The Handbook of
EVOLUTIONARY PSYCHOLOGY

Second Edition

Volume 1: Foundations

Edited by

DAVID M. BUSS

WILEY

The Handbook of Evolutionary Psychology

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Cover design: Wiley

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Published by John Wiley & Sons, Inc., Hoboken, New Jersey.
Published simultaneously in Canada.

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Library of Congress Cataloging-in-Publication Data:

Handbook of evolutionary psychology (Hoboken, N.J.)
The handbook of evolutionary psychology / edited by David M. Buss. — 2nd edition.
volumes cm
Includes bibliographical references and index.
Contents: Volume 1. Foundations — volume 2. Application.
ISBN 978-1-118-75588-4 (cloth) — ISBN 978-1-118-76399-5 (set) — ISBN 978-1-118-75602-7 (pdf) — ISBN 978-1-118-75597-6 (epub)
1. Evolutionary psychology. 2. Human evolution. I. Buss, David M. II. Title.
BF698.95.H36 2016
155.7—dc23
2015008090

Printed in the United States of America

Second Edition

10 9 8 7 6 5 4 3 2 1

To Charles Darwin

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Foreword

STEVEN PINKER

FOR MANY YEARS after I decided to become a psychologist I was seriously frustrated by my chosen field, and fantasized about a day when it would satisfy the curiosity that first led me to devote my professional life to studying the mind. As with many psychology students, the frustration began with my first class, in which the instructor performed the ritual that begins every Introduction to Psychology course: disabusing students of the expectation that they would learn about any of the topics that attracted them to the subject. Forget about love and hate, and family dynamics, and jokes and their relation to the unconscious, they said. Psychology was a rigorous science that investigated quantifiable laboratory phenomena; it had nothing to do with self-absorption on an analyst's couch or the prurient topics of daytime talk shows. Accordingly, the course confined itself to "perception," which meant psychophysics, and "learning," which meant rats, and "the brain," which meant neurons, and "memory," which meant nonsense syllables, and "intelligence," which meant IQ tests, and "personality," which meant personality tests.

When I proceeded to advanced courses, they only deepened the disappointment, by revealing that the psychology canon was a laundry list of unrelated phenomena. The course on perception began with Weber's law and Fechner's law and proceeded to an assortment of illusions and aftereffects familiar to readers of cereal boxes. There was no there there—no conception of what perception *is* or of what it is for. Cognitive psychology, too, consisted of laboratory curiosities analyzed in terms of dichotomies like serial/parallel, discrete/analog, and top-down/bottom-up (inspiring Alan Newell's famous jeremiad "You can't play twenty questions with nature and win"). To this day, social psychology is driven not by systematic questions about the nature of sociality in the human animal but by a collection of situations in which people behave in strange ways.

But the biggest frustration was that psychology seemed to lack any sense of *explanation*. Like the talk-show guest on *Monty Python's Flying Circus* whose theory of the brontosaurus was that "the brontosaurus is skinny at one end; much, much thicker in the middle; and skinny at the other end," psychologists were content to "explain" a phenomenon by redescribing it. A student rarely enjoyed the flash of insight that tapped deeper principles to show why something *had* to be the way it is, as opposed to some other way it could have been.

My gold standard for a scientific explanation was set when I was a graduate student—not by anything I learned in graduate *school*, mind you, but by a plumber who came to fix the pipes in my dilapidated apartment and elucidated why they had sprung a leak. Water, he explained, obeys Newton's second law. Water is dense. Water is incompressible. When you shut off a tap, a large incompressible mass moving at high speed has to decelerate quickly. This imparts a big force to the pipes, like a car slamming into a wall, which eventually damages the threads and causes a leak. To deal with this problem, plumbers used to install a closed vertical section of pipe, a "pipe riser," near each faucet. When the faucet is shut, the decelerating water compresses the column of air in the riser, which acts like a shock absorber, protecting the pipe joints. Unfortunately, this is a perfect opportunity for Henry's law to apply, namely that gas under pressure is absorbed by a liquid. Over time, the air in the column dissolves into the water, filling the pipe riser and rendering it useless. So every once in a while a plumber has to bleed the system and let air back into the risers, a bit of preventive maintenance the landlord had neglected. I only wished that psychology could meet that standard of explanatory elegance and show how a seemingly capricious occurrence falls out of laws of greater generality.

It's not that psychologists never tried to rationalize their findings. But when they did, they tended to recycle a handful of factors like similarity, frequency, difficulty, salience, and regularity. Each of these so-called explanations is, in the words of the philosopher Nelson Goodman, "a pretender, an impostor, a quack." Similarity (and frequency and difficulty and the rest) are in the eye of the beholder, and it is the eye of the beholder that psychologists are responsible for explaining.

This dissatisfaction pushed me to the broader interdisciplinary field called cognitive science, where I found that other disciplines were stepping into the breach. From linguistics I came across Noam Chomsky's criteria for an adequate theory of language. At the lowest level was observational adequacy, the mere ability to account for linguistic behavior; this was the level at which most of psychology was stuck. Then there was descriptive adequacy, the ability to account for behavior in terms of the underlying mental representations that organize it. At the highest level was explanatory adequacy, the ability of a theory to show why *those* mental representations, and not some other ones, took root in the mind. In the case of linguistics, Chomsky continued, explanatory adequacy was rooted in the ability of a theory to solve the problem of language acquisition, explaining how children can learn an infinite language from a finite sample of sentences uttered by their parents. An explanatory theory must characterize Universal Grammar, a part of the innate structure of the mind. This faculty forces the child to analyze speech in particular ways, those consistent with the way human languages work, rather than in any of the countless logically possible ways that are consistent with the input but dead ends in terms of becoming an expressive language user (for example, memorizing every sentence, or combining nouns and verbs promiscuously). As a result, a person's knowledge of language is not just any old set of rules, but ones that conform to an algorithm powerful enough to have acquired an infinite language from a finite slice of the environment.

Artificial intelligence, too, set a high standard of explanation, largely through the ideas of the vision scientist David Marr. A theory of vision, he suggested, ought to characterize visual processing at three levels: the neurophysiological mechanism, the algorithm implemented by this mechanism, and crucially, a "theory of the computation" for that domain. A theory of the computation is a formal demonstration that an algorithm can, in principle, compute the desired result, given certain assumptions about the way the world works. And the desired result, in turn, should be characterized in terms of the overall "goal" of the visual system, namely to compute a useful description of the world from the two-dimensional array of intensity and wavelength values falling on the retina. For example, the subsystem that computes the perception of shape from shading (as when we perceive the contours of a cheek, or the roundness of a ping-pong ball) relies on a fact of physics that governs how the intensity of light reflecting off a surface depends on the relative angles of the illuminant, the surface, and the observer, and on the physical properties of the surface. A perceptual algorithm can exploit this bit of physics to work backward from the array of light intensities, together with certain assumptions about typical illuminants and surfaces in a terrestrial environment, and thereby compute the tangent angle of each point on a surface, yielding a representation of its shape. Many perceptual phenomena, from the way makeup changes the appearance of a face to the fact that turning a picture of craters upside down makes it look like a picture of bumps, can be explained as by-products of this shape-from-shading mechanism. Most perception scientists quickly realized that conceiving the faculty of vision as a system of neural apps that supply the rest of the brain with an accurate description of the visible environment was a big advance over the traditional treatment of perception as a ragbag of illusions, aftereffects, and psychophysical laws.

Language and perception, alas, are just two out of our many talents and faculties, and it was unsatisfying to think of the eyes and ears as pouring information into some void that constituted the rest of the brain. Might there be some comparable framework for the rest of psychology, I wondered, that addressed the engaging phenomena of mental and social life, that covered its subject matter systematically rather than collecting oddities like butterflies, and that explained its phenomena in terms of deeper principles? The explanations in language and vision appealed to the *function* of those faculties: in linguistics, acquiring the language of one's community; in vision, constructing an accurate description of the visible world. Both are extraordinarily difficult computational problems (as yet unsolvable by artificial intelligence systems) but ones that any child can perform with ease. And both are not esoteric hobbies but essential talents for members of our species, affording obvious advantages to their well-being. Couldn't other areas of psychology, I wondered, benefit from an understanding of the problems our mental faculties solve; in a word, what they are *for*?

When I discovered evolutionary psychology in the 1980s through the work of Donald Symons, Leda Cosmides, and John Tooby, I realized my wait was over. Evolutionary psychology was the organizing framework—the source of "explanatory adequacy" or a "theory of the computation"—that the science of psychology had been missing. Like vision and language, our emotions and cognitive faculties are complex, useful, and nonrandomly organized, which means that they must be a product of the only physical process capable of generating complex, useful, nonrandom organization, namely natural selection. An appeal to evolution was already implicit in the metatheoretical directives of Marr and Chomsky, with their appeal to the function of a mental faculty, and evolutionary psychology simply shows how to apply that logic to the rest of the mind.

Just as important, the appeal to function in evolutionary psychology is itself constrained by an external body of principles—those of the modern, replicator-centered theory of selection from evolutionary biology—rather than being made up on the spot. Not just any old goal can count as the function of a system shaped by natural selection, that is, an adaptation. Evolutionary biology rules out, for example, adaptations that work toward the good of the species, the harmony of the ecosystem, beauty for its own sake, benefits to entities other than the replicators that create the adaptations (such as horses that evolve saddles), functional complexity without reproductive benefit (e.g., an adaptation to compute the digits of pi), and anachronistic adaptations that benefit the organism in a kind of environment other than the one in which it evolved (e.g., an innate ability to read, or an innate concept of "carburetor" or "trombone"). Natural selection also has a positive function in psychological discovery, impelling psychologists to test new hypotheses about the possible functionality of aspects of the mind that previously seemed functionless. For example, the social and moral emotions (sympathy, trust, guilt, anger, gratitude) appear to be adaptations for policing reciprocity in nonzero sum games; an eye for beauty appears to be an adaptation for detecting health and fertility in potential mates. None of this research would be possible if psychologists had satisfied themselves with a naïve notion of function instead of the one licensed by modern biology.

Evolutionary psychology also provides a motivated research agenda for psychology, freeing it from its chase of laboratory curiosities. An explanatory hypothesis for some emotion or cognitive faculty must begin with a theory of how that faculty would, on average, have enhanced the reproductive chances of the bearer of that faculty in an ancestral environment. Crucially, the advantage must be demonstrable by some independently motivated causal consequence of the putative adaptation. That is, laws of physics or chemistry or engineering or physiology, or some other set of laws independent of the part of our psychology being explained, must suffice to establish that the trait is useful in attaining some reproduction-related goal. For example, using projective geometry, one can show that an algorithm can compare images from two adjacent cameras and calculate the depth of a distant object using the disparity of the two images. If you write out the specs for computing depth in this way—what engineers would specify if they were building a robot that had to see in depth—you can then examine human stereoscopic depth perception and ascertain whether humans (and other primates) obey those specs. The closer the empirical facts about our psychology are to the engineering specs for a well-designed system, the greater our confidence that we have explained the psychological faculty in functional terms.

A similar example comes from the wariness of snakes found in humans and many other primates. We know from herpetology that snakes were prevalent in Africa during the time of our evolution, and that getting bitten by a snake is harmful because of the chemistry of snake venom. Crucially, these are not facts of psychology. But they help to establish that something that *is* a fact of psychology, namely the fear of snakes, is a plausible adaptation. In a similar manner, robotics can help explain motor control, game theory can explain aggression and appeasement, economics can explain punishment of free riders, and mammalian physiology (in combination with the evolutionary biology of parental investment) makes predictions about sex differences in sexuality. In each case, a "theory of the computation" is provided by an optimality analysis using a set of laws outside the part of the mind we are trying to explain. This is what entitles us to feel that we have explained the operation of that part of the mind in a noncircular way.

In contrast, it's not clear what the adaptive function of music or religion is. The popular hypothesis that the function of music is to keep the community together may be true, but it is not an *explanation* of why we like music, because it just begs the question of why sequences of tones in rhythmic and harmonic relations should keep the group together. Generating and sensing sequences of sounds is not an independently motivated solution to the problem of maintaining group solidarity, in the way that, say, the emotion of empathy, or a motive to punish free riders, is part of such a solution. A similar problem infects the "explanation" that people are prone to believe in incredible religious doctrines because those doctrines are comforting—in other words, that the doctrines of a benevolent shepherd, a universal plan, an afterlife, and divine retribution ease the pain of being a human. There's an element of truth to each of these suggestions, but they are not legitimate adaptationist explanations, because they beg the question of *why* the mind should find comfort in beliefs that it is capable of perceiving as false. In these and other cases, a failure to find an adaptationist explanation does not mean that no explanation is forthcoming at all. Religious belief may be a by-product of adaptations (such as a capacity to mentalize and free-rider detection mechanisms) that are demonstrably useful for solving *other* adaptive problems.

Evolutionary psychology is the cure for one last problem ailing traditional psychology: its student-disillusioning avoidance of the most fascinating aspects of mental and social life. Even if evolutionary psychology had not provided psychology with standards of explanatory adequacy, it has proved its worth by opening up research in areas of the human experience that have always been fascinating to reflective people but that had long been absent from the psychology curriculum. It is no exaggeration to say that contemporary research on topics like sex, attraction, jealousy, love, food, disgust, status, dominance, friendship, religion, art, fiction, morality, motherhood, fatherhood, sibling rivalry, and cooperation has been opened up and guided by ideas from evolutionary psychology, even if the initial ideas did not always prove to be correct. At the same time, evolutionary psychology is changing the face of theories in more traditional areas of psychology, making them into better depictions of the real people we encounter in our lives, and making the science more consonant with common sense and the wisdom of the ages. Before the advent of evolutionary thinking in psychology, theories of memory and reasoning typically didn't distinguish thoughts about people from thoughts about rocks or houses. Theories of emotion didn't distinguish fear from anger, jealousy, or love. And theories of social relations didn't distinguish among the way people treat family, friends, lovers, enemies, and strangers.

For many reasons, then, the second edition of this *Handbook* represents a significant milestone in the science of psychology. The theoretical rigor and empirical richness showcased in these chapters have more than fulfilled evolutionary psychology's initial promise, and they demolish lazy accusations that the field is mired in speculative storytelling or rationalizations of reactionary politics. The chapters don't, of course, summarize a firm consensus or present the final word in any of the areas they cover. But in topics from parenting to fiction, from predation to religion, they deliver subtle and deep analyses, genuinely new ideas, and eye-opening discoveries. *The Handbook of Evolutionary Psychology* is far more than a summary of the state of the art of evolutionary psychology. It is the realization of the hope that psychology can be a systematic and explanatory science of the human condition.

Acknowledgments

THE CREATION OF this *Handbook* owes a special thanks to friends and colleagues who offered suggestions about coverage, provided reviews of individual chapters, and helped me on the long journey. For the first edition of the *Handbook* (2005), these include Sean Conlan, Leda Cosmides, Martin Daly, Todd DeKay, Randy Diehl, Diana Fleischman, Steve Gangestad, Martie Haselton, Sarah Hill, Joonghwan Jeon, Barry X. Kuhle, Steven Pinker, David Schmitt, Todd Shackelford, Don Symons, John Tooby, Jerry Wakefield, and Margo Wilson. Their contributions carry over to this second edition.

Cristine Legare played a key role for the current edition of the *Handbook*. In addition to generous feedback on several chapters, she was instrumental in convincing me to broaden the scope of the *Handbook* to include topics such as cultural evolution, social group cognition, learning over ontogeny, and religion—domains of huge importance to human affairs.

Dan Conroy-Beam deserves singling out for special and enormous thanks. He helped me shepherd this *Handbook* at all stages of the 3-year process: decisions about key contributors, providing key reviews of a dozen or so chapters, tracking the status of each chapter, and offering key suggestions about final organization. I owe Dan a great debt.

Many scholars generously provided external reviews of draft of one or more chapters: Bill von Hippel, Anne Campbell, Pascal Boyer, Daniel Nettle, Ray Hames, Joe Henrich, Ryan McKay, Coren Apicella, Alyssa Crittenden, Willem Frankenhuis, Todd Shackelford, H. Clark Barrett, Kristina Durante, David Rakison, Elizabeth Cashdan, Steve Gangestad, Dave Schmitt, Cristine Legare, Randy Nesse, Jonathan Gotschall, Josh Tybur, Dominic Johnson, Aaron Sell, Gad Saad, Robert Kurzban, Jerone Wakefield, Kelly Asao, and Rebecca Burch. I am much in their debt.

An editor could not ask for a more superlative team than those at John Wiley & Sons. Patricia Rossi's unflagging enthusiasm for the *Handbook* provided the inspiration needed to bring the project to fruition, and Rachel Livsey and Amanda Orenstein helped enormously in the final stages.

I owe a special thanks to Steven Pinker for furnishing the foreword, Don Symons for writing a special essay for the section on mating, Martin Daly for providing an introduction to the section on parenting and kinship, and Richard Dawkins for furnishing the afterword. Most important, I thank the authors who provided the 52 chapters that form the core of the *Handbook*. Within their domains of expertise, they help the next generation of scientists by showing the light and the way.

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Introduction: The Emergence and Maturation of Evolutionary Psychology

DAVID M. BUSS

EVOLUTIONARY PSYCHOLOGY, BROADLY conceived, dates back to Darwin. He offered this scientific vision at the end of his monumental book, *On the Origin of Species:* "In the distant future I see open fields for more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation" (Darwin, 1859). This *Handbook of Evolutionary Psychology* (second edition), published 156 years after these prophetic words, symbolizes the emergence of evolutionary psychology based on Darwin's vision.

Evolutionary psychology is still a young scientific field, and there's a long and exciting road ahead. Aspects of the field's conceptual foundations remain legitimate topics of debate, such as the nature and specificity of psychological adaptations and the importance of individual differences. Many phenomena remain unexamined, awaiting new explorers of the human mind equipped with the conceptual tools that evolutionary psychology provides. Many of the conceptual foundations are now in place, offering a solid metatheoretical framework from which to build. Hundreds of psychological and behavioral phenomena have been documented empirically, findings that would never have been discovered without the guiding framework of evolutionary psychology. Evolutionary psychology has proved its worth many times over in its theoretical and empirical harvest. If a viable alternative metatheoretical framework to evolutionary psychology exists for understanding the origins and nature of the human mind, it has not been revealed to the scientific community. The second edition of this *Handbook*, published a decade after the first, takes stock of where the field is today and where it needs to go.

Until recently, a handbook of this scope would have been impossible. The empirical corpus of research testing evolutionary psychological hypotheses was too slim. Now the body of work has mushroomed at such a rapid rate that I had to make difficult decisions about what to include for this volume to keep it to a reasonable length. Some important areas regrettably could not be covered. Most chapters had to be shortened, sometimes dramatically. The extensity of coverage, however, reveals that evolutionary psychology has penetrated every existing branch of psychology.

Psychologists working in some subdisciplines in times past could safely disregard evolutionary psychology. Now the robustness of evolutionary hypotheses and the rapid accumulation of empirical findings make it impossible to ignore for all but those who remain conceptually insular. Scientists working in cognitive, social, developmental, personality, neuroscience, or clinical psychology, and more recently cultural psychology, cannot afford to close their eyes to the insights offered by evolutionary psychology.

Some view evolutionary psychology as an optional perspective, an explanation of last resort, to be brought in only when all other alternatives have been exhausted. In my view, this position is naïve. Evolutionary psychology represents a true scientific revolution, a profound paradigm shift in the field of psychology. The human mind can no longer be conceived as it has been in mainstream psychology, implicitly or explicitly, as a blank slate onto which parents, teachers, and culture impose their scripts; or as a domain-general learning device; or a set of content-free information processing mechanisms; or as a content-free neural or connectionist network. Instead, the human mind comes factory-equipped with an astonishing array of dedicated developmental programs for psychological mechanisms, designed over deep time by natural and sexual selection, to solve the hundreds of statistically recurring adaptive problems that our ancestors confronted. Understanding these mechanisms of mind requires understanding their evolved functions—what they were designed by selection to accomplish, the adaptive problems that selection favored them to solve, the specific manner in which they contributed to fitness. Just as a medical researcher's insights into the heart, liver, or kidney would be viewed as woefully incomplete without knowledge of their functions, explanations of psychological mechanisms will almost invariably be incomplete without specifying their functions. Evolutionary psychology is no longer a discretionary or elective theoretical option for psychology. It is essential, necessary, and indispensable.

At the current point in the history of psychology, the mainstream field is partitioned into subdisciplines—cognitive, social, personality, developmental, clinical, and hybrid areas such as cognitive neuroscience. Evolutionary psychology provides the metatheoretical foundation that unites the disparate branches of the sprawling field of psychology, and suggests that the human mind cannot be logically parsed in the manner the subdisciplines imply. Consider "stranger anxiety" as a candidate psychological adaptation. Its function is to motivate the infant to recoil from potentially dangerous humans and to maintain close proximity to caregivers, thereby avoiding hazards that strangers might pose. Stranger anxiety possesses a number of well-articulated design features. It shows universality, emerging in infants in all cultures in which it has been studied. It emerges predictably during ontogeny at roughly six months of age, coinciding with the time when infants begin crawling away from their mothers and potentially encountering strangers. And its focus centers on strange males rather than strange female because strange males historically have been more hazardous to infants' health. Stranger anxiety shows all the characteristics of "improbable design" for achieving a specific function.

In which subdiscipline of psychology does stranger anxiety belong? It obviously involves information processing, and so could be claimed by cognitive psychology. It shows a predictable ontogenetic unfolding, so it could be claimed by developmental psychology. It is activated by interactions with others, so clearly it belongs to social psychology. Individual infants differ in the intensity of stranger anxiety, so it falls within the province of personality psychology. The mechanism can malfunction in a minority of infants, so it is relevant to clinical psychology. And its biological substrate must include the brain, so neuroscience can also lay claim. Obviously, stranger anxiety belongs simultaneously to all or to none.

Evolutionary psychology breaks down these traditional disciplinary boundaries and reveals them to lack logical or scientific warrant. Viewed through the theoretical lens of adaptive problems and their evolved psychological solutions, evolutionary psychology offers the only cogent nonarbitrary means for carving the mind at its natural joints. It provides the conceptual unification of the disparate branches of psychology that currently operate in virtual isolation. And it integrates psychology theoretically with the rest of the natural sciences in a unified causal framework.

It is a great honor and privilege to serve as editor for *The Handbook of Evolutionary Psychology* (second edition), which contains such a high-powered assembly of outstanding scientists. Whereas the first edition of the *Handbook* contained 34 chapters, this second edition contains 52 chapters (plus essays by Steven Pinker, Donald Symons, and Richard Dawkins), reflecting both the rapidly expanding empirical base of evolutionary psychology and its penetration into new and previously uncharted domains ranging from food to culture to public policy implications. The dramatic expansion of topical coverage includes entirely new chapters on food, the behavioral immune system, inbreeding avoidance, hunter-gatherer parenting and families, prejudice, warfare, cultural evolution, morality, ritual, religion, group selection, leadership, evolutionary genetics, evolutionary endocrinology, evolutionary political psychology, and evolutionary consumer psychology. Its authors are housed in diverse disciplines, including psychology, anthropology, biology, political science, business school, law school, and the humanities.

This *Handbook* begins with a foreword from Steven Pinker, who provides a powerful narrative of his intellectual journey to evolutionary psychology, and describes his views about why evolutionary psychology is necessary for psychological science. The *Handbook* ends with an eloquent afterword by evolutionary biologist Richard Dawkins, whose theoretical contributions have informed much work in the discipline. In between are 52 chapters, parsed into nine parts. Each part has its own introduction.

Part One, Foundations of Evolutionary Psychology, contains five chapters that outline the logic of the enterprise, the methods used, and controversial issues surrounding the field. Part Two, Survival, contains five chapters that deal, respectively, with struggles with the physical environment, with other species (predators and prey), and with other humans. Part Three, Mating, begins with an insightful essay by Donald Symons, in which he articulates the logic of adaptationism and offers a novel hypothesis about mate-rejection anxiety. It is followed by eight chapters that range in content from attraction to contest competition, from sexual coercion to love in long-term mating, highlighting the breadth and depth of theory and research in the domain of human mating. Part Four, Parenting and Kinship, contains an excellent introductory essay by Martin Daly, and is followed by chapters on cooperation and conflict among kin, parental investment, parent-offspring conflict, the evolution of the human family, and hormones, and human sociality.

Group living, which all scholars recognize is one of the most crucial contexts in which humans evolved, is so important that it warranted two parts. The first, Part Five, Group Living: Cooperation and Conflict, deals with social exchange, aggression, prejudice, and social exclusion, and ends with a new chapter on leadership in warfare. The second, Part Six: Culture and Coordination, contains seven entirely new chapters. These focus on cultural evolution, morality, status hierarchies, ritual, religion, and group selection. Taken together, these chapters reflect the explosion of theoretical and empirical work on the monumental importance of group living, and the upsurge of interest in understanding previously neglected aspects of group living such as ritual, religion, morality, and culture.

Part Seven, Interfaces With Traditional Psychology Disciplines, contains eight chapters on how the conceptual foundations of the current disciplines within psychology can be informed by an evolutionary framework. Part Eight, Interfaces Across Traditional Academic Disciplines, contains five chapters, four entirely new and one heavily revised. The new chapters focus, respectively, on evolutionary anthropology, evolutionary genetics, evolutionary psychology and endocrinology, and evolutionary political psychology; the revised chapter deals with evolutionary literary study. Collectively, these key chapters reflect the degree to which evolutionary sciences have become centrally integrated with so many far-flung disciplines within the life sciences.

Part Nine, Practical Applications of Evolutionary Psychology, provides the concluding section of the *Handbook*. Chapters deal with evolutionary approaches to public policy, consumer behavior, organizational leadership, and legal issues.

After a long succession of conceptual advances and empirical discoveries, a robust field of evolutionary psychology has finally emerged. Darwin's prophetic vision is being realized—a psychology based on a new foundation. And beyond psychology, evolutionary approaches to human behavior are penetrating domains Darwin is unlikely to have envisioned, from evolutionary genetics to a deep understanding of human culture. I like to think Charles Darwin would have been both humbled and gratified, and perhaps even awed, by the intellectual flowering forecast by his scientific prophecy.

PART I

FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

DAVID M. BUSS

JOHN TOOBY AND Leda Cosmides have been true pioneers in developing the conceptual foundations of evolutionary psychology, so it's fitting that they supply the first foundational chapter. They provide a fascinating tour of the discipline's intellectual origins, showing how a series of conceptual advances, from the cognitive revolution to evolutionary game theory, led to the emergence of evolutionary psychology. Tooby and Cosmides then discuss foundational premises on which the field rests. They explicate principles of organic design, the logic of reverse engineering, the nature of evidence for special design, and discuss how theories of good design provide powerful heuristics for psychological scientists. They describe how the framework of evolutionary psychology differs from that of traditional psychology. Finally, Tooby and Cosmides offer an intriguing novel framework for conceptualizing the functional architecture of cognition, motivation, and emotion. The original theoretical papers of Tooby and Cosmides over the past 30 years have informed virtually all work being conducted in the field of evolutionary psychology. This chapter, heavily revised from the first edition, consolidates and expands the conceptual foundations of the field.

Marco Del Giudice, Steven Gangestad, and Hillard Kaplan argue for the integration of life history theory and evolutionary psychology, suggesting that adaptations are designed to make different budget-allocation trade-offs over the lifespan. They begin with a presentation of the fundamentals of life history theory. All energy budgets of an organism are finite, so trade-offs are inevitable. They discuss the most important trade-offs—between present and future reproduction, quality and quantity of offspring, and mating effort and parental effort. They proceed to illuminate the important effects of ecological factors such as food supply and mortality hazards on optimal life history strategies. Del Giudice and coauthors then turn to *humans* specifically, showing how life history theory informs, and can be successfully integrated with, evolutionary psychology. Most intriguingly, they propose that these adaptations cannot be independent of each other in at least two ways. First, effort allocated to one (e.g., preventing cuckoldry) necessarily takes away effort allocated to others (e.g., foraging for food). Second, humans must possess *coevolved bundles* of psychological mechanisms, such as those for long-term mating linked with those for heavy-investment parenting. They make a persuasive argument that the integration of life history theory with evolutionary psychology provides a means for uncovering psychological adaptations designed to make important budget allocation trade-offs. This approach also promises to reveal how different psychological mechanisms are linked with each other, illuminated by an economic cost–benefit analysis of selection pressures.

Jeffrey Simpson and Lorne Campbell argue convincingly that programs of research in evolutionary psychology can and should be strengthened methodologically by using a wider array of methods and measurement techniques specifically tailored to testing "special design" predictions that follow from hypothesized psychological adaptations. They present a persuasive case for multiple research methods and multiple outcome measures, as well as increased attention to issues of the validity of these measures, in successfully illuminating the "special design" qualities of hypothesized psychological adaptations. Evolutionary psychology ultimately will convince the residue of remaining skeptics by *empirical* discoveries that cannot successfully be explained by more traditional competing "nonevolutionary" explanations. This chapter provides an informative and insightful guide for anyone conducting, or aspiring to conduct, empirical research in evolutionary psychology.

Edward Hagen provides an insightful analysis of recurrent controversies surrounding evolutionary psychology and the misconceptions that stubbornly persist. He makes a compelling case for a universal human nature with adaptations as the central pillars of that nature. Hagen incisively addresses misconceptions about evolutionary psychology that are tiresomely repeated by those critical of the enterprise, such as misconceptions about the concept of the environment of evolutionary adaptedness (no, it is not a specific time or place, an error that seems a stubborn meme that resists attempts at correction). Hagen explores evolution before the Pleistocene era, as well as evolution within the past 10,000 years. He concludes by noting that most critics of evolutionary psychology essentially accept its basic premises.

Pascal Boyer and Clark Barrett offer an extended argument for domain specificity, using intuitive ontology—adaptations for different domains of information—as a vehicle for illuminating the tight integration of neural, developmental, and behavioral components of evolved psychological mechanisms. They describe evidence from cognitive psychology and neuroscience that strongly supports a key foundational premise of evolutionary psychology, namely that humans possess, in their words, "a federation of evolved competencies." Boyer and Barrett outline the features that specific inference systems possess, including semantic knowledge, a specialized learning logic, a dedicated set of developmental pathways, and a close correspondence with specific adaptive problems solved. They then explore several broad evolved competencies in detail, such as the ability to read the minds of others (intuitive psychology) and the ability to grapple with the physical environment (intuitive physics). They argue persuasively that evolved competencies, in fact, are more fine-grained than these ontological categories imply. Indeed, adaptations cross these ontological categories. Boyer and Barrett provide an example *par excellence* of how evolutionary psychology dissolves traditional disciplinary boundaries by bringing developmental, cognitive, and neuroscience evidence to bear in illuminating evolved psychological mechanisms.

CHAPTER 1

The Theoretical Foundations of Evolutionary Psychology

JOHN TOOBY and LEDA COSMIDES

THE EMERGENCE OF EVOLUTIONARY PSYCHOLOGY: WHAT IS AT STAKE?

THE THEORY OF evolution by natural selection has revolutionary implications for understanding the design of the human mind and brain, as Darwin himself was the first to recognize (Darwin, 1859). Indeed, a principled understanding of the network of causation that built the functional architecture of the human species offers the possibility of transforming the study of humanity into a natural science capable of precision and rapid progress. Yet, more than a century and a half after *On the Origin of Species* was published, many of the psychological, social, and behavioral sciences continue to be grounded on assumptions that evolutionarily informed researchers know to be false; the rest have only in the past few decades set to work on the radical reformulations of their disciplines necessary to make them consistent with findings in the evolutionary sciences, information theory, computer science, physics, the neurosciences, molecular and cellular biology, genetics, behavioral ecology, hunter-gatherer studies, biological anthropology, primatology, and so on (Pinker, 1997, 2002; Tooby & Cosmides, 1992). Evolutionary psychology is the long-forestalled scientific attempt to assemble out of the disjointed, fragmentary, and mutually contradictory human disciplines a single, logically integrated research framework for the psychological, social, and behavioral sciences—a framework that not only incorporates the evolutionary sciences and information theory on a full and equal basis, but that systematically works out all the revisions in existing belief and research practice that such a synthesis requires (Tooby & Cosmides, 1992).

The first long-term scientific goal toward which evolutionary psychologists are working is the mapping of our universal human nature. By mapping human nature, we mean the progressive construction and refinement of a set of empirically validated, high-resolution models of the evolved adaptations (genetic, developmental, anatomical, neural, information processing, etc.) that collectively constitute universal human

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We dedicate this chapter to the late Irven DeVore, professor emeritus, Department of Anthropology, Harvard University, dear mentor and friend.

nature. Because the focus in the behavioral and social sciences is on explaining mind, behavior, and social interactions, initially the emphasis has been placed on adaptations that are behavior-regulating, and which researchers may call a variety of names, such as evolved psychological (mental, cognitive) programs, neurocomputational programs, behavior-regulatory programs, adaptive specializations, "modules," information-processing mechanisms, and so on. However, because the architecture of the human species evolved as a set of functional interactions at all physical and temporal scales, it follows that genetic, cellular, developmental, anatomical, physiological, endocrinological, and life-historical processes are also considered as fully part of human nature, and, therefore, part of the systems of evolved interrelationships that evolutionary psychology needs to deal with. Because the evolved function of a regulatory mechanism is computational—to regulate behavior, development, and the body adaptively (over the short term and the long term) in response to informational inputs—such a model consists of a description of the functional circuit logic or information-processing architecture of the mechanism, in a way that eventually should incorporate its physical implementation (Cosmides & Tooby, 1987; Tooby & Cosmides, 1992). More completely, these models must sooner or later include descriptions of the regulatory logic of the developmental programs that, in interaction with environments, lead to the unfolding succession of designs that constitute the organism's changing phenotype across its life history (Tooby & Cosmides, 1992; Tooby, Cosmides, & Barrett, 2003—see review in Del Giudice, Gangestad, & Kaplan, Chapter 2, this volume). As scientific knowledge grows in the longer term, these models will eventually come to incorporate descriptions of the neural and genetic implementations of these mechanisms.

The second long-term scientific goal toward which evolutionary psychologists and their allies are working is a comprehensive reconstruction of the social sciences (and many of the humanities) that an accurate, natural science–based model of human nature will both make possible and require. At present, the social sciences are a stew of mutually contradictory claims, with no theoretical unity or clear progressive direction. Major components of the social sciences are sufficiently incoherent to qualify—in Paul Dirac's phrase—as not even wrong. Genuine, detailed specifications of the circuit logics of the neuroregulatory programs that compose human nature are expected to become the theoretical centerpieces of a newly reconstituted set of social sciences. This is because each model of an evolved component of human nature (e.g., the human-language competence) makes predictions about (and explains) those sets of developmental, psychological, behavioral, and social phenomena that its circuits generate or regulate (e.g., the existence of and the patterns found in human language; Pinker, 1994; the existence of and patterns found in incest aversion and kin-directed altruism; Lieberman, Tooby, & Cosmides, 2007). The resulting changes to the social sciences are expected to be dramatic and far-reaching because the traditional conceptual framework for the social and behavioral sciences—what we have called the Standard Social Science Model (SSSM)—was built from defective assumptions about the nature of the human psychological and developmental architecture (for an analysis of the SSSM, see Pinker, 2002; Tooby & Cosmides, 1992). The most consequential assumption is that the human psychological architecture consists predominantly of learning and reasoning mechanisms that are general purpose, content independent, and equipotential (Pinker, 2002; Tooby & Cosmides, 1992). That is, the mind is blank-slate–like, and lacks specialized circuits that were designed by natural selection to respond differentially to inputs by virtue of their evolved significance. This presumed psychology justifies a crucial foundational claim: Just as a blank piece of paper plays no causal role in determining the content that is inscribed on it, the blank-slate view of the mind rationalizes the belief that the evolved organization of the mind plays little causal role in generating the content of human social and mental life. The mind with its learning capacity absorbs its content and organization almost entirely from external sources. These processes are thought to be analogous to the operation of a video camera— the content of the recording originates in the world, whereas the mechanism of recording adds no content of its own to the mix. As Thomas Aquinas put this seemingly self-evident view, "There is nothing in the mind that was not first in the senses." Hence, according to the standard model, the social and cultural phenomena studied by the social sciences are autonomous and disconnected from any nontrivial causal patterning originating in our evolved psychological mechanisms. Organization flows inward to the mind from the processes in the social world (what we call the Durkheimian causal arrow). More importantly, social scientists have considered it to be unshakably well-established that content does not flow outward from evolved organization in individual minds to organize culture or the social world (Geertz, 1973; Sahlins, 1976). Now that this hypothesis is being empirically tested, however, it is regularly falsified (e.g., Buss, 1989; Lieberman, Tooby, & Cosmides, 2003, 2007; Petersen, Sznycer, Sell, Cosmides, & Tooby, 2013; Sell, Tooby, & Cosmides, 2009).

Yet if—as evolutionary psychologists have been demonstrating—the blank-slate view of the mind is wrong, then the social science project of the past century is not only wrong but radically misconceived. The blank-slate assumption removes the central causal organizers of social phenomena—evolved psychological programs—from the analysis of social events, rendering the social sciences powerless to understand the animating logic of the social world. Evolutionary psychology provokes so much reflexive opposition because the stakes for many social scientists, behavioral scientists, and humanists are so high: If evolutionary psychology turns out to be well founded, then the existing superstructure of the social and behavioral sciences—the Standard Social Science Model—will have to be dismantled. Instead, a new social science framework will need to be assembled in its place that recognizes that models of psychological mechanisms are essential constituents of social theories (Boyer, 2001; Sperber, 1994, 1996; Tooby & Cosmides, 1992).

Within such a framework, the circuit logic of each evolved mechanism contributes to the explanation of every social or cultural phenomenon it influences or helps to generate. For example, the nature of the social interactions between the sexes are partly rooted in the design features of evolved programs that underlie sexual behavior, mate choice, attractiveness, intrasexual competition, intersexual conflict, and mateship maintenance, reviewed in many chapters in this volume (for notable earlier work, see Buss, 1994, 2000; Daly & Wilson, 1988; Symons, 1979). The patterned incidence of violence is partly explained by the evolved programs governing our species' psychology of aggression, parenting, and sexuality (Campbell & Loving, Chapter 18, this volume; Daly & Wilson, 1988); the foundations of trade can be located in evolved cognitive specializations for social exchange (Cosmides & Tooby Chapter 25, this *Handbook*, Volume 2; Cosmides & Tooby, 1992); both incest avoidance and love for family members are rooted in evolved mechanisms for kin recognition (Lieberman et al., 2003, 2007). Similarly, the evolutionarily specialized mechanisms underlying human alliance psychology help to explain phenomena such as racism, coalitions, morality, social sanctions, and group dynamics (e.g., Delton, Cosmides, Guemo, Robertson, & Tooby, 2012; Kurzban, Tooby, & Cosmides, 2001; Pietraszewski, Cosmides, & Tooby, 2014; Tooby & Cosmides, 2010; Tooby, Cosmides, & Price, 2006).

A growing inventory of such models will catalyze the transformation of the social sciences from fields that are predominantly descriptive, soft, and particularistic into theoretically principled scientific disciplines with genuine predictive and explanatory power. Evolutionary psychology in the narrow sense is the scientific project of mapping our evolved psychological and developmental mechanisms; in the broad sense, it includes the project of reformulating and expanding the social sciences (and medical sciences, as somatic adaptations become incorporated into the synthesis) in the light of the progressive mapping of our species' evolved architecture. This *Handbook* contains reviews of the rich harvest of projects and discoveries that have already emerged out of this young paradigm. Even though the field is in its infancy, evolutionary psychologists have already identified a very large set of examples that touch almost every aspect of human life. In the light of such rapidly accumulating findings, many hallowed beliefs in anthropology, sociology, political science, social psychology, cognitive psychology, and (to a lesser extent) economics will have to be completely revised. However, we are only in the earliest phases of what is expected to be an ever-widening transformation of the human and nonhuman behavioral sciences, an enterprise so large that it may take the remainder of this century, and which is sure to include surprises as more and more strands of conceptual unification proceed.

It is important to emphasize that evolutionary psychology in the broad sense is not just about the design of the individual, nor is it just a revision of the present academic field of psychology. Instead, this reformulation encompasses and integrates the entire sweep of the human sciences. This is because our minds' programs evolved in ancestral social, demographic, and informational environments that gradually produced and refashioned various epidemeological and population- and group-level phenomena such as cultural traditions, languages, social groups, and demographic structures. These, in turn, acted as selection pressures that collectively engineered our constellation of evolved programs to operate functionally with respect to these supra-individual phenomena. That is, these programs evolved to functionally produce some of these phenomena (e.g., alliances; language); they also evolved to act functionally within environments that included these phenomena (e.g., fitness-promoting behavior guided by an alliance detector; communication made possible by language competence). Hence, the extended phenotypes (in Dawkins' 1982 sense) that these programs produce are not only individual traits (in the folk sense), but are designed to interact with each other to produce or exploit complex collective phenotypes (e.g., languages, cultural elements, traditions, exchange networks, social groups, agent-like coalitions, mobs, wars, small-scale hierarchies, some small-scale institutions). Moreover, on their way to producing the functional socially extended phenotypes they were designed ancestrally to produce, our evolved programs and their outputs also produce many modern and complex group and population-level phenomena as by-products (e.g., global networks of exchange, fashions, supply and demand curves, aristocracies, social classes, complex hierarchies, complex institutions, religions, different languages, etc.).

All these are objects of study for social scientists, and because these are patterned by our evolved programs, evolutionary psychology provides the integrating framework for the social sciences. It is the specifics of our adaptations' decision-making architectures that strongly shape how individuals assemble themselves into larger social structures in the modern world, and that generate the cultural outputs that our minds dynamically build and reshape over time.

Because the Standard Social Science Model's claim for the source of essentially all human mental content is free-form culture downloaded into individual minds, it is vital to realize how different the evolutionary psychological explanation is of the origin of mental content, and the nature of culture. The evolutionary psychological claim is that—for our evolved computational problem solvers to actually solve the adaptive problems faced by our ancestors (food acquisition, parenting, mate acquisition)—they had to be richly structured by selection in a content-specific way. That is, they are endowed by what philosophers would once have called innate ideas or a priori concepts (e.g., food, child, my child, male-female, ingroup-outgroup, mother, kin, cheater, free rider, snake, spider, animacy, number, noun, object, aggressive formi-dability, friend, enemy, predator, leader, and perhaps thousands of others). These may be built in to evolved modes of interpretation, conceptual-motivational systems, or evolved intuitive ontologies, in what might be thought of as a Darwinian-Kantian-computational synthesis of how our evolved programs organize experience (Boyer & Barrett, Chapter 5, this volume; Cosmides & Tooby, 1994b; Tooby, Cosmides, & Barrett, 2003). This different approach explains and often predicts the (previously unappreciated) set of human universals (see, e.g., Brown, 1991) as reliably developing adaptations, their by-products, and their interactive products. It predicts and explains principled cross-cultural variation; for example, adaptations have been designed by selection to take relevant local conditions as input to produce output that is calibrated to local circumstances (e.g., Gaulin & Schlegel, 1980; Schmitt, 2005; Sznycer et al., 2012). This approach can even explain highly particularistic cultural phenomena as unique patterns of activation of species-typical evolved mechanisms (e.g., Boyer, 2001).

Hence, our content-inflected mental adaptations reliably develop, as well as generate, some of the particular content of human culture, and form the raw materials out of which the rest is developmentally and socially elaborated in an immense and endlessly shifting play of combinatorics. This content is then present to be adopted or modified by evolved programs situated in other members of the population, or shaped by social interactions. This gives rise to epidemiological and historical population-level processes, located in particular ecological, economic, demographic, and intergroup social contexts or environments, which themselves impact their cross-individual and cross-generational dynamics. From this perspective, culture is the manufactured product of our evolved neurocomputational programs situated in individuals living in groups. To flag how different this theory of culture is from classical general learning transmission approaches, we gave our book *The Adapted Mind* (Barkow, Cosmides, & Tooby, 1992) the subtitle *Evolutionary Psychology and the Generation of Culture*. The recognition that the mind contains a large array of evolved programs leads to another departure from standard thought: Culture is not a unitary stuff, nor is culture in any way independent of evolved psychological processes. Instead, "culture" is located inside our evolved programs, and different kinds of culture are located inside different programs (and their combinations). Different types of information live inside distinct computational habitats as their native settings—that is, habitats built out of different evolved mental programs. The computational specifics of these different habitats give meaning to these data structures; they impose meaningful structure on content; they determine the rules by which potential changes to content can happen; they determine what inputs from which other programs provide the raw material that a given program operates on; they determine which contents in which internal habitats can become outputs. "Culture" and "learning" are not theoretical rivals to evolutionary psychology; they are instead phenomena to be explained by reference to and in terms of the design of the evolved neural programs that produce them (plus a description of the local inputs provided to these mechanisms).

So there is fear-of-snakes culture (living "inside" the snake-phobia system, that can be transmitted as intensities of fear-response passed to others), grammar culture (living "inside" the language competence), food-preference culture, group-identity culture, disgust culture, contempt culture, sharing culture, aggression culture, and so on. The set of cultural competences arose as a response to the opportunity afforded by the fact that other humans with their own calibrated programs are rich potential sources of information. Any time a program can cost effectively improve its performance by censusing programs situated in other brains, then selection will favor the evolution of inference systems to do so. All these distinct effects have been confusingly aggregated under the single name "culture," misleading people into thinking "culture" is a homogeneous stuff moving according to unitary principles free of the influence of our evolved psychology. Instead, brains are linked by many causally distinct pathways, built to perform distinct functions. Each brain is bristling with many independent "tubes" that propagate many distinct kinds of stuff to and from a diversity of brain mechanisms in others. This is why evolutionary psychology is not restricted to studying the static determinants of individual behavior taken in isolation from culture or social and historical setting. Instead, this is why evolutionary psychology in the broad sense integrates with and provides a nonoptional foundational framework for the social sciences (e.g., Boyer, 2001; Pinker, 2002; Sperber, 1996; Tooby, 2014; Tooby & Cosmides, 1992).

For almost a century, adherence to the Standard Social Science Model has been strongly moralized within the scholarly world, immunizing key aspects from criticism and reform (Pinker, 2002; Tooby & Cosmides, 1992). As a result, in the international scholarly community, criteria for belief fixation have often strayed disturbingly far from the scientific merits of the issues involved, whenever research trajectories produce results that threaten to undermine the credibility of the SSSM. Nevertheless, in recent decades, the strain of ignoring, exceptionalizing, or explaining away the growing weight of evidence contradicting traditional theories has become severe. Equally, reexaminations of the arguments advanced in favor of the moral necessity of the SSSM suggest that they—at best—result from misplaced fears (Pinker, 2002; Tooby & Cosmides, 1992). Indeed, we may all have been complicit in the perpetuation of vast tides of human suffering—suffering that might have been prevented or alleviated if the scientific community had not chosen to postpone or forgo a more accurate social and behavioral science.

THE INTELLECTUAL ORIGINS OF EVOLUTIONARY PSYCHOLOGY

Despite the marginalization of Darwinism within the behavioral and social sciences during the 20th century, a diverse minority of thinkers tried to think through how Darwinian insights could be applied to behavior. These efforts led to many valuable approaches, including: the instinct psychology of William James and William McDougall; the ethological approach of Tinbergen, Lorenz, and von Frisch, which integrated the careful observation of animal behavior in natural contexts with investigations of its adaptive significance and physiological basis; the sociobiological approach of Richard Alexander, William Hamilton, Robert Trivers, Edward O. Wilson and many others, which often tried to explain patterns of social behavior—differences as well as universals—in humans and other species in terms of their fitness consequences; nativist approaches to language pioneered by Chomsky (1959, 1965), Lenneberg (1967) and others, which brought to wider attention the question of whether one general-purpose learning system could account for all learning; and even behaviorist psychology—quite orthodox with respect to the Standard Social Science Model—looked for phylogenetic continuities in the laws of learning that would apply across species. As valuable as each of these approaches turned out to be, conceptual handicaps internal to each program limited their scope of application and their capacity to usefully reorganize the human psychological, behavioral, and social sciences.

The way past these limitations involved isolating or deriving a core set of foundational concepts from the intersection of physics, biology, and information theory, elucidating their logical and causal interrelationships, and then building back upward from this groundwork. (A few representative concepts are *function, regulation, information, computational architecture, adaptation, organization, design, entropy, selection, replication, selection pressure, by-product, environment of evolutionary adaptedness,* and *task environment.*) These concepts could then be used to trace out the necessary interconnections among several previously distinct scientific programs, so that the previously independent (and often inconsistent) disciplinary building blocks could be integrated into a single unified framework (for discussion, see Tooby & Cosmides, 1992). The building blocks from which evolutionary psychology was assembled include (a) the modern adaptationist revolution in theoretical evolutionary biology (Williams, 1966); (b) the rise of information theory and the computational sciences (Shannon, 1948; Weiner, 1948); (c) the emergence of serious attempts to reconstruct the ancestral conditions and ways of life of humans and prehumans and the selection pressures they imposed on our lineage (e.g., Cheney, Seyfarth, Smuts, & Wrangham, 1987; Isaac, 1989; Kaplan & Hill, 1985; Lee & DeVore, 1968, 1976); and (d) an adaptationist/computationalist resolution of the debate between environmentalists and nativists (e.g., Cosmides & Tooby, 1987; Pinker, 1997; Tooby & Cosmides, 1990a, 1990b, 1992; Tooby, Cosmides, & Barrett, 2003).

The first building block of evolutionary psychology was the strain of theoretical evolutionary biology that started in the late 1950s and early 1960s, especially with the work of George Williams (Williams & Williams, 1957; Williams, 1966); William D. Hamilton (1964); and John Maynard Smith (1982). By being placed on a more rigorous, formal foundation of replicator dynamics, evolutionary biology was transformed over the ensuing decades from a vaguely conceptualized and sometimes implicitly teleological field into a principled discipline that rivals physics in its theoretical beauty and explanatory power. One face of this transformation has been the derivation of a series of elegant selectionist theories—theories of how natural selection acts on altruism, kinship, cooperation, mating, foraging, reproduction, parenting, risk-taking, aggression, senescence, host-parasite interactions, intragenomic conflict, life-history, communication, and many other dimensions of life. Research in biology (and the human sciences informed by these theories) has been called sociobiology, behavioral ecology, evolutionary ecology, or simply evolutionary biology. In addition to evolutionary genetics, a key foundation of the improvements in our understanding of replicator dynamics was the application of game theory (von Neumann & Morgenstern, 1944) to genetic and organismal interactions—a program that rapidly developed into evolutionary game theory (Maynard Smith, 1982). (We think this process will continue as evolutionary game theory morphs into what might be called *adaptationist game theory* (e.g., Delton, Krasnow, Cosmides, & Tooby, 2011; Krasnow, Delton, Cosmides, & Tooby, 2015).[1] The other face of this revolution in biology is modern adaptationism (Williams, 1966)—a set of deductions that are still often misunderstood, even in biology (Alcock, 2001; Thornhill, 1997; Tooby & Cosmides, 1992; Tooby, Cosmides, & Barrett, 2003). Adaptationism is based on the recognition that selection is the only known natural physical process that builds highly ordered functional organization (adaptations) into the designs of species, in a world otherwise continuously assaulted by the ubiquitous entropic tendency of physical systems to become increasingly disordered with time. Thus, although not everything is functional, whenever complex functional organization is found in the architectures of species, its existence and form can be traced back to a previous history of selection. Moreover, for a given selection pressure to drive an allele systematically upward until it is incorporated into the species-typical design, the same selective cause-and-effect relationship must recur across large areas and for many generations. Complex adaptations necessarily reflect the functional demands of the cross-generationally long-enduring structure of the organism's ancestral world, rather than modern, local, transient, or individual conditions. This is why evolutionary psychology as an adaptationist field concerns the functional design of mechanisms given a recurrently structured ancestral world, rather than the idea that behavior is the fitness striving of individuals tailored to unique circumstances (Symons, 1992; Tooby & Cosmides, 1990a).

Consequently, systems of complex, antientropic functional organization (adaptations) in organisms require explanation wherever they are found; their correct explanation (barring supernatural events or artificial intervention) always involves a specific history of selection in ancestral environments; and so the prediction, discovery, mapping, and understanding of the functional architecture of organisms can be greatly facilitated by analyzing the recurrent structure of a species' ancestral world, in conjunction with the selection pressures that operated ancestrally. The foundational recognition that psychological (neurocomputational) mechanisms are evolved adaptations connects evolutionary biology to psychology in the strongest possible fashion, allowing everything we know about the study of adaptations to be applied to the study of psychological mechanisms. Whatever the sociology of

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[1] We think that, although there are many valuable results that have emerged from evolutionary game theory, other widely cited and influential results are not truly applicable to real species such as humans. The goal of adaptationist game theory is to replace a series of limitations in standard evolutionary game theory (such as highly biologically implausible conditions, radically impoverished strategy-types, etc., that were adopted to make the mathematics tractable or other reasons of preference or convenience) with modeling decisions chosen to make the results more biologically realistic. This is made possible by moving from primarily analytic approaches to agent-based population simulations; by endowing the simulated world with, for example, more plausible information ecologies; giving agents locations; by endowing agents with richer and more realistic strategies—specified psychologies—that include background capacities humans actually have, such as individual recognition; by allowing relevant decision-making variables to evolve—that is, not restricting strategy sets to a small number of discontinuous types such as defector and cooperator but, instead, for example, allowing the probability of cooperation allowed to evolve from 0 to 1. For example, it was widely thought that humans were irrationally generous, by cooperating in one-shot games, purportedly showing individual selection could not explain human game performance. By simply recognizing that interactions don't come pre-typologized for the agent as either one-shot or repeated, and that the organism must make this discrimination under uncertainty, simulations demonstrate that reciprocity under biologically plausible conditions spontaneously evolves to manifest the observed (and no-longer mysterious) generosity bias (Delton, Krasnow, Cosmides, & Tooby, 2011; see also Krasnow, Delton, Cosmides, & Tooby, 2013).

academic tribes, scientifically psychology (along with the other social and behavioral sciences) is a subbranch of evolutionary biology and can no longer be defensibly divorced from it.

George Williams's 1966 volume, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*, was central to both the adaptationist and selectionist revolutions. In it, Williams provided the first fully modern statement of the relationship between selection and adaptive design; clarified that selection operates at the genic level; developed strict evidentiary standards for deciding what aspects of a species' phenotype were adaptations, by-products of adaptations, or noise; and usefully distinguished the present usefulness of traits (if any) from their evolved functions (if any).[2] The second building block of evolutionary psychology was the rise of the computational sciences and the recognition of the true character of mental phenomena. Boole (1848) and Frege (1879) formalized logic in such a way that it became possible to see how logical operations could be carried out mechanically, automatically, and hence through purely physical causation, without the need for an animate interpretive intelligence to carry out the steps. This raised the irresistible theoretical possibility that not only logic but other mental phenomena such as goals and learning also consisted of formal relationships embodied nonvitalistically in physical processes (Weiner, 1948). With the rise of information theory (Shannon, 1948), the development of the first computers (von Neumann, 1945), and advances in cybernetics and neuroscience (Weiner, 1948), it became widely understood that mental events consisted of transformations of structured informational relationships embodied as aspects of organized physical systems in the brain. This spreading appreciation constituted the cognitive revolution. The world of the mental was no longer a mysterious, indefinable realm, but locatable in the physical world in terms of precisely describable, highly organized causal relations. Why do these informational relationships emerge in physical systems in organisms? The adaptive problem of regulating behavior in a fitness-promoting way could be seen as the selection pressure that led to the emergence of systems for natural computation—that is, as naturally engineered behavior control systems for organisms—adaptationist cybernetics.

Evolutionary psychology can, therefore, be seen as the inevitable intersection of the computationalism of the cognitive revolution with the adaptationism of Williams's evolutionary biology: Because mental phenomena are the expression of complex functional organization in biological systems, and complex organic functionality is the downstream consequence of natural selection, then it must be the case that the sciences of the mind and brain are adaptationist sciences, and psychological mechanisms are computational adaptations. In this way, the marriage of computationalism with adaptationism marks a major turning point in the history of ideas, dissolving the intellectual tethers that had limited fundamental progress, and opening the way forward. Like Dalton's wedding of atomic theory to chemistry, computationalism and adaptationism solve each other's deepest problems, and open up new continents of

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[2] The arguments that not every trait is an adaptation, not all beneficial effects of a trait are its functions, that phenotypes are full of by-products, and that there are constraints on developing systems were all central to Williams's 1966 critique of evolutionary biology. Thus, many of us were surprised when, 13 years later, Stephen Jay Gould and Richard Lewontin (1979) began to repeat the same critique without attribution, writing as if it were unknown to the evolutionary community they were criticizing. One striking difference between the two critiques was Williams's development of strict standards of evidence can be used to distinguish adaptations from nonadaptations, rendering the issue a matter of empirical research rather than post hoc rhetoric.

scientific possibility (Cosmides & Tooby, 1987; Tooby & Cosmides, 1992; Tooby, Cosmides, & Barrett, 2003, 2005).

Sociologically speaking, the single most significant factor in triggering the renewed efforts to apply evolution to behavior was the selectionist revolution in evolutionary biology, which subsequently (if temporarily) became known as sociobiology (Wilson, 1975). Across the world, biologists and allied researchers were electrified by the potential predictive and explanatory power of the new selectionist theories that were emerging, together with how elegantly and systematically they could be derived. Dynamic research communities formed at Oxford, Cambridge, Sussex, Michigan, Harvard, the University of California, and elsewhere. As a result of the flood of empirical and theoretical work coming out of these communities, the adaptationists/ selectionist revolution rapidly established itself in the biological journals as the dominant theoretical approach biologists apply to understanding the behavior of nonhumans—a position behavioral and social scientists are surprised to find that it occupies today (often under other names such as behavioral or evolutionary ecology).[3]

At Harvard, for example, under the sponsorship of Irven DeVore and E.O. Wilson, one of the most influential and dynamic of these communities gathered and matured. This research community fluoresced in Irven DeVore's living room, where Harvard's Simian Seminar was held from 1971 through the mid-1980s. In this atmosphere of ongoing discovery, ideas and findings sparked each other in an endless chain reaction. A remarkable procession of figures in evolutionary biology, behavioral ecology, primatology, and ethology spoke at DeVore's Simian Seminar, participating in this chain reaction, and sometimes staying for extended periods. Among many others, these included George Williams, Bill Hamilton, John Maynard Smith, Ernst Mayr, Edward O. Wilson, Richard Alexander, Richard Dawkins, Tim Clutton-Brock, Paul Harvey, Lionel Tiger, Robin Fox, Diane Fosse, Jane Goodall, Robert Hinde, Richard Leakey, Joseph Shepher, Richard Lee, Stephen Jay Gould, Martin Daly, and Margo Wilson, and the editor of this *Handbook*, David Buss. Among the students or proteges DeVore mentored in this environment were Bob Bailey, Peter Ellison, John Fleagle, Steve Gaulin, Henry Harpending, Paul Harvey, Sarah Blaffer Hrdy, Melvin Konner, Jeff Kurland, Jim Moore, Nadine Peacock, Peter Rodman, Robert Sapolsky, John Seger, Marjorie Shostak, Barbara Smuts, Karen Strier, Bob Trivers, Carol Worthman, Richard Wrangham, John Yellen, and ourselves (John Tooby and Leda Cosmides). Although Wilson's contributions are deservedly famous through his books and publications, DeVore's intellectual impact is less well known because his ideas were realized through his students, proteges, and colleagues. Deeply interested in human origins, DeVore pioneered three major research movements. He initiated and then championed the systematic study of primate social behavior under natural conditions (DeVore, 1962, 1965). This led him to want to incorporate human hunter-gatherers into the same careful scientific framework. With Lee and many other colleagues, in 1963 he inaugurated the systematic, empirical, quantitative investigation of living

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[3] Intellectuals wedded to the blank slate generated an unslakable demand for seemingly authoritative dismissals of the new biology. As a result, the handful of biologists who were willing to ignore the data and supply these dismissals came to be seen as the authentic voices of scientific biology to the intellectual world at large (e.g., Gould & Lewontin, 1979). The decisive empirical success of the paradigm within biology itself—what Alcock (2001) calls "the triumph of sociobiology"—is largely unknown outside of the field, and the majority of nonbiologists labor under the misimpression that sociobiology was substantively discredited by "real" biologists.

hunter-gatherers with the Kalahari Research Project and the famous Man the Hunter meetings (Lee & DeVore, 1968, 1976). Then, together with Chagnon, Irons, and many anthropologists, he worked on applying the new selectionist biology to anthropological questions.

DeVore and his colleague, Richard Lee, eschewed the "lone anthropologist" model (with its typological baggage), in which a single individual spends time documenting "the" culture of a people. In its place, they innovated a team-based approach like that found in other sciences. (Imagine the state of physics if one physicist studied the electron, another the mu meson, etc.) Their Kalahari San project brought scientists and scholars from a broad array of disciplines—anthropologists, demographers, physicians, linguists, folklorists, psychologists, ethologists, archeologists—in an attempt to document as completely as possible the behavior, health, and lives of the !Kung San people in Botswana's Kalahari desert, before hunting and gathering as a way of life disappeared from the planet. His goal in studying the San was to provide a detailed database that, when triangulated with other similarly detailed databases drawn from other hunter-gatherer groups, would allow new and powerful inferences to be made about the selection pressures that operated on hunter-gatherers to shape human design. Behavioral ecologists would be able to test optimal foraging models by matching foraging patterns to ecological conditions. Archaeologists could better interpret patterns found at ancestral sites by seeing patterns of campfires, animal remains, tool-making debris, and midden heaps produced by the social life of living hunter-gatherers. Medical researchers could gain insight into diseases of civilization by comparing diets and conditions in industrialized countries to the diets and stressors produced by a way of life that more closely resembles the conditions in which our species evolved. Developmental psychologists could gain insights into the mother-infant bond and human attachment by seeing the demands placed on infants and mothers in foraging contexts. Anthropologists could learn what social conditions foster risk pooling and food sharing; what kinds of knowledge hunter-gatherers have about animal behavior and plant life; how they use this knowledge in foraging; and how people negotiate the problems and opportunities of social life in a tiny community of interdependent, extended families (see, e.g., Lee & DeVore, 1976; Shostak, 1981). Although commonplace now, these ideas were pathbreaking at the time. After all, if the human mind consists primarily of a general capacity to learn, then the particulars of the ancestral hunter-gatherer world and our prehuman history as Miocene apes left no interesting imprint on our design. In contrast, if our minds—as evolutionary psychologists argue—are collections of mechanisms designed to solve the adaptive problems posed by the ancestral world, then hunter-gatherer studies and primatology become indispensable sources of knowledge about the adaptations that constitute modern human nature, and how our evolved psychology and soma organizes modern social, cultural, and economic processes. DeVore's insistence on situating the operation of natural selection within the detailed contexts of hunter-gatherer and nonhuman primate life was a signal contribution to the application of the evolutionary sciences to humans.

Many members of the evolutionary research communities believed that the new selectionist theories straightforwardly applied to humans, although others continued to welcome the SSSM arguments that learning had insulated human life from evolutionary patterning. On the one hand, human behavior exhibited many patterns that offered ready selectionist interpretations (e.g., sex differences in the psychology of mating), but many other phenomena resisted easy interpretation and seemed to lack clear nonhuman analogues (e.g., morality, the arts, language, culture, etc.). The result was a rich and contradictory pluralism of ideas about how evolution relates to human affairs—a pluralism that is still with us.

One of the most widespread approaches to emerge is what might be called fitness teleology. Teleological explanations are found in Aristotle (invited by his observations, because he was in fact largely a biologist), and arguably constitute an evolved mode of interpretation built into the human mind. Humans find explaining things in terms of the ends they lead to intuitive and often sufficient (Baron-Cohen, 1995; Dennett, 1987; Leslie, 1987, 1994). Social science theories have regularly depended on explicitly or implicitly teleological thinking. Economics, for example, explains choice behavior not in terms of its antecedent physical or computational causes but in terms of how the behavior serves utility maximization (involving the future pursuit and realization of valued goals). Of course, the scientific revolution originated in Renaissance mechanics, and seeks ultimately to explain everything (non-quantum mechanical) using forward physical causality—a very different explanatory system in which teleology is not admissible. Darwin outlined a forward causal physical process—natural selection—that produces biological outcomes that had once been attributed to natural teleological processes (Darwin, 1859). The theory of natural selection explains how biological systems could have sets of properties (adaptations) that naturally emerged because of the functions they served. Williams (1966) mounted a systematic critique of the myriad ways teleology had nonetheless implicitly infected evolutionary biology (where it persists in Darwinian disguises). Computationalism assimilated the other notable class of apparently teleological behavior in the universe—the seeming goal directedness of living systems—to physical causation by showing how informational structures in a regulatory system can operate in a forward causal way and yet be directed toward goals (either apparently or actually) (Weiner, 1948). The teleological end that seems to exist in the future as the point toward which things tend is in reality a feedback-driven regulatory process—a regulatory process that need not but sometimes does include a representation of a goal state in the organism in the present. The modern scientific claim would be that adaptationism and computationalism in combination can explain by forward physical causation all events that once would have been explained teleologically.

Yet, because the human mind evolved in the midst of biological and mental phenomena that can be compactly and efficiently represented and predicted using intuitive teleology, our brains evolved teleological representations as one natural causal format: We are all implicitly drawn to explain things in teleological terms. Hence, the implicit or explicit substrate underlying many attempts to apply Darwinism to human behavior was a return to the intuition that human behavior was explained by the ends it serves. For a Darwinian, it was argued, choices, practices, culture, and institutions were explained to the extent that they could be interpreted as contributing to individual (or sometimes group) reproduction: That is, the explanation for individual human behavior is that it naturally tends toward the end of maximizing reproduction in the present and future. This theory—Darwinism transmuted into fitness teleology—parallels the economic view of individuals as selfish utility maximizers, except that Hamilton's (1964) concept of inclusive fitness is substituted for the economists' concept of utility. Both approaches implicitly assume that unbounded rationality is possible and that the mind is a general-purpose computer that can figure out, in any situation, what will maximize a given quantity over the long term (whether utility, children, or inclusive fitness). Indeed, the concept of "learning" within the SSSM itself tacitly invokes unbounded rationality, in that "learning" is often implicitly treated as the tendency of the general-purpose, equipotential mind to grow—by an unspecified and as yet undiscovered computational means—whatever functional information-processing abilities it needs to serve its purposes, given time and experience in the task environment.

Evolutionary psychologists depart from fitness teleologists, nonmodularist cognitive scientists, blank-slate learning theorists, and traditional economists (but not neuroeconomists or behavioral economists) by arguing that neither human engineers nor evolution can build a computational device that exhibits these forms of unbounded rationality, because such architectures are impossible, even in principle (for arguments, see Cosmides & Tooby, 1987; Symons, 1989, 1992; Tooby & Cosmides, 1990a, 1992). In any case, observed human behavior dramatically and systematically departs from the sociobiological predictions of generalized fitness striving (as well as the predictions of economic rationality and blank-slate learning abilities). To take one simple contrast, large numbers of men will pay to have nonreproductive sex with prostitutes they believe and hope are contracepting, but have to be paid to contribute to sperm banks that, with high probability, may lead to offspring. More generally, across a range of wealthy nations, those able to afford more children choose to have fewer children—a striking disconfirmation of the prediction that humans teleologically seek to maximize reproduction or fitness (Vining, 1986). Human life is permeated with systematic deviations away from rationally maximized child-production and kin assistance. Humans are not mesmerized by accounts of Hutterites or Tsimane—people who average roughly 10 children per family.

For those eager to leap directly from theories of selection pressures to predictions of fitness maximization, there remains a missing level of causation and explanation: the level of informational or computational adaptations. This level cannot be avoided if the application of Darwin's theory to humans is ever to achieve the necessary level of scientific precision. Natural selection does not operate on behavior per se; it operates on a systematically caused *relationship* between information and behavior. Running—a behavior—is neither good nor bad. Running away from a lion can promote survival and reproduction; running toward a lion will curtail both. To be adaptive, behavioral regulation needs to be functionally contingent on information; for example, *flee when you see a stalking lion*. But a systematic relationship between information and a behavioral response cannot occur unless some reliably developing piece of organic machinery *causes* it. These causal relations between information and behavior are created by reliably developing neural circuits in the brain, which function as programs that process information. By altering the neural circuitry that develops, mutations can alter the information-processing properties of these programs, creating alternative information-behavior relationships. Selection should retain or discard alternative circuit designs from a species' neural architecture on the basis of how well the information-behavior relationships they produce promote the propagation of the genetic bases of their designs. Those circuit designs that promote their own proliferation will be retained and spread, eventually becoming species-typical (or stably frequency-dependent); those that do not will eventually disappear from the population. The idea that the evolutionary causation of behavior would lead to rigid, inflexible behavior is the opposite of the truth: Evolved neural architectures are specifications of richly contingent systems for generating responses to informational inputs.

As a result of selection acting on information-behavior relationships, the human brain is predicted to be densely packed with programs that cause intricate relationships between information and behavior, including functionally specialized learning systems, domain-specialized rules of inference, default preferences that are adjusted by experience, complex decision rules, concepts that organize our experiences and databases of knowledge, and vast databases of acquired information stored in specialized memory systems—remembered episodes from our lives, encyclopedias of plant life and animal behavior, banks of information about other people's proclivities and preferences, and so on. All these programs and the databases they create can be called on in different combinations to elicit a dazzling variety of behavioral responses. These responses are themselves information, subsequently ingested by the same evolved programs, in endless cycles that produce complex eddies, currents, and even singularities in individual, social, and cultural life. To get a genuine purchase on human behavior and society, researchers need to know the architecture of each of these evolved programs. Knowing the selection pressures will not be enough. Our behavior is not a direct response to selection pressures or to a "striving" to increase our reproduction.

Hence, one of several reasons that evolutionary psychology is distinct from the fitness-teleological branch of human sociobiology and other similar approaches lies in its rejection of fitness maximization as an explanation for behavior (Cosmides & Tooby, 1987; Daly & Wilson, 1988; Symons, 1987, 1989, 1992; Tooby & Cosmides, 1990a, 1992). The relative degree of fitness promotion under ancestral conditions is simply the design criterion by which alternative mutant designs were sorted in the evolutionary past. (The causal role that fitness plays in the present is in changing the relative frequencies of alternative designs with respect to future generations.) Although organisms sometimes appear to be pursuing fitness on behalf of their genes, in reality they are executing the evolved circuit logic built into their neural programs, regardless of whether this corresponds to current fitness maximization. Organisms are adaptation executers, not fitness pursuers. Mapping the computational architecture of the mechanisms will give a precise theory of behavior, whereas relying on predictions derived from fitness maximization will give a very impoverished and unreliable set of predictions about behavioral dynamics.

To summarize, evolutionary psychology's focus on psychological mechanisms as evolved programs was motivated by new developments from a series of different fields:

> *Advance 1:* The cognitive revolution was providing, for the first time in human history, a precise language for describing mental mechanisms as programs that process information. Galileo's discovery that mathematics provided a precise language for expressing the mechanical and physical relationships enabled the birth of modern physics. Analogously, cognitive scientists' discovery that computational-informational formalisms provide a precise language for describing the design, properties, regulatory architecture, and operation of psychological mechanisms (and developmental regulation) enables a modern science of mind (and its physical basis). Computational language is not just a convenience for modeling anything with complex dynamics. The brain's evolved function is inherently and fundamentally computational—to use information to adaptively regulate the body and behavior—so computational and informational formalisms are by their nature the most appropriate to capture the functional design of behavior regulation.

Advance 2: Advances in paleoanthropology, hunter-gatherer studies, primatology, and behavioral ecology were providing data about the adaptive problems our ancestors had to solve to survive and reproduce and the environments in which they did so.

Advance 3: Research in animal behavior, linguistics, and neuropsychology was showing that the mind is not a blank slate, passively recording the world. Organisms come "factory-equipped" with knowledge about the world, which allows them to learn some relationships easily and others only with great effort, if at all. Skinner's hypothesis—that there is one key learning process governed by reward and punishment—was wrong.

Advance 4: Evolutionary biology was revolutionized by (a) being placed on a more rigorous, formal foundation of replicator dynamics (e.g., Hamilton, 1964; Maynard Smith, 1982; Williams, 1966), leading to the derivation of a diversity of powerful selectionist theories, and by the development of adaptationism, which includes the analytic tools to recognize and differentiate adaptations, from by-products, and stochastically generated evolutionary noise (Williams, 1966). Enduring selection pressures (recurrent adaptive problems), operating over evolutionary time within sets of enduring environmental regularities, act to construct in species reliably developing solutions (adaptations) to their enduring adaptive problems. Evolutionary change involves the change in a population's gene frequencies, and those environmental characteristics that are transient and variable cannot, by their very nature, systematically push gene frequencies directionally upward for long enough to cumulatively produce complex functional species-typical design. Hence adaptationists necessarily emphasize the role that a species-particular history of enduring selection pressures and environmental regularities plays in explaining complex functional design (see the discussion of the *environment of evolutionary adaptedness* or *EEA* following). The composite of enduring selection pressures (the EEA) that pushed the alleles underlying adaptation upward to stably high frequencies are that specific part of the past that caused the adaptation and hence explains its existence and design.

Ethology had brought together Advances 2 and 3, sociobiology had connected Advances 2 and 4, sometimes with 3; nativist cognitive science connected Advances 1 and 3, but neglected and still shrinks from Advances 2 and 4. Standard cognitive neuroscience partially and erratically accepts 1 and 3, but omits 2 and 4. Aside from cognitive approaches, the rest of psychology lacks much of Advance 1, most of Advance 3, and all of Advances 2 and 4. Evolutionary anthropology appreciates Advances 2 and 4, but neglects 1 and 3. Social anthropology and sociology lack all four. So it goes. If one counts the adaptationist/computationalist resolution of the nature-nurture issue as a critical advance, the situation is even bleaker.

We thought these new developments could be painstakingly pieced together into an integrated framework that successfully addressed the difficulties that had plagued evolutionary and nonevolutionary approaches alike. The reason that the synthesis had not emerged earlier in the century was because the key concepts and theories (e.g., adaptationism, computationalism, etc.) were scattered across fields that were institutionally and intellectually distant from each other. Consequently, relatively few were in the lucky position of being professionally equipped to see all the necessary connections at once. This limited the field's initial appeal, because what seems self-evident from the synoptic vantage point seems esoteric, pedantic, or cultish (and immoral) from other vantage points. Nevertheless, those researchers working along these and similar lines were confident that by bringing all four advances together, the evolutionary sciences could be united with the computationalist revolution in a way that provided a framework not only for psychology but for all of the social and behavioral sciences. To signal its distinctiveness from other approaches, the field was named *evolutionary psychology*.[4] Its long-term goal is to eradicate disciplinary boundaries, and unify the evolutionary, genetic, neural, cognitive, psychological, behavioral, and social sciences, because the idea that these are different fields is a sociological vestige rooted in the isolated perspectives native to the independent disciplines when they were founded. Reality has no such boundaries, and the eventual theoretical unification of these fields should reflect the undivided nature of the reality we are studying.

EVOLUTIONARY PSYCHOLOGY

Like other cognitive scientists, when evolutionary psychologists refer to *the mind*, they mean the set of information-processing devices, embodied in neural tissue, that is responsible for all conscious and nonconscious mental activity, that generates all behavior, and that regulates the body. Like other psychologists, evolutionary psychologists test hypotheses about the design of these computational devices using laboratory methods from experimental cognitive and social psychology, developmental psychology, experimental economics, cognitive neuroscience, and cross-cultural fieldwork.

The primary tool that allows evolutionary psychologists to go beyond traditional psychologists in studying the mind is that they take full advantage in their research of

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[4] We sometimes read that the term *evolutionary psychology* is simply sociobiology, with the name changed to avoid the bad political press that sociobiology had received. Although it is amusing (given the record) to be accused of ducking controversy, these claims are historically and substantively wrong. In the first place, evolutionary psychologists are generally admirers and defenders of sociobiology (or behavioral ecology, or evolutionary ecology). It has been the most useful and most sophisticated branch of modern evolutionary biology, and various evolutionary psychologists have themselves made contributions to this literature. Nonetheless, the lengthy and intense debates about how to apply evolution to behavior made it increasingly clear that markedly opposed views needed different labels if any theoretical and empirical project was to be clearly understood. In the 1980s, Martin Daly, Margo Wilson, Don Symons, John Tooby, Leda Cosmides, and David Buss had many discussions about what to call this new field, some at Daly and Wilson's kangaroo rat field site in Palm Desert, some in Santa Barbara, and some at the Center for Advanced Study in the Behavioral Sciences. Politics and the press did not enter these discussions, and of course we anticipated (correctly) that the same content-free ad hominem attacks would pursue us throughout our careers. What we *did* discuss was that this new field focused on characterizing the adaptations comprising the psychological/developmental architecture—whereas sociobiology had not. Sociobiology had focused mostly on selectionist theories, with no consideration of the computational level, and little interest in mapping psychological mechanisms. Both the subject matter of evolutionary psychology and the theoretical commitments were simply different from that of sociobiology, in the same way that sociobiology was quite different from the ethology that preceded it and in the same way that cognitive psychology was different from behaviorist psychology—necessitating a new name in each case.

an overlooked reality: The programs comprising the human mind were designed by natural selection to solve the adaptive problems regularly faced by our hunter-gatherer ancestors—problems such as finding a mate, cooperating with others, hunting, gathering, protecting children, navigating, avoiding predators, avoiding exploitation, and so on. Knowing this allows evolutionary psychologists to approach the study of the mind like an engineer. You start by carefully specifying an adaptive information-processing problem; then you do a task analysis of that problem. A task analysis consists of identifying what properties a program would have to have to solve that problem well. This approach allows you to generate hypotheses about the structure of the programs that comprise the mind, which can then be tested. Indeed, evolutionary psychology is unique among theoretical orientations in psychology in the degree to which it derives from independently established theories principled predictions about previously unknown aspects of the species-typical psychological architectures of humans and other species (see, e.g., Buss, 1999; Daly & Wilson, 1988; Gaulin, 1995; Symons, 1979).

From this point of view, there are precise causal connections that link the four developments discussed earlier into a coherent framework for thinking about human nature and society (Tooby & Cosmides, 1992):

- Each organ in the body evolved to serve a function: The intestines digest, the heart pumps blood, and the liver detoxifies poisons. The brain's evolved function is to extract information from the environment and use that information to generate behavior and regulate physiology. Hence, the brain is not just like a computer. It is a computer—that is, a physical system that was designed to process information (Advance 1). Its programs were designed not by an engineer, but by natural selection, a causal process that retains and discards design features based on how well they solved adaptive problems in past environments (Advance 4).

  The fact that the brain processes information is not an accidental side effect of some metabolic process. The brain was designed by natural selection *to be* a computer. Therefore, if you want to describe its operation in a way that captures its evolved function, you need to think of it as composed of programs that process information. The question then becomes: What programs are to be found in the human brain? What are the reliably developing, species-typical programs that, taken together, comprise the human mind?
- Individual behavior is generated by this evolved computer, in response to information that it extracts from the internal and external environment (including the social environment, Advance 1). To understand an individual's behavior, therefore, you need to know both the information that the person registered *and* the structure of the programs that generated his or her behavior.
- The programs that comprise the human brain were sculpted over evolutionary time by the ancestral environments and selection pressures experienced by the hunter-gatherers from whom we are descended (Advances 2 and 4). Each evolved program exists because it produced behavior that promoted the survival and reproduction of our ancestors better than alternative programs that arose during human evolutionary history. Evolutionary psychologists emphasize hunter-gatherer life because the evolutionary process is slow—it takes hundreds of generations to build a program of any complexity. The industrial revolution—

even the agricultural revolution—is too brief a period to have selected for new neurocomputational programs of any complexity.[5]

- Although the behavior our evolved programs generate would, on average, have been adaptive (reproduction promoting) in ancestral environments, there is no guarantee that it will be so now. Modern environments differ importantly from ancestral ones, particularly when it comes to social behavior. We no longer live in small, face-to-face societies, in seminomadic bands typically of 50 to 150 people, many of whom were close relatives. Yet, our cognitive programs were designed for that social world.
- Perhaps most importantly, natural selection will ensure that the brain is composed of many different programs, many (or all) of which will be specialized for solving their own corresponding adaptive problems. That is, the evolutionary process will not produce a predominantly general-purpose, equipotential, domain-general architecture (Advance 3).

In fact, this is a ubiquitous engineering outcome. The existence of recurrent computational problems leads to functionally specialized application software. For example, the demand for effective word processing and good digital music playback led to different application programs because many of the causal design features that make a program an effective word processing program are different from those that make a program a good digital music player. Indeed, the greater the number of functionally specialized programs (or subroutines) your computer has installed, the more intelligent your computer is, and the more things it can accomplish. The same is true for organisms. Armed with this insight, we can lay to rest the myth that the more evolved organization the human mind has, the more inflexible its response. Interpreting the emotional expressions of others, seeing beauty, learning language, loving your child—all these enhancements to human mental life are made possible by specialized neural programs built by natural selection.

To survive and reproduce reliably as hunter-gatherers required the solution of large and diverse arrays of adaptive information-processing problems. These ranged from predator vigilance and prey stalking to plant gathering, mate selection, childbirth, parental care, coalition formation, and disease avoidance. Design features that make a program good at choosing nutritious foods, for example, are ill suited for finding a fertile mate or recognizing free riders. Some sets of problems would have required differentiated computational solutions.

This difference can be most clearly seen by using results from evolutionary game theory (Advance 4) and data about ancestral environments (Advance 2) to define adaptive problems and then carefully dissecting the computational requirements of any program capable of solving those problems. For example,

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[5] Simple, unidimensional traits, caused by quantitative genetic variation (e.g., taller, shorter), can be adjusted in less time; see Tooby and Cosmides, 1990b. Moreover, intense selection pressures, such as those caused by diseases (e.g., malaria) or new food sources (milk from domesticated animals) can propel some alleles rapidly upward in frequency on a timescale of centuries. For example, all mammals have the adaptations to digest milk in infancy and then lose it after weaning, but some human populations who get milk from livestock benefited from the tweaking of the lactose-digesting enzyme production system so that the preexisting ability to digest milk is maintained into adulthood. In contrast, despite being surrounded, for millions of years, by forests of sugar (cellulose) whose digestion would have prevented all starvation, no humans have evolved the appropriate enzymes to break down the beta acetal linkages that prevent the digestion of cellulose. Complex adaptations are difficult to evolve rapidly.

game theoretic analyses of conditional helping show that programs designed for logical reasoning would be poorly designed for detecting cheaters in social exchange and vice versa; this incommensurability selected for programs that are functionally specialized for reasoning about reciprocity or exchange (Cosmides & Tooby, Chapter 25, this *Handbook*, Volume 2).

- Finally, descriptions of the computational architecture of our evolved mechanisms allow a systematic understanding of cultural and social phenomena. The mind is not like a tape recorder, passively recording the world but imparting no content of its own. Domain-specific programs organize our experiences, create our inferences, inject certain recurrent concepts and motivations into our mental life, give us our passions, and provide cross-culturally universal frames of meaning that allow us to understand the actions and intentions of others. They invite us to think certain kinds of thoughts; they make certain ideas, feelings, and reactions seem reasonable, interesting, and memorable. Consequently, they play a key role in determining which ideas and customs will easily spread from mind to mind and which will not (Boyer, 2001; Sperber, 1994, 1996; Tooby & Cosmides, 1992). That is, they play a crucial role in shaping human culture.

Instincts are often thought of as the opposite of reasoning, decision-making, and learning. But the reasoning, decision-making, and learning programs that evolutionary psychologists have been discovering (a) are complexly specialized for solving an adaptive problem, (b) reliably develop in all normal human beings, (c) develop without any conscious effort and in the absence of formal instruction, (d) are applied without any awareness of their underlying logic, and (e) are distinct from more general abilities to process information or behave intelligently. In other words, they have all the hallmarks of what we usually think of as an instinct (Pinker, 1994). In fact, we can think of these specialized circuits as *reasoning instincts, decision instincts, and learning instincts.* They make certain kinds of inferences and decisions just as easy, effortless, and natural to us as humans as catching flies is to a frog or burrowing is to a mole.

Consider this example from the work of Simon Baron-Cohen (1995). Like adults, normal 4-year-olds easily and automatically note eye direction in others, and use it to make inferences about the mental states of the gazer. For example, 4-year-olds, like adults, infer that, when presented with an array of candy, the gazer wants the particular candy he or she is looking at. Children with autism do not make this inference. Although children with this developmental disorder can compute eye direction correctly, they cannot use that information to infer what someone wants. Normal individuals know, spontaneously and with no mental effort, that the person wants the candy he or she is looking at. This is so obvious to us that it hardly seems to require an inference at all. It is just common sense. But "common sense" is caused: It is produced by neurocomputational mechanisms. To infer a mental state (wanting) from information about eye direction requires a computation. There is an inference circuit—a reasoning instinct—that produces this inference. When the circuit that does this computation is broken or fails to develop, the inference cannot be made. Those with autism fail this task because they lack this reasoning instinct, even though they often acquire very sophisticated competences of other sorts. If the mind consisted of a domain-general knowledge-acquisition system, narrow impairments of this kind would not be possible.

Reasoning instincts are invisible to our intuitions, even as they generate them. They are no more accessible to consciousness than our retinal cells and line detectors but are just as important in manufacturing our perceptions of the world. As a species, we have been blind to the existence of these instincts, not because we lack them but precisely because they work so well. Because they process information so effortlessly and automatically, their operation disappears unnoticed into the background. Moreover, these instincts structure our thought and experience so powerfully we mistake their products for features of the external world: Color, beauty, status, friendship, charm—all are computed by the mind and then experienced as if they were objective properties of the objects we attribute them to. These mechanisms limit our sense of behavioral possibility to choices people commonly make, shielding us from seeing how complex and regulated the mechanics of choice is. Indeed, these mechanisms make it difficult to imagine how things could be otherwise. As a result, we take normal behavior for granted: We do not realize that normal behavior needs to be explained at all.

As behavioral scientists, we need corrective lenses to overcome our instinct blindness. The brain is fantastically complex, packed with programs, most of which are currently unknown to science. Theories of adaptive function can serve as corrective lenses for psychologists, allowing us to see computational problems that are invisible to human intuition. When carefully thought out, these functional theories can lead us to look for programs in the brain that no one had previously suspected.

PRINCIPLES OF ORGANIC DESIGN

Biology is the study of organisms, and psychology is—in a fundamental sense—a branch of biology. It is the study of the evolved designs of the behavior-regulating tissues of organisms. To be effective researchers, psychologists will need to become at least minimally acquainted with the principles of organic design.

NATURAL SELECTION IS AN ENGINEER THAT DESIGNS ORGANIC MACHINES

The phenomenon that Darwin was trying to explain is the presence of functional organization in living systems—the kind of organization found in artifacts, such as clocks, spectacles, or carriages; indeed, the kind of organization that appeared to be designed by an intelligent engineer to solve a problem. Darwin realized that organisms can be thought of as *self-reproducing machines*. What distinguishes living from nonliving machines is reproduction: the presence in a machine of devices (organized components) that cause it to produce new and similarly reproducing machines. Given a population of living machines, this property—self-reproduction—drives a system of positive and negative feedback—natural selection—that can explain the remarkable fit between the design of organisms and the problems they must solve to survive and reproduce.

In contrast to human-made machines, which are designed by inventors, living machines acquire their intricate functional design over immense lengths of time, as a consequence of the fact that they reproduce themselves. Indeed, modern Darwinism has an elegant deductive structure that logically follows from Darwin's initial insight that reproduction is the defining property of life:

When an organism reproduces, genes that cause the development of its design features are introduced into its offspring. But the replication of the design of the parental machine is not always error free. As a result, randomly modified designs (i.e., mutants) are introduced into populations of reproducers. Because living machines are already exactingly organized so that they cause the otherwise improbable outcome of constructing offspring machines, random modifications will usually introduce disruptions into the complex sequence of actions necessary for self-reproduction. Consequently, most newly modified but now defective designs will remove themselves from the population: a case of negative feedback.

However, a small number of these random design modifications will, by chance, improve the system's machinery for causing its own reproduction. Such improved designs (by definition) cause their own increasing frequency in the population: a case of positive feedback.

This increase continues until (usually) such modified designs outreproduce and thereby replace the alternative designs in the population, leading to a new species-standard (or population-standard) design: a new retinal design, or blood cell, or reasoning circuit, or food preference ordering. After such an event, the population of reproducing machines is different from the ancestral population. The population has taken a step "uphill" toward a greater degree of functional organization for reproduction than it had previously. Over the long run, down chains of descent, this feedback cycle pushes designs through state-space toward increasingly well-engineered—and increasingly improbable—functional arrangements. These arrangements are *functional* in a specific sense: The elements are well organized to cause their own reproduction in the environment in which the species evolved.

For example, if a mutation appeared that caused individuals to find family members sexually repugnant, they would be less likely to conceive children incestuously. They would produce children with fewer genetic diseases, and more of these children would mature and reproduce than would the children of those who were not averse to incest. Such an incest-avoiding design would produce a larger set of healthy children every generation, down the generations. By promoting the reproduction of its bearers, the incest-avoiding circuit thereby promotes its own spread over the generations, until it eventually replaces the earlier-model sexual circuitry and becomes a universal feature of that species' design (for a map of the design of this system, see Lieberman et al., 2007). This spontaneous feedback process—natural selection—causes functional organization to emerge naturally, without the intervention of an intelligent designer or supernatural forces.

Genes and Design Self-reproducing systems could not exist unless there were adaptations that conserved the functional design against entropy from one generation to the next. Genes are the means by which functional design features replicate themselves from parent to offspring. They can be thought of as particles of design. These elements are transmitted from parent to offspring and together with stable features of an environment, cause the organism to develop some design features and not others. Genes have two primary ways they can propagate themselves: by increasing the probability that offspring will be produced by the organism in which they are situated or by increasing reproduction in others who are more likely than random members of the population to carry the same gene.

An individual's genetic relatives carry some of the same genes, by virtue of having received some of the same genes from a recent common ancestor. Thus, a gene in an individual that causes an increase in the reproductive rate of that individual's kin will, by so doing, tend to increase its own frequency in the population. A circuit that motivates individuals to help feed their sisters and brothers, if they are in sufficiently greater need, is an example of a program that increases kin reproduction (for evidence about the design of such a system, see Lieberman et al., 2007). As Hamilton (1964) pointed out, design features that promote both direct reproduction and kin reproduction and that make efficient trade-offs between the two will replace those that do not (a process called *kin selection*).

Reproduction and Function How well a design feature systematically promotes direct and kin reproduction is the bizarre but real engineering criterion determining whether a specific design feature will be added to or discarded from a species' design.

The concept of *adaptive behavior* can now be defined with precision. Adaptive behavior, in the evolutionary sense, is (in the general case) behavior that increased the frequency of the alleles underlying the behavior; typically, this means behavior that systematically promoted the net lifetime reproduction of the individual and/or (with appropriate trade-offs) that individual's genetic relatives. By promoting the replication of the genes that built them, circuits that—systematically and over many generations—cause adaptive behavior become incorporated into a species' neural design. In contrast, behavior that undermines the reproduction of the individual or his or her genetic relatives removes the circuits causing those behaviors from the species. Such behavior is maladaptive.

Evolutionists analyze how design features are organized (in ancestral environments) to contribute to lifetime kin-weighted reproduction because reproduction was the final causal pathway through which a functionally improved design feature caused itself to increase in frequency until it became standard equipment in all (or in an enduring subset of) ordinary members of the species.

Adaptive Problems Select for Adaptations Darwin's detailed studies of plants and animals revealed complex structures composed of parts that appeared to be organized to overcome reproductive obstacles (e.g., the presence of predators) or to take advantage of reproductive opportunities (e.g., the presence of fertile mates). Enduring conditions in the world that create reproductive opportunities or obstacles constitute *adaptive problems*, such as the presence of pathogens, variance in the food supply, the vulnerability of infants, or the presence of family in an individual's social group. Adaptive problems have two defining characteristics. First, they are conditions or cause-and-effect relationships that were regularly encountered by members of a population or species, and that recurred across sufficiently many generations such that natural selection has enough time to design adaptations in response. Second, they are that subset of enduring relationships that could, in principle, be exploited by some property of an organism to increase its reproduction or the reproduction of its relatives. Alternative designs are retained or discarded by natural selection on the basis of how well they function as solutions to adaptive problems.

Over evolutionary time, more and more design features accumulate that fit together to form an integrated structure or device (e.g., a retina, a claw, an incest-avoidance program) that is well engineered to solve its particular adaptive problem. Such a structure or device is called an *adaptation*. Indeed, an organism can be thought of as a collection of adaptations, together with the engineering by-products of adaptations, and evolutionary noise. The functional subcomponents of the ear, hand, intestines, uterus, or circulatory system are examples. Each of these adaptations exists in the human design now because it contributed to the process of self- and kin reproduction in the ancestral past. Adaptive problems are the only kind of problem that natural selection can design machinery for solving. They are the source of and explanation of our evolved functional design.

The Environment of Evolutionary Adaptedness One key to understanding the functional architecture of the mind is to remember that its programs were not selected for because they solved the problems faced by modern humans. Instead, they were shaped by how well they solved adaptive problems among our hunter-gatherer ancestors. The second key is to understand that the developmental processes that build each program, as well as each program in its mature state, evolved to use information and conditions that were reliably present in ancestral environments. The design of each adaptation assumes the presence of certain background conditions and operates as a successful problem solver only when those conditions are met. The *environment of evolutionary adaptedness* (EEA) refers jointly to the problems hunter-gatherers had to solve and the conditions under which they solved them (including their developmental environment).

Although the hominin line is thought to have originated in African open woodlands, the EEA is not a particular place or time. The EEA for a given adaptation is the statistical composite of the enduring selection pressures or cause-and-effect relationships that pushed the alleles underlying an adaptation systematically upward in frequency until they became species-typical or reached a frequency-dependent equilibrium (most adaptations are species-typical; see Hagen, Chapter 4, this volume). Because the coordinated fixation of alleles at different loci takes time, complex adaptations reflect enduring features of the ancestral world. The adaptation is the consequence of the EEA, and so the structure of the adaptation reflects the structure of the EEA. The adaptation evolved so that when it interacted with the stable features of the ancestral task environment, their interaction systematically promoted fitness (i.e., solves an adaptive problem). The concept of the EEA is essential to Darwinism, but its formalization was prompted by the evolutionary analysis of humans because human environments have changed more dramatically than the environments most other species occupy. The research problems faced by most biologists do not require them to distinguish the modern environment from a species' ancestral environment. Because adaptations evolved and assumed their modern form at different times and because different aspects of the environment were relevant to the design of each, the EEA for one adaptation may be somewhat different from the EEA for another. Conditions of terrestrial illumination, which form (part of) the EEA for the vertebrate eye, remained relatively constant for hundreds of millions of years—and can still be observed by turning off all artificial lights. In contrast, the social and foraging conditions that formed (part of) the EEA that selected for neural programs that cause human males to provision and care for their offspring (under certain conditions) is almost certainly less than 2 million years old.

When a program is operating outside the envelope of ancestral conditions that selected for its design, it may look like a poorly engineered problem solver. Efficient foraging, for example, requires good probability judgments, yet laboratory data suggested that people are poor intuitive statisticians, incapable of making simple inferences about conditional probabilities (Kahneman, Slovic, & Tversky, 1982). Evolutionary psychologists recognized that these findings were problematic, given that birds and bees solve similar problems with ease. The paradox evaporates when you consider the EEA for probability judgment. Behavioral ecologists presented birds and bees with information in ecologically valid formats; psychologists studying humans did not.

Being mindful of the EEA concept changes how research is designed and what is discovered. Giving people probability information in the form of absolute frequencies—an ecologically valid format for hunter-gatherers—reveals the presence of mechanisms that generate sound Bayesian inferences (Brase, Cosmides, & Tooby, 1998; Cosmides & Tooby, 1996a; Gigerenzer, 1991; Gigerenzer, Todd, & the ABC Group, 1999). Indeed, EEA-minded research on judgment under uncertainty is now showing that the human mind is equipped with a toolbox of "fast-and-frugal heuristics," each designed to make well-calibrated judgments quickly on the basis of limited information (Gigerenzer & Selten, 2002; Gigerenzer et al., 1999; Todd, Hertwig, & Hoffrage, Chapter 37, this *Handbook*, Volume 2). These procedures are *ecologically rational,* providing good solutions when operating in the task environments for which they evolved (Cosmides & Tooby, 1996b; Delton, Krasnow, Cosmides, & Tooby, 2011; Tooby, Cosmides, & Barrett, 2005, Tooby & Cosmides, in press).

Knowing the Past It is often argued that we can know nothing about the past that is relevant to psychology because behavior doesn't fossilize. Thus, the whole field of evolutionary psychology is claimed to rest on uncertain speculation or conjecture. In reality, we know with certainty thousands of important things about our ancestors and the world they inhabited, many of which can be useful in guiding psychological research. Some of these should be obvious, although their implications may not be. For example, it is a certainty that our ancestors lived in a world in which certain principles of physics governed the motions of objects: facts that allowed Shepard (1984, 1987) to discover how the mind represents the motion of objects, both in perception and imagination. It is equally certain that hominins had eyes, looked at what interested them, and absorbed information about what they were looking at, making eye-gaze direction informative to onlookers: facts that helped Baron-Cohen (1995) and others to create a far-reaching research program on the cognitive basis of mind reading, the ability to infer the mental states of others. It is certain that our ancestors, like other Old World primates, nursed; had two sexes; chose mates; had color vision calibrated to the spectral properties of sunlight; lived in a biotic environment with predatory cats, venomous snakes, and spiders; were predated on; bled when wounded; were incapacitated from injuries; were vulnerable to a large variety of parasites and pathogens; and had deleterious recessives rendering them subject to inbreeding depression if they mated with siblings. All these conditions (along with tens of thousands of others) are known, and all pose adaptive problems. By considering these selection pressures, a careful, well-informed, intelligent researcher can develop plausible, testable theories of the adaptations that arose in response to them. Selection would not plausibly have built an equipotential cognitive architecture that had to encounter the world as if it were unprepared for functionally significant sets of evolutionarily recurrent relationships. It is remarkable that such a model is so vigorously defended.

By triangulating the work of researchers in many disciplines, many other sound inferences can be made. Evolutionary psychologists, behavioral ecologists, and evolutionary biologists have already created a library of sophisticated models of the selection pressures, strategies, and trade-offs that characterize fundamental adaptive problems (Advance 4), which they use in studying processes of attention, memory, decision-making, and learning in nonhuman animals. Which model is applicable for a given species depends on certain key life-history parameters. Findings from paleoanthropology, hunter-gatherer archaeology, and studies of living hunter-gatherer populations locate humans in this theoretical landscape by filling in the critical parameter values (Advance 2). Ancestral hominins were ground-living primates; omnivores,[6] exposed to a wide variety of plant toxins and meat-borne bacteria and fungi; they had a sexual division of labor involving differential rates of hunting and gathering. They were mammals with altricial young, long periods of biparental investment in offspring, enduring male-female mateships, and an extended period of physiologically obligatory female investment in pregnancy and lactation. They were a long-lived, low-fecundity species in which variance in male reproductive success was higher than variance in female reproductive success. They lived in small, typically nomadic, kin-based bands often of 20 to 150; they would rarely have seen more than 1,000 people at one time; they had only modest opportunities to store provisions for the future; they engaged in cooperative hunting, raiding, defense, and aggressive coalitions; and they made tools and engaged in extensive amounts of implicit and explicit exchange, food-sharing, cooperation, and deferred reciprocation. When these parameters are combined with formal models from evolutionary biology and behavioral ecology, a reasonably consistent picture of ancestral life begins to appear (e.g., Tooby & DeVore, 1987). From this, researchers can refine theories of adaptive problems, develop models of their computational requirements, and test for the presence of mechanisms equipped with design features that satisfy these requirements. Most chapters in this volume provide examples of this process.

Many adaptive problems can be further illuminated by the use of evolutionary game theory (see Cosmides & Tooby, Chapter 25, this *Handbook*, Volume 2) and/or optimal foraging models. For example, variance in the food supply can be buffered through food sharing, a method of pooling risk, which is stable only when the variance is primarily due to luck rather than effort. Studies of modern hunter-gatherers have allowed quantitative estimates of how much variance there is in successfully finding different kinds of foods; for example, among the Ache of Paraguay, meat and honey are high-variance foods even for skilled foragers, whereas the variance in gathering vegetable foods is low and comes from effort rather than luck. As might be predicted from an analysis of the adaptive problems posed by variance in the food supply, Ache hunter-gatherers risk-pool with meat and honey by sharing widely at the band level, but they share gathered vegetable foods only within nuclear families (Kaplan & Hill, 1985). This analysis suggests that our minds house at least two different decision rules for sharing, each creating a different sense of what is appropriate or fair, and each triggered by a different experience of variance. This, in turn, led to the successful prediction that we have mechanisms designed to be effectively calibrated to variance and its causes (e.g., Rode, Cosmides, Hell, & Tooby, 1999; Wang, 2002). Indeed, the "irrational" risk aversion posited in Kahneman and Tversky's (1979) prospect theory can be replaced by an evolutionarily revised prospect theory (Rode et al., 1999), in which individuals can be shown to be adaptively risk-seeking or adaptively risk averse depending on their need level and the probability distribution they faced.

Knowledge of ancestral life, ancestral conditions, and ancestral adaptive problems are like treasure maps that can supercharge the discovery of previously unknown

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[6] Fossil sites show extensive processing sites for animal products. Large East African woodland primates hunt and eat meat. Hunter-gatherers are observed to get a major fraction of their diet from hunting, and for hunting to be a dispropoportionately male activity not only in humans but in chimpanzees and baboons.

psychological and developmental mechanisms. Although behavioral scientists can be certain about a huge inventory of facts about the ancestral world that has not yet been harnessed to guide psychological research, certainty about the past is not necessary for building better hypotheses. We can derive valuable experimental hypotheses from likely rather than certain features of the ancestral world. At worst, such a hypothesis is no more likely to be falsified than the hypotheses advanced by nonevolutionary researchers, who have no principled source from which to derive their hypotheses and must rely on the random walk of blind empiricism. There are certainly many features of the ancestral world about which we are completely ignorant: These features simply do not form the basis for experiments. Traditional research programs involve proceeding either with blind empiricism, on the basis of no theory of function, or to proceed guided by necessarily false theories of function. It is difficult to see any valid argument for doing either, because (a) random empirical tests are unlikely to efficiently guide researchers to the correct experimental procedures that are capable of detecting and mapping complex neural or developmental programs, and (b) invalid nonevolutionary theories are even less likely to be productive. (The physics of entropy together with replicator dynamics tell us that the only origin of complex functional design in undomesticated species is natural selection; hence, all correct theories of function will be and must be evolutionary.)

PSYCHOLOGY IS REVERSE ENGINEERING

As engineers go, natural selection is superlative. It has produced exquisitely engineered biological machines—the vertebrate eye, the four-chambered heart, the liver, and the immune system—whose performance at solving problems is unrivaled by any machine yet designed by humans. (Consider the poor quality of machine vision compared to evolved vision, artificial pacemakers compared to the evolved system regulating the heart, pharmaceuticals with their negative side effects compared to the body's immune and detoxification systems.)

Psychologists—evolutionary or otherwise—are engineers working in reverse. The brain/mind is a complex functional system, composed of programs whose design was engineered by natural selection to solve specific adaptive problems. Our job is to reverse-engineer the human brain/mind: to dissect its computational architecture into functionally isolable information-processing units—programs—and to determine how these units operate, both computationally and physically. To arrive at the appropriate construal, the neurocomputational and developmental architecture must be conceptualized as a set of parts designed to interact in such a way that they solve adaptive problems. This conceptualization requires theories of adaptive function—engineering specifications, which provide analyses of what would count as good design for a particular problem. In so doing, they also provide the criteria necessary to decide whether a property of an organism is a design feature, a functionless by-product, or noise.

Many Properties of Organisms Are Not Adaptations The cross-generationally recurrent design of an organism can be partitioned into (a) adaptations, which are present because they were selected for, (b) by-products of adaptations, which were not themselves targets of selection but are present because they are causally coupled to or produced by traits that were, and (c) noise, which was injected by the stochastic components of evolution. Consider, for example, that all brain-intact persons learn to speak (or sign) the language of their surrounding community without explicit instruction, whereas reading and writing require explicit schooling, are not mastered by every individual, and are entirely absent from some cultures. The neural programs that allow humans to acquire and use spoken language are adaptations, specialized by selection for that task (Pinker, 1994; Pinker & Bloom, 1990). But once an information-processing mechanism exists, it can be deployed in activities that are unrelated to its original function. Because we have evolved learning mechanisms that cause language acquisition, we can, through laborious study and schooling, learn to write and read. But the learning mechanisms that enable these activities were not selected for *because* they caused reading and writing. The ability to read and write are by-products of adaptations for spoken language, enabled by their causal structure. Random evolutionary noise exists as well—for example, the gene variants that cause dyslexia (difficulties with learning to read). Indeed, entropy is pervasive, and so the designs of organisms are the product of mutation-selection balance. All organisms contain many negative genetic mutations, on the way to being selected out, and the environments of development change, generating environmental "mutations"—changes—that induced developmental perturbations. Moreover, organisms may only have been exposed to an adaptive problem recently. So evolutionarily informed researchers do not expect optimality, and are not confounded when nonoptimality is found. They only expect that designs are to be found in regions of design-space that are vastly better than random from a functional perspective, and that by modeling or considering "optimality" or good design, these rare regions can be identified.

Adaptations are present because of a prior history of selection. They are not defined as any ability or trait, however rare or modern, that is beneficial by virtue of enabling a particular individual to have more children. Suppose, for example, that a computer programmer were to become wealthy through writing code and used that wealth to conceive many children. This would not make computer programming, which is a very recent cultural invention, an adaptation, nor would it mean that the cognitive mechanisms that enable computer programming are adaptations designed *for* producing computer programs. The ability to write code is a beneficial side effect of cognitive adaptations that arose to solve entirely different problems, ones that promoted reproduction in an ancestral past.[7]

Thus, although selection creates functional organization, not all traits of organisms are functional. In fact, most "parts" of an organism are not functional for a simple reason: Most ways of conceptually dissecting a species' phenotype into parts will fail to capture functional components.[8] To see the organization that exists in a complex

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[7] In the case of computer programming, these adaptations might include the numerical abilities that underwrite foraging (Wynn, 1998), recursion for producing metarepresentations (Leslie, 1987), grammatical mechanisms (Pinker, 1994), certain deductive capacities (Rips, 1994), and so on. To determine which adaptations underwrite the ability to program computers would require cognitive experimentation aimed at discovering which information-processing mechanisms are activated when someone is engaged in this evolutionarily novel activity. Moreover, different constellations of mechanisms might be activated when different individuals program, precisely because there has not been enough time for natural selection to produce an integrated design specifically for this purpose.

[8] Imagine you are looking inside a television and considering ways to conceptually divide its innards into parts. A random parsing is unlikely to isolate the functional units that allow a TV to transduce electromagnetic radiation into a color bitmap (its function). Indeed, most ways of dividing its insides will fail to capture *any* functional components, and any such nonfunctional "parts" will be by-products of the functional ones (Hagen, Chapter 4, this volume).

system, researchers need to be able to distinguish its functional components from the by-products and noise.

With a well-specified theory of an adaptive problem, researchers can identify functional and nonfunctional parts of an organism. Of the three kinds of properties, adaptations are the most important and illuminating because they explain why a system has certain parts, why these participate in certain cause-and-effect relationships with one another, and why they interact with the world in the way that they do. Adaptations are problem-solving machines and can be identified using design evidence. This entails probability judgments about the degree to which a set of design features nonrandomly solve an independently defined ancestral adaptive problem.

DESIGN EVIDENCE

To determine a system's adaptive function, researchers need to produce evidence of a fit between its design and the proposed function, This requires the application of engineering standards. As an analogy, consider the relation between design and function in human-made artifacts. A ceramic mug is made of an insulating material that does not dissolve or melt when it contacts hot drinks; its shape stably contains about 8 ounces of liquid and allows a mouth access to it; and it has a heat-dissipating handle that allows it to be lifted without burning the lifter. These properties of a mug are *design features*: properties that exist *because* they are good solutions to the problem of drinking hot beverages without burning your hands.

These properties are unlikely to occur together by chance. Moreover, other uses to which mugs are put (e.g., paperweights, pencil holders) neither predict nor explain these features (paperweights need only be heavy; pencil holders must have a containing shape, but many materials will do—the container need not be watertight, and no handle is needed). A mug can produce many beneficial effects, but only one of these is its function, that is, the explanation for why it was constructed in the way that it was. We can tell which design explanation is correct by analyzing the fit between the mug's design and a proposed function. Mugs have many interlocking properties that are good solutions to the problem of drinking hot drinks, and their properties are poorly explained by alternative theories of their function; that is how we know that they were designed for that function. The more complex the architecture, the more powerful design evidence can be. For example, there are many design features that can decide whether a toaster was intended to be a vehicle, a nutrient, a cleaner, a geological accident, a device for executing bathers, or a means for toasting slices of bread (for discussion, see Dawkins, 1996).

In the same way, design evidence is the criterion for claiming that a property of an organism is an adaptation, whether that property is a knee, a heart, or a neural circuit that processes information. Does the organic machinery in question have properties that cause it to solve an adaptive problem precisely, reliably, and economically? If not, then its ability to solve the problem at issue may be incidental, a side effect of a system that is well designed to perform some alternative adaptive function (Williams, 1966). For example, zoologists found that nocturnal bats have a sonar system with many of the same intricate and interlocking features of human-engineered sonar and radar systems, including features that make bat sonar a good design for finding insects and avoiding obstacles at night (e.g., higher pulse rates when hunting small moving targets than when cruising; for discussion, see Dawkins, 1986). At the same time, bat sonar is poorly suited for solving most other problems (e.g., judging the relative ripeness of fruit during the day). And there is no physical law or general metabolic process that produces bat sonar as a side effect.

Finding and pursuing small flying food items in the dark without crashing into things pose intricate computational problems, which very few arrangements of matter can solve. The bat's sonar solves these problems well. There is a tight fit between the problems' requirements and the evolved solution. It is by virtue of this excellence in design that we recognize finding insects and avoiding obstacles at night as the adaptive function of bat sonar.

Researchers can identify an aspect of an organism's physical, developmental, or psychological structure—its phenotype—as an adaptation by showing that (a) it has many design features that are improbably well suited to solving an ancestral adaptive problem, (b) these phenotypic properties are unlikely to have arisen by chance alone, and (c) they are not better explained as the by-product of mechanisms designed to solve some alternative adaptive problem or some more inclusive class of adaptive problem. Finding that a reliably developing feature of the species' architecture solves an adaptive problem with reliability, precision, efficiency, and economy is prima facie evidence that an adaptation has been located. This is like showing that an oddly shaped piece of metal easily opens the lock on your front door. It is almost certainly a key designed for your door because door locks are not easily opened by random bits of metal, by can openers or candlesticks, or even by keys designed for other doors.

To show that something is a by-product, researchers must first establish that something else is an adaptation (e.g., blood as an oxygen transport system) and then show how the feature is a side effect of the adaptation (e.g., the redness of blood is a side effect of the oxygen-carrying iron in hemoglobin). Features that are uncoordinated with functional demands are evolutionary noise (e.g., the locations of flecks of color in the eye).

Theories of Good Design Are a Heuristic for Discovery

If design evidence were important only for explaining why known properties of organisms have the form that they do (i.e., why the lens of the eye is transparent rather than opaque), its use in psychology would be limited. After all, most properties of the human mind are currently unknown. The concept of good design for solving an adaptive problem is important because it allows researchers to discover new mechanisms within the human mind. There is a systematic method for using theories of adaptive function and principles of good design for discovering new programs.

One starts with an adaptive problem encountered by human ancestors, including what information would potentially have been present in past environments for solving that problem (i.e., its *information ecology*). From the model of an adaptive problem, the researcher develops a task analysis of the kinds of computations necessary for solving that problem, concentrating on what would count as a well-designed program given the adaptive function under consideration. Based on this task analysis, hypotheses can be formulated about what kinds of programs might actually have evolved. Next, their presence can be tested experimentally, using methods from cognitive, social, and developmental psychology, cognitive neuroscience/neuropsychology, experimental economics, cross-cultural studies—whichever methods are most appropriate for illuminating programs with the hypothesized properties.

If the predicted properties are found, tests can be conducted to make sure they are not better explained by alternative hypotheses about the programs responsible. Testing includes making sure the program in question is distributed cross-culturally in the way predicted by the theory (usually adaptations are predicted to be species-typical). However, a universal program may often produce different expressions triggered by different environmental or social conditions, or show local calibration by specific circumstances.

Research on the architecture of kin detection in humans provides an example of how this process of discovery can work (Lieberman et al., 2003, 2007). Avoiding the deleterious effects of inbreeding was an important adaptive problem faced by our hominin ancestors. The best way to avoid the costs of inbreeding is to avoid having sex with close genetic relatives. This, in turn, requires a system for distinguishing close genetic relatives from other individuals: a kin detection system, which computes a kinship estimate for each individual with whom one lives in close association. Because genetic relatedness cannot be directly observed, it is important to consider what information relevant to estimating degrees of kinship would have been available to ancestral hunter-gatherers. To be useful, kinship estimates would have to be based on cues that reliably predicted genetic relatedness in the social conditions under which our ancestors lived. We are looking for cues that would have been stably present across a broad variety of ancestral social conditions and habitats. For example, hunter-gatherers often live and forage in groups that fuse and fission along nuclear family lines, such that parents more frequently stay together with children, adult siblings and their families maintain association, but to a lesser degree, and so on. This would allow the cumulative duration of childhood co-residence to function as a cue to genetic relatedness. An individual who observed his or her mother caring for another infant (what we call maternal perinatal association) would be a more direct cue that the infant was a sibling. A third cue might be an olfactory signature indicating similarity of the major histocompatibility complex. Based on the stable information structure of the ancestral world, the kin detection system is expected to evolve to monitor ancestrally valid cues, and use them to compute a relatedness estimate (that we call a kinship index) for each individual in the person's social world. The kinship index serves as an input to systems that compute the sexual value of another individual to himself or herself: All else equal, close genetic relatives should be assigned a lower sexual value than unrelated people. This sexual-value estimate—another internal regulatory variable—should regulate the motivational system that generates sexual attraction. A low kinship estimate should upregulate sexual attraction whereas a high kinship estimate should downregulate sexual attraction, perhaps by activating disgust in response to the prospect of sex with that person. Independently, the kinship index in one individual's mind about a particular other individual should regulate altruism: The higher the kinship index, the more an individual should be motivated to sacrifice for the relative. These and other theoretically derived predictions about the existence and architecture of the human kin detection system were empirically confirmed, along with a parallel set of predictions about kin-directed altruism. The two predicted cues—maternal perinatal association and duration of childhood co-residence—regulate sexual disgust toward genetic relatives and kin-directed altruism as well (as predicted by Hamilton, 1964). The cues used by older siblings in detecting younger ones differ from those used by younger siblings detecting older ones. The results are incompatible with a variety of alternative theories that could be put forth to explain the results (e.g., Leiberman, Tooby, & Cosmides, 2003, 2007). So far, the pattern found holds in a variety of different cultural settings, consistent with the hypothesis that the kin detection system develops cross-culturally as a universal mechanism of the human mind.

Note that by starting with an adaptive problem—inbreeding avoidance—and analyzing the computational requirements of a system that solves this problem, a significant neurocomputational system was predicted, tested for, and discovered—a system that was previously unknown and uninvestigated by traditional psychologists and cognitive scientists.

It may not seem so at first glance, but notice that the kin detection system is a *learning mechanism*. Its function is to learn which individuals in a person's environment are kin and which are not, and it is designed to make this categorization on the basis of certain cues present during development, while ignoring others. For example, an individual's consciously held beliefs about who is a sibling do not predict degree of sexual aversion, once duration of childhood coresidence is controlled for (but coresidence does predict sexual aversion, controlling for beliefs about who is a sibling; Lieberman et al., 2003, 2007). The kin detection system is not, however, a *general-purpose* learning mechanism. It is highly specialized for a narrow task and has nothing in common with mechanisms of classical and operant conditioning, the way facts are learned in school, or any other more general-purpose method of learning.[9]

NATURE AND NURTURE: AN ADAPTATIONIST PERSPECTIVE

To fully understand the concept of design evidence, we need to consider how evolutionary psychologists think about nature and nurture. Debates about the relative contribution (as it is misleadingly put) of genes and environment during development have been among the most contentious in psychology. The premises that underlie these debates are flawed, yet they are so deeply entrenched that many people, scientists and nonscientists alike, have difficulty seeing that there are better ways to think about these issues. (For an excellent, early treatment of these issues, see Tinbergen, 1963.)

Rather than there being one nature-nurture issue, there are many independent issues. Unfortunately, they have become so tangled that most discussions in psychology and the social sciences are hopelessly confused. We pull the major questions apart and look at them one by one. Some of them are conceptual confusions, whereas others are genuine scientific questions whose resolution will depend on research, rather than on clear thinking alone.

Despite widespread belief to the contrary, evolutionary psychology is not another swing of the nature-nurture pendulum (Tooby & Cosmides, 1992). It shatters the traditional framework and the old categories entirely, rather than siding with any position within the old debate. Indeed, a defining characteristic of the field is the explicit rejection of the usual nature-nurture dichotomies—instinct versus reasoning, innate versus learned, biological versus cultural, nativist versus environmentalist, socially determined versus genetically determined, and so on—because they do not correspond to the actual distinctions that need to be made in the real world.

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[9] It is not known how children learn facts in school—the notion that it is via some form of general-purpose learning is an assumption, not a finding for which there is evidence. Indeed, there is starting to be evidence that school learning piggybacks off domain-specific inference mechanisms such as being fed linguistic representations (e.g., Hirschfeld & Gelman, 1994).

Evolutionary psychologists do not see nature and nurture as existing in an explanatory zero-sum relationship. Nonevolutionary researchers have typically assumed that there is a spectrum in the nature-nurture debate, that it runs from the nativist extreme (most things are "genetically determined") to the environmentalist extreme (most things are "environmentally determined"), and that the true position (the subject of the debate) lies somewhere along this spectrum. But all properties of the organism equally develop through 100% gene-environment interaction. The key point at which the adaptationist approach pivots to a new framework for understanding development lies in the following recognition: As will be explained in greater depth, a species' history of selection acted over evolutionary time to organize and tune the interaction between genes and environment to produce the reliable development of that species' adaptations—adaptations whose program logic, in turn, specifies how environmental inputs are operated on to become behavioral outputs. (Whereas selection acts antientropically to functionally tune gene-environment interactions, random genetic and environmental changes—mutations—act to entropically disrupt reliable development.)

Innate Is Not the Opposite of Learned Everyone is a nativist, regardless of whether she knows it. Even the most extreme advocates of the role of the environment in shaping human behavior, from Skinner to the postmodernists, make nativist claims about the "innate" structure of the evolved neural machinery that learns or responds to the environment. The only difference is whether they make the nature of their claims about this machinery explicit or allow them to remain implicit, forcing the reader to deduce them from their arguments about why people act as they do.

Imagine that you are an engineer and your project is to create a brain that can learn. To be able to learn, this brain would have to have a certain kind of structure—after all, 3-pound cauliflowers do not learn, but 3-pound brains do. To get your brain to learn, you would have to arrange the neurons in particular ways. You would have to create circuits that cause learning to occur. In short, you would have to equip your brain with programs that *cause* it to learn. The same is true when natural selection is the engineer.

Even if a program that causes a particular kind of learning was itself learned, there had to be a prior program that caused that learning to occur, and so on. Logic forces us to conclude that there had to be, at some point in the developmental causal chain, a program that caused learning but that was itself unlearned. These unlearned programs are a part of the brain by virtue of being part of its evolved architecture. They are programs that reliably develop across the ancestrally normal range of human environments.

Both environmentalists and nativists—Pavlov, Skinner, and Chomsky alike—must agree on this point. They may disagree strongly about the computational structure of the evolved programs that cause learning but not about whether evolved learning programs exist. For example, classical and operant conditioning are widely viewed as the simplest and most general forms of learning in humans and other animals. Yet, even operant conditioning presumes the existence of evolved mechanisms that change the probability of a behavior by a certain amount, as a function of its consequences (and according to particular equations). It also presumes that a handful of consequences—food, water, pain—are "intrinsically" reinforcing (i.e., the fact that these consequences are capable of changing the probability of a subsequent behavior is a design feature of the brain). Classical conditioning presumes the existence of a great deal of innate equipment. In addition to the programs that compute contingencies, the animal is filled with unconditioned—that is, *unlearned*—responses, such as salivating in response to meat. Salivating in response to meat is considered to be part of the dog's evolved architecture, and what the evolved learning program does is calculate when an arbitrary stimulus, such as a bell, predicts the appearance of the meat (Gallistel & Gibbon, 2000). Thus, even in classical conditioning, the learned link between information and behavior—salivating to the sound of the bell—is caused by an evolved learning program, which takes as input both innate stimulus-response pairs (meat and salivation) and information from the external environment (the contingency between the sound of the bell and the appearance of meat). The only substantive disagreement between a Skinner and a Chomsky is about the structures of the evolved programs that cause learning.

Consequently, any learned behavior is the joint product of "innate" equipment interacting with environmental inputs and, therefore, cannot be solely attributed to the action of the environment on the organism. Thus, *innate* cannot be the opposite of *learned*. It is just as mistaken to think of *evolved* as the opposite of *learned* because our evolved learning programs were organized by evolution to learn some things and not others.

To say a behavior is learned in no way undermines the claim that the behavior was organized by evolution. Behavior—if it was learned at all—was learned through the agency of evolved mechanisms. If natural selection had built a different set of learning mechanisms into an organism, that organism would learn a different set of behaviors in response to the same environment. It is these evolved mechanisms that organize the relationship between the environmental input and behavioral output and thereby pattern the behavior. For this reason, *learning is not an alternative explanation to the claim that natural selection shaped the behavior*, although many researchers assume that it is. The same is true for culture. Given that cultural ideas are absorbed via learning, inference, and interaction payoffs—which themselves are caused by evolved programs of some kind in interaction with the environment—a behavior can be, at one and the same time, *cultural, learned,* and *evolved.* (For excellent discussions of how evolved inference mechanisms produce and structure cultural transmission, see Boyer, 2001; Sperber, 1996.)

Moreover, there does not appear to be a single program that causes learning in all domains (consider kin detection, food aversions, snake phobias, alliance detection, and grammar acquisition). Evidence strongly supports the view that learning is caused by a multiplicity of programs (Gallistel, 2000; Tooby & Cosmides, 1992). Without specifying which program is the cause (and knowing its functional architecture), nothing whatsoever is explained by invoking learning as an explanation for a behavior. Labeling something as learning does not remove the requirement to spell out the evolved machinery involved; it only makes the weak claim that interaction with the environment participated in the process (which is always the case, anyway, in all anatomical and behavioral phenotypes). In short, learning (like culture) is a phenomenon that itself requires explanation, rather than being any kind of explanation itself. A coherent explanation for how humans and nonhumans learn about a given domain must include (a) a description of what the evolved learning program looks like (that is, its circuit logic, code, or program architecture); (b) what selection pressures and other evolutionary effects led it to acquire its present structure over evolutionary time; (c) what set of gene-environment interactions lead it to develop its structure at any given point in the organism's life history; and (d) what information was and is available to the organism that is executing that evolved program.

Everyone is also an environmentalist, regardless of whether she knows it. Even the most die-hard nativist understands that organisms learn—or, even more broadly, that an organism's evolved mechanisms extract information from the environment and process it to regulate behavior. Hence the environment regulates behavior, and it is the presence of evolved mechanisms that makes this possible. Indeed, the entire function of a brain is to allow the organism's responses to be sensitively contingent to the information provided by the environment.

Thus, evolved programs—instincts—are not the opposite of learning. They are the engines or programs through which learning takes place. We learn only through instincts—learning and reasoning instincts. There are instincts in songbirds for learning songs, instincts in geese for learning which individual is one's mother, instincts in desert ants for learning how to return home, and instincts in humans for learning a language or who our genetic relatives are. The greater the number of specialized learning (or cognitive) programs we come equipped with, the more we can learn from experience. Evolved programs do not constrain a "flexibility" that organisms otherwise would have; each additional program endows the organism with competences it would not otherwise have. To take just one example, the evolved language competence vastly multiplies the behavioral repertoire of humans. Humans can respond with intricate contingency to the world because of these endowments. This is why nature and nurture do not exist in a zero-sum relationship, but in a positive-sum relationship. More nature (evolved systems of regulation and computation) allows more nurture (exquisitely sensitive responsiveness to the world) (Boyer, 2001; Tooby & Cosmides, 1992).

Specialized or General Purpose? If the *innate versus learned* controversy is meaningless, there is a genuine and illuminating question to be answered: What is the precise structure of these evolved learning and regulatory programs? Are there many or just a few? Which embody knowledge about enduring aspects of the world, and what knowledge do their procedures reflect? To what extent is a program—regardless of whether it governs learning—functionally specialized to produce the outcome that you have observed?

What effect a given environmental factor will have on an organism depends critically on the details of the designs of its evolved neurocomputational programs. So the discovery of their structure is a pivotal question. Indeed, one of the few genuine nature-nurture issues concerns the extent to which each evolved program is specialized for producing a given outcome (Cosmides & Tooby, 1987; Symons, 1987; Tooby & Cosmides, 1992). Most nature-nurture issues disappear when more understanding is gained about evolution, cognitive science, and developmental biology, but this one does not.

Thus, the important question for any particular behavior is not, "Is it learned," but, "What kind of evolved programs produced it?" More specifically, "What is the architecture of the evolved cognitive programs through which the organism learns this particular type of behavior, acquires this kind of knowledge, or produces this form of behavior?"

For any given (functional) outcome, there are three alternative possibilities: (1) It is the product of domain-general programs, (2) it is the product of cognitive programs that are specialized for producing that outcome (or a more inclusive set of which the outcome in question is one instance), or (3) it is a by-product of specialized cognitive programs that evolved to solve a different problem.

The debate about language acquisition, which began in 1959 when Noam Chomsky reviewed B. F. Skinner's book, *Verbal Behavior,* brings this issue into sharp focus, because Chomsky and Skinner disagreed about precisely these issues (Chomsky, 1959; Skinner, 1957). Both sides in the ensuing controversy admit, as coherence demands, that the human mind contains innate learning programs. But the two camps differ in their answer to the question: Does a single set of general-purpose, cognitive programs cause children to learn everything, with language as one incidental example? Or is language learning caused, in part or in whole, by programs that are specialized for performing this task: by what Chomsky called a *language acquisition device*?

Questions about functional specialization cannot be answered a priori by theory or logic alone. Each hypothesis about the computational architecture of a learning mechanism—general, or specialized—must be evaluated on the basis of its coherence, explanatory economy and power, retrodictive consistency with known phenomena, and its ability to make successful, novel predictions. The theoretical tools and empirical studies necessary will differ, depending on whether the proposal is about language learning, inferring mental states, acquiring gender roles, developing friendships, eliciting jealousy, or something else. For language, 55 years of research support the hypothesis that humans have evolved programs specialized for various aspects of language acquisition, although the debate remains heated (Pinker, 1994). With the emergence of evolutionary psychology and under the weight of discoveries about large numbers of diverse, specialized adaptive problems in many areas of biology, the debate over adaptive specializations has now widened to include all human competences.

Present at Birth? Sometimes people think that to show that a program is part of our evolved architecture, researchers need to show that it is present from birth. Otherwise, the behavior is "learned" (by which they implicitly mean learned through general-purpose processes). But this assumes that all the evolved programs that cause maturational development operate before birth and none after birth.

This assumption is clearly false. Teeth and milk-delivering breasts are uncontroversially standard parts of our evolved architecture, but they develop after birth, years after in the case of breasts. Newborns lack teeth, but does this mean that infants and toddlers acquire their first set through learning? Does cultural pressure lead them to lose the first set in favor of the second?

Organs and design features can mature at any point of the life cycle, and this applies to the adaptations in our brains just as much as it does to the features of our bodies. Thus, the fact that a behavior emerges after birth tells us very little about how it was acquired or why it has a certain organization. Organs can be disassembled on schedule as well: Consider the placenta, umbilical cord, and fetal hemoglobin. Evolutionists expect, and the evidence appears to bear them out, that many mechanisms will appear and disappear on a condition-specific or life-history linked timetable based on when they would have been needed, under ancestral conditions, to solve the challenges of that life stage. Infants need the sucking reflex but not sexual desires; adolescents need sexual desires but not the suckling reflex. For an example of a condition-specific adaptation, consider pregnancy sickness. It does not manifest itself according to a developmental schedule, but is triggered by a condition: Women during the first trimester of pregnancy (that is, during fetal organogenesis) need a different set of thresholds inhibiting the ingestion of substances that could cause birth defects than do nonpregnant women, so their disgust thresholds are adaptively adjusted by the condition of pregnancy (Profet, 1992).

Presence at birth is only a function of what is needed at birth, not an indicator of whether something is or is not part of our evolved architecture. Accordingly, much of what is present in adult minds may have been put there by evolution and activated through neural maturation, without depending on the accidents of personal experience. For example, infants who cannot crawl do not need a fear of heights, whereas infants who can crawl do. But experiments have demonstrated that a fear of heights is not learned by trial and error; rather, it is an evolved competence that is triggered when the baby starts to self-locomote, even if researchers contrive the situation such that the baby never experiences a fall (Campos, Bertenthal, & Kermoian, 1992).

Of course, the early presence of features is not completely irrelevant when evaluating alternative hypotheses about our evolved design. For example, the early emergence of a competence, before the social world could plausibly have acted, may falsify or undermine a particular social constructionist hypothesis. But the early *absence* of a competence does not by itself in any way undermine the claim that it is part of our evolved design. We all start out as a single-celled zygote, so everything develops.

The Twin Fallacies of Genetic Determinism and Environmental Determinism Traditional researchers hold a series of beliefs that are widely accepted and that sound eminently reasonable. Unfortunately, they are based on a series of fallacies about how development works. The first belief is that some behaviors are genetically determined whereas others are environmentally determined. The second is that evolutionary psychology deals only with behavior that is genetically determined, not the much larger set of behaviors that are environmentally determined. These beliefs are wrong for many reasons (Tooby & Cosmides, 1990b, 1992; Tooby et al., 2003), of which we mention just two (see also Hagen, Chapter 4, this volume).

First, genes are regulatory elements that use environments to construct organisms. Thus, as discussed, every single component of an organism is co-determined by the interaction of genes with environments. Moreover, some of those components are computational mechanisms, designed to produce behavior on the basis of information from the environment. Seen in this way, it is senseless to ask whether kin detection or language acquisition or snake phobias are caused by the genes or the environment: These phenomena are caused by evolved mechanisms that operate on information from the environment in particular ways, and these evolved mechanisms were themselves constructed by the interaction of genes with the environment.

Second, the view that evolutionary psychology deals only with "genetic" behaviors (a nonexistent class) erroneously assumes that environmental causation is nonevolutionary. In order to understand why environmental causation is every bit as "evolved" as the genes, it is useful to distinguish "the environment" (in the sense of all properties of the universe) from a given species' developmentally relevant environment. By *developmentally relevant environment* we mean the subset of properties of the world that evolution has made relevant to the development of the adaptations of a given species.

Evolution acts by selecting some genes over others, but in so doing it acts on the *relationship* between the genes and the environment, choreographing their interaction to cause evolved design. Genes are the so-called units of selection, which are inherited, selected, or eliminated, so they are indeed something that evolves. But every time one gene is selected over another, one design for a developmental program is selected as well. (We all start as a single cell—brainless, limbless, gutless. Every cell and organ system subsequently develops from that cell, nonrandomly climbing toward specific organizational forms despite the onslaughts on entropy. For manifest organization to emerge, there must be naturally selected processes that cause this to happen: developmental programs.)

Developmental programs, by virtue of their design, make some parts of the world relevant to development and other parts irrelevant. Over evolutionary time, genetic variation in developmental programs (with selective retention of advantageous variants) explores the properties of the environment, discovering those that are useful sources of information in the task of regulating development and behavior. Selection tailors developmental programs to engage in organized interactions with facets of the developmentally relevant environment to successfully produce highly ordered, functional phenotypes. Selection also acts to render those features of the environment that are unreliable or disruptive irrelevant to development. Step by step, as natural selection constructs the species' gene set (chosen from the available mutations), it selects in tandem which enduring properties of the world will be relevant to development. Thus, a species' *developmentally relevant environment*—that set of features of the world that a zygote and the subsequently developing organism depend on, interact with, or use as inputs—is just as much the creation of the evolutionary process as the genes are. Hence, natural selection can be said to store information necessary for development both in the environment and the genes. Because for humans the amount of information stored in the environment is much vaster than the quantity of genetic information, one can think of the zygote, its genome, and its parentally supplied cellular and uterine environment as analogous to a computer's basic input/output system (BIOS)—self-extracting kernels that bootstrap the single cell toward its highly organized, realized set of adaptations (as expressed at a given point in life history). We manifest species-typical (or population-tuned) evolved designs not because genes are the only things that influence phenotypes, but because selection orchestrates the interplay of gene-environment interactions through genes.

Hence, the developmentally relevant environment can be viewed as a second system of inheritance comparable in some ways to genetic systems of inheritance. A zygote in an environment can be seen as inheriting a set of genetic determinants (including cellular machinery) and simultaneously a set of environmental determinants. The environmental determinants are transmitted or inherited in a peculiar fashion: They simply endure as physical arrangements in the world across generations over the range in which the lineal series of zygotes appears. They must regularly recur often enough that they select for developmental programs that interact with them to cause reliable development every generation of the functional species-typical design. From the point of view of any given subcomponent of the organism, other parts of the organism are, of course, stable features of the environment, and so high levels of functional interrelationship and developmental interdependence accumulate among a body's parts. In addition, some aspects of the environment outside the organism are also enduring features of the ancestral world that interacted reliably with the organism's design, and so subcomponents of the organism typically manifest highly functional interrelationships with them (e.g., wings and air; eyes and light; digestive enzymes and available diet), as well as developmentally interdependent relationships with them (e.g., lung size and altitude during development). Some environmental determinants are perfectly replicated across generations (e.g., the three-dimensional nature of space, the properties of light, the properties of chemical compounds, the existence of two sexes, the presence of caretakers for infants that survive); others are replicated reliably but imperfectly (e.g., mother smiling in response to an infant's smile, the presence of fathers during childhood, a correlation between duration of childhood co-residence and genetic relatedness). In spite of omnipresent, order-destroying entropy, organismic designs successfully develop the functional species-typical design (and its locally tuned expressions) based on the degree to which their genetic and environmental inheritances were functionally coordinated with each other by selection adjusting them over evolutionary time so that they interactively produced an adaptive phenotype. Gene–organism–environment webs have been experimentally tested generation after generation; those interactions that led to maladaptive development were discarded by selection. This evolutionarily orchestrated coordination of genome and environment is how organisms are able to overcome entropic processes that would otherwise preclude the existence of life (Tooby, Cosmides, & Barrett, 2003). Change in either of the two inheritances (either through genetic mutation or change in the developmentally relevant environment) disrupts the coordination, and the greater or more rapid the change, the greater is the disruption in the always imperfect actual phenotype.

This view of development is not gene centered or a form of "genetic determinism" if that is interpreted to mean that genes by themselves determine everything, immune from environmental influence—or even that genes determine "more" than the environment does. Although not gene centered, however, this view is very much natural selection centered, because it is natural selection that chooses some genes rather than others and, in so doing, orchestrates the interaction between the two inheritances so that high degrees of recurrent functional order can emerge and persist, such as eyes, kin-directed altruism, language, or maternal love.

Moreover, this view explains how reliable development both can and does ordinarily occur—that is, it explains why a robust, species-typical design emerges in almost all individuals (e.g., what can be seen in *Gray's Anatomy* [Gray, 1918]). The species-typical features of the genome interact with the features of evolutionarily long-enduring, species-typical environments to produce the species-typical design observable in organisms. Failures of reliable development are attributable to genetic mutation, to environmental mutation (change), or to both.

The closest that the world comes to the fallacious distinction between biologically or genetically determined traits versus environmentally or socially determined traits is in the following real distinction: Some neural programs were designed by natural selection to take in substantial amounts of environmental input (e.g., the language acquisition device) whereas others were designed to take in less information and express themselves less contingently (e.g., the typical form of the anger facial display of emotion; Sell, Cosmides, & Tooby, 2014). But in all cases, there is an underlying regulatory or neural program designed by natural selection and a set of environmental regularities necessary for that program's reliable development. Indeed, as we discuss later, there is not a zero-sum relationship between nature and nurture: More nature (more evolved content specificity) allows more nurture (richer stores of ontogenetically elaborated data and locally contingent behavior). For example, the highly organized language acquisition device allows marvelously rich and variable verbal expression (Pinker, 1994).

From this perspective, successful development has to accomplish two tasks (Tooby & Cosmides, 2001). The first is the reliable construction of the set of (largely species-typical) adaptations required at each point in the organism's life history (given its sex). The second is to bring each adaptation into a state of readiness to perform its evolved functions, given the organism's situation. Accordingly, adaptations can be conceptualized as operating in two different modes (Cosmides & Tooby, 2000a; Tooby & Cosmides, 2001). The first is its functional mode, when it is performing its evolved function (e.g., the incest-avoidance system, calling up aversion at the prospect of sex with a close relative). This is the aspect of the adaptation we normally think about. The second is its organizational mode. This mode of operation is designed to construct the adaptation, and in so doing, to furnish it with the information, neuroendocrinological pathways, correct weightings in decision variables, procedures, and representations it needs to behave adaptively when called upon to do so. In general, the goal of the organizational mode of an adaptation is to cause it to develop a better organization for carrying out its function so that, when it is called on to operate, it discharges its function well (e.g., the kin detection front-end of the incest-avoidance system, processing cues in its local environment into a kinship map of who the individual's genetic relatives are).

Although a natural first step for researchers is mapping adaptations operating in their functional mode, it may be that solving the problem of correct assembly and calibration of an adaptation is a much harder problem for the organism (given entropy) than merely running the device, once it has been assembled. So, for example, babbling, word learning, local syntax acquisition, the intrinsically entertaining nature of verbal play, and so on, all seem to be the language system operating in its organizational mode, so that when the individual needs to speak or understand, the underlying adaptations are ready to perform their function. Rough and tumble play are adaptations for fighting and defense operating in their organizational mode (Symons, 1978). The organizational mode of an adaptation or set of adaptations will generate different organizations (such as bodies of knowledge, habits, neuroendocrinological calibration, fear sensitivity, etc.) in the minds of each individual, given the individual's unique experience or ontogenetic trajectory. This is the most basic way that the evolved adaptations that compose our species-typical design lead to large sets of functionally intelligible individual differences, without this outcome being in any tension with an adaptationists perspective on human psychology and behavior (Cosmides & Tooby, 2000a; Tooby & Cosmides, 2001).

Universal Architectural Design Versus Genetic Differences How are we to reconcile the claim that there is a universal species-typical design—including a universal human nature—with the existence of individual differences, especially those caused by genetic differences among people?

At a certain level of abstraction, every species has a universal, species-typical evolved architecture. For example, we humans all have a heart, two lungs, a stomach, and so on. This is not to say there is no biochemical individuality, especially in quantitative features. Stomachs, for example, vary in size, shape, and amount of hydrochloric acid produced. Yet, all stomachs have the same basic *functional* design: They are attached at one end to an esophagus and at the other to the small intestine, they secrete the same chemicals necessary for digestion, they are made of the same cell types, and so on. Indeed, when humans are described from the point of view of their complex adaptations, differences tend to disappear, and a universal architecture emerges. This universality is not only theoretically predicted, but is empirically established (e.g., *Gray's Anatomy* describes this architecture in minute detail). This phenotypic universality is expected to be reflected at the genetic level through a largely universal and species-typical genetic architecture ("the" human genome) as well.

The logic is as follows (see Tooby, 1982, and Tooby & Cosmides, 1990b, for a more complete explanation, and a discussion of how to relate individual differences to universal design):

1. Complex adaptations are intricate machines. Adaptations that consist of complexly structured functional elements require, in turn, complex specification at the genetic level. That is, they require coordinated gene expression, often involving hundreds or even thousands of genes to regulate their development.
2. Like any other intricate machine, the parts of a complex adaptation must all be present and fit together precisely if the adaptation is to work properly. Parts of complex adaptations are functionally interdependent. All the genes necessary to build each component part and assemble them correctly must be reliably brought together in the same individual. Fitting together the parts specified by new genetic combinations is not a problem for organisms that reproduce by cloning but it is for sexual reproducers.
3. Each new human originates sexually. A randomly selected half of the mother's genes is recombined with a randomly selected half of the father's genes. During gamete and zygote formation, sexual reproduction automatically breaks apart existing sets of genes and randomly generates in the offspring new combinations at those loci that vary from individual to individual. This would not be a problem if the mother and father were genetically identical at all loci. But it is a problem to the extent that their genes differ at those loci underlying complex adaptations.
4. Hence, the successful assembly of a complex adaptation in a new individual requires that all the genes necessary for that adaptation be supplied by the two gametes, even though gametes are both randomly generated and consist of only half of each parent's DNA. Successful assembly would not be possible if only some individuals in the population had the complex adaptation (and the suite of genes that specified all its necessary component parts). If in a given generation, different individuals had different complex adaptations, each of which was coded for by a different suite of genes, then during the formation of the gametes for the next generation the random sampling of subsets of the parental genes would break apart each suite. During zygote formation, these incomplete specifications of incompatible adaptations would be shuffled together. Consequently, the offspring generation would be a handicapped jumble of fragments of functionally incompatible adaptations. The simultaneous demand for functional compatibility of complex adaptations and sexual reproduction places strong constraints on the nature and distribution of functional variation.
5. Specifically, the only way that each generation can be supplied with the genetic specification for complex adaptations is if the entire suite of genes necessary for coding for each complex adaptation is effectively universal and hence reliably supplied by each parent regardless of which genes are sampled. By analogy, if you attempted to build a new car engine by randomly sampling parts from two parent cars, you would fail if one parent were a Toyota and the other a Jaguar. To build a new engine whose component parts fit together, you would have to salvage parts from two parents that were of the same make and model.
6. By the same token, sexually reproducing populations of organisms freely tolerate genetic variation to the extent that this variation does not impact the complex

adaptive organization shared across individuals. In the car engine example, the color of the parts is functionally irrelevant to the operation of the car and thus can vary arbitrarily and superficially among cars of the same make and model. But the shapes of the parts are critical to functional performance and cannot vary if the offspring design is to function successfully.

7. The constraint of functional universality applies to only adaptations whose genetic basis is complex—that is, whose genetic basis involves multiple independently segregating loci. This selection pressure starts when there are two independent loci and becomes combinatorially more powerful with each additional locus. However, if an adaptation can be coded for by a single gene in a way that is not impacted by genes at other loci, then sexual recombination does not disassemble it, and individuals may vary locally or regionally. Similarly, quantitative genetic variation (e.g., height, arm length, how easily an individual is angered) is not constrained by sexual reproduction and functional compatibility and thus may also vary locally or regionally. Quantitative genetic variation is genetic variation that shifts phenotypes quantitatively, but not outside the boundaries imposed by the demand for functional compatibility.
8. Some evolved outcomes are the result of frequency-dependent selection. That is, the population stabilizes at intermediate frequencies with two or more alternative designs, such as male and female, because the relative reproductive advantage of being one over the other decreases with increasing frequency (Fisher, 1930). If the adaptation involves only a single locus, two or more alternative designs can persist indefinitely in the species.
9. Finally, selection for genetic universality in complex adaptations does not rule out the possibility that some individuals express complex adaptations that others do not (as the two sexes and different life stages do, with, for example, the placenta, fetal hemoglobin, teeth, the reproductively mature uterus, testes). Such expression, however, must be based on a genetic architecture that is largely universal and simply activated by an environmental trigger or a simple genetic switch such as a single locus (e.g., the unrecombining regions of the Y chromosome). For example, women express a different set of complex reproductive organs than men, but not because men lack the genes necessary to code for ovaries and a uterus. If males and females were different because each lacked the complex genetic specification of the adaptations of the other sex, then, when they produced offspring, they would be nonreproductive individuals of intermediate sex. In other words, *functional* aspects of the architecture tend to be universal at the genetic level, even though their expression may be typically limited to a particular sex or age or be contingent on the presence of an eliciting condition (e.g., pregnancy adaptations) or at a single nonrecombining stretch of DNA (e.g., biological sex in humans).
10. The living world sharply clusters into sets of organisms that share properties—species—because of the demand for functional compatibility among sexual reproducers. Indeed, it is striking the degree to which species are characterized by complex, shared, and instantly recognizable designs (like different car models). Still, the degree to which functional variation can be tolerated in a species is a function of a number of variables, such as fecundity, migration rate, and population density. In species in which successful parents have large numbers of offspring, reproductive rates are high and migration rates are low between populations, populations may diverge in some complex adaptations because local mates are more likely to share functionally compatible genotypes even if there is

> variation elsewhere in the species. Compared with the great majority of other species, however, ancestral humans had very low fecundity, had an open breeding structure, and migrated across substantial distances. For these reasons, humans are both expected to be, and are observed to be, characterized by a greater tendency toward species typicality than many other species.

Thus, humans are free to vary genetically in their superficial, nonfunctional traits but are constrained by natural selection to share a largely universal genetic design for their complex, evolved functional architecture. Even relatively simple adaptive programs must contain a large number of interdependent processing steps, limiting the nature of the variation that can exist without violating the program's functional integrity. The psychic unity of humankind—that is, a universal and uniform human nature—is necessarily imposed to the extent and along those dimensions that our psychologies are collections of complex adaptations. In short, selection, interacting with sexual recombination, tends to impose at the genetic level near uniformity in the latent or potential functional design of our complex neurocomputational machinery, and very high levels of expressed architecture uniformity at a given sex and age.

Evolutionary Psychology and Behavior Genetics Ask Different Questions The preceding discussion provides a framework for thinking about universal design and genetic differences. Behavior geneticists, through twin studies and comparisons of kin raised together and apart, explore the extent to which *differences* among individuals are accounted for by *difference*s in their genes. This difference is expressed as a heritability statistic—$h = Vg/Vg + Ve + Vge$—which tells you the proportion of variance in a population of individuals that is caused by differences in their genes (compared to all causes: variance due to differences in environment, genes, and their interaction). In contrast, evolutionary psychologists primarily explore the design of the universal, evolved psychological and neural architecture that we all share by virtue of being human.

Evolutionary psychologists are usually less interested in human characteristics that vary due to arbitrary genetic differences because they recognize that these differences are unlikely to be evolved adaptations central to human nature. Of the three kinds of characteristics that are found in the design of organisms—adaptations, by-products, and noise—traits caused by genetic variants are predominantly (but not exclusively) evolutionary noise, with little adaptive significance, while complex adaptations are likely to be universal in the species.

Why is uniformity generally associated with functionality and variability typically associated with lack of function? The first reason involves the constraints on organic design imposed by sexual recombination, as explained earlier. Second, alternative genes at the same locus (the same location in the human genome) are in a zero-sum competition for relative frequency in the species: The more common one allele is, the less common the others are. Natural selection tends to eliminate genetic differences whenever two alternative alleles (genes) differ in their ability to promote reproduction (except in the case of frequency-dependent selection). Usually, the better functioning gene increases in frequency, squeezing out the less functional gene variant, until it disappears from the species. When this happens, there is no longer genetic variability at that locus: Natural selection has produced genetic uniformity instead. The more important the function, the more natural selection tends to enforce genetic uniformity.

Thus, our important functional machinery tends to be universal at the genetic level, and the heritability statistic associated with this machinery will be close to zero (because there is little variation between individuals caused by genes). In contrast, whenever a mutation fails to make a functional difference, selection will not act on it, and such minor variants can build up at the locus until there is substantial genetic variability for the trait, and its heritability statistic will be high (because most variation between individuals in the trait will be caused by variation in genes). For this reason, genetic variability tends to be predominantly nonadaptive or maladaptive evolutionary noise: neutral or nearly neutral variants, negative mutations on their way to being eliminated, and so on. Such variants may be, of course, of the greatest medical, personal, or practical significance, as, for example, in the search for possible genetic causes of schizophrenia, depression, and autism or the discovery that a formerly neutral variant causes differential drug metabolism. The point is, however, genetic variants causing medical vulnerabilities or personality differences are generally unlikely to be adaptations designed to cause those effects. If something is highly functional, selection usually acts to spread its genetic basis to the entire species. Fundamentally, selection acts to decrease entropy in phenotypic design, while mutation acts to increase it. Because of entropy, genomes are never close to flawless, but are instead a balance between mutation and selection.

There is, nonetheless, a great deal of genetic variability within species, which is in tension with the functional advantages of genetic uniformity. Aside from mutations and neutral variants, there is a third reason for this genetic diversity. Genetic variability, such as the ABO blood group system, is retained in the species because genetically based, biochemical individuality interferes with the transmission of infectious diseases from host to host (Tooby, 1982). Diseases that use or depend on a protein found in their present host are thwarted when the next individual they jump to has a different protein instead. Hence, natural selection sifts for genetic variants that supply approximately the same functional properties to the adaptations they participate in but that taste different from the point of view of disease organisms. Because we catch diseases from those we have contact with—such as our family, neighbors, and other locals—selection favors maximizing genetically based protein diversity locally, which requires pulling into every local population as many of the genetic variants found anywhere in the species as possible. Thus, this explains why individuals are so genetically different from one another, but different populations tend to be so surprisingly genetically similar.

This large collection of genetic differences introduces minor perturbations into our universal designs. The result is that each normal human expresses the universal human design, but, simultaneously, each human is slightly different from every other in personality, structure, temperament, health, anatomy, and appearance. These differences tend to be quantitative in nature—a little more of this, a little less of that—whereas the overall functional architecture remains the same.

Another category is the possibility of alternative, genetically based psychological designs that are maintained through frequency-dependent selection. The existence of male and female—two alternative designs—shows that such frequency-dependent equilibria are not only possible but real for humans. Moreover, multiple behavioral strategies often emerge in theoretical models through frequency-dependent selection (e.g., cooperators and free riders). Nevertheless, the constraints created by sexual reproduction place strong limitations on the emergence of such systems in real species (even the system of two sexes is based almost entirely on genetic uniformity). Indeed, as the case of the sexes shows, alternative phenotypic strategies can be based more easily on substantial genetic uniformity and alternative developmental pathways than on genetic differences encoding the alternative adaptations. It remains unclear the extent to which humans exhibit allele-based frequency-dependent behavioral strategies, and so far there are no well-established cases aside from the two sexes. For most challenges, strategy selection might most advantageously take place when the challenge is faced, so the strategy matches the challenge; this may be why genetic commitments to strategies seem rare and would be generally disadvantageous. However, the longer the period it will take to develop a good phenotype for a future adaptive problem (as is arguably the case in mammals for developing a male or female phenotypic design), the more it might pay to make an early commitment, undertaken in greater ignorance of what future conditions will be like. Commitment by genetic switch (e.g., XY sex determination) is the extreme case, where strategy commitment occurs randomly at conception.The question of why there should be systems of heritable dimensional personality variation will be addressed in the section on epigenetics and parametric coordinative adaptations.

EVOLUTIONARY VERSUS TRADITIONAL APPROACHES TO PSYCHOLOGY: HOW ARE THEY DIFFERENT?

If all psychologists are engineers working in reverse, if the goal of all psychologists is to discover the design of the human mind, then how does evolutionary psychology differ from traditional approaches?

Traditional approaches to psychology are not guided by any specific theory of what the mind was designed to do. As animal species go, humans are startling in their capabilities; from making lemon chiffon pies to writing waka to sending probes to Titan, we are capable of solving many problems that no hunter-gatherers ever had to solve (and that no other animal does solve). It, therefore, seemed obvious to many that our minds are not designed to do anything in particular; rather, they must be designed to reason and to learn, by virtue of mechanisms so general in function that they can be applied to any domain of human activity. Reasoning and learning require certain auxiliary processes: a memory to retain what is learned or inferred, perceptual systems to bring sense data to the learning and reasoning mechanisms, and attention to spotlight some aspects of perception for further analysis. But these auxiliary processes were also thought to be domain-general. Noting the disconnection between assumptions in psychology and biology, Gallistel (2000, p. 1179) made the following observation about the study of learning:

> Biological mechanisms are hierarchically nested adaptive specializations, each mechanism constituting a particular solution to a particular problem. . . . One cannot use a hemoglobin molecule as the first stage in light transduction and one cannot use a rhodopsin molecule as an oxygen carrier, any more than one can see with an ear or hear with an eye. Adaptive specialization of mechanism is so ubiquitous and so obvious in biology, at every level of analysis, and for every kind of function, that no one thinks it necessary to call attention to it as a general principle about biological mechanisms. In this light, it is odd but true that most past and contemporary theorizing about learning does not assume that learning mechanisms are adaptively specialized for the solution of particular kinds of problems. Most theorizing assumes that there is a general-purpose

> learning process in the brain, a process adapted only to solving the problem of learning. There is no attempt to formalize what the problem of learning is and thereby determine whether it can in fact be conceived as a single or uniform problem. From a biological perspective, this assumption is equivalent to assuming that there is a general-purpose sensory organ, which solves the problem of sensing.

The same passage could have been written about reasoning, memory, or attention. The reigning assumption has been that the function of the mind is general—to acquire information that is (roughly) true—which requires programs general enough to handle content drawn from any and all domains. Thus, the study of reasoning has concentrated on procedures that are content free. Examples include logical procedures (which are designed to produce true conclusions from true premises, no matter what the subject matter of the premises is); mathematical procedures, such as Bayes's theorem or multiple regression (which operate over quantities of anything); and heuristics of judgment that use very general principles such as similarity (the representativeness heuristic), frequency (the availability heuristic), or what came first (anchoring and adjustment; e.g., Kahneman, Slovic, & Tversky, 1982; Rips, 1994; but see Cosmides & Tooby, 1996a; Gigerenzer et al., 1999). Memory has been conceived as a single system—after all, it had to be able to store and retrieve information from all domains of human life. When multiple memory systems are proposed, they are usually individuated by information modality or source (a storage system for perceptual representations? motor skills? general knowledge?) rather than by information content (Schacter & Tulving, 1994; but see Caramazza & Shelton, 1998; Klein, 2005; Klein, Cosmides, Tooby, & Chance, 2002; Sherry & Schacter, 1987). Attention has primarily been seen as a content-free mechanism that selects some information in an array for further processing. If true—if attention contains no domain-specialized selection procedures—it should be safe to study it using artificial stimuli that are easy to modify and manipulate in a controlled fashion (Posner, 1978; Triesman, 2005). If true, principles derived from experiments involving artificial stimuli should easily generalize to natural scenes and stimuli—but they do not (Braun, 2003; Li, Van Rullen, Koch, & Perona, 2002; New, Cosmides, & Tooby, 2007).

The traditional view of the mind is radically at variance with the view that emerges from evolutionary psychology. Evolutionary psychologists expect a mind packed with domain-specific, content-rich programs specialized for solving ancestral problems. For example, evolutionary psychologists would view *attention* not as a single mechanism, but as an umbrella term for a whole *suite* of mechanisms, each designed to select different information from a scene for different processing purposes. Some of these may be relatively domain-general and deployed via volitional systems to any task-relevant element in a scene—these are the attentional mechanisms that have been studied most, using artificial stimuli. The mistake is not to think these exist, but to think they are *all* that exist (Braun, 2003). For example, research with change detection and attentional blink paradigms is uncovering attentional systems that are highly domain specific and deployed in the absence of any specific task demand. One system preferentially attends to human faces (Ro, Russell, & Lavie, 2001). A similar system snaps attention to the location at which a pair of eyes is gazing (Friesen & Kingstone, 2003). Yet another monitors animals for changes in their state and location: Changes to animals are detected more quickly and reliably than changes to buildings, plants, tools—even vehicles (New, Cosmides, & Tooby, 2007). Better change detection for animals than vehicles is significant because it shows a monitoring system tuned to ancestral rather than modern priorities. Our ability to quickly detect changes in the state and location of cars on the highway has life or death consequences and is a highly trained ability in 21st-century America, where the studies were done. Yet, we are better at detecting changes in the states and locations of animals—an ability that had foraging or sometimes predatory consequences for our hunter-gatherer ancestors but is merely a distraction in modern cities and suburbs. By applying adaptationist approaches, it is easy to predict and discover new principles of visual attention, such as the evolved animacy bias, which would never have been discovered by a metatheory that the brain consists primarily of general-purpose processes (New, Cosmides, & Tooby, 2007).

The point is not just that attention will be composed of many different domain-specific mechanisms, but that each domain-specialized attentional mechanism will be part of a vertically integrated system linking the attended objects to domain-specialized inferential, learning, and memory systems. True, animals needed to be closely monitored because they presented either dangers (e.g., predators) or opportunities for hunting (prey), but once detected, other specialized processing is needed. Barrett has shown that a predator-prey inference system develops early, regardless of relevant experiences: 3- and 4-year-old children have a sophisticated understanding of predator–prey interactions, whether they grow up in urban Berlin or in a Shuar village in the jaguar- and crocodile-infested Amazon, eating animals that their fathers hunted and killed (Barrett, Chapter 9, this volume; Barrett, Tooby, & Cosmides, in press). Steen and Owens (2001) have shown that chase play in toddlers and preschoolers has features of special design as a system for practicing and perfecting escape from predators (see also Marks, 1987).

Learning about animals is specialized as well. Mandler and McDonough (1998) have shown that babies distinguish animals from vehicles by 7 months of age and make different inferences about the two by 11 to 14 months. A detailed knowledge of animal behavior is necessary for successful hunting (Blurton Jones & Konner, 1976; Walker, Hill, Kaplan, & McMillan, 2002), and preschoolers as well as adults are equipped with systems specialized for making inductive inferences about the properties of animals (Keil, 1994; Markman, 1989; Springer, 1992; and discussion thereof in Boyer, 2001; Boyer & Barrett, Chapter 5, this volume; Barrett, Cosmides, & Tooby, in press). Atran and colleagues (Atran, 1998; López, Atran, Coley, Medin, & Smith, 1997) provide cross-cultural evidence for a system specialized for sorting living kinds into hierarchically organized, mutually exclusive taxonomic categories, which organize inductive inferences: The closer two species are in this taxonomic structure, the more likely someone is to assume that a trait of one is present in the other. Barrett, Cosmides, and Tooby (in press) have found a second parallel inductive system that uses the predatory role to guide inferences. This system assumes that two species are more likely to share a trait if they are both predators than if one is a predator and the other an herbivore. This system categorizes animals as predators or not on the basis of minimal dietary information scattered amidst other facts about the species' natural history. That is, the category *predator* is triggered by the information "eats animals" and guides inductive learning; the effect on trait induction is strong—twice the size of the taxonomic effect (Barrett, Chapter 9, this volume; Barrett, Cosmides, & Tooby, in press). Animal-specialized memory systems appear to exist as well. For example, Caramazza provides neuropsychological evidence that information about animals is stored in a category-specific memory system, functionally and neurally separate from that which stores information about artifacts (Caramazza, 2000; Caramazza & Shelton, 1998). From a traditional psychological perspective, content effects concerning animals are no more significant that hypothetical effects about door knobs, floorings, or words that rhyme with Quetzalcoatl. From an evolutionary perspective, however, animals were a selective agent of great magnitude and duration, and it would be a surprise if our brains were not strongly shaped by their hundreds of millions of years of interaction with other species.

We are emphasizing the content-specialized nature of processing about animals to illustrate an important point. The benefit of an attentional system specialized for monitoring animals is enhanced if its output is fed into inferential systems that infer their mental states and use this information to predict their likely behavior. The inferences and predictions generated by the mental state system are more useful if they are reliably fed into decision rules that determine whether escape is necessary. The monitoring system should also feed learning mechanisms that incidentally acquire information about the animal's properties; these, in turn, should feed memory systems designed to encode, store, and retrieve information about the animals monitored, according to ecologically relevant categories such as *predator, taxonomically related*, and so on. Animal-specialized attentional, inferential, behavioral, learning, and memory systems should be *functionally integrated with one another*, forming a distinct, category-based *system.* The same should be true for other content domains. Distinct, content-based information-processing systems will exist to the extent that the computational requirements for adaptive problem solving for one content area are functionally incompatible with those for another (Sherry & Shacter, 1987; Tooby & Cosmides, 1992; Tooby et al., 2005).

Seen from this perspective, the ordinary categories of psychology dissolve. To have a textbook chapter on attention and a separate one on memory and then learning and reasoning does not divide the mind in the most appropriate way. Evolutionary psychologists suspect that there may be a domain-specialized system for dealing with animals, with its own associated attentional, inferential, behavioral, learning, and memory circuitry that are designed to work together as an integrated system.

The organization of these specialized systems are expected to look nothing like Fodor's (1983, 2000) "pipelines" (for discussion, see Barrett, 2005, 2015; Boyer & Barrett, Chapter 5, this volume). Some components of the system for making inferences about animals will also be activated for plants and other living things as well (e.g., taxonomic organization [Atran, 1990] or inferences that parts have functions [Keil, 1994]). Other components of the animal system will be activated only in response to animals—or, more precisely, to things manifesting those psychophysical properties the system uses to detect animals, such as contingent reactivity or self-propelled motion—whether the manifesting entity is a meerkat, a robot, or a cartoon. Because many components of the animal system will be functionally specialized for solving animal-specific adaptive problems, they will be composed of representations and procedures that have little in common with those in a system for making inferences about plants, artifacts, or cooperation between people (Boyer & Barrett, Chapter 5, this volume). Nor will the boundaries between category-based systems be clean. People may be attended by the animal monitoring system but also by the system for monitoring social gestures; for inferences about growth and bodily functions, people may be processed as animals but perhaps not for inferences about social behavior. The organization of specializations will be complex and heterarchical, but with a functional logic that arose because of its excellence at solving ancestral problems of survival and reproduction.

The old categories of psychological research have not led to robust models of the human mind because they do not carve nature at the joints. Content specialization is the rule, not the exception. The easiest way to make a domain-general model of learning, reasoning, attention, or memory collapse is to introduce stimuli drawn from different adaptive domains (e.g., Anderson & Phelps, 2001; Boyer & Barrett, Chapter 5, this volume; Braun, 2003; Cosmides & Tooby, Chapter 25, this *Handbook*, Volume 2; Gallistel, 2000). A more reasoned research strategy is to start developing some formal (or even informal) analyses of specific adaptive problems and let these guide research. If there are general systems or principles to be found, they will eventually emerge as we gain a clear understanding of how each content-specialized system functions (for an example, see Leslie, German, & Polizzi, 2005).

Biology is not split into evolutionary biology and nonevolutionary biology: All of biology is organized by evolutionary principles. At some point, all psychology will be evolutionary psychology, simply because it will make no sense to wall off the study of humans from the rest of the natural world. When that happens, textbooks in psychology will no longer be organized according to folk psychological categories, such as attention, memory, reasoning, and learning. Their chapter headings will be more like those found in textbooks in evolutionary biology and behavioral ecology, which are organized according to adaptive problems animals must solve to survive and reproduce: foraging (hunting, gathering), kinship, predator defense, resource competition, cooperation, aggression, parental care, dominance and status, inbreeding avoidance, courtship, mateship maintenance, trade-offs between mating effort and parenting effort, mating system, sexual conflict, paternity uncertainty and sexual jealousy, signaling and communication, navigation, habitat selection, and so on (e.g., see Buss, 1999). Future psychology textbooks will surely contain some additional chapters that capture zoologically unusual aspects of human behavior, such as language acquisition, coalition formation, deep engagement friendships, counterfactual reasoning, metarepresentation, and autobiographical memory. But theories of the computational mechanisms that make these unusual abilities possible will include how they interact with and are supported by a wide variety of adaptive specializations (e.g., Boyer, 2001; Cosmides & Tooby, 2000a; Klein, German, Cosmides, & Gabriel, 2004; Leslie et al., 2005; Sperber, 1994; Sperber & Wilson, 1995; Tooby & Cosmides, 1996).

COMPUTATIONAL ADAPTATIONIST APPROACHES TO MOTIVATION AND EMOTION

In principle, all modern behavioral scientists should understand that any mechanism that processes information must have a computational description. This should include psychological mechanisms that are responsible for motivation. For example, mechanisms that cause fear, gratitude, sexual aversion to close relatives, romantic love, guilt, anger, sexual jealousy, sexual attraction, the perception of beauty, or disgust should all be describable in computational terms, which specify the relevant inputs, representations, the procedures that act on them, and regulatory outputs. Yet, until recently, most cognitive scientists, for example, would not even recognize these topics as within their domain of study.

One reason for why even cognitive psychologists arbitrarily limit their scope is the folk psychological distinction made between knowledge acquisition on the one hand and motivation, emotion, feeling, and preferences on the other. Those who make this distinction view cognition as the study of knowledge acquisition and leave motivation, emotion, and action to other research communities—a practice that presumes that knowledge and motivation are separable rather than coevolved aspects of the same unified systems of representation and action (see Fodor, 2000, for an example).

The Weakness of Content-Free Architectures

To some, it may seem as if an evolutionary perspective supports the case that our species-typical psychological architecture consists primarily of powerful, general-purpose problem solvers, inference engines that embody the content-free normative theories of mathematics and logic. After all, wouldn't an organism be better equipped and better adapted if it could solve a more general class of problems over a narrower class? And won't mathematical and logical inference engines produce knowledge that is true, thereby providing a sound basis for choosing the most adaptive course of action? The difficulty with this intuition is that the more general the problem-solving strategy is, the weaker and more nonfunctional it is. What makes something a more general problem-solving strategy is that it can be applied across a broader class of problems; to do this, it must be stripped of strategies that yield correct answers on some subsets of problems and incorrect answers on others. Domain-specific or content-sensitive architectures are not limited in this way; if they can appropriately apply a program that evolved to solve a specific subset of problems (e.g., kin detection), and others on other problem types (optimal foraging; language acquisition), then it can solve a broader array of problems than the one using content-independent general strategies. So our brains should use the principle of preemptive specificity—use the program specialized for the content, if there is one, and if there is not, fall back to strategies that work on more inclusive problem types.

To be a plausible model of how the mind works, any hypothetical domain-general neurocomputational architecture would have had to reliably generate solutions to all of the problems that were necessary for survival and reproduction ancestrally. For humans and most other species, this is a remarkably diverse, highly structured, and very complex set of problems. If it can be shown that there are essential adaptive problems that humans must have been able to solve to have propagated and that domain-general mechanisms cannot solve them, the view of the mind as consisting solely or primarily of domain-general programs fails. There appear to be a very large number of such problems; at minimum, any kind of information-processing problem that involves motivation and many others as well. This leads to the inference that the human cognitive architecture contains many information-processing mechanisms that are domain specific, content dependent, and specialized for solving particular adaptive problems (Cosmides, 1985; Cosmides & Tooby, 1987, 1994a, 1994b; Tooby, 1985; Tooby & Cosmides, 1990a, 1992; Tooby et al., 2005).

Content-Free Is Content-Poor Some inferences are usefully applied to some domains but not to others. For example, when predicting the behavior of people, it is useful to assume they have *beliefs* and *desires*: invisible mental states that can be inferred but never observed. When predicting the behavior of rocks rolling down a hill, computing their beliefs and desires is useless. Accordingly, the human psychological architecture has evolved two separate inference systems for these two domains: a mind-reading system for inferring the mental states of people (which can be selectively impaired in autism; Baron-Cohen, 1995; Leslie & Thaiss, 1992) and an object mechanics system for understanding the interactions of inanimate objects (Leslie, 1994; Spelke, 1990). Each inference system is designed to be activated by cues particular to its domain of applicability (e.g., human behavior for the mind-reading system, inanimate motion for the object mechanics system). Because their domain of applicability is restricted, specialized inferences appropriate for one domain can be made without producing absurd inferences for another. This property allows domain-specific systems to include rich, contentful inferential rules. For example, in content-free logics, "If *P*, then *Q*" does not imply, "If *Q*, then *P*" because it would lead to absurd inferences ("If you saw a horse, then you saw an animal" does not imply, "If you saw an animal, then you saw a horse"). But a "logic" restricted to situations of social exchange, operating over a more content-restricted set of representations (e.g., benefits, entitlement, obligation, and so on), can usefully specify, "If you take the benefit, then you are obligated to satisfy the requirement" implies, "If you satisfy the requirement, then you are entitled to take the benefit"—an inference that is invalid for any content-free logic (see Cosmides & Tooby, Chapter 25, this *Handbook*, Volume 2). Because they can have content-restricted, specialized inference rules, domain-specific systems can arrive at correct conclusions that more general rules are necessarily barred from making. As a result, small inputs of information can generate many inductions or deductions.

Notice, however, that these powerful, content-rich inference systems are unavailable to a truly domain-general system. To maintain its domain generality, a general system must be equipped only with rules that generate valid inferences across all domains—people, rocks, plants, tools, nonhuman animals, and so on. It cannot take advantage of any inference rules that are useful for one domain but misleading if applied to another. It can have no mind-reading system, no object mechanics system, no predator-prey inference system, or no specializations for tool use (e.g., Defeyter & German, 2003; German & Barrett, 2005). The only kinds of inference rules that are left are content-free ones, such as those found in logic and mathematics. Domain-general systems are crippled by this constraint.

Combinatorial Explosion Combinatorial explosion paralyzes even moderately domain-general systems when encountering real-world complexity. Imagine trying to induce what caused your nausea in the absence of any privileged hypotheses. Your entire life preceded the nausea, and a truly open-minded system would have to consider every action, thought, sight, smell, taste, sound, and combination thereof as a potential cause. In deciding how to respond, every possible action would have to be considered singly and in combination. There would be nothing to privilege the hypothesis that the cause was a recently consumed food and nothing to privilege vomiting or future avoidance of that food as behavioral responses.

As the generality of a system is increased by adding new dimensions to a problem space or new branch points to a decision tree, the computational load increases with catastrophic rapidity. A content-free, specialization-free architecture contains no rules of relevance, procedural knowledge, or privileged hypotheses and thus could not solve any biological problem of routine complexity in the amount of time an organism has to solve it (for further discussion, see, e.g., Carruthers, 2006; Gallistel, Brown, Carey, Gelman, & Keil, 1991; Gigerenzer & Selten, 2002; Keil, 1989; Markman, 1989; Tooby & Cosmides, 1992).

Acknowledging the necessity of a few "constraints" on learning will not solve this problem. As Gallistel (2000, p. 1180) notes:

> Early work focusing on the role of adaptive specialization in learning tended to formulate the problem in terms of the constraints . . . or boundaries . . . that biological considerations placed on *the* learning process. . . . [The contrasting argument] is that there is no such thing as *the* learning process; rather there are many different learning processes. While it is true that the structure of these processes constrain the outcome of learning in interesting ways, the more important point is that it is the problem-specific structure of these processes that makes learning possible.

Problem-specific learning specializations are necessary because the problem of combinatorial explosion cannot be overcome by placing a few constraints on a single, general learning process. Instead of asking, "How much specialization does a general-purpose system require?" psychologists should be asking, "How many degrees of freedom can a system *tolerate*—even a specialized, highly targeted one—and still compute decisions in useful, real-world time." Combinatorics guarantee that real systems can tolerate only a small number. Without domain-specialized learning mechanisms, we would learn nothing at all. Because the set of problems our ancestors had to solve was not a random sample of the set of all logically possible information relationships, the highly clustered relationships in real adaptive problems would have selected, in many (perhaps all) cases, for networks of efficient specialization, along with whatever strategies worked over broader sets of problems.

Clueless Environments Animals subsist on information. The single most limiting resource to reproduction is not food or safety or access to mates, but what makes them each possible: the information required for making adaptive behavioral choices. Many important features of the world cannot be perceived directly, however. Content-free architectures are limited to knowing what can be validly derived by general processes from perceptual information, and this drastically limits the range of problems they can solve. When the environment is clueless, the mechanism will be, too.

Domain-specific mechanisms are not limited in this way. When perceptual evidence is lacking or difficult to obtain, they can fill in the blanks by using cues (perceivable states or events) to infer the status of important, nonperceivable sets of conditions, provided there was a predictable probabilistic relationship between the cues and the unobservable states over evolutionary time. For example, it is difficult or impossible to tell from experience that sex with siblings has a higher chance of producing defective offspring—many conceptions are lost in utero, and whatever problems exist in children born of such matings could have been caused by any number of prior events. In contrast, a domain-specialized system can trigger disgust at the prospect of sex with a sibling, drastically reducing the probability of inbreeding. This will work, without individuals having to obtain any knowledge, conscious or otherwise, about the pitfalls of inbreeding. Incestuous sex will simply seem disgusting and wrong (Haidt, 2001; Lieberman et al., 2003, 2007). Similarly, ancestral hominins had no method by which they could directly see another person's genes to tell whether they are genetic siblings or not. But a mind equipped with a domain-specific kin detection system can estimate kinship on the basis of cues, such as maternal perinatal association, or co-residence during childhood, that were correlated with genetic relatedness ancestrally. The person need not be aware of the cues used by this system, the computational process employed, or even the concept of *genetic relative*.

What Counts as Adaptive Behavior Differs Markedly From Domain to Domain An architecture equipped only with content-free mechanisms must succeed at survival and reproduction by applying the same procedures to every adaptive problem. But there is no domain-general criterion of success or failure that correlates with fitness (for argument, see Cosmides & Tooby, 1987). For example, what counts as a "good" mate has little in common with a "good" lunch or a "good" brother or a "good" person to assault or a "good" place to set up camp. Designing a computational program to choose foods based on their kindness or to choose friends based on their flavor and the aggregate calories to be gained from consuming their flesh suggests the kind of functional incompatibility issues that naturally sort human activities into incommensurate motivational domains. Because what counts as the wrong thing to do differs from one class of problems to the next, there must be as many domain-specific subsystems as there are domains in which the definitions of successful behavioral outcomes are incommensurate.

A *motivational domain* is a set of represented inputs, contents, objects, outcomes, or actions that a functionally specialized set of evaluative procedures was designed by evolution to act over (e.g., representations of foods, contaminants, animate dangers, people to emulate, potential retaliations to provocations). For a given species, there are an irreducible number of these motivational domains; within each motivational domain, there are an irreducible set of domain-specific criteria or value-assigning procedures operating. For the domain of *food* in humans, for example, criteria and value-assigning operations include salt, sweet, bitter, sour, savory, fat affordances, putrefying smell avoidance, previous history with the aversion acquisition system, temporal tracking of health consequences of specific foods by the immune system,[10] stage of pregnancy (because of the vulnerability of fetal organogenesis to chemical disruption), boundaries on entities and properties considered by the system, perhaps maggot-ridden food avoidance, and scores of other factors. When the required assignments of value within a domain (e.g., food) cannot all be derived from a common neurocomputational procedure, the number of motivational elements must necessarily be multiplied to account for the data.

Thus, by evolved design, different content domains should activate different evolved criteria of value, including different trade-offs between alternative criteria.

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[10] Humans and omnivorous nonhumans have a surprising ability to pick efficacious herbs to medicate themselves with, to avoid foods with slow- as well as fast-acting toxins, to match nutritionally complementary foods, to identify effective nutrient releasing or detoxifying food processing practices, and to differentially select foods with nutrients they are deficient in even with no obvious odor clues. To explain these facts, we hypothesize that there is a set of adaptations that (a) exploits the immune system's ability to recognize alien proteins to construct recognition profiles of the digestive products of ingested substances; (b) maps these recognition profiles to the sensory properties of foods ingested in temporal proximity to the immune system's exposure to the protein breakdown products; (c) identifies various components of health (which specific detoxification pathways are overloaded, essential nutrient profile, immune categorization of health, other short-term and long-term health consequences); (d) performs the matrix algebra of backward inducing the temporal profiles of the health consequences of dietary substances onto the immune database of recognized foods (plausibly using the Gallistelian time-series analysis component of conditioning); and (e) maps the computational outputs of these analyses back to sensory food recognition templates, along with valences that reweight how desirable or undesirable the food is to the organism.

Cases of motivational incommensurability are numerous and easily identified via careful analyses of adaptive problems. Distinct and incommensurable evolved motivational principles exist for food, sexual attraction, mate acquisition, parenting, kinship, incest avoidance, coalitions, disease avoidance, friendship, predators, provocations, snakes, spiders, habitats, safety, competitors, being observed, behavior when sick, motor skill acquisition, certain categories of moral transgression, and scores of other entities, conditions, acts, and relationships.

There has been little progress over the past century toward constructing an inventory of motivational domains. Without any proof or even an informal argument, psychologists have presumed that most values are derived from the environment, by computing contingencies between environmental conditions and a tiny set of reinforcers (food, water, sex, pain; Herrnstein, 1977). As a field, we have been shrugging off the issue of evolved motivations through the shell game of implying that any given motivation is secondarily acquired, without obliging ourselves to specify computationally how and from what. Yet, there are strong reasons to doubt that a system of this kind would track fitness at all (Cosmides & Tooby, 1987; Tooby et al., 2005).

Value and behavior cannot be induced from the environment alone. No environmental stimulus intrinsically mandates any response or any value hierarchy of responses. In the tangled bank of coevolved organisms that Darwin memorably contemplated at the end of *On the Origin of Species*, naturally selected differences in the brains of different species cause them to treat the same objects in a rich and conflicting diversity of ways. The infant that is the object of caring attention by one organism is the object of predatory ambition by another, an ectoparasitic home to a third, and a barrier requiring effortful trajectory change to a fourth. It is the brains of these organisms that introduce behavior-regulatory valuation into the causal stream and natural selection that introduced into brains the neural subsystems that accomplish valuation. The same stimulus set cannot, by itself, explain differences in the preferences and actions they provoke, nor indeed, the preferences themselves.

Value is not in the world even for members of the same species. Members of the same species view the same objects differently. The very same object is one person's wife and another's mother—an object of sexual preference in one case and sexual aversion in the other. Moreover, because each evolved organism is by design the center of its own unique valuer-centered web of valuations, evolved value, by its nature, cannot have an objective character (Cosmides & Tooby, 1981; Hamilton, 1964). Because of the structure of natural selection, social organisms are regularly in social conflict, so that the objective states of the world that are preferred by some are aversive or neutral to others (e.g., that this individual and not that should get the contested food, mating opportunity, territory, parental effort, status, grooming, and so on). This structure gives value for organisms an intrinsically indexical quality. Indeed, fitness "interests"—the causal feedback conditions of gene frequency that value computation evolved to track—cannot be properly assigned to such a high-level entity as a person but are indexical to sets of genes inside the genome defined in terms of their tendency to replicate under the same conditions (Cosmides & Tooby, 1981). Whatever else might be attainable by sense data and content-free operations, value or its regulatory equivalents must be added by our evolved architecture.

Values and Knowledge We can now address why knowledge acquisition cannot be computationally divorced from motivation, valuation, and preferences.

To behave adaptively, some actions, entities, or states of affairs must be valued more than others, with a motivational system organized to pursue higher- over lower-valued options. The computations whereby value is assigned typically involve many of the same elements of conceptual structure that are the traditional objects of cognitive science (representations of persons, foods, objects, animals, actions, events). Thus, the evolution of motivational elements will mandate the evolution of an irreducible set of conceptual elements as well. Why? A valuation is not meaningful or causally efficacious for regulating behavior unless it includes some specification of *what is valued*. That is, the specification of what the value applies to generally involves conceptual structure.

For example, for natural selection to cause safe distances from snakes to be preferred to closeness to snakes, it must build the recognition of snakelike entities into our neurocomputational architecture. This system of recognition and tagging operations is, for certain purposes, equivalent to having a snake *concept*, albeit a skeletally specified one. Evidence supports the view that humans and related species do indeed have a valuation system specialized to respond to snakes (e.g., Marks, 1987; Mineka & Cook, 1993; Mineka, Davidson, Cook, & Keir, 1984; Yerkes & Yerkes, 1936). This one consideration alone forces us to add a fourth "innate idea" to Kant's trinity of space, time, and causality. Yerkes's finding of evolved snake fear in chimpanzees counts as empirically based philosophical progress and as straightforward progress in the cognitive science of knowledge—derived (*pace* Fodor) from evolutionarily motivated theories of function.

This argument not only establishes the necessity of evolved motivational elements but also resurrects the argument for the necessity of "innate ideas," that is, evolved conceptual procedures within the cognitive architecture that embody knowledge about the world and are triggered by evolved cue recognition systems that evolved to be specifically responsive to stimuli with certain cues (however abstractly described in the nervous system). It is the specificity of the coupling to the particular valuation procedure (closer is negative) that individuates the concept with respect to the set of motivational functions (e.g., *beloved* [your children], *wary* [snakes]).

Consider, for example, the series of interacting conceptual components necessary to build a snake avoidance system. The system needs a psychophysical front-end: One of its subcomponents assigns the evolved, internal tag *snake* through visual and biomechanical motion cues to a perceptual representation of some entity in the world. It has a second subcomponent that maps in a parameter, *distance*, between the *snake* and the valued entity (e.g., *self* or *child*). The distance-representing component is used by many systems. However, it also must have a component that assigns and updates different specific valuation intensities for different distances, so that farther away is better than closer for snakes (but not for food or other motivational domains). A particular bad event (e.g., an imagined snake bite) need not be specifically represented as a negative goal state in the snake avoidance system, with distance acquiring its significance through backward induction and means-ends analysis. The distance-fear relationship could fill the representation of space with a motivational manifold that itself motivates avoidance (closeness is increasingly unpleasant). But such action-inviting affordances are not the same, computationally, as a represented goal state.

The metric of valuation against distance (and its update rules) is proprietary to snakes, but the output value parameter it produces must be accessible to other systems (so that distance from snakes can be ranked against other goods, like getting closer to extract your child from the python's coils). Snake, distance, person, and the *distance* (person, snake) valuation metric all necessarily operate together for this simple system to work. Snakes, the entity to be protected, and distance cannot be assigned to one computational process, with valuation assigned to another. Even in this simple example, conceptual and valuation functions indivisibly interpenetrate each other, with the representations necessarily coexisting within the same structure.

Learning, another clearly cognitive topic, is implicated in snake aversion as well, but the learning process is domain specific. It appears that the snake avoidance system recalibrates based on individual experience, possibly slowly habituating in the absence of negative experiences or observations and increasing sharply if snake contact leads to injury. It also narrowly accepts inputs from the social world—a conspecific expressing fear toward a snake (but not toward other stimuli such as rabbits or flowers)—and uses this information to recalibrate the individual's snake valuation (Mineka & Cook, 1993; Mineka et al., 1984). Presumably, recalibration from observing conspecifics evolved because the system operates more functionally by upregulating or downregulating fear as a function of the local distribution of fear intensities in others, which index to some degree the local rate at which venomous snakes are encountered. (It is also worth pointing out that degrees of snake fear are, therefore, "cultural"—weights in snake fear calibrate each other in interacting primate communities.)

The key point is that even this apparently simple, one-function motivational system involves a series of evolved content-specific conceptual elements, including snakes, distance, conspecifics, that fear-faces have specific referents in the world, that snakes are one of the privileged referents of a fear-face, and the output of fear itself. Not all these elements are unique to the snake system (e.g., snake-recognition is; distance-to-self, fear-faces, fear-output are not), but their pattern of distribution among motivational systems is heterarchical and itself not something that could be derived by content-independent operations acting on unmediated experience.

As this form of analysis is applied to the other tasks humans perform, we think it will be impossible to escape the general conclusion that cognitive science intrinsically involves motivation and that the science of motivation intrinsically involves cognition. The brain evolved as a control system (Weiner, 1948), designed to generate action. From this perspective, there is not just a cognitive science of knowledge such as language, intuitive physics, and number, but also a cognitive science of parenting, eating, kinship, friendship, alliance, groups, mating, status, fighting, tools, minds, foraging, threat, collective action, natural history, and scores of other ancient realms of human action. Separating knowledge acquisition from motivation has placed the study of motivation in cognitive eclipse and diverted cognitive scientists from studying conceptual structure, motivation, and action as integrated systems (which they will inevitably turn out to be). It ignores the many causal pathways whereby our evolved architecture should have been designed to manufacture, store, communicate, and act on the basis of representations that would not qualify as a rational architecture's efficient attempt at constructing true beliefs (Gigerenzer & Murray, 1987; Haselton & Buss, 2000; Tooby & Cosmides, 1990a, in press). Evolved systems for motivational computation use conceptual structure in targeted ways, so motivational computation and knowledge computation cannot be isolated from each other into separate systems, but instead evolves together. (For a more complete discussion, see Tooby et al., 2005.) Indeed, many evolved concepts arguably exist so we can have functional motivations about them (e.g., food, free rider, mother, child, predator, snake, unclean, sexually attractive).

EMOTIONS AS A SOLUTION TO THE SHORT-TERM PROBLEM OF MECHANISM COORDINATION

The preceding discussion leads us to view the mind as a crowded network of evolved, domain-specific programs. Each is functionally specialized for solving a different adaptive problem that arose during hominin evolutionary history, such as face recognition, foraging, mate choice, heart-rate regulation, sleep management, or predator vigilance, and each is activated by a different set of cues from the environment. But the existence of all these microprograms itself creates an adaptive problem: Programs that are individually designed to solve specific adaptive problems could, if simultaneously activated, deliver outputs that conflict with one another, interfering with or nullifying one another's functional products (e.g., digest food versus devote maximum blood resources to the cardiopulmonary system and muscles executing escape). They may also make conflicting demands on common computational resources. The existence of attention itself, where some things are selected to be processed with higher priority than others, demonstrates this. For example, sleep and flight from a predator require mutually inconsistent actions, computations, and physiological states. It is difficult to sleep when your heart and mind are racing with fear, and this is no accident: Disastrous consequences would ensue if proprioceptive cues were activating sleep programs at the same time that the sight of a stalking lion was activating ones designed for predator evasion. To avoid such consequences, the mind must be equipped with superordinate programs that override some programs when others are activated (e.g., a program that deactivates sleep programs when predator evasion subroutines are activated). Furthermore, many adaptive problems are best solved by the simultaneous activation of many different *components* of the neurocomputational architecture, such that each component assumes one of several alternative states (e.g., predator avoidance may require simultaneous shifts in both heart rate and auditory acuity). Again, a superordinate program is needed that coordinates these components, snapping each into the right configuration at the right time given the array of challenges prioritized by likely fitness consequences.

We have proposed that emotions are such programs (Tooby, 1985; Tooby & Cosmides, 1990a, 2008). To behave functionally according to evolutionary standards, the mind's many subprograms need to be orchestrated so that their joint product at any given time is functionally coordinated to produce a best-bet set of responses, rather than clashing in a cacophonous and self-defeating fashion. This coordination is accomplished by a set of superordinate programs, namely the emotions. On this view, emotions are adaptations that have arisen in response to the adaptive problem of mechanism orchestration. This view implies that the exploration of (a) the statistical structure of ancestral situations (the EEA) and (b) their relationship to the mind's battery of functionally specialized programs is central to mapping the emotions because the most useful (or least harmful) deployment of programs at any given time will depend critically on the exact nature of the immediate situation being confronted.

How did emotions arise and assume their distinctive structures? Fighting, falling in love, responding to mistreatment by another, escaping predators, seeing a potential sexual or mate-recruitment opportunity, confronting sexual infidelity, experiencing a failure-driven loss in status, responding to the death of a family member, and so on each involved conditions, contingencies, situations, or event types that recurred innumerable times in hominin evolutionary history. Repeated encounters with each kind of situation selected for adaptations that guided information processing, behavior, and the body adaptively through the clusters of conditions, demands, and contingencies that characterized that particular class of situation. These functions could be accomplished by engineering superordinate programs, each of which jointly mobilizes a subset of the psychological architecture's other programs in a particular configuration. Each configuration would be selected to deploy computational and physiological mechanisms in a way that, when averaged over individuals and generations, would have led to the most fitness-promoting subsequent lifetime outcome given that class of ancestral situation type. So those designs that responded to large felid predators by approaching to better appreciate their beauty were selected out; those designs that motivated avoidance but did not accelerate heart rate and breathing were also selected out compared to designs that increased the maximum possible speed of retreat by accelerating heart rate and breathing (and suspend digestion, long-run somatic repair, attention to competing non-time-fused goals, and so on). Step by step, design variants that more thoroughly coordinate effective response sets become incorporated into the species design.

When we use the term *emotions*, we are linking these evolved programs to evolutionarily recurrent situations (whether challenges or opportunities) that have a short-term or moderately extended duration. These situations may terminate (e.g., with a rescuer killing the predator), gradually lose their structure (with the predator wandering away from your arboreal refuge, so that the predator risk returns to baseline levels), or be replaced by other situations that trigger new emotions (your child makes a misstep and is struggling not to fall out of the tree). Moreover, there is not only an abstract structure of a recurrent situation (to which we have evolved an organized response), but there will be recurrent dimensions of variation in the abstract structure of the recurrent situation, which are used to calibrate the response. That is, not only will there be predator-threat, but predator-threat varied in terms of speed, surprise, number, distance to safety, number of allies, and so on (Cosmides & Tooby, 2000b). Hence individual ontogenetically encountered situations will be responded to in terms of the long-term abstract structure of a situation, as parameterized by psychological variables that serve to meaningfully individuate the immediate situation in a way in which the architecture can recognize and to which it can deploy appropriately.

Moreover, the world does not dichotomously chop itself into short-term situations and long-term conditions. For convenience, we term programs that coordinate responses to short-term conditions *emotions;* we term coordinated responses to conditions of intermediate duration that recalibrate a constellation of decision-variables *calibrational adaptations* or (if related to traditionally recognized emotions) *moods*; and we term coordinated responses to enduring conditions *parametric coordinative adaptations*. As discussed later, the major dimensions of personality variation (including perhaps what researchers sometimes call temperaments) may be constructed by various parametric coordinative adaptations.

The coordinated adjustment and entrainment of mechanisms (emotions) functions as a mode of operation for the entire neurophysiological architecture and serves as the basis for a precise computational and functional definition of each emotion state. Each emotion entrains various other adaptive programs—deactivating some, activating others, and adjusting the modifiable parameters of still others—so that the whole system operates in a particularly harmonious and efficacious way when the individual is confronting certain kinds of triggering conditions or situations. The conditions or situations relevant to the emotions are those that (a) recurred ancestrally, (b) could not be negotiated successfully unless there was a superordinate level of program coordination (i.e., circumstances in which the independent operation of programs caused no conflicts would not have selected for an emotion program and would lead to emotionally neutral states of mind), (c) had a rich and reliable repeated structure, (d) had recognizable cues or situation-representations signaling their presence,[11] and (e) an error would have resulted in larger fitness costs than the remedy. When a condition or situation of an evolutionarily recognizable kind is detected, a signal is sent out from the emotion program that (a) activates the specific constellation of subprograms appropriate to solving the type of adaptive problems that were regularly embedded in that situation, and (b) deactivates programs whose operation might interfere with solving those types of adaptive problems. Programs directed to remain active may be cued to enter subroutines that are specific to that emotion mode and were tailored by natural selection to solve the problems inherent in the triggering situation with special efficiency.

According to this theoretical framework, an emotion is a superordinate program whose function is to direct the activities and interactions of many subprograms, including those governing perception, attention, inference, learning, memory, motor planning, goal choice, motivational priorities, categorization and conceptual frameworks, physiological reactions (e.g., heart rate, endocrine function, immune function, gamete release), reflexes, behavioral decision rules, motor systems, communication processes, energy level and effort allocation, affective coloration of events and stimuli, and the recalibration of probability estimates, situation assessments, values, and regulatory variables (e.g., self-esteem, estimations of relative formidability, relative value of alternative goal states, efficacy discount rate). An emotion is not reducible to any one category of effects, such as effects on physiology ("arousal"), behavioral inclinations, situation interpretations ("appraisals"), facial expressions, or consciously accessible feeling states, because it involves evolved instructions for all of them together, as well as other mechanisms distributed throughout the human mental and physical architecture.

For example, some emotion researchers consider that definitional to a basic emotion is an identifiable emotional expression, causing them to focus on a set of six or seven (happiness, sadness, anger, fear, surprise, disgust, and perhaps contempt). However, an evolutionary computational approach makes it plausible that emotions are far more numerous, but for only seven of these (identified so far) did it pay to broadcast the individual's emotional state to others (Tooby & Cosmides, 2008). We would add confusion to this list (since it is recognizable on the face), and because we think it is a mode of operation.[12] All psychological programs—including superordinate programs

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[11] If there is no repeated structure or no cues to signal the presence of a repeated structure, selection cannot build an adaptation to address the situation.

[12] An evolutionary recurrent situation can be extremely abstract, provided that there is a deployment of the architecture that improves performance given the detection of this abstract situation. To give a flavor of just how strangely abstract a "situation" can be, consider the hypothesis that confusion as a mental state might not be a failure of processing, as it is usually thought of, but rather itself an adaptation. Indeed, it seems likely that humans even have adaptations for confusion—that is, that confusion as a detected situation selected for a mode of operation (confusion) that improves resolution of the problem posed by confusion (the situation). What is the recurrent situation that confusion (the mode of operation) is a response to? Confusion may be defined as having insufficient information to decide on a single coherent representation of the organism's circumstances relevant to selecting a best response; this can involve feedback to behavior being highly inconsistent with expectation; being exposed to conflicting cues that imply mutually inconsistent conditions, or a situation requiring contradictory responses. Evolved best responses to the situation of confusion may be such computational adjustments as a suspension of ongoing action; a broadening of attentional focus beyond ongoing goal-pursuit; increasing the search for disambiguating cues; rapid shifts between different interpretations of data to see which has the best fit; increasing uncertainty weightings on decision-relevant variables; and dropping down the ladder of interpetations and responses to more conservative computational or behavioral strategies that yield positive returns over broader sets of conditions.

of this kind—are sometimes mistaken for "homunculi," that is, entities endowed with "free will." A homunculus scans the environment and freely chooses successful actions in a way that is not systematic enough to be implemented by a program. It is the task of cognitive psychologists to replace theories that implicitly posit such a computationally impossible entity with theories that can be implemented as information-processing architectures with open parameters. Emotion programs, for example, have a front end that was designed to detect evolutionarily reliable cues that a situation exists (regardless of whether these cues still reliably signal the presence of that situation in the modern world); when triggered, they entrain a specific set of subprograms: those that natural selection chose as most useful for solving the problems that a situation posed in ancestral environments. Just as a computer can have a hierarchy of programs, some of which control the activation of others, the human mind can as well. Far from being internal free agents, these programs execute their evolved code regardless of the needs and circumstances of the modern individual; they were designed to create states (fury) and implement actions that worked effectively in ancestral situations (e.g., murder a weaker rival), regardless of their consequences in the present (e.g., prison).

Fear (an Example)

The ancestrally recurrent situation is being alone at night and a situation-detector circuit perceives cues that indicate the possible presence of a human or animal predator. The emotion mode is a fear of being stalked. (In this conceptualization of emotion, there might be several distinct emotion modes that are lumped together under the folk category *fear* but that are computationally and empirically distinguishable by the different constellation of programs each entrains.) When the situation detector signals that the individual has entered the situation "possible stalking and ambush," the following kinds of mental programs are entrained or modified:

- There are shifts in perception and attention. You may suddenly hear with far greater clarity sounds that bear on the hypothesis that you are being stalked but that ordinarily you would not perceive or attend to, such as creaks or rustling. Are the creaks footsteps? Is the rustling caused by something moving stealthily through the bushes? Signal detection thresholds shift: Less evidence is required before you respond as if there were a threat, and more true positives will be perceived at the cost of a higher rate of false alarms.
- Goals and motivational weightings change. Safety becomes a far higher priority. Other goals and the computational systems that subserve them are deactivated. You are no longer hungry; you cease to think about how to charm a potential mate; or practicing a new skill no longer seems rewarding. Your planning focus narrows to the present; worries about yesterday and tomorrow temporarily vanish. Hunger, thirst, and pain are suppressed.
- Information-gathering programs are redirected. Where is my baby? Where are others who can protect me? Is there somewhere I can go where I can see and hear what is going on better?
- Conceptual frames shift, with the automatic imposition of categories such as *dangerous* or *safe*. Walking a familiar and usually comfortable route may now be mentally tagged as dangerous. Odd places that you normally would not

occupy—a hallway closet, the branches of a tree—suddenly may become salient as instances of the category *safe* or *hiding place*.

- Memory processes are directed to new retrieval tasks. Where was that tree I climbed before? Did my adversary and his friend look at me furtively the last time I saw them?
- Communication processes change. Depending on the circumstances, decision rules might cause you to emit an alarm cry or be paralyzed and unable to speak. Your face may automatically assume a species-typical fear expression.
- Specialized inference systems are activated. Information about a lion's trajectory or eye direction might be fed into systems for inferring whether the lion saw you. If the inference is yes, a program automatically infers that the lion knows where you are; if no, the lion does not know where you are (the seeing-is-knowing circuit identified by Baron-Cohen, 1995, and inactive in people with autism). This variable may automatically govern whether you freeze in terror or bolt (Barrett, Chapter 9, this volume). Are there cues in the lion's behavior that indicate whether it has eaten recently and thus is unlikely to be predatory in the near future? (Savanna ungulates, such as zebras and wildebeests, commonly make this kind of judgment; Marks, 1987.)
- Specialized learning systems are activated, as the large literature on fear conditioning indicates (e.g., LeDoux, 1995; Mineka & Cook, 1993; Öhman & Mineka, 2001; Pitman & Orr, 1995). If the threat is real and the ambush occurs, the victim may experience an amygdala-mediated recalibration (as in posttraumatic stress disorder) that can last for the remainder of his or her life (Pitman & Orr, 1995).
- Physiology changes and the immune system adjusts. Gastric mucosa turn white as blood leaves the digestive tract (another concomitant of motivational priorities changing from feeding to safety); adrenalin spikes; heart rate may go up or down (depending on whether the situation calls for flight or immobility), blood rushes to the periphery, and so on (Cannon, 1929; Tomaka, Blascovich, Kibler, & Ernst, 1997); instructions to the musculature (face and elsewhere) are sent (Ekman, 1982). Indeed, the nature of the physiological response can depend in detailed ways on the nature of the threat and the best response option (Marks, 1987).
- Behavioral decision rules are activated. Depending on the nature of the potential threat, different courses of action will be potentiated: hiding, flight, self-defense, or even tonic immobility (the latter is a common response to actual attacks, both in other animals and in humans).[13] Some of these responses may be experienced as automatic or involuntary.

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[13] Marks (1987) vividly conveys how many aspects of behavior and physiology may be entrained by certain kinds of fear: "During extreme fear humans may be 'scared stiff' or 'frozen with fear'. A paralyzed conscious state with abrupt onset and termination is reported by survivors of attacks by wild animals, by shell-shocked soldiers, and by more than 50% of rape victims (Suarez & Gallup, 1979). Similarities between tonic immobility and rape-induced paralysis were listed by Suarez & Gallup (features noted by rape victims are in parentheses): (1) profound motor inhibition (inability to move); (2) Parkinsonian-like tremors (body-shaking); (3) silence (inability to call out or scream); (4) no loss of consciousness testified by retention of conditioned reactions acquired during the immobility (recall of details of the attack); (5) apparent analgesia (numbness and insensitivity to pain); (6) reduced core temperature (sensation of feeling cold); (7) abrupt onset and termination (sudden onset and remission of paralysis); (8) aggressive reactions at termination (attack of the rapist after recovery); (9) frequent inhibition of attack by a predator . . ." (pp. 68–69).

From the point of view of avoiding danger, these computational changes are crucial: They are what allowed the adaptive problem to be solved with high probability, on average, over evolutionary time. In any single case they may fail because they are only the evolutionarily computed best bet, based on ancestrally summed outcomes; they are not a sure bet, based on an unattainable perfect knowledge of the present.

Whether individuals report consciously experiencing fear is a separate question from whether their mechanisms assumed the characteristic configuration that, according to this theoretical approach, defines the fear emotion state. Individuals often behave as if they are in the grip of an emotion, while denying they are feeling that emotion. It is perfectly possible that individuals sometimes remain unaware of their emotion states, which is one reason subjective experience should not be considered the sine qua non of emotion. At present, both the function of conscious awareness and the principles that regulate conscious access to emotion states and other mental programs are complex and unresolved questions. Mapping the design features of emotion programs can proceed independently of their resolution, at least for the present. This computational approach also allows testing for the presence of emotion programs cross-culturally. The design features of an emotion mode should be present and ascertainable experimentally, whether the language has a word for an emotion state or not (pace Lutz, 1988).

The Functional Structure of an Emotion Program Evolved to Match the Evolutionarily Summed Structure of Its Target Situation

According to this framework, the sets of human emotion programs assumed their evolved designs through interacting with the statistically defined structure of human environments of evolutionary adaptedness. Each emotion program was constructed by a selective regime imposed by a particular evolutionarily recurrent situation—a cluster of repeated probabilistic relationships among events, conditions, actions, and choice payoffs. These would have had to have (a) endured over a sufficiently long stretch of evolutionary time (and proportion of the species range) to have had selective consequences on the design of the mind; and (b) be probabilistically associated with cues detectable by humans. To the extent that situations exhibit such a structure, their statistical properties are expected to have been used by selection to build an emotion program whose detailed design features are favored given that recurrent situation. That is, the architecture of the emotion program should manifest an advantageous complementarity with the structure of the recurrent situation, so that their interaction produces a better outcome (given ancestral conditions) than would have been produced without the program.

Emotion programs have evolved to take features of the recurrent statistical and causal structure into account, whether they could have been perceived ontogenetically or not. This tailoring is accomplished by selection, acting over evolutionary time, differentially incorporating program components that dovetail with individual items on the list of properties probabilistically associated with the situation. Thus, embedded in an emotion mode is a way of interpreting the world in terms of parameters made meaningful by the recurrent structure, assuming causal connections (even unobservable ones) that were typically present, and being motivated to take action related to the ancestral cluster of probabilistically associated elements. So, for example, if ancestrally a new group moving into one's locale statistically foreshadowed eventual zero-sum conflict, competition, and potential expulsion from their existing resource base by the new group at some nontrivial rate, then humans should be designed to be more liable to experience intergroup fear, hostility, and rivalry. Similarly, if anger is an emotion program that evolved to orchestrate negotiative behaviors in conflicts of interest, and being perceived as stronger increases one's bargaining power (Sell, Tooby, & Cosmides, 2009), then evolution should have incorporated elements into the facial display of anger that enhanced the appearance of strength (as it appears to have done: Sell et al., 2014).

For example, the condition of having a mate plus the condition of your mate copulating with someone else constitutes a situation of sexual infidelity—a situation that has recurred over evolutionary time, even though it has not happened to every individual. Associated with this situation were cues reliable enough to allow the evolution of a "situation detector" (e.g., observing a sexual act, flirtation, or even the repeated simultaneous absence of the suspected lovers are cues that could trigger the categorization of a situation as one of infidelity). Even more importantly, there were many necessarily or probabilistically associated elements that tended to be present in the situation of infidelity as encountered among our hunter-gatherer ancestors. Additional elements include: (a) a sexual rival with a capacity for social action and violence, as well as allies of the rival; (b) a discrete probability that an individual's mate has conceived with the sexual rival; (c) changes in the net lifetime reproductive returns of investing further in the mating relationship; (d) a probable decrease in the degree to which the unfaithful mate's mechanisms value the victim of infidelity (the presence of an alternative mate lowers replacement costs); (e) a cue that the victim of the infidelity will likely have been deceived about a range of past events, leading the victim to confront the likelihood that his or her memory is permeated with false information; and (7) the victim's status and reputation for being effective at defending his or her interests in general would be likely to plummet, inviting challenges in other arenas. These are just a few of the many factors that constitute a list of elements associated in a probabilistic cluster; they constitute the evolutionary recurrent structure of a *situation* of sexual infidelity. The emotion of sexual jealousy evolved in response to these properties of the world—this situation—and there should be evidence of this in its computational design (Buss, 2000; Daly, Wilson, & Weghorst, 1982).

For example, if in ancestral situations of sexual infidelity, there was a substantially higher probability of a violent encounter than in its absence, the sexual jealousy program will have been shaped by the distillation of those encounters, and the jealousy subroutines will have been adjusted to prepare for violence (e.g., with heart rate increase) in proportion to the raised probability in the ancestral world. (Natural selection acts too slowly to have significantly updated the mind to post-hunter-gatherer conditions.) Each of these subelements and the adaptive circuits they require can be added to form a general theory of sexual jealousy (e.g., Buss, 2000).

The emotion of sexual jealousy constitutes an organized mode of operation specifically designed to deploy the programs governing each psychological mechanism so that each is poised to deal with the exposed infidelity. Physiological processes are prepared for things such as violence, sperm competition, and the withdrawal of investment; the goal of deterring, injuring, or murdering the rival emerges; the goal of punishing, deterring, or deserting the mate appears; the desire to make yourself more competitively attractive to alternative mates emerges; memory is activated to reanalyze the past; confident assessments of the past are transformed into doubts; the general estimate of the reliability and trustworthiness of the opposite sex (or indeed everyone) may decline; associated shame programs may be triggered to search for situations in which the individual can publicly demonstrate acts of violence or punishment that work to counteract an imagined or real social perception of weakness; and so on.

It is the relationship between the summed details of the ancestral condition and the detailed structure of the resulting emotion program that makes this approach so useful for emotion researchers. Each functionally distinct emotion state—fear of predators, gratitude, guilt, sexual jealousy, anger, grief, and so on—corresponds to an integrated mode of operation that functions as a solution designed to take advantage of the particular structure of the recurrent situation or triggering condition to which that emotion corresponds. This approach can be used to create theories of each individual emotion, through three steps: (a) reconstructing the clusters of properties of ancestral situations, (b) constructing engineering analyses about how each of the known or suspected psychological mechanisms in the human mental architecture should be designed to deal with each ancestral condition or cluster of conditions and integrating these into a model of the emotion program, and (c) constructing or conducting experiments and other investigations to test and revise the models of emotion programs.

Evolutionarily recurrent situations can be arrayed along a spectrum in terms of how rich or skeletal is the set of probabilistically associated elements that defines the situation. A richly structured situation, such as sexual infidelity or predator ambush, will support a richly substructured emotion program in response to the many ancestrally correlated features. Many detailed adjustments will be made to many psychological mechanisms as instructions for the mode of operation. In contrast, some recurrent situations have less structure (i.e., they share fewer properties in common), so the emotion mode makes fewer highly specialized adjustments, imposes fewer specialized and compelling interpretations and behavioral inclinations, and so on. For example, surges of happiness or joy are an emotion program that evolved to respond to the recurrent situation of encountering unexpected positive events. The class of events captured by "unexpectedly positive" is extremely broad and general and has only a few additional properties in common, selecting for differential responses (e.g., adjusting the reserve price for taking action down or up, so that joy makes people more energetic, whereas sadness deters action). Emotion programs at the most general and skeletal end of this spectrum correspond to what some call *mood* (happiness, sadness, excitement, anxiety, playfulness, homesickness, and so on).

Motivational Systems, Internal Regulatory Variables, and Recalibrational Emotions

Although traditional theories of motivation have tended to be general-purpose or very simple (e.g., motivation as goal seeking; motivation driven by a general-purpose operant conditioning system shaped by histories of reinforcement, linked to a small number of drives or reinforcers, such as food, water, sex, etc.), evolutionary research has identified a large and expanding number of adaptive problems for which there exist no corresponding motivational theories in traditional psychology (e.g., kin-directed altruism, incest avoidance, exchange partner management, power-based negotiation, habitat selection, prevention of partner infidelity, contagion avoidance, child care, status-seeking, affiliation by association value, punitive deterrence of free-riding, advancement of one's coalition's interests with respect to competing coalitions, and so on). These do not involve freely chosen goals, nor do they appear to be well-captured by any extant drive-reduction theory. These adaptive problems are each so different from each other that they require distinct adaptive specializations to solve them (how much sexual aversion should you feel toward this half-sibling—incest avoidance; how much cost should you incur to struggle for a resource against this adversary—anger; how much should you recalibrate your disposition to help someone who helped you more than you expected to consolidate a higher level of mutual cooperation—gratitude; how determined should you be to punish a free rider—punitiveness; how much effort should you devote to your group, given the likely costs—loyalty).

Motivational adaptive problems are, abstractly, information-processing problems involving evaluating expected fitness payoffs to alternative courses of action, given information available to the organism about its situation, in order to make decisions that are best bet responses. Ancestrally recurrent situations that required choices (e.g., have sex with this person given cues that he might be your brother?; punish or ignore free-riding?) can be organized into distinct sets or clusters with statistically recurrent features, cues, invisible concomitants, outcomes, and payoff distributions. This in turn led to selection for distinct motivational subsystems tailored to the special properties of each motivational problem-type (incest avoidance; child care; sacrifice for the coalition; mateship maintenance; exploitation of opportunities for gain through aggression; satisfaction of curiousity). To operate, each of these will generally be associated with proprietary interpretive systems with reliably developing conceptual primitives such as *free rider* (Delton, Cosmides, Guerno, Robertson, & Tooby, 2012), so that motivations such as punitive sentiment can be directed toward their functional targets (e.g., the transgressing person; see also Price, Cosmides, & Tooby, 2002). Conveniently, evolutionary biologists have developed a number of models of adaptive problems—that is, how selection acts in specific domains (such as kin selection, inbreeding depression, sexual selection, the asymmetric war of attrition); these models can be used to develop models of the computational architectures that specific motivational subsystems should have in order to be able to solve their respective adaptive problems.

In order to construct a theoretical framework capable of incorporating this new range of cases, we need to introduce a new class of computational elements that have no present counterpart in the cognitive sciences, traditional approaches to motivation, or folk psychology. That is, they are not thoughts, or feelings, or desires as ordinarily conceptualized. For sake of simplicity, we call these computational elements *internal regulatory variables* (Tooby & Cosmides, 2008; Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008). They are needed to register properties of persons, acts, and situations that are needed to compute, implicitly or explicitly, the value and probability of an outcome of a particular kind, given a course of action; to segregate elements in the world into classes that can then be assigned motivationally relevant meanings (e.g., my child, a sexual opportunity, or a potential friend); or to store decision-making thresholds that partition the set of possible actions in the immediate situation that are fitness-promoting from those that are fitness-reducing (e.g., a welfare trade-off threshold). They not only encode necessary precursors (e.g., co-residence as one input into relatedness computation) necessary to specialized next-step input computations (e.g., update kinship index estimating how genetically related this person is); but they also can encode values themselves (a high kinship index can then lead to a computation that this specific relative is *valuable* to *this* degree); this in turn can be used to provide values (as parameters) to decision-making circuits (e.g., place a high weight on this person's welfare when making choices that affect the welfare of self versus other—welfare trade-off magnitudes).

According to this view, internal regulatory variables evolved to track those narrow, targeted properties of the body, the social environment, and the physical environment whose computation provided inputs needed by evolved decision-making programs in order to generate motivations relevant to choice and action. At their simplest, internal regulatory variables have discrete parameter values (e.g., target person represented as being male or female) or continuous magnitudes (target person is represented as having a kinship index ranging between 0 and some evolutionarily set possible upper bound). Final outputs of different motivational systems about the value of various outcomes need also to be expressed in a common neural currency, so that trade-offs and opportunity costs are incorporated into choice behavior for mutually exclusive choices. That is, ultimately, you choose to deliver the gazelle haunch to your band or to your sick brother in the neighboring village.

Therefore, we expect that the architecture of the human mind is full of evolved variables, existing embedded in evolved circuits, whose function is to store proprietary parameters that are useful for regulating valuation, choice behavior, and prospective computational preparation for future choice-forcing situations. Internal regulatory variables are not explicit concepts, representations, or goal states, but rather registers or indices that acquire their meaning by their location in the architecture—for example from the situational cues that feed into them (e.g., co-residence, perinatal association), and the evolved behavior-controlling and computation-controlling procedures that they in turn feed into (e.g., an estimated kinship index between self and individual *i*, in turn leading to aversion at the prospect of sex with *i*, a family member). Such regulatory variables may include measures of how valuable to the individual a mate is, a child is, your own life is, and so on; how stable or variable the food productivity of the habitat is; the distribution of condition-independent mortality in the habitat; how long you have co-resided with an individual; your expected future life span or period of efficacy; how good a friend someone has been to you; the extent of your social support; how durable your social partnerships are expected to be; your association value to others; your own and others ability to inflict costs—aggressive formidabilities; your sexual attractiveness; your status or self-esteem; the status of the coalition you belong to; present energy stores; present health; how advantageous conception would be given your somatic condition and circumstances; the degree to which subsistence requires collective action, and so on.

Most evolutionarily recurrent situations and choice contexts that select for motivational subsystems and associated emotion programs involve the ongoing discovery of information that allows and requires the recomputation of one or more of these variables. Recalibration is, therefore, a major functional component of most emotion programs. *Recalibrational programs* are components of emotion programs such as guilt, gratitude, grief, depression, compassion, and shame whose primary function is to carry out such recomputations of internal regulatory variables (Cosmides & Tooby, 2013; Tooby & Cosmides, 1990a, 2008; Tooby et al., 2008), rather than to orchestrate any specific short-run behavioral response. Jealousy, for example, involves several sets of recalibrations (e.g., decrease in estimate of own mate value, decrease in trust in mate, decrease in paternity confidence, increase in the benefit of eliminating the rival).

But information relevant to internal regulatory variables is not equally spread throughout all points in time and throughout all situations. Some situations are information dense, full of informative, ancestrally stable cues that reliably allowed more accurate calibrations of what these variables should be set at (e.g., discovering your child is dead; that your love is returned; your husband has not been faithful; who your father really is; or that someone you know sacrificed a great deal on your behalf). A well-designed architecture would exploit these information-dense situations to update the parameters in the system. This is particularly true since these variables would logically exist in mutually interrelated networks. Among other things, these networks need to exist to internally solve what microeconomists would call pricing problems—computational problems that exist when there a large variety of factors of production with different costs (e.g., different possible mutually constraining courses of action), different possible products (outcomes with different and mutually interacting payoffs), and so on. Externally caused changes in these factors require extensive and spreading recomputation through the motivational system. That is, new information relevant to opportunities, factors of production, payoffs, and uncertainties will necessarily have to ramify through the system that governs the thousands of decisions a person makes each day. Accidentally spilling your dinner in the dirt may require just a quick pang of annoyance or disappointment to update; at the other extreme, discovering that your husband is dead will require major changes in tens of thousands of decision-variables, trade-offs, and habit-elements distributed throughout the architecture that have been calibrated in the past to assume his presence (Who are you going to turn to when you are in trouble? Who do you share food with? How vigilant do you have to be at night? Who will help care for the children? How much food do you need to forage tomorrow?). For reasons that are theoretically unclear, our brains are organized so that these recalibrational processes often appear to require conscious attention to allow the appropriate reweightings of the associated variables, and are associated with rich and distinct affective feeling states that constitute a major dimension of human experience. These emotions have often appeared puzzling from a functional perspective because the feelings they engender interfere with short-term utilitarian action that an active organism might otherwise be expected to engage in. For example, people voluntarily or involuntarily take time out from obviously productive activities like foraging, eating, or sleeping in order to spend time feeling grief, depression, guilt, the onset of romantic love, and so on. The suggestion here is that customary actions and stored dispositions that were productive under one set of circumstances may no longer pay off when the landscape suddenly changes, and people feel less motivated to act. Indeed, people in grief or depression or infatuation show high levels of brain activity; they want to be left alone, without outside demands on their attention. The brain needs to revise large networks of regulatory and decision variables. The cognitive sciences have devoted far more attention to cold cognition—perception, categorization, language processing, object recognition—than to hot cognition. But we suspect that far more of the brain may be organized to computationally implement feeling, valuing, motivation, and emotion—hot cognition. Knowing what is in the world ("objective" knowledge) is generally a far easier computational problem than knowing what to do, and how much to value different courses of action ("subjective" valuation that is fitness-enhacing).

The environment of evolutionary adaptedness was full of event relationships (e.g., mother is dead) and psychophysical regularities (e.g., blood indicates injury) that cued reliable information about the functional meanings and properties of things, events, persons, and regulatory variables to the psychological architecture. For example, certain body proportions and motions indicated immaturity and need, activating emotion programs for nurturing in response to "cuteness" releasers (see Eibl-Eibesfeldt, 1970). Others indicated sexual attractiveness (Buss, 1994; Symons, 1979). To be moved with gratitude, to be glad to be home, to see someone desperately pleading, to hold your newborn baby in your arms for the first time, to see a family member leave on a long trip, to encounter someone desperate with hunger, to hear your baby cry with distress, to be warm while it is storming outside—these all *mean* something to us. How does this happen?

In addition to the situation-detecting algorithms associated with major emotion programs such as fear, anger, or jealousy, humans have a far larger set of evolved specializations that we call *recalibrational releasing engines* that involve situation-detecting algorithms and whose function is to provide inputs into internal regulatory variables, and trigger appropriate recalibrations, including affective recalibrations, when certain evolutionarily recognizable situations are encountered. Although these pervasive microprograms construct a great deal of our world, investigations are only beginning into adaptations of this nature.

Welfare Trade-Off Functions and Recalibrational Emotions

Humans, like members of other social species, face a continuous flow of choices that force them either to sacrifice another's welfare to increase their own (selfish choices), or to sacrifice their own welfare to increase the welfare of one or more others (altruistic choices). Evolutionary biologists have identified a number of selection pressures for which (under specified conditions) selection can favor trading off the immediate welfare of the actor in favor of specific others. These include, among others, kin selection (Hamilton, 1964; for evidence of adaptations in humans, see Lieberman et al., 2007), reciprocation or exchange (Trivers, 1971; for adaptations in humans, see Cosmides & Tooby, Chapter 25, this *Handbook*, Volume 2; Krasnow, Cosmides, Pedersen, & Tooby, 2012), the asymmetric war of attrition (Hammerstein & Parker, 1982; for adaptations in humans, see Sell et al., 2009), and externality management and partner choice (Tooby & Cosmides, 1996; see also Noë & Hammerstein, 1994).

For the human mind to solve the adaptive problem of motivating the actor to make the fitness-promoting set of trade-offs between her own welfare and the welfare of another under a given set of conditions, it must have adaptations designed to compute regulatory variables that correspond to the relevant decision parameters (genetic relatedness to this person—kinship index; did the person reciprocate previously?; how much does the other person need this benefit?; the formidability index of this person—how much can this person injure me?; the association value of this person; etc.). We and our colleagues think these are organized through a human-universal motivational subsystem in the mind which calculates, for each familiar individual, a welfare trade-off function that sets thresholds (welfare trade-off thresholds) partitioning sacrifices the individual is motivated to make on behalf of that familiar other from sacrifices the individual is unwilling to make (Tooby & Cosmides, 2008; Tooby et al., 2008). These thresholds should correspond, to the extent the system is well-engineered and operating under ancestral-like conditions, to sacrifices that were fitness-promoting, and sacrifices that were fitness-reducing. This system also has to make estimates of how valuable the act or resource is not only to the self, but also to the other party.

Each evolutionary theory of social interaction contains within it variables that help specify how fitness-promoting a given welfare trade-off threshold from *i* to *j* would be (the kinship index, how reliable an exchange partner is, how much they value you, the magnitude of benefits they can confer or withhold, etc.). This welfare trade-off threshold (WTT) should be a quasi-stable variable—that is, it should be stable until the system receives new information. When new information about these variables is received, then the welfare trade-off threshold should be recalibrated to the magnitude that is fitness-promoting under the new conditions.

When motivational problems are analyzed in terms of the internal regulatory variables that would be needed to solve them, a pleasing finding is that many hypothesized regulatory variables must be shared by a number of distinct motivational systems with different adaptive functions. For example, both of the independent adaptive problems of how altruistic one should be toward relative *i* and how sexually aversive one should find relative *i* require the same regulatory variable: the kinship index between self and *I* (Lieberman et al., 2007). One regulatory variable—the welfare trade-off threshold—keeps reappearing in a broad variety of independent adaptive motivational problems. For example, it is relevant to kin-directed altruism; to exchange and reciprocation; to mateships and parenting; to aggression-based negotiation; to benefit-based negotiation; to integrating externalities into social relationships; to the management of social valuation, and so on.

Indeed, welfare trade-off thresholds and their recalibration appear to be deeply embedded in the designs of a series of emotion programs: gratitude, anger, guilt, compassion, shame, and contempt, to take leading examples. *Anger* appears to be triggered when another person places too little weight on one's own welfare (their expressed WTT toward the self is too low), given the mind's implicit estimation of what welfare trade-off threshold it can plausibly enforce, given the person's ability to confer or withhold benefits, or inflict or withhold harms (Sell et al., 2009). That is, its function is to bargain for a better WTT of the other to the self (or, if their WTT was correct, but they did not understand how much you valued the service or resource, to reeducate them). In cooperative relationships, the incentivization provided by the angry individual to the other party is a threatened reduction in the angry individual's WTT toward the other: The other will no longer be able to expect the same delivery of benefits through sacrifices unless their own welfare trade-off threshold toward the angry individual is increased to acceptable levels. Guilt functions to recalibrate your own welfare trade-off function toward a specific other when you get new information indicating either that your previous welfare weighting on the other (as expressed behaviorally) was too low, or that your estimation of the value of a service or good to the other person was too low—you did not know they cared that much (Tooby & Cosmides, 1990a, 2008). Shame is the recalibrational emotion designed to deal with the threat or actuality of negative information about you reaching others' minds, so that they would devalue you—that is, the adaptive threat is others recalibrating their welfare trade-off threshold toward you downwards in response to new information about you (Sznycer et al., 2012).

Gratitude, correspondingly, is the recalibrational emotion program that is activated in order to (1) increase the welfare trade-off threshold in the self toward another person (2) upon discovery of new information that the association value of the other person to the self is greater than previously estimated. For example, gratitude is triggered when another person trades off their welfare for yours at a much higher level than you had expected: They were unexpectedly kind to you, in a way not justified by your previous treatment of them. Good cooperative relationships are rare, and the higher the mutual welfare trade-off thresholds toward each other can become, (other things being equal) the more efficiently your joint welfare can be promoted. In order to stabilize this potential high level of mutual assistance, it is important to show the act was noticed, attributed to the correct person, appreciated, and led to an increase in the weight you place on your benefactor's welfare. So the emotion program creates communicative intent, and upregulates your welfare trade-off threshold toward the other. This leads to a model of cooperation that is stabilized by the threat of the other's welfare trade-off threshold being downregulated (through the anger program) if your WTT toward the other is too low; and your WTT toward the other being upregulated (through the gratitude program) if their trade-off threshold toward you is higher than yours presently justifies (Lim et al., forthcoming). A second kind of gratitude is not based on exchange, but on association value and externalities (Tooby & Cosmides, 1996). Gratitude is triggered by high valuation toward the other party. The individual may benefit by sacrificing for the welfare of a highly valued person, and the feeling of valuation toward the person is also often called gratitude (i.e., you are grateful your child lives; we are thankful for our blessings). Third, partner choice may be based on the magnititude of positive externalities given off by the potential partner.

RECURRENT DIMENSIONS OF ENVIRONMENTAL AND ORGANISMIC VARIATION SELECT FOR PARAMETRIC COORDINATIVE ADAPTATIONS

When discussing the relationship between behavior genetics and human universal design earlier, we postponed addressing one question: Why should some kinds of individual differences in organisms be organized into a small number of dimensions of variation? Over evolutionary time, many aspects of the world (including environments, organisms, and organism-environment interactions) shift within a evolutionarily recurrent covariant structure. That is, not only are there stable regularities in the world (e.g., gravity, the properties of light, the proportion of oxygen in the atmosphere), and stable regularities in the dimensions along which conditions and phenotypes vary, but there are also higher order covariant relationships in conditions and in phenotypes. For example, regional temperature may shift, but if the temperature increases then humidity increases in a coupled fashion. Moreover, aspects of the environment and internal species organization may systematically co-vary as well. For example, the environment may sometimes select for an increase in species size, and at other times a decrease in species size. For a functionally scaled organism to be maintained if (for example) head size increases, larger vertebrae are required, as are greater neck and torso muscles as well. If all the size dimensions of the organism were under independent genetic control, then for the species to grow (or shrink), selection would have to independently occur in all functionally interrelated traits throughout the organism, slowing down the rate at which the lineage can respond. A mutation in one of these may not even be advantageous without others. The ability of the lineage to shift in size in response to selection would be considerably impeded. Alternating selection for larger and smaller size ought to therefore also select for welding together formerly independent growth in various traits into a far smaller number of developmental growth fields. This would be favored because then the organism's traits maintain functional allometric interrelationships while undergoing directional selection. That is, mutations will be favored that developmentally link formerly independent traits whose payoffs vary in response to a particular recurrently varying environmental dimension. Thus, genetic correlation among traits is not, as is often thought, a given, but is itself an evolved outcome. Given such genetic and developmental adaptations, expressed phenotypes should track recurrently variable environments with far less lag time, and remain somewhat closer to fitness optima. The covariant structure of conditions, and the covariant structure of the developmental system should evolve to complement each other over evolutionary time.

In the case of allometry, the number of (for example) growth fields ought to be reduced to the number of phenotypic dimensions that benefit by being tuned by selection independently. Quantitative genetic variation that moves designs along these dimensions is expected to have accumulated because adding numerous loci to the determination of a quantitative trait slows loss of variants, maintaining the ability of the lineage to respond more rapidly to reversals in directional selection. This reduces the risk of being stuck at fixation at a ceiling or floor when directional selection reverses again. (Surprisingly, Gould and Lewontin (1979) considered observed allometric relationships to be "constraints" on development and hence constraints on adaptive design itself, rather than adaptations themselves. Not only does simple mechanics support the functional nature of many of these scaling relationships, but selection must be actively maintaining these allometric relationships, because there are always outliers in populations and species that deviate from these relationships that selection could act on; and related species deviate from each other as well.)

Of course, a better design would be to have developmental adaptations that facultatively regulate trait expression so that the expressed phenotype matches the demands of the specific environment the organism matures in (rather than, if the phenotype was determined by inherited genetic differences, a random sample out of a cross-generationally lagging quantitative genetic distribution). Indeed, many individual differences appear to be due to the operation of calibrational adaptations (muscle increase due to increased exercise; the development of calluses in response to abrasion; increased storage of fat in response to a history of calorie flow variance). Regardless of whether the phenotype is facultatively calibrated or just determined by alleles, the dimensions of variation would be the product of selection. For developmental adaptations for matching local demands, both the dimensions of variation and the regulation of the individual outcome would be an expression of the adaptative system. That is, adaptations would take environmental or organismic condition as input, and produce a facultatively calibrated phenotypic outcome. In contrast, for systems of individual differences caused directly by quantitative genetic variation, the system would be the product of selection, but the particular outcome for an individual would be a random but beneficially biased outcome. A third (and likely) possibility is that given there is genetic noise throughout the system, there should be phenotypic differences (like differences in strength) which species-typical adaptations would respond functionally to—what we have called reactive heritability (Tooby & Cosmides, 1990b)—see discussion of anger, strength, and heritable factors leading to differences in strength below. More generally, if over evolutionary time there is covariation in the independent adaptive demands placed by the environment on the organism (called here a *selective regime*), and a set of independent traits with shifting parameter values that are best responses to these demands, then one expects the evolutionary emergence of parameterized dimensions of covariation in the developmental expression for these formerly independent adaptations. There need be no logical coherence or functional necessity to the set of properties that are phenotypically scaled together: Just that the organism did better when these properties were increased (or decreased) together when an environmental variable (or covariant set of variables) moved together.

Dimensions of personality variation are potential candidates for adaptationist explanations of this kind. Although there ought to be individual differences caused by genetic noise permeating the human neurocomputational architecture, the consistent emergence (for some sets of individual differences) of a far smaller number of robust dimensions in personality suggest that patterns like the five factor model or the HEXACO model (Ashton et al., 2004) might be the product of adaptations to the covariant structure of selective regimes. In exploring this hypothesis, it is always preferable to begin with theoretically well-motivated theories of adaptive function, rather than simply constructing explanations after the fact.

Consider, for example, the hypothesis that the human anger program is a species-typical adaptation that evolved to orchestrate an individual's bargaining behavior in conflicts of interest so that they secure for themselves an advantageous resolution of the conflict (Sell et al., 2009). Power in bargaining comes from the ability to confer or withhold benefits, and the ability to inflict or refrain from inflicting harm. This theory predicts that individual differences in the ability to inflict harm (for example, by upper body strength) and the ability to confer or withhold benefits (for example, by attractiveness) should calibrate how successfully the individual will be able to incentivize better treatment for him- or herself using these advantages. Therefore, upper body strength and attractiveness were predicted to calibrate how readily the individual angers; how entitled they feel to better treatment; how successful they are in resolving conflicts of interest in their favor; (for strength) how useful they think force is in resolving disputes, and so on (these predictions were supported; Sell et al., 2009). This provides a case study of a theoretically derived, empirically supported adaptationist theory of some types of individual differences: Individual differences in inputs (strength, attractiveness, being male, being female) fed into the species-typical negotiative system then outputs advantageously calibrated behaviors and motivational settings. The species-typical adaptation creates a systematic and adaptively calibrated functional relationship between the magnitudes of some individual differences and the magnitudes of others. This is simultaneously consistent with the possibility of high heritability in anger proneness and entitlement (for example), because there is likely to be genetic variation in the factors that produce upper body strength and beauty (e.g., reactive heritability; Tooby & Cosmides, 1990b). These are processed by the organism just as if they were environmentally caused individual differences: The organism must respond adaptively to its own condition, however caused. Hence, a human-universal adaptation (the anger program) can, by taking in heritable inputs (individual differences in strength caused by individual differences in genes), produce functionally calibrated individual differences in anger proneness.

These results only scratch the surface of the potential ramifications of the evolved bargaining system on individual differences. Stronger and more attractive people will have less to fear from interacting with larger numbers of less familiar others, and because of the nature of social markets, will have more to gain. This predicts that there should be a functionally calibrated relationship between strength and attractiveness and the extraversion-introversion dimension. Lukaszewski and Roney (2011) did superb work testing this hypothesis in two studies, along with simultaneously investigating the contribution of specific genetic polymorphisms (the AR CAG repeat polymorphism) to extraversion. They found the relationship between strength and attractiveness and extraversion to be, as they predicted, high (and varying by sex in the expected directions). They also found that the AR CAG polymorphism accounted for some of the variance in extraversion.

So we know that at least some dimensions of personality variation are the product of parametric coordinative adaptations similar to, but more slowly changing than emotional states (e.g., strength persists far longer than a snake appearing in the path). Just as emotion programs involve adaptively coordinating multiple mechanisms within the architecture to the adaptive demands posed by an evolutionarily recurrent short term adaptive problem, personality factor (and especially subfactor) phenotypes are proposed to be parameterized coordinative adaptations to evolutionarily recurrent and longer-lasting selective regimes. That is, they are hypothesized to be best-bet deployments of the mechanisms in the psychological architecture and body, given the developmental adaptations' reading of the individual's location within the covariant structure of adaptive demands posed by the environment and the individual's own condition. These conditions may disappear over the lifespan (e.g., with loss of strength), but might last several generations (e.g., a high-warfare social ecology).

Consider dimensions of the biotic and social ecology: Some environments will have higher rates of predation; some will have higher rates of warfare and/or within-group exploitation; some biotic and social ecologies impose zero-sum relationships between individuals and groups (where resource extraction by some intrinsically decreased resource extraction by others; some environments will be less abundant, or have periodic famines; some will have higher rates of disease; some individuals will be weaker or less attractive or have fewer kin). Optimal settings on anxiety, fear, thresholds for project abandonment in the face of risks or setbacks (i.e., proneness to discouragement or depression), vulnerability by gender, willingness to defer gratification, willingness to trust, rivalrousness, anger, and so on should all shift depending on predictable features of the self, the social ecology, and the biotic ecology. These would provide a straightforward functional interpretation for the dimension of neuroticism, and for subfactors in agreeableness or HEXACO's honesty-humility.

This suggests an entirely different framework for research into personality. Instead of starting with empirical relationships of unknown functional significance and unknown ecological validity, it might be useful to (1) make or adopt models of adaptations that (2) need to take as inputs—in order to perform their function—locations along adaptively salient dimensions in ancestral environments and individual conditions, and (3) attempt to identify which adaptations should facultatively shift in response to movement along the same dimensions. By starting with specific adaptations and adaptive problems, and considering how sets of them should jointly vary by individual condition and ecology, one might be able to derive a principled series of empirically validated theories of personality variation. One might work upward, from specific adaptive problems and associated subscales, to larger sets of adaptations with more weakly associated responses to dimensions of ecological or phenotypic variation.

Indeed, there is no reason to attempt to force dimensions of personality variation to be statistically independent. On the contrary, one would expect from first principles that dimensions would derive from how the structure of variation in the environment drives demands for coordinated adaptive responses. There is no reason whatsoever to expect these dimensions of variation to all be orthogonal to each other (e.g., the degree to which social interactions in the social ecology are highly positive-sum might impact both agreeableness and honesty-humility, but neuroticism to a lesser degree). Also, researchers ought to be open to the discovery of major, previously unknown personality dimensions, since existing dimensions were empirically derived overwhelmingly in developed mass societies and abundant environments, rather than by (impossibly) censusing the range of fitness regimes that characterized the ancestral world.

For example, ancestrally, the fitness of individuals or sets of individuals might have been inversely related, unrelated, or positively related. Our normal intuitive expectations of rationality (characterized by a set of social orientations, emotional calibrations, ways of interpreting events, and motivated appetites forged in cooperative and positive-sum social ecologies) we suspect is just one parameterization of a coordinative adaptive system capable of creating very different rationalities, including what might be called predatory rationality. In a fitness regime where those who socially interact are typically in intense negative-sum or zero-sum relationships with each other (because competition is local), win-win strategies are not seen to be best-bet responses; strength and aggressive formidability are highly prized and cultivated; there are no inhibitions on preying on the weaker; audacious predatory attacks and the extermination or humiliation of the antagonist is more attractive to the predatory-minded than to whose who have a cooperative orientation; cooperativeness, paranoia, generosity, revenge-proneness, envy, sensitivity to cues of fitness differentials and status differentials, propensity to exploit—all these are set at surprisingly different levels (Sznycer et al., forthcoming; Tooby et al., forthcoming).

WHY MIGHT SOME COORDINATIVE CALIBRATIONS BE PARAMETERIZED BY ONTOGENETIC INPUTS, SOME BY QUANTITATIVE GENETIC INHERITANCE, AND SOME BY INHERITED EPIGENETIC INFORMATION?

For aspects of the world where the variance in the situation distribution is small (e.g., the geometry and physics of light), then a single design can uniformly develop (e.g., the visual system) to reliably improve the behavioral output of members of the species. In contrast, where variance in the situation distribution is large, a uniform expressed phenotype will rarely be the best solution. In such cases, fitness is enhanced to the extent that regulatory designs match their phenotypic outputs (e.g., mature early; invest in larger musculature; extend less credit in cultivating cooperative relationships) to the demands of actual conditions (e.g., greater extrinsic mortality; a social ecology of greater competition; a social ecology of lower payoffs to cooperation). In this case, the underlying uniform adaptation lies in the design of the regulatory machinery that parameterizes the expressed phenotypes to the particular situations that it will be facing.

What is key is that there be a principled guidance system whose evolved architecture decides on and then implements those targeted phenotypic modifications that correctly close the gap between the needed phenotype (in a given situation) and the realized phenotype, over the range of situations the species typically faces (Tooby & Cosmides, 1992). Success in the game of matching phenotype to circumstances would be impossible for the architecture unless there existed (1) information that (with computation) systematically predicted which circumstances the organism was going to face, (2) a repertoire of phenotypic alternatives that encoded the phenotypic modifications that would be needed for the organism to develop a high-performing response for those circumstances, and (3) a function that mapped the information about circumstances to the best bet phenotypic alternative. Fortunately for organisms, there are many such systematic relationships that natural selection has exploited to build developmental or facultative adaptations that successfully solve these problems (e.g., skin darkening in response to sun exposure).

The two key questions governing how these systems evolve are (Tooby, 1976; Tooby & Cosmides, 2003; Tooby, Cosmides, & Barrett, 2003):

1. When does the information become available that is needed to decide on the best-bet phenotype?; and,
2. How much lead time does the organism need to generate or construct the best-bet phenotype in time for it to discharge its function?

For the startle reflex, the information needed to protect the eyes does not become available until a few hundred milliseconds before impact; but the system needs around 50 milliseconds to begin to respond. So flinching is linked to rapid looming (and if it is faster than that, you are out of luck). It would make no sense to determine the time of the flinch minutes, hours, days, or years in advance, because the time the flinch is needed could not be known to sufficient precision earlier. The best design (where possible) is one in which response selection can be cost-effectively postponed until the environmental demand can be assayed with high reliability (e.g., through perception); and only then is the phenotypic response selected and implemented. To take a more interesting example, some fish species change sex based on their relative size and the death of the dominant local male (Warner, 1988). Humans and other mammals, in contrast, use a genetic sex determination system, presumably because you can build a better woman or man if you start very early in development differentiating the adaptations of the two phenotypes, long before there is any useful information about what the adult sex ratio will be at maturation. We have to place our gender bets before we have information (so genetic sex determination flips a coin). For systems involving major tissue differentiation, intricate wiring, and/or long-term nutrient flow (like becoming female or male), construction needs to begin very early. Similarly, to acquire large databases of intricately patterned information (as in acquiring a skill given a sexual division of labor), the human child also may not be able to afford to wait too long. It seems likely that there exist developmental adaptations whose function is to make predictive inferences about the adult fitness regime by sampling self and world early in life, and then using these predictions to calibrate life history (see, e.g., Griskevicius et al., 2011). However, for many traits, early life does not predict the best bet later in life, either because the correlation is too low, or the sample is too brief and unrepresentative to be useful.

What then? It must often be the case that there is a correlation of conditions among adjacent generations in certain respects (e.g., if a mother faces an exceptionally competitive, predatory, or food-limited environment, then there is an increased probability that offspring will too—and with some decay function, that subsequent generations will as well). If this information exists, it is available long before development even begins. Such cases would select for coopting non-DNA-based systems of inheritance that could transmit regulatory signals from one or more generations to the next. Although several of these systems have been suspected or known for decades (Cosmides & Tooby, 1981; Tooby, 1976; Tooby et al., 2003), only recently have they become a focus of interest (see Jablonka & Lamb, 2005, for review).

We believe that cross-generational epigenetic effects are not simply accidental by-products, but that they are evolved adaptations with functions. Most generally, the function of these signals is to parameterize individual development so it goes along pathways that better suit it to the conditions it is likely to face across its life. Given the operation of such systems, individual differences in phenotypes would be partly calibrated from environmental cues during ontogeny (conditions less far away in time should be more diagnostic); partly epigenetically inherited (i.e., frequencies of events summed over multiple generations are going to provide an independent method of improving predictive validity); these systems should cause heightened parent–offspring phenotypic similarity in a way not attributable to DNA-sequence differences. Indeed, these additional systems of inheritance would be selected to use non-DNA-based mechanisms, because DNA sequence transmission is too high fidelity to be useful for tracking rapid changes across multiple generations.

To take a hypothetical example, if the mother is made repeatedly fearful by exposure to predators in an enduringly predator-rich environment, then signals transmitted by methylation, in utero, or in early maternal care to the offspring could be designed to cause it to develop a predator-cautious phenotype usefully in advance of experiencing attacks by local predators. Depending on the temporal structure of the environmental change, these systems could be designed to be passed on signals according to a multigenerational decay function to subsequent generations. That is, by including (say) three generations of information gathering on the frequency of droughts, the system could make better predictions than if it simply used one. Similarly, if the parents (and/or other close lineal ancestors) are food limited, and such a condition often persists across generations, then the offspring would benefit by developing a more frugal metabolism, selecting for an inheritance system that regulates metabolism and life-history across generations. To take a third case, if the parents are in an exceptionally competitive environment, then offspring would benefit by developing a more aggressive, territorial, competitive phenotype, with a greater tendency to emigrate, delayed maturation, and a greater tendency to bias uterine sex ratio toward the more dispersing sex. Not only have many of these empirical relationships been observed (Clark & Galef, 1995; Clark, Karpiuk, & Galef, 1993; Francis, Diorio, Liu, & Meaney, 1999), but they fit elegantly into an evolutionary psychological theory of functional development.

From this theoretical vantage point, cross-generational inheritance effects are not only unsurprising but are instead predicted for traits whose value depends on conditions (a) that frequently endure across more than one generation; or (b) whose probability of occurrence in the upcoming generation can be better estimated using their incidence over multiple recent generations; and (c) that repeatedly cycle along dimensions of variation across generations (Tooby, 1976; Tooby et al., 2003). We predict that such inheritance systems should be especially prominent in regulating traits that are used starting early in the life cycle (e.g., frugal metabolism, predator-evasion tactics, physiology tuned to local conditions; affiliativeness to coalitions; ecological incidence of positive vs. zero-sum/negative-sum interactions) or that are less costly or more effective if the organism begins to develop them prior to directly detecting the conditions it will be facing (e.g., life history trajectory, competitive ability, size reduction and heightened fat stores to better survive food interruptions).

One might also expect that the sex that disperses less would be selected to engage in more epigenetic inheritance, since the correlation of environments of parent and offspring would be higher (Tooby, 1976).

In sum, these systems should evolve and regulate development cross generationally when (1) the dimensional covariation they track is autocorrelated on time scales longer than a generation—i.e., conditions persist long enough in the environment (or in the lineage); (2) when the optimal developmental coordinative response or strategy is dependent on being parameterized by information about the position of the system in its dimensions of variation; (3) for developmental processes such as physiological adjustment or expertise acquisition that need to begin early in development (or at least before the task environment that must be prepared for can be directly perceived). It is important to recognize that not just physical features of the environment (e.g., climate) fit these criteria. Local social ecologies (cooperative hunting; warfare; intensity of individual competition) and biotic ecologies (disease, food abundance, predation) fit these criteria, as do individual heritable somatic features such as strength, reflexes, or genetic impairment.

Finally, it bears noting that the methods used by behavior geneticists would tend to misattribute systems of epigenetically regulated individual differences in behavior to genetic differences. Epigenetic states, like the genes they adhere to, are passed down from parents to offspring, and make family members more similar to each other than they would be to nonrelatives. Since these are the sources of data that behavior geneticists use to compute heritability it is indeed possible that a great proportion of the variance in individual behavioral (and somatic) phenotypes that has been attributed to DNA sequences are instead due to epigenetic systems. This would make particular sense for dimensional systems of personality variation which may well be the product of parameterized coordinative adaptations. This would explain why it has been so difficult to track down and identify many DNA sequences that can be shown to explain observed behavioral differences. If epigenetic systems can process information more rapidly that selection acting on quantitative genetic variation (which they can), and if they can efficiently parameterize coordinative adaptations so phenotypes are better matched to ontogenetic conditions (which seems likely), then behavior genetics findings may mostly be behavior epigenetics findings. An examination of the subtly discordant empirical models of heritability across different familial pathways might be more consistent with more rapidly mutating epigenetic transmission. One might predict that traits that turn out to be determined by quantitative genetic variation will be ones where the temporal structure of successive environments cannot be better predicted by sampling over small numbers of generations (that is, environmental autocorrelation is too low to be useful), and the best that can be done is to sample randomly quantitative genetic variation from the broader population.

How could this make sense of dimensions of personality variation? In the first place, one would expect that—just as selection has merged independent traits into allometric growth fields so that the species or population responds to selection more rapidly—selection would have done the same to quantitative settings in sets of psychological adaptations that would benefit from being adjusted together. If, cross-generationally, ecologies shift periodically into conditions where male-male competition is more intense, then all of the parameterizations of psychological adaptations that improve performance in male competition might be linked together so the dial can be turned up or down (leading to parameterizations of, e.g., the shame-honor system). Initially, this would select for systems of quantitative genetic variation in such a dimension. Similarly, where extrinsic mortality is high, this might link fear-anxiety sensitivity to a lower propensity to defer gratification (e.g., showing up in personality psychology as psychoneuroticism). Second, where reliable information exists during development, then cues may parameterize the coactivation of adaptations functionally. Third, where the parameterization bet can be improved by information transmitted from previous generations, epigenetic systems would be one adaptive calibrational system that natural selection could construct. So personality variation would be the functional product of the program architecture of psychological adaptations, as calibrated by cues during development; heritable differences in other parts of the organism (e.g., strength) being functionally responded to by these adaptations (e.g., bargaining power, anger); epigenetic signals sent from past generations, which improve the ability of the developmental system to bet on the best parameterizations of adaptations for the organism; or, failing that, falling back of quantitative genetic variation responding slowly to recent selection on the population.

THE FUTURE OF EVOLUTIONARY PSYCHOLOGY AND A UNIFIED SOCIAL SCIENCE

The amazingly high levels of functional order that are found in evolved systems is so dazzlingly intricate, that originally the machinery of life clearly seemed to be the handiwork of an omniscient transcendental craftsman, who built physical systems far beyond human comprehension. Since Darwin's discovery of how blind causality can push replicating systems uphill against the physical tendency of ordered systems to deteriorate, and the other natural sciences made rapid strides in understanding microscale causation, we now have an emerging skeletal framework around which to organize our understanding of life forms. Yet it remains important to recognize that at every scale and level of organization, the structure of biological systems is so labyrinthine and sophisticated that what that we so far understand is merely the nearest edge of a vast space of unseen and uncharted evolved organization.

Therefore, we are only at the beginning of an age of extraordinary discovery, and we should be open to surprising transformations and additions to our knowledge. To judge by the systems (like the visual system) we understand to some limited degree, natural selection produces exquisitely subtle and sophisticated functional complexity that may be likened to a high technology developed by extraterrestrials millions of years ahead of us. The key idea is that natural selection tends to build subtle adaptations out of the enduring structure of the world, the information ecology provided by that structure, and by the computational or regulatory power provided wherever biological structure can be hijacked to provide it. So, we can expect many unexpected and major discoveries about how these are woven together functionally. For example, the DNA and RNA machinery inside individual cells provide all the elements necessary for each cell to function as an assemblage of Turing machines. It seems unlikely that selection would have left this vast computational power untapped, which means that a great deal of computation might be taking place within and not just between neurons. So we expect that the neuron—once regarded as a mere on-off switch—will eventually be found to be something much more like an integrated circuit. Similarly, we expect that the epigenetic machinery underlying cellular differentiation in ordinary development has also been hijacked to transmit and process information across generations through the genetic machinery in gametes and other biologically active molecules provided by parents to offspring. Similarly, the immune system is both capable of recognizing immense numbers of proteins, and simultaneously monitoring various components of health, and so we consider it likely that this has been conscripted as a powerful organ of perception and dietary regulation.

Finally, we briefly return to an earlier question. We began our discussion of traditional versus evolutionary approaches to psychology by noting that humans are able to solve a wide array of problems that were not part of their evolutionary history, and that this observation lent appeal to the view that the mind is a general-purpose machine. But this is to confuse the range of problems solved with the architecture that solves it. One could get breadth not only by having a general purpose architecture (an unspecified, hypothetical and arguably incoherent entity), but alternatively by bundling an increasing number of specializations together, each capable of solving an additional class of problems. Moreover, it leaves open the possibility of evolved architectures that include numerous specializations, plus additional components designed to exploit the specializations by integrating information from across these systems to manufacture a flexibly deployable array of tools to attack novel problems (e.g., the concept of causation in the object mechanics system provided the core concept that was used to develop modern science).

The evolved architecture of the mind includes specialized mechanisms that permit offline, decoupled cognition. These include metarepresentations, imagery, and a scope syntax, which together can interact with the outputs of domain-specific mechanisms to allow counterfactual and suppositional thinking that is basic to human evaluation, decision-making, and causal reasoning (Cosmides & Tooby, 2000a; Leslie, 1987; Sperber, 1994). Decoupled cognition may have evolved to help calibrate or recalibrate mechanisms through experiencing evaluative feedback from imagined or planned outcomes, infer other people's mental contents, or imagine solutions to social, tool use, or other ancestral problems. But it seems likely that, whether as by-products or not, decoupled cognition also permits the kind of thinking that underlies scientific discovery, religious ideas, and other uniquely human preoccupations (Boyer, 2001; Cosmides & Tooby, 2000a, 2001; Sperber, 1994; Tooby & Cosmides, 2001).

In sum, the century long scientific program that assumed that the human psychological architecture consisted predominantly of general purpose, content-independent, equipotential mechanisms has failed to explain much of human behavior. Indeed, it has failed even to develop a set of persuasive models about what the computational architecture of putatively general purpose learning, rationality, or intelligence would look like, and cannot account for any significant kind of human activity. In contrast, evolutionary theory when joined with a computational approach to the mind leads to the conclusion that the human psychological architecture is very likely to include a large array of adaptive specializations. Evolutionary psychologists, and others, have found detailed empirical confirmation of a large series of narrow, deductive predictions derived from models of evolutionarily specialized computational adaptations.

Accordingly, we think that, over the next four or five decades, as a large scale collaborative program by the scientific community, it may be possible to turn human nature from a vague idea into a set of precise, high-resolution models of our evolved computational architecture—models that can be cashed out genetically, at the cellular level, developmentally, physiologically, and neurally. These in turn can then inform models of social interactions and culture, providing a foundation for a more rigorous and integrated social science. It will be a fundamental advance for our species once we have constructed a true, natural science of humanity.

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CHAPTER 2

Life History Theory and Evolutionary Psychology

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THE EVOLUTION OF LIFE is the result of a process whereby variant forms compete to harvest energy from the environment and convert it into replicates of those forms. Individuals "capture" energy from the environment—for example through foraging, hunting, or cultivating—and "allocate" it to reproduction and survival-enhancing activities. Selection favors individuals who efficiently capture energy and effectively allocate it to enhance fitness within their ecological niche.

Energy does not come free. Were individuals able to expend unlimited energy at no cost, in principle they could grow and develop so rapidly they would begin reproducing immediately after birth, produce massive numbers of offspring, and preserve themselves such that they never age. In biological reality, however, individuals must live within finite energy "budgets"—themselves earned through energy and time expenditures—and can never spend more than they have available. Allocation of a finite budget entails trade-offs and hence forces decisions about the relative value of possible ways to spend. Acquiring one expensive item means giving up others; more consumption today may entail less tomorrow.

Selection favors organisms' strategies for allocating energy budgets on the basis of one criterion: The strategy that leads to the allocation of energy that, on average, results in the greatest inclusive fitness (see West & Gardner, 2013) is the one that wins out over others. In this sense, selection is expected to result in fitness-maximizing or "optimal" strategies. Of course, they are optimal in a restricted sense, that is, under the constraints imposed by trade-offs between allocations of energy (see Parker & Maynard Smith, 1990).

Crucially, optimal allocations depend on the characteristics of an individual and its environment: Newborns optimally allocate energy differently from adults; healthy individuals optimally allocate differently from those infected with disease; the best allocation strategy for individuals in stable circumstances differs from that of individuals whose future circumstances are unpredictable.

Life history theory (LHT) provides a framework that addresses how, in the face of trade-offs, organisms should allocate time and energy to tasks and traits in a way that maximizes their fitness. Life history trade-offs have profound ramifications, affecting virtually every aspect of an organism's development and behavior. The concepts of LHT have steadily gained prominence within evolutionary psychology and are now core components of the discipline's toolkit, but with many potential avenues for further integration and application yet to be explored.

We begin with an overview of LHT. We then discuss the proximate mechanisms that enact allocation decisions, including hormonal systems and cognitive adaptations. Finally, we review current psychological applications of LHT and offer suggestions for advancing the integration of LHT into evolutionary psychology.

LIFE HISTORY THEORY: AN OVERVIEW

Fundamental Trade-Offs in Life History Theory

Individuals can enhance fitness in two primary ways: They can invest either in traits that affect the age-schedule of survival, or in traits that affect the age-schedule of fertility (in this chapter, fertility refers to an organism's number of offspring rather than its ability to conceive). Ultimately, the influence of traits on inclusive fitness must be mediated through changes in survival or fertility or both (though they may do so by enhancing the survival and/or fertility of related individuals—e.g., offspring—as well as self). Because of allocation trade-offs, many if not most traits have opposing effects on survival and fertility, on the same fitness component at two different points in time, or on a fitness component of self (e.g., own fertility) and that of a related individual (e.g., offspring survival and/or fertility). For example, a trait that increases fertility by increasing mating frequency (e.g., a mating display) may simultaneously reduce survival by compromising immune function; energetic allocations to growth suppress fertility during youth, but may increase it later in life; allocations to offspring viability through parental investment may reduce one's own survival or future fertility.

Trade-offs between two traits do not necessarily lead them to be negatively correlated. Large individual differences in the availability of, ability to acquire, or efficiency in utilizing resources generate positive covariation among traits; e.g., individuals with larger budgets can invest more than others in both fertility *and* parental care. This positive covariation may overshadow negative covariation produced by trade-offs (see Reznick, Nunney, & Tessier, 2000).

Allocation problems can be conceptualized at multiple levels of detail (see Roff, 2002). We focus on three broad, fundamental trade-offs: *current vs. future reproduction*, *quality vs. quantity of offspring*, and *mating vs. parenting effort*.

The Trade-Off Between Current and Future Reproduction At any point in time, an organism can convert its available energy into a variety of activities. Some facilitate reproduction now (e.g., copulation, gestation). Others prolong life, thereby creating opportunities to reproduce later (e.g., additional energy harvesting, growth, predator avoidance, tissue repair, etc.). Allocation of energy to future opportunities draws it away from efforts to reproduce now, and vice versa. The first modern LHT framework for this trade-off was developed by Gadgil and Bossert (1970). Organisms capture energy (*resources*) from the environment. Their capture rate (or *income*) determines their energy budget. Through time, they can "spend" income on three different activities. Through *growth*, organisms can increase their energy capture rates in the future, thus increasing their future fertility. Through *maintenance*, organisms repair somatic tissue, allocate energy to immune function, engage in further energy production, and so on. Through *reproduction*, organisms replicate genes. How organisms solve this energetic trade-off shapes their life histories. Organisms typically have a juvenile phase during which fertility is zero, and then cease growth when allocation to reproduction increases fitness more than growth. Because maintenance and growth affect fitness through impacts on *future* reproduction, the tripartite trade-off collapses into a trade-off between current and future reproduction (Bell & Koufopanou, 1986; Hill, 1993; Lessells, 1991; Stearns, 1992). The loss of future survival, energy capture, and reproduction because of energy allocation to current reproduction is referred to as the *cost of reproduction* (Williams, 1966).

The current–future reproduction trade-off has been invoked to explain *senescence*, a pattern of gradual deterioration of somatic functionality and increased mortality occurring after reproductive maturity (Jones et al., 2014; Williams, 1957). According to *disposable soma theory*, senescence arises as a by-product of optimal allocation design (Kirkwood, 1990). Perfect maintenance of somatic tissues would result in zero senescence, with no mortality due to internal deterioration. Because the organism is still subject to mortality due to external causes, however, it optimally diverts some resources away from maintenance and invests them in present reproduction. Accordingly, organisms invest less in maintenance than would be required to avoid senescence, thus allowing the soma to decay at a nonzero rate. Kaplan and Robson (2009) offer a model that explains differences in rates of senescence across the lifespan. Since maintenance costs increase as the *quantity* of tissue to maintain increases during growth, optimal allocations to maintenance progressively shrink across the life course. The combination of early growth, decaying somatic quality, and reproductive trade-offs leads to a U-shaped mortality curve that decreases early in life but increases later on (Kaplan & Robson, 2009).

The Trade-Off Between Quality and Quantity of Offspring A second major life history trade-off, first discussed by Lack (1954, 1968), concerns a division within the resources allocated to current reproduction: allocation to increase offspring *quality* vs. allocation to increase offspring *quantity*. This trade-off arises because parents have limited resources to invest in reproduction and, hence, additional offspring must reduce average investment per offspring in terms of parental care, provision of resources, and so on. Models of the quantity–quality trade-off usually operationalize quality as offspring survival (e.g., Fischer, Taborsky, & Kokko, 2011; Harpending, Draper, & Pennington, 1990; Smith & Fretwell, 1974). More complex multigenerational models consider not only offspring survival but also the adult fertility of offspring, which can vary due to body size, health, skills, status, and so on, accrued as a result of parental investment (e.g., Kaplan, 1996).

The basic principle underlying the quality–quantity trade-off is that it is adaptive to increase investment in the quality of existing offspring until the fitness return on investment equals the return of a comparable allocation of resources to fertility (i.e., producing an additional offspring). This optimal level of investment is typically lower than the level that would ensure maximum offspring quality (Harpending et al., 1990; Pennington & Harpending, 1988). Specific solutions to the quantity–quality trade-off depend critically on the shape of the functions that translate parental investment into offspring quality, and, in particular, on whether those functions show diminishing returns (the benefit to offspring levels off as investment increases) or increasing returns (as investment increases, offspring benefit disproportionately more; see Kaplan, 1996).

The Trade-Off Between Mating and Parenting Effort Sexual reproduction adds another layer of complexity to life history allocations. To reproduce, individuals need to find potential mates, choose and be chosen by a specific mate, and secure copulation. All these activities take time and may involve substantial energy expenditures (e.g., costly displays, competition with rivals) as well as exposure to danger (e.g., increased predation risk). Individuals who already have offspring also can invest time and energy to increase their survival and quality. When mating effort and parental investment compete for time and resources, a trade-off arises so that the opportunity of gaining additional mating must be weighted against a reduction in the fitness of existing offspring (Trivers, 1972). For many sexual organisms, the mating–parenting trade-off clearly overlaps with the quality–quantity trade-off, but only in part; offspring number can be regulated by many means other than mating frequency—for example egg production, spontaneous abortion, or even infanticide.

The mating–parenting trade-off is an important factor in the evolution of sex differences in patterns of mating competition and parental care (Kokko & Jennions, 2008). When mating and parenting conflict, the sex that experiences stronger sexual selection and higher mortality should invest more in mating competition, whereas the other sex should provide more parental care and become choosier. In addition, uncertainty of paternity is expected to select against male care (Kokko & Jennions, 2008). When the value of biparental care is substantial, females partly select males for their willingness to invest in parenting, leading to smaller sex differences in allocation toward mating and parenting and favoring the evolution of mutual mate choice (Edward & Chapman, 2011). Models suggest that strong female preferences for caring males may be able to overcome the effect of paternity uncertainty, leading to high levels of male care even in the face of a low probability of paternity (Alonzo, 2012).

Although trade-offs between mating and parenting are widespread, they are by no means inevitable; even the distinction between mating and parenting is not always a sharp one (Stiver & Alonzo, 2009). Most notably, when females base mating decisions on males' ability to care and invest in offspring, the same male behavior (e.g., protecting offspring) may simultaneously contribute to both mating and parenting effort. Conversely, when allocations to mating effort severely affect one's ability to invest in parenting (e.g., because of somatic investments in traits that aid competition), alternative reproductive strategies within a sex (usually males) may evolve, whereby some individuals invest heavily in parental effort whereas others specialize in mating strategies involving little if any parental investment (see Stiver & Alonzo, 2009; Taborsky & Brockmann, 2010).

Embodied Capital Growth and development can be viewed as investments in stocks of *embodied capital:* investments in self that can be translated into future reproduction. In a physical sense, embodied capital is organized somatic tissue (muscles, digestive organs, brains, and so on). In a functional sense, embodied capital includes strength, speed, immune function, skill, knowledge, and other abilities (Hill & Kaplan, 1999). Because allocations to maintenance counteract the depreciation of stocks of embodied capital with time, they, too, can be treated as investments in embodied capital (Kaplan & Robson, 2009). In this perspective, the current–future reproduction trade-off can be framed as a trade-off between investments in own embodied capital versus reproduction, while the quality–quantity trade-off is a trade-off between investments in the embodied capital of offspring versus their number (Kaplan, 1996).

When translated and extended into an embodied capital framework, LHT allows one to entertain possibilities not explicitly conceptualized by standard treatments. Standard models tend to treat investment in the future as physical growth. But growth is only one form of such investment, as illustrated by brain development. The brain has the capacity to transform present experiences into future performance. Brain expansion among higher primates represents an increased investment in this capacity (Fleagle, 2013; van Schaik, Isler, & Burkart, 2012). But this investment is realized not only in growth of neural tissue; substantial energy and time may be allocated to encountering experiences that, through changes in neural tissue, yield benefits realized over time—investments in the future.

How selection affects these investments depends on costs and benefits realized over an organism's lifetime. Growing and maintaining neural tissue entails substantial energetic costs (see Kuzawa et al., 2014) and, by curtailing "preprogrammed" behavioral routines, compromises performance early in life (consider for example the motoric incompetence of human infants). Hence, the *net* benefits of learning are only fully realized as the organism ages. In a niche where there is little to learn, benefits never offset early costs and smaller brains are favored. In a more challenging niche, small brains might be better early in life but much worse later, such that large brains are favored. Other systems may similarly become more functional through time—for example, the immune system, which requires exposure to antigens to become fully functional. The concept of embodied capital can address the evolution of any form of investment in a stock of capital that pays off over time.

LIFE HISTORY STRATEGIES

Taken together, the allocation decisions made in response to life history trade-offs constitute an organism's *life history strategy.* A common approach to life history evolution employs demographic (age-structured) models of population growth (Charlesworth, 1994). In this modeling framework, a life history strategy is ultimately defined by three basic or "direct fitness" traits (Roff, 2002): age at maturity, age-specific fertility, and age-specific survival (or, equivalently, age-specific mortality). These traits are sufficient to determine the fitness of a given strategy, operationalized as the population growth rate associated with the strategy; they also determine the organism's lifespan and lifetime fertility. Other traits that have been classically investigated in LHT include size at birth, rate of physical growth, size at maturity, and offspring size (Stearns, 1992), with body size often used as a proxy for phenotypic quality. Although the age-based approach is adequate to model the current–future reproduction trade-off (as well as many narrower trade-offs; see Roff, 2002), investigating the quality–quantity trade-off requires tracking an individual's state in addition to age (McNamara & Houston, 1996). Individual quality can be recast as embodied capital, which extends the logic of LHT to traits such as health, skills, and status (e.g., Kaplan, 1996). In a broader perspective, life history strategies are expressed as synergistic combinations of co-adapted *morphological, physiological,* and *behavioral* traits (Braendle, Heyland, & Flatt, 2011). For example, in many organisms the transition to reproductive status involves a range of motivational and behavioral shifts, including the onset of sexual receptivity and competitiveness and the activation of behavioral systems that support parental care (e.g., nest building, offspring protection). Life history strategies that delay reproduction should be characterized by protracted behavioral immaturity and inhibition of reproduction-related behavioral systems. Moreover, delayed reproduction should usually be associated with risk aversion, so as to minimize the likelihood of dying before reaching maturity.

The bottom line is that life history strategies organize behavior in multiple domains—including risk-taking, self-regulation, aggression, exploration, mating, and caregiving (see Del Giudice, 2014a; Réale et al., 2010; Stamps, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007). In species with complex social lives, life history strategies have deep implications for behaviors that depend on future rewards—such as long-term cooperation and reciprocity—as well as behaviors that affect investment in offspring quality, including pair-bonding and the multigenerational transmission of knowledge and resources. In addition, different life history strategies likely benefit from different arrays of cognitive traits involved in learning, memory, and decision-making (Réale et al., 2010; Sih & Del Giudice, 2012).

Evolution of Life History Strategies at the Population Level Variations in ecological factors (e.g., food supply, mortality hazards) imply different optimal allocation strategies, leading to across- and within-species variation in life histories. Mathematical models can be developed to predict the evolution of life history strategies. The standard approach is to model life history outcomes as a function of age-specific rates of *extrinsic mortality*—the risk of death due to difficult-to-avoid causes such as predation, accidents, epidemics, and so on (see Charlesworth, 1994; Roff, 2002). The broader concept of *extrinsic morbidity-mortality* (Ellis, Figueredo, Brumbach, & Schlomer, 2009) includes unavoidable causes of deterioration and disability (e.g., the long-term consequences of nonlethal injuries and diseases) that limit an organism's reproductive potential. Another important factor is the degree of *unpredictable variation* in environmental conditions (e.g., unpredictable mortality rates). Finally, the *availability of resources* sets the baseline for all sorts of allocation problems.

In general, high levels of extrinsic adult mortality select for early maturation and reproduction, early senescence (Kirkwood & Rose, 1991), and concentration of reproductive effort in a shorter period of time; high mortality in juveniles also favors early maturation, but promotes life history strategies that spread reproductive effort over an extended window (Charlesworth, 1994; Roff, 2002). The effects of unpredictable temporal variation are more complex. Like high mortality, variation in adult mortality selects for concentrated reproductive effort and, typically, early reproduction (Murphy, 1968), although the latter effect depends on patterns of correlation between risks across time. By contrast, unpredictable variation in juvenile mortality favors delayed maturation and an extended reproductive schedule (Charlesworth, 1994). In general, the impact of unpredictable variation on the distribution of reproductive effort should be small compared to effects of average extrinsic mortality (Roff, 2002).

Another adaptive response to unpredictable variation in juvenile survival/fertility is *bet-hedging* (Roff, 2002; Ellis et al., 2009). Bet-hedging reduces the average individual fitness of offspring in the short term, but enhances the long-term reproductive success of the genetic lineage by decreasing fitness variance across generations (see Starrfelt & Kokko, 2012). *Diversified bet-hedging* does so by generating stochastic variation in life history traits across offspring, thereby increasing phenotypic diversity. *Conservative* *bet-hedging* produces a "generalist" phenotype that does relatively well in a broader range of environments and is thus less vulnerable to unpredictable fluctuations in fitness (Ellis et al., 2009; Starrfelt & Kokko, 2012). When temporal or spatial environmental variation can be anticipated by relying on predictive cues, selection often favors *plasticity* in life history strategies (e.g., Roff, 2002). As prediction is typically imperfect, plasticity and bet-hedging and are not mutually exclusive; they may coexist in the same species or population (e.g., Donaldson-Matasci, Bergstrom, & Lachmann, 2013).

In models of the quality–quantity trade-off, high extrinsic mortality in both juveniles and adults favors lower levels of investment in somatic capital (Harpending et al., 1990; Kaplan, 1996). Moreover, optimal fertility derives from the available investment budget divided by the optimal investment per offspring (Kaplan, 1996; Smith & Fretwell, 1974). All else equal, then, higher resource availability increases optimal fertility, whereas lower mortality tends to decrease it.

In sexually reproducing species, males and females usually face different trade-offs as a result of sexual selection, which leads to the evolution of sexually differentiated life history strategies. For example, when male-male contests determine male access to mates, males tend to mature later than females to accumulate competitive ability (Roff, 2002). More generally, species-typical patterns of sexual selection and competition determine systematic sex differences in reproductive timing, allocation to mating and parenting, age-specific mortality, and investment in different components of embodied capital (e.g., McDonald, 1993; Promislow, 1990).

Development of Life History Strategies at the Individual Level Individual differences in life history strategy are routinely observed within species and populations. Individual strategies reflect the combination of genotypic effects, plasticity in response to environmental inputs, and stochastic processes. Genotypic variance in life histories can be maintained by various processes including mutation-selection balance (Roff, 2002), frequency-dependent selection (e.g., the fitness of a parenting-oriented strategy may depend on the frequency of mating-oriented strategists in the population; see Sinervo, Clobert, Miles, McAdam, & Lancaster, 2008), and shifting selective optima due to environmental variation across space and time (e.g., Del Giudice, 2012).

Plasticity in life history traits in response to environmental states and individual conditions is widespread. Plastic organisms have *reaction norms,* which reflect contingent phenotypic expression. For reaction norms to be adaptive, the cues used to predict the future state of the environment must have sufficient reliability, and the benefits of matching the phenotype to the environment must exceed the costs of plasticity (e.g., maintaining the relevant physiological machinery, energetic costs). The evolution of reaction norms in life history traits and allocations can be modeled explicitly (e.g., Fischer et al., 2011). For example, Berrigan and Koella (1994) showed that, in a simple developmental model, the optimal strategy in response to high juvenile mortality is early maturation and, in response to energetic scarcity, delayed maturation. More generally, developmental responses to recurrent changes in environmental characteristics can be often expected to parallel evolutionary responses to the same characteristics. Thus, the logic of population-level models can usefully inform predictions about developmental plasticity in life history traits (see Ellis et al., 2009; West-Eberhard, 2003).

Individual reaction norms can be affected by genotypic factors. Two individuals may show a similar amount of plasticity, but different *average* levels of the trait.

Conversely, one individual may be more plastic than the other, his or her phenotypes more responsive to environmental variation. The reaction norms of males and females typically differ, so that the two sexes respond differently to the same environmental cues. For example, when females invest heavily in offspring, they are more likely than males to delay reproduction (e.g., by suppressing fecundity) in response to cues of temporary energetic scarcity (Beehner & Lu, 2013; Wasser & Barash, 1983; on humans, see Ellison, 2001, 2003).

Chance affects life history development in various ways. The probabilistic nature of life history events inevitably produces large stochastic variations in direct fitness traits, such as longevity and lifetime fertility (Steiner & Tuljapurkar, 2012). At the same time, bet-hedging strategies in response to unpredictable chance events may adaptively increase offspring diversity. Notably, sexual organisms can increase their offspring's diversity by simply having more of them, and by mating with multiple partners. Increased offspring quantity and promiscuous mating may constitute adaptive bet-hedging in response to unpredictable variation in juvenile survival (e.g., Fox & Rauter, 2003; see Ellis et al., 2009).

The Fast-Slow Continuum Life history traits do not evolve independently from one another; both within and across species, different traits covary in clusters. At the broadest level of analysis, the life history strategies of different species can be arranged on a continuum from "fast" (early maturation and reproduction, fast growth, small body size, high fertility, short lifespan, and low investment in offspring quality) to "slow" (late maturation and reproduction, slow growth, large body size, low fertility, long lifespan, and high investment in offspring; Promislow & Harvey, 1990; Sæther, 1987). Within-species variation often falls along the same continuum (see Réale et al., 2010).

The fast-slow continuum captures the pattern initially described by models of *r-K selection* (MacArthur & Wilson, 1967; Pianka, 1970). Those models assumed that life history evolution was driven by density-dependence, with "*K*-selection" (slow growth, late reproduction, low fertility) occurring in stable and densely populated ecologies and "*r*-selection" (fast growth, early reproduction, high fertility) resulting from fluctuating, sparsely populated ecologies. These claims have since been largely rejected or revised, as factors such as costly-to-avoid mortality risks and their unpredictability are seen as more important drivers of life history variation (see Ellis et al., 2009; Jeschke, Gabriel, & Kokko, 2008). The existence of a fast-slow continuum has nonetheless proven empirically robust.

When body size is controlled for, the fast-slow continuum has been claimed to either dissolve into two independent dimensions (Bielby et al., 2007) or be defined by markedly different life history traits (Jeschke & Kokko, 2009). However, reanalysis of the same data shows that, despite some meaningful differences between taxa—for example, high fertility is a "slow" trait in fish but not in birds or mammals—the fast-slow continuum is a stable dimension of life history variation, even controlling for differences in body size (Appendix in Del Giudice, 2014b). That said, the fast-slow continuum does not fully account for life history variation. Comparative data invariably show the existence of other meaningful axes of variation, such as the "lifestyle" dimension identified by Sibly and Brown (2007), or the two dimensions of reproductive timing (current versus future) and reproductive output (quality versus quantity) identified by Bielby et al. (2007; see also Del Giudice, 2014b).

In part, the fast-slow continuum emerges from fundamental constraints on the relationship between mortality and age at maturity (e.g., Roff, 2002; see also Brown et al., 2004, on constraints on metabolic rates). But life history traits may also coevolve because they adaptively respond to the same characteristics of the environment: For example, high levels of extrinsic morbidity mortality typically favor early maturation and reproduction, higher fertility, lower levels of investment in offspring quality, and, often, additional investment in mating effort.

Limitations of Standard LHT As noted earlier, the standard approach in LHT assumes an extrinsic component of mortality not subject to selection, which then explains variation in other life history traits. Ultimately, this approach is theoretically unsatisfying. Organisms, after all, exert control over virtually all causes of mortality (e.g., by altering patterns of travel to avoid predators, by investing in immune function). By treating a component of mortality as assumed rather than explained, this approach fails to offer a full understanding of how mortality rates evolve. A more complete approach assumes that ecological factors do not directly entail mortality rates, but rather affect the *functional relationships* between mortality and efforts allocated to reducing it (Figure 2.1). They do so, at least in part, by imposing particular "assault" types and rates on the organism. For example, warm, humid climates favor the evolution of disease organisms and, therefore, increase the assault rate and diversity of diseases affecting organisms, which in turn affect the relationship between efforts to combat disease and mortality reduction. Mortality reduction can then affect the payoffs of other efforts; for example, dynamic optimization modeling (see Frankenhuis, Panchanathan, & Barrett, 2013) shows that growing larger brains should coevolve with the allocation of effort to reduce mortality (Robson & Kaplan, 2003). Relatedly, standard models lump all causes of mortality into a single mortality rate. In fact, allocations to different components of somatic capital (e.g., immune function versus

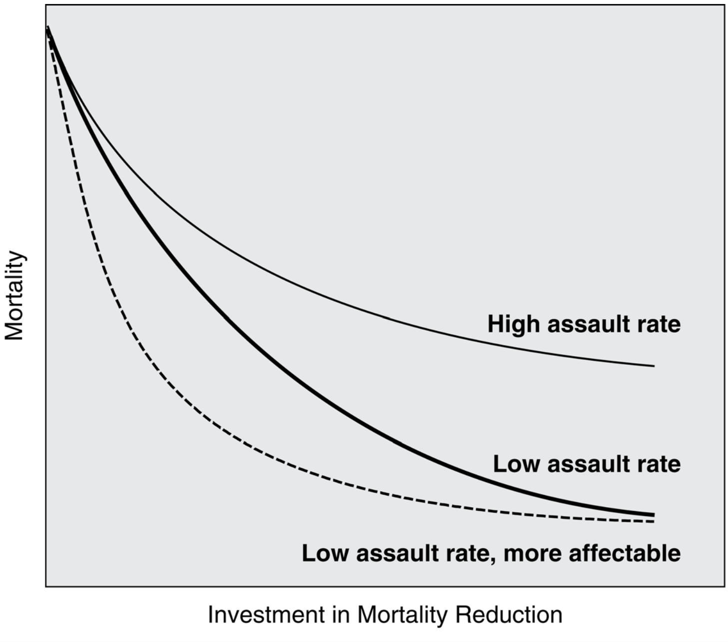

Figure 2.1 Mortality as a Function of Investments. Adapted with permission from Kaplan and Gangestad (2005).

antipredator defenses) may track different sources of mortality in a finer-grained way (see Kaplan, 1996).

MECHANISMS OF LIFE HISTORY ALLOCATION

Thus far, we have considered forces of selection that shape the evolution of life histories. We now turn to the proximate mechanisms that evolve to enact life history decisions.

Endocrine Systems

Adaptive allocation typically requires coordinated tuning of multiple physiological and behavioral systems. Increased allocation to reproduction, for instance, should be coordinated with less allocation to growth. Increased effort to immune function in response to infection may best be synchronized with lower overall expenditure. Such adaptive coordination usually requires systems of communication and control distributed across a variety of somatic systems. These roles are often filled by endocrine systems (Finch & Rose, 1995; Lancaster & Sinervo, 2011). Indeed, the primary function of endocrine systems, giving rise to them and shaping their specific nature, may well be the adaptive, coordinated allocation of energetic and other resources in the face of trade-offs.

Endocrine systems are internal communication devices. Hormones released at one site (e.g., the gonads, the adrenal cortex) are "picked up" by receptors at multiple other sites (e.g., brain structures), thereby affecting them in a modular fashion. Accordingly, hormonal signals can simultaneously regulate many different features and modulate allocation decisions at various timescales, from short-term adjustments to major transitions between life stages. Consider, for instance, reproductive hormones during human puberty. In females, mechanisms regulating energy balance lead to fat storage and regular menstrual cycling. As mediated by estrogen and other hormones, increased energy is allocated to reproductive traits and functions, including secondary sexual characteristics. Males begin producing androgens in substantial quantities, leading to greater musculature and investments in forms of mating effort, including social competition and physical performance. Simultaneously, other investments (e.g., in certain immune functions) are withdrawn. For both sexes, modulation of psychological processes (e.g., desires, motives, situation-specific responses) is integral to the matrix of coordinated responses (see Ellis, 2013; Ellison, 2001).

Reproductive hormones also regulate differential investments on shorter time scales. For example, testosterone levels decrease when men enter committed romantic relationships (e.g., marriage), arguably facilitating reallocation of reproductive effort from mating to parenting (e.g., Burnham et al., 2003; Gettler, McDade, Agustin, Feranil, & Kuzawa, 2013). As well, individual differences in the timing and amount of hormone production partly mediate the development of individual differences in life history strategy; for example, male testosterone levels show robust associations with status-oriented competitiveness and lifetime number of sexual partners (e.g., Eisenegger, Haushofer, & Fehr, 2011; Pollet, van der Meij, Cobey, & Buunk, 2011).

The same developmental mechanisms that mediate species-specific transitions between life history stages may mediate individual plasticity by acting as *developmental switches* (West-Eberhard, 2003). A developmental switch is a regulatory mechanism activated at a specific point in development. Based on input about the external environment and state of the organism, it shifts the individual along alternative pathways, ultimately resulting in the development of alternative phenotypes. Human puberty involves two major transition points, *adrenarche* (the onset of androgen production by the adrenal glands) and *gonadarche* (the onset of androgen/estrogen production by the ovaries and testes), both potentially key switches in the development of life history strategies (Del Giudice, 2014c; Ellis, 2013).

Endocrine systems involved in life history allocations are remarkably conserved across species. Testosterone typically regulates trade-offs between mating, parenting, and survival in male vertebrates (Hau & Wingfield, 2011). In vertebrates and invertebrates alike, insulin-like growth factor 1 (IGF-1) is involved in the trade-off between survival and growth/reproduction (Gerish & Antebi, 2011; Swanson & Dantzer, 2014). The major life history regulators in vertebrates include the hypothalamic-pituitary-adrenal (HPA), hypothalamic-pituitary-gonadal (HPG), and hypothalamic-pituitary-thyroid (HPT) axes, the insulin/insulin-like growth factor 1 (IGF-1) signaling system, and pathways involving prolactin, oxytocin, vasopressin/vasotocin, and immune cytokines (Lancaster & Sinervo, 2011).

These systems are characterized by extensive interplay and cross-regulation. Within the broader network they define, some nodes may play key roles in decision-making processes, by integrating information from multiple sources and redistributing it to other systems. In vertebrates, the HPA axis seems to play such a central role in life history development, as it encodes and integrates crucial information about many characteristics of the social and nonsocial environment (e.g., danger, unpredictable/uncontrollable events, crowding; see Crespi, Williams, Jessop, & Delehanty, 2013; Lancaster & Sinervo, 2011). The role of the stress response system in the development of human life history strategies has been explored in the adaptive calibration model of stress responsivity (Del Giudice, Ellis, & Shirtcliff, 2011; Ellis & Del Giudice, 2014).

PSYCHOLOGICAL PROCESSES

Endocrine systems may play very important roles in modulating coordinated allocation decisions. Because adaptive allocations are often contingent on environmental circumstances, psychological processes—the perception, interpretation, and evaluation of life circumstances—ultimately guide many allocation decisions, regardless of whether they are mediated by endocrine processes.

Consider, for example, a cortisol response to a current or impending threat. Circulating cortisol causes changes in energy mobilization and allocation, as part of a system shaped by selection posited by life history theory. Prior to the release of cortisol, however, a cascade of processes occurs. An event must first be perceived, appraised, and judged to be a threat. Various cortical regions of the brain are involved in this perception, depending on the nature of threat. The amygdala, which receives input from, as well as directs output to these regions, plays a special role in interpreting the event as a threat and initiating the HPA response (see Gunnar & Quevedo, 2007). Psychological processes, then, initiate the re-allocation of energy that cortisol entails; corticotropin-releasing hormone (CRH) and cortisol may feed back on the brain regions involved in appraising and evaluating threats, so that different levels of the control cascade influence one another. In a word, this system is psychoneuroendocrinological.

The same reasoning applies to changes in the HPG system regulating the production and secretion of men's testosterone in the testes. The reduction in gonadal secretion of testosterone that men experience when they enter romantic relationships (e.g., Gettler et al., 2013) is a final outcome of a series of steps, initiated in the brain. Though the precise proximate mechanisms are not fully understood, romantic relationships probably elicit appraisals of long-term commitment and relative exclusivity (e.g., McIntyre et al., 2006). These appraisals, whether experienced consciously or not, ultimately leads to down-regulation of the HPG axis—a process possibly mediated by oxytocin production in the brain (Weisman, Zagoory-Sharon, & Feldman, 2014).

Psychological processes may regulate life history allocations in a number of ways. Consider the optimal age of first birth for females. Nettle (2011a) examined several psychological processes that may be involved in the decision (conscious or not) to initiate reproduction. First, experiences during early childhood, such as poor maternal care or household instability, may affect timing of menarche through developmental induction (discussed in detail later). Second, social learning processes may affect decisions. Copying of close social others, for instance, may be adaptive, if an aggregate of multiple individuals' sense of, say, mortality rates has greater validity than a single individual's. Third, contextual factors such as mortality cues may trigger adaptive, domain-specific responses that take the form of relatively simple (and often unconscious) heuristics. For example, research has found that local birth rates increase following death-causing events (e.g., hurricanes; Cohan & Cole, 2002); even thinking about death can increase desires to have children (e.g., Wisman & Goldenberg, 2005). Finally, women may engage in conscious planning, reasoning about their life situation, and considering the costs and benefits of different options. Culturally transmitted knowledge and values should be especially relevant at this level. Of course, the subjective perception of goals, costs, and benefits involved in conscious decision-making is itself influenced by nonconscious evaluation processes taking place in the brain/body.

A concept that may offer a useful way to conceptualize the psychological processes that mediate life history trade-offs is that of the *internal regulatory variable*. Tooby, Cosmides, and their colleagues introduced this term as a means of explaining how motivational and emotional processes are instantiated (e.g., Lieberman, Tooby, & Cosmides, 2007; Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008). As Tooby et al. conceptualize them, they are "evolved variables whose function is to store summary magnitudes (or parameters) that allow value computation to be integrated into behavior regulation" (Tooby et al., 2008, p. 253). Put otherwise, selection would have forged cognitive systems that adaptively direct behavior contingent on circumstances that recurred in our ancestral history. An internal regulatory variable functions as an index of a circumstance upon which adaptive behavior is contingent.

A next step toward understanding how psychological processes affect life history allocations would involve positing the internal regulatory variables involved—how the mind computes specific summary stores of experiences that affect pertinent decisions. For instance, how are accumulated stores of environmental harshness of the kind informative of mortality rates registered and represented psychologically? What kinds of short-term indexes of mortality risk become represented, and through what processes do they affect decisions? How does information about the behavior of others become synthesized with these personal experiences? Research in this area has identified some promising psychological variables such as the perceived controllability of the environment (Mittal & Griskevicius, 2014) and the subjective estimate of one's life expectancy (Chisholm, 1999). To date, however, there are no explicit models of how these variables may be computed and how they are used to regulate behavioral and physiological processes.

Here we illustrated how psychological processes may regulate life history allocations with the example of age at first reproduction. But there are countless decisions demanding explanation at a proximate, psychological level—for example, allocations of energy to immune function; allocations of effort to increase offspring quality, as a function of returns on investment; investment in skill acquisition, dependent upon usage; dedication to developing and strengthening particular social relationships, in light of time horizons; allocation of efforts to aid kin, dependent on likely relative returns to such investment versus investment in efforts enhancing self; male efforts to protect paternity, at the risk of cuckoldry, as a function of mortality rates; and many more. Scientists have available life history theoretic models specifying how selection might operate on how optimal decision-making in these instances is affected by circumstances (e.g., for an analysis showing how males' tolerance of investment in offspring not their own—cuckoldry—should be influenced by mortality rates, in ways not intuitively obvious but understandable through life history modeling, see Mauck, Marschall, & Parker, 1999). Yet in most cases, we know very little about the psychological processes involved in these decisions. More generally, very little is now known about the precise nature of the adaptations by which people solve the major trade-off problems that life history theory identifies. A primary task for the future of evolutionary psychology, in our view, should be to specify the nature of these adaptations.

PSYCHOLOGICAL APPLICATIONS

We now review several areas of application of LHT in psychological research, organized around four overlapping themes: species-typical patterns of growth and development; individual differences in developmental trajectories; personality; and psychopathology.

Patterns of Growth and Development

Human Life History and the Human Adaptive Complex Humans have several distinctive life history features (Kaplan, Hill, Lancaster, & Hurtado, 2000)—a late onset of reproduction, an extended period of vulnerability and dependence during infancy and childhood, and a long lifespan with extended post-reproductive life (menopause). Relative to primate life histories, humans clearly fall at the slow end of the fast-slow continuum in most respects. At the same time, human populations that have not undergone the demographic transition show higher fertility and shorter interbirth intervals compared to close primate relatives.

This combination of traits can be understood in the context of the *human adaptive complex*—a suite of coevolved traits that define humans' socioecological niche (Kaplan, Gurven, & Lancaster, 2007). Relative to chimpanzees, humans consume a diet consisting of nutrient-dense but difficult-to-extract foods such as meat, roots, and nuts (Kaplan et al., 2000). The techniques employed to acquire and process food (including hunting and fishing) are learning- and skill-intensive and often require extensive cooperation between related and unrelated individuals, with a special role played by pair-bonded couples (marriage). Attaining the skills to forage effectively and manage the complex social games that originate from cooperation and division of labor requires huge investments in embodied capital—including a large and flexible brain—and a long, slow phase of learning and dependency. As this way of thinking posits that social capabilities that permit one to choose and be part of cooperative ventures importantly affect foraging efficiency, it proposes that ecological and social intelligence coevolved and led to large investments in brains (Kaplan et al., 2007; Sterelny, 2007). It is compatible with data showing that both high-quality diet (emphasized by those who give priority to ecological intelligence) and social group size (emphasized by those who give priority to social intelligence, especially pertaining to close social bonds; e.g., Dunbar & Shultz, 2007) predict larger brains and slower development in primates (e.g., Walker, Burger, Wagner, & von Rueden, 2006).

In humans, delayed maturation and intensive learning are made energetically sustainable by massive intergenerational transfers of resources from parents, grandparents, and others. Children do not pay their own way: They accumulate large calorie deficits that, in forager populations, are not repaid until about 20 years of age; after that, adults start producing large amounts of surplus calories, peaking around age 40 and continuing well into the seventh decade of life (Kaplan et al., 2000). By comparison, chimpanzees pay off their own calorie debt by age 5, generate relatively little surplus, and do so only while reproductively active (Figure 2.2).

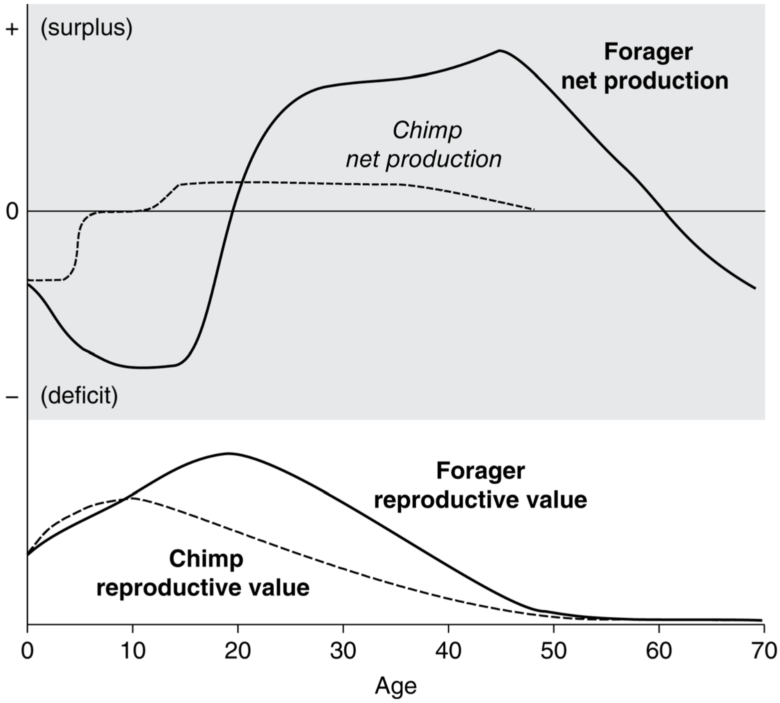

Figure 2.2 Net Energetic Production and Reproductive Value (expected future reproduction at a given age) in Chimpanzees and Human Foragers. Adapted with permission from Kaplan and Gangestad (2005) and Gurven et al. (2012).

High-quality foraging, delayed development, and large energy debts entail considerable risks: Returns from hunting and fishing can be highly variable, adverse conditions may reduce food availability, and one's parents may die before maturity. Complex cooperative strategies and resource transfers within and between generations absorb risk (Gurven, Stieglitz, Hooper, Gomes, & Kaplan, 2012). The costs of extended childcare are shared between mothers and others such as grandparents and older siblings (*cooperative breeding*; see Hrdy, 2007); juveniles are routinely recruited to help with household activities and small-scale foraging, freeing parents to dedicate additional time and energy to high-quality foraging, breastfeeding, and so on (Kramer, 2011).

Developmental Stages and Transitions This analysis provides a background for conceptualizing human developmental stages and transitions in a LHT framework, one aspiring to offer an integrated model of physical and psychological development. For example, a central feature of early childhood (~2–6 years) is sustained, expansive brain growth; the proportion of glucose consumed by the brain peaks at age 4, when it accounts for about 65% of the child's resting metabolic rate (Kuzawa et al., 2014). These allocations deplete fat reserves accumulated during infancy, and entail a compensatory slowing of body growth (Kuzawa et al., 2014; Figure 2.3).

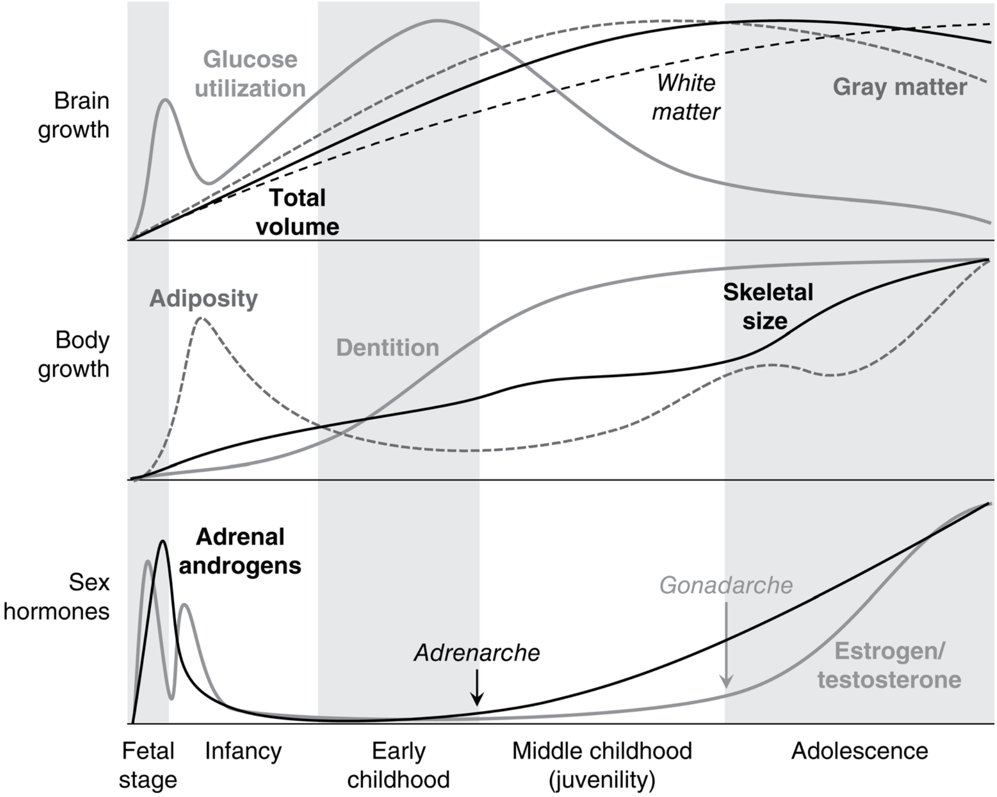

Figure 2.3 Developmental Trajectories of Human Growth and Sex Hormone Production, From Conception to Adolescence. Adapted with permission from Del Giudice (2014c).

In turn, brain development permits the acquisition of language, the foundations of which are achieved by age 5. As language is arguably one of the most computationally complex processes in which humans engage, one may wonder why children acquire the ability to understand and produce a near-infinite number of utterances before they can even coordinate smooth running? An LHT framework offers a principled framework for answering such questions: Because language greatly increases the rate at which children learn about the world—such that benefits, post-acquisition, accrue rapidly—its development may be front-loaded, even at the expense of delaying the acquisition of other, computationally less-demanding capabilities. Similar considerations apply to the development of basic mind-reading abilities (see Bjorklund, 2011).

Middle childhood (human juvenility; about 6 to 11 years) is characterized by intense learning. In traditional societies, children start practicing foraging techniques as well as social roles (Bogin, 1997). The transition to this phase is marked by adrenarche. Adrenal androgens shift energy allocation from the brain to the body, and trigger the accumulation of muscle and fat in preparation for sexual maturation (Campbell, 2011; see Figure 2.3). A cascade of cognitive and motivational changes accompany these changes: for example, marked increases in self-regulation, memory, and problem solving, the onset of sexual/romantic attraction, and the emergence and intensification of sex differences across domains (play, aggression, and so on; see Del Giudice, 2014c). Whereas language development in early childhood focuses on syntax and vocabulary, middle childhood witnesses a dramatic increase in pragmatic skills such as teasing, gossiping, joking, and verbal competition (Locke & Bogin, 2006). These remarkable physical, cognitive, and motivational changes can be understood in the light of shifting allocation priorities, both between different types of embodied capital and from exclusive investment in somatic effort to initial investment in mating effort through social competition (Del Giudice, 2014c). Mating effort and sexual selection take center stage with the transition to adolescence, entraining yet another suite of coordinated physical and psychological changes (see Ellis, 2013; Hochberg & Belsky, 2013).

Individual Differences in Developmental Trajectories

Starting with seminal work by Belsky, Steinberg, and Draper (1991), LHT has been increasingly applied to explain individual differences in physical and psychological development. In Belsky et al.'s "psychosocial acceleration" theory, harsh, insensitive parenting acts as a cue of ecological stress and promotes the development of fast life history strategies: earlier puberty, earlier sexual debut, higher investment in short-term mating effort, and an opportunistic-exploitative interpersonal orientation, typically expressed as aggression/noncompliance in males and anxiety/depression in females. They hypothesized that attachment security mediates the effects of parenting. Subsequently, Chisholm (1993, 1999) stressed the theoretical importance of local mortality rates (a proxy for extrinsic mortality) and argued that time preference—the preference for smaller immediate rewards versus larger, delayed rewards—importantly mediates life history development at the psychological level, (see also Kruger, Reischl, & Zimmerman, 2008).

Research has supported most of the theory's core predictions, while also guiding theoretical elaborations and modifications. In both sexes, early familial and ecological stress predicts earlier sexual debut and increased mating effort. At the same time, effects of early experience on pubertal timing appear largely specific to females (reviewed in Belsky, 2012; James & Ellis, 2013). Women's first potential reproduction is especially sensitive to sheer reproductive capability; moreover, women's reproductive window is shorter than that of men, and the requirements of pregnancy and lactation make women's fertility especially dependent on timing constraints. By contrast, male pubertal timing appears to be more strongly influenced by perceptions of mate quality (health, attractiveness, popularity) and availability of economic resources (James & Ellis, 2013; see also Copping, Campbell, & Muncer, 2014). The theory has been extended to incorporate systematic sex differences in insecure attachment styles (Del Giudice, 2009). Furthermore, research has aimed to unpack the construct of early stress by examining unique effects of environmental harshness and unpredictability (e.g., Belsky, Schlomer, & Ellis, 2012). Related studies have linked childhood illness, early sexual debut, and insecure attachment with preferences for exaggerated sex-typical features in opposite-sex faces and potential partners who display cues of short-term mating (e.g., Cornwell et al., 2006; de Barra et al., 2013; Kruger & Fisher, 2008).

Work inspired by LHT in this area has generally focused on developmental plasticity and focused on the family as a source of environmental cues. But other factors also play important roles. Genetic factors clearly affect developmental trajectories, including puberty timing and mating behavior (see Belsky, 2012). Some effects likely result from adaptively contingent development. For instance, as alluded to earlier, genetic factors affecting attractiveness and health may, in turn, affect life history outcomes. Gene-environment interactions are also possible; for example, attractiveness may be especially important in some environments (e.g., Gangestad, Haselton, & Buss, 2006), and certain genetic variants may increase life history plasticity by amplifying an individual's sensitivity to the environment (see Belsky, Pluess, & Widaman, 2013; Ellis, Boyce, Belsky, Bakersmans-Kranenburg, & van IJzendoorn, 2011).

Family stress does not appear to fully mediate the effects of broader ecological factors such as mortality and violence rates. Other plausible mechanisms include social learning (e.g., copying one's mother's behavior) and direct observation of mortality cues (Copping, Campbell, & Muncer, 2013; Nettle, 2011a). Recently, Rickard, Frankenhuis, and Nettle (2014) advanced the intriguing hypothesis that early stress may speed up life history strategies not only because it predicts a dangerous future environment ("external prediction"), but also because it predicts increased morbidity-mortality due to stress itself and associated somatic damage ("internal prediction"). Internal prediction can be adaptive even when external prediction fails. The degree of stability required for successful external prediction remains a matter of debate (Nettle, Frankenhuis, & Rickard, 2013, 2014; Del Giudice, 2014d). In addition, these models have not been tested against predictions explicitly derived from embodied capital theory. For example, gains from investments in embodied capital, especially education, will correlate with early events and with community-level mortality rates. It still remains to be resolved whether the early events set the psychology or the costs and benefits realized over developmental time determine whether the gains from delaying pregnancy in terms of future life prospects are worth the costs.

CONTINGENT RESPONSES TO THREAT

Recently, researchers have begun to investigate the effects of early experience on contingent responses to subtle threats of mortality and scarcity (e.g., Griskevicius, Delton, Robertson, & Tybur, 2011; Griskevicius et al., 2013; Mittal & Griskevicius, 2014; White, Li, Griskevicius, Neuberg, & Kenrick, 2013). Participants are asked about their childhood socioeconomic status (SES), then experimentally primed with stimuli suggesting threats of mortality or resource scarcity (i.e., news stories about rising homicide rates or looming economic recession). The hypothesis is that people raised in low-SES environments should have faster life history strategies and a tendency to appraise potential threats as unavoidable/uncontrollable (i.e., more "extrinsic"), whereas people with a high-SES upbringing should have slower life history strategies and a bias toward perceiving future threats as avoidable/controllable ("intrinsic").

People with low SES childhoods respond to mortality threats by expressing a desire for having children earlier, even at the cost of delaying one's education or career development, whereas those with high SES childhoods react with a preference shift in the opposite direction (Griskevicius et al., 2011). Mortality threats prompt participants with low-SES childhoods to choose riskier but more diversified options over safer and less diversified ones (e.g., different stock packages; White et al., 2013). Participants with low-SES childhoods respond to scarcity threats with increased risk-taking and shorter time preferences (i.e., spending more now and saving less for the future), whereas participants with high-SES childhoods show increased risk avoidance and longer time preferences. Perceptions of personal control may mediate the psychological effects of the scarcity threat (Griskevicius et al., 2013; Mittal & Griskevicius, 2014). Intriguingly, behavioral differences between the two groups only emerge in the threat condition; absent threat, participants from different socioeconomic backgrounds make similar choices and express similar preferences.

Taken together, these studies open a window on the psychological mechanisms that mediate life history allocations through real-time behavioral adjustments to environmental change. They also offer an intriguing adaptationist alternative to the standard view that impulsivity and risk taking in low-SES environments are the outcomes of poor decision-making or deficits in coping strategies (see Frankenhuis & de Weerth, 2013). It remains unclear which aspects of a low-SES upbringing drive the development of threat-contingent strategies, because low income is associated with a wide range of life history-relevant experiences including—but not limited to—nutritional stress, harsh or neglectful parenting, household instability, exposure to violence, and exposure to infectious agents. Moreover, the association between SES and threat-contingent strategies may be partly mediated by genetic factors rather than induced by early experience.

PERSONALITY

The idea that stable personality traits partly reflect individual differences in life history strategy has been gaining ground in biology and psychology. In their framework for understanding personality variation in nonhuman animals, Réale et al. (2010) proposed that fast strategies should typically be associated with increased boldness, activity, and aggression, lower sociability, and superficial (versus thorough) exploration. This list can be expanded to include impulsivity, risk taking, and neophilia (Del Giudice, 2014a; Sih & Del Giudice, 2012; Wolf et al., 2007). These features may be expressed differently in different species.

In humans, the personality traits of agreeableness, conscientiousness, and honesty-humility consistently relate to reduced mortality, high investment in predictors of parental effort (e.g., relationship stability), reduced investment in mating effort (e.g., restricted sociosexuality and fewer sexual partners), and prosocial/cooperative behaviors. Conversely, impulsivity and some facets of extraversion and openness to experience (e.g., dominance, sensation seeking, imagination) predict fast life history traits such as increased mortality, relationship instability, unrestricted sociosexuality, larger numbers of sexual partners, and exploitative/antisocial behaviors (reviewed in Del Giudice, 2012, 2014a). How emotional stability (low neuroticism) contributes to life history strategies is less clear. There is initial evidence that anxiety and worry affect women's quality–quantity trade-off through effects on parenting (Alvergne, Jokela, & Lummaa, 2010). A recent study in Tsimane forager-horticulturalists showed that individual variation in this population is best described by two personality dimensions (*prosociality* and *industriousness*) rather than a standard "Big Five" (Gurven, von Rueden, Massenkoff, Kaplan, & Lero Vie, 2013). Intriguingly, these dimensions largely reflect mixtures of conscientiousness, agreeableness, and aspects of extraversion, consistent with the idea that these traits reflect fundamental behavioral trade-offs.

Although the existence and meaning of a "general factor of personality" (GFP) are still debated in the literature, some scholars have argued that the GFP—essentially, a dimension of socially desirable personality emerging from the covariation between emotional stability, extraversion, conscientiousness, agreeableness, and openness—is associated with slow strategies (see Figueredo, Woodley, & Jacobs, Chapter 40, this *Handbook*, Volume 2). Also, profiles of personality and cognitive ability seem to become increasingly differentiated toward the slow end of the spectrum, perhaps reflecting benefits of behavioral specialization in slow strategists (Figueredo et al., Chapter 40, this *Handbook*, Volume 2).

All personality traits are at least moderately heritable (Ebstein, Israel, Chew, Zhong, & Knafo, 2010). Their associations with life history trade-offs leave open the question of what evolutionary processes have maintained genotypic variation. Personality traits may be subject to directional selection (maximal fitness associated with high or low levels of the trait) or stabilizing selection (maximal fitness associated with intermediate trait values). In either scenario, genetic variation is maintained through mutation-selection balance. Genetic variation may also be maintained by balancing selection, whereby selection pressures vary spatially, temporally, between the sexes, or depending on the frequency of a phenotype in the population (see Gangestad, 2011; Nettle, 2011b). In the Tsimane, personality traits predict fitness in ways that vary systematically across regions and between the sexes (Gurven, von Rueden, Stieglitz, Kaplan, & Rodriguez, 2014). Another potential source of balancing selection on personality is temporal fluctuation in local sex ratios; the relative proportion of males and females in the mating pool modulates the costs and benefits of life history allocations, such as that between mating and parenting effort (Del Giudice, 2012).

PSYCHOPATHOLOGY

By organizing physiology and behavior across domains, life history strategies also contribute to increased or decreased risk for mental disorders. Some putative disorders may be best understood as adaptive behavioral strategies, albeit with socially or personally undesirable consequences. Several authors have argued that externalizing disorders such as psychopathy, antisocial personality disorder, and conduct disorder are (male-typical) behavioral manifestation of fast life history strategies (e.g., Barr & Quinsey, 2004; Belsky et al., 1991; Mealey, 1995). Potentially, borderline personality disorder is a (female-typical) manifestation of fast life history strategy (Brüne, 2014; Brüne, Ghiassi, & Ribbert, 2010). For many other disorders, it is much less clear to what extent they represent adaptive strategies, maladaptive phenotypic extremes, or dysregulation of adaptive mechanisms. Nonetheless, individual differences in life history may play a role in their origin. For example, the spectrum of eating disorders appears to covary with increased sexual competition and fast life history indicators in women (Salmon, Figueredo, & Woodburn, 2009). Associations of attention-deficit and hyperactivity symptoms with fast life history indicators such as lower birth weight and unrestricted sociosexuality have been documented as well (Frederick, 2012).

Del Giudice (2014a, 2014b) advanced a comprehensive framework for psychopathology inspired by LHT. The framework identifies four pathways from life history strategy to psychopathology: First, adaptive life history-related traits may be regarded as symptoms; second, life history-related traits may be expressed at maladaptive levels (e.g., as a result of assortative mating between individuals high in the trait); third, adaptive strategies may yield individually maladaptive outcomes (e.g., defensive mechanisms may "misfire" with catastrophic consequences); finally, life history-related traits may increase vulnerability to dysfunction (e.g., upregulated defensive mechanisms may be more vulnerable to deleterious mutations or environmental insults).

Del Giudice (2014a) argued that many mental disorders can be classified as *fast spectrum* or *slow spectrum* conditions, depending on their correlates in the domains of motivation, self-regulation, personality, sexual maturation, and environmental predictors. Putative fast spectrum disorders include externalizing disorders, borderline personality disorder, schizophrenia spectrum and bipolar disorders (possibly a heterogeneous category), and specific subtypes of eating disorders, obsessive-compulsive disorder, and attention-deficit/hyperactivity disorder. Putative slow spectrum disorders include autism spectrum disorders (possibly heterogeneous), obsessive-compulsive personality disorder, and specific subtypes of eating disorders, (see Del Giudice, 2014a, 2014b). Depression appears to be a highly heterogeneous category, with some indications that fast life history strategies may be especially conducive to depressive disorders with high levels of somatic (stress-related) symptoms (Del Giudice, 2014a).

This proposal is theoretically ambitious, and much research is needed to flesh out the breadth of its applicability. Certain factors that increase vulnerability to disease (e.g., deleterious mutations) are likely to do so through pathways other than ones directly implicating life history strategies (e.g., compromised neural integrity, affecting schizophrenia and other neurodevelopmental disorders; see Yeo, Pommy, & Padilla, 2014). For this reason, the domain of adaptive *function* captured by life history strategies must be integrated with that of *functionality*, as instantiated in the efficiency and integrity of psychological and neurobiological processes (see Del Giudice, 2014b). Classifying disorders based on motivation, self-regulation, and so on is complicated by the overdetermination of behavioral traits, which reflect life history strategies only in part (Gangestad, 2014). A strength of the framework, however, is its theory-grounded empirical generativity. Applications of LHT to psychopathology should continue to yield useful insights in the structure and meaning of mental disorders.

PRESENT LIMITATIONS AND FUTURE DIRECTIONS

Theoretical Challenges LHT is a theoretical foundation of modern evolutionary biology, one that speaks very broadly to how selection operates on what organisms do and how they develop. The major concepts drawn upon to date within evolutionary psychology pertain to the fast-slow continuum of life histories, and specifically as they inform an understanding of developmental trajectories and individual differences. Although this continuum is an important topic in biology, it is merely one aspect of the theory. Life history theory is far broader in scope and much more ambitious as an explanatory framework. It pertains to trade-offs between allocations of energy of many types, arguing that an understanding of how selection shapes organisms to execute them is a function of their fitness effects integrated across the life span. At a broad level, they may be few in type (e.g., current versus future reproduction, quality versus quantity of offspring). But at a more specific level, they are numerous; at any point in its existence, an organism could be allocating its energy to an extraordinary range of fitness-enhancing features and activities (e.g., bodily features with various impacts on survival and access to mates, brain structures, multiple elements of immune function, somatic repair, food search, mate search, mate retention, assisting kin—as merely a start). Within evolutionary psychology, the strong identification of life history theory with the fast-slow continuum limits appreciation of its richness and leads to an overly simplified understanding of its foundational nature.

Life history theory is expressed in mathematical models; work in evolutionary psychology could benefit from greater development of formal models of life history evolution and development in humans. For example, the approach to developmental trajectories inaugurated by Belsky et al. (1991) depends on the assumption that children can reliably forecast future conditions based on cues received during the first 5–7 years of life. However, only recently (Nettle et al., 2013) was this assumption formalized in a mathematical model. Subsequent debate (Del Giudice, 2014d; Nettle et al., 2014) has attempted to clarify the conditions under which the assumption may be plausible and, equally important, the kinds of empirical data that can test its validity. Future research should combine evolutionary and cognitive modeling to better understand the psychological processes involved in life history allocations, as well as the origin and nature of relevant internal regulatory variables. Work in this area could benefit by interfacing with literatures on heuristics and decision-making, as well as with the expanding biological literature on the integration of adaptive functions and behavioral mechanisms (see McNamara & Houston, 2009).

Empirical Challenges Biologists interested in understanding the life history of a species often adopt a whole-organism approach that combines behavior, morphology, and physiology. Although behavioral components are often of key interest, they must be understood in combination with growth, metabolism, immune function, and so on. Psychologists have tended to focus on behavior at the exclusion of the other dimensions of life history allocation. Relatedly, research has often assessed life history strategies solely through questionnaire measures of behavioral and psychological traits, assuming that clusters of these variables map well onto allocations that define life histories. As individual behaviors are typically multiply determined, linkages with other dimensions of life histories may be modest (see also Copping et al., 2014). Research could benefit from a broader array of measures, including parameters of immune function, reproductive and metabolic hormones, energy utilization, growth trajectories, oxidative damage, and other indicators of somatic degradation. Metabolic regulators such as thyroid hormones and IGF-1 should be investigated alongside more commonplace reproductive and stress hormones.

Because of the focus on the fast-slow continuum and its emphasis on the transition from prereproductive growth to the reproductive phase of life, life history work in psychology has paid much attention to adolescence and early adulthood. Allocation decisions at other stages of the life course—the prenatal period, infancy and early childhood, the postreproductive phase, and the aging process more generally—have received much less attention (see Del Giudice & Belsky, 2011). Broadening the current perspective on life history trade-offs and decisions will be especially important in view of the disproportionate force of selection on early survival (Jones, 2009) and the severe metabolic trade-offs involved in brain growth through infancy and childhood (Kuzawa et al., 2014). Also, very little attention has been paid to rates of cognitive decline with age, and on changing endocrine profiles late in life in evolutionary life history models. Do we expect cognitive aging to proceed at the same rate as cardiovascular or immune system aging? Do changing endocrine profiles with age reflect dysregulation of those systems or are they adaptive responses to deteriorating phenotypic condition? Research designed to answer these questions is likely to be quite productive.

Increasingly, concepts and insights inspired by LHT permeate the field of evolutionary psychology, particularly with respect to individual differences and their developmental trajectories. We believe the discipline is ready to embrace the life history approach in its full richness, and look forward with excitement to the theoretical and empirical fruits of this integration.

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CHAPTER 3

Methods of Evolutionary Sciences

JEFFRY A. SIMPSON and LORNE CAMPBELL

METHODS IN EVOLUTIONARY PSYCHOLOGY

Charles Darwin (1859) began formulating the theory of evolution by natural selection almost 20 years before he published *On the Origin of Species*. One of the main reasons he waited to publish his iconoclastic book was that he did not have sufficient evidence to support his theory (Desmond & Moore, 1991). Testing the theory of evolution by natural selection was a truly major and complicated task, so Darwin used several different methods to marshal support for the theory. He spoke, for example, with animal breeders to learn about artificial selection. Over time, he discovered that heritable variation in domesticated traits was shaped by the preferences of breeders, a process similar to the natural selection of traits. He also surveyed the existing scientific literature on myriad species in their natural environments, carefully describing and cataloguing the large amount of variation that existed both within and between species. And he spent countless days experimenting with seeds to determine whether they germinated after being exposed to different types of conditions. Armed with a huge amount of information from all his observations, field studies, and experiments, Darwin was eventually able to marshal sufficient initial support for the basic principles of the theory of evolution by natural selection. It was partly Darwin's relentless tenacity at gathering and analyzing data from multiple sources that resulted in his theory eventually being accepted by the wider scientific community.

Both the theory and science of evolution have progressed remarkably since 1859. Indeed, Darwin's vision that his theory of evolution would provide the foundation for the study of psychology is coming to fruition in a growing number of academic disciplines. This is a very exciting time for the evolutionary sciences. However, a larger number of researchers need to emulate Darwin by adopting a more multifaceted approach when studying psychological adaptations. To do so, researchers must take advantage of all the many different investigative methods that are currently available.

To facilitate this process, this chapter revisits some of the fundamental principles and concepts that have anchored research methods in the social and behavioral sciences for several decades. Our hope is that it will also kindle (or rekindle) greater interest in methodological issues by not only showcasing the many research methods currently available to evolutionary scientists, but also by clarifying *how* different research methods, measures, and statistical techniques can be utilized to make clearer, stronger, and more precise tests of evolutionary-based predictions.

The chapter has three overarching themes. The first is that, to provide stronger and more definitive tests of theories, multiple research methods and outcome measures must be used to test alternate models *within* ongoing programs of evolutionary research. Each major research method (e.g., laboratory experiments, surveys, computer simulations) and each type of outcome measure (e.g., self-reports, peer ratings, behavioral ratings) have strengths and limitations. No single method or measure is optimal in every research context because different methods, measures, and techniques entail trade-offs between maximizing internal validity, external validity, and the generalizability of findings across participants. Both methodological triangulation within programs of research (i.e., adopting a multiple-method/multiple-measure approach when testing for effects) and the testing of alternative models are required to arrive at strong, clear inferences.

A second theme is that there has been a general overreliance on certain research methods (e.g., correlational approaches) and certain measures (e.g., self-reports) in some areas within the evolutionary sciences. In some cases, this mono-method/mono-measure focus has impeded the rigorous testing of certain evolutionary-based phenomena; in others, it has not allowed investigators to discern whether the results predicted by evolutionary theories fit observed data better than alternative competing theories. This problem was remedied by greater knowledge and appreciation of the numerous strengths and advantages that multiple research methods and different paradigms can offer.

A third organizing theme is the need to test and provide better evidence for the "special design" properties of psychological adaptations. In some situations, a multimethod/multimeasure approach can help researchers provide better and stronger evidence for the "special design" features of certain purportedly evolved traits, behaviors, or characteristics in humans. The telltale signs of selection and adaptation should be most evident when specific stimuli (triggering events) produce specific effects (responses) across different levels of measurement (ranging from molecular to macro levels). Converging patterns of findings from well-conducted multimethod/multimeasure studies can appreciably *increase* our confidence that certain "specially designed" adaptations probably did, in fact, evolve. We now turn to the first major topic of the chapter, which centers on theory testing, special design, and "strong" research methods.

THEORY TESTING, SPECIAL DESIGN, AND STRONG RESEARCH METHODS

Many evolutionary theories confront relatively high evaluation standards given the sheer complexity—and sometimes imprecision—of the metatheories in which they are grounded. As a rule, evolutionary theories tend to be more complex than other theories, including historical origin theories that do not have an evolutionary basis such as certain social structuralist theories (e.g., Eagly, 1987). One reason for this is that inferring simple associations between distal biologically based adaptations and how current psychological processes operate is more complicated than inferring associations between cultural or social structural factors and current psychological processes. More complex theories usually generate a larger number of "internal" alternative explanations, which makes it more difficult to derive straightforward predictions about whether and how certain traits or behaviors were—or should have been—adaptive in our ancestral past (see Caporael & Brewer, 2000; Dawkins, 1989).

This problem has been magnified by the relative lack of attention often devoted to (a) clarifying how different middle-level evolutionary theories are or are not interrelated, and (b) specifying the conditions under which different theories make similar versus different predictions about specific outcomes (Simpson & Belsky, 2008). Evolutionary theories are hierarchically organized and they have several levels of explanation, ranging from broad metatheoretical assumptions, to domain-relevant middle-level principles, to specific hypotheses, to specific predictions (Buss, 1995; Ketelaar & Ellis, 2000). Most middle-level evolutionary theories (such as parental investment, attachment, parent-offspring conflict, reciprocal altruism) extend the core assumptions of their metatheories to specific psychological domains, such as the conditions under which individuals invest in their offspring, bond with them, experience conflict with them, or assist others who are not biologically related to them. In some cases, middle-level theories generate competing hypotheses and predictions. Parental investment theory, for instance, makes different predictions than reciprocal altruism theory does regarding when men should invest in young, biologically unrelated children of unattached women (see Ketelaar & Ellis, 2000). In other cases, middle-level evolutionary theories spawn hypotheses that vie with nonevolutionary theories (e.g., the debate about why homicide is so prevalent in "families"; see Daly & Wilson, 1988). Little attention is typically paid to which outcomes different competing theories or models—either evolutionary based or otherwise—logically anticipate. *Whenever possible, tests between predictions that have been logically derived from competing models should be built into evolutionary research programs.*

At times, evolutionary researchers also do not fully explain the deductive logic that connects one level of explanation (such as the basic principles of a middle-level theory) to adjacent levels (such as a specific set of hypotheses). One reason for this is that evolutionary hypotheses exist along a "continuum of confidence," which ranges from: (a) clear and firm hypotheses that are unequivocally and directly derived from a middle-level theory, to (b) expectation-based hypotheses that can be logically deduced from a theory, but cannot be directly derived from it without making auxiliary assumptions, to (c) speculative hypotheses based on casual or intuitive hunches.

HOW CAN MORE COMPELLING EVIDENCE BE GENERATED?

How can the evolutionary sciences overcome these limitations? As a start, researchers must articulate clearer, more specific, and more detailed models of the historical events that should have produced an evolved trait or attribute (Conway & Schaller, 2002). Supportive evidence must also be gathered from a wide range of disciplines (e.g., anthropology, zoology, genetics, evolutionary biology) to justify the "starting assumptions" of a proposed historical theory or model and to explain why it is more probable than other theories or models. To accomplish this, evolutionary scientists must conduct more refined cost–benefit analyses relevant to the evolutionary history of each purported adaptation (Cronin, 1991). Specifically, greater attention must focus on the probable costs, constraints, and limitations—social, physical, behavioral, physiological, and otherwise—that might have counterweighted the conjectured benefits associated with a hypothesized adaptation (see Eastwick, 2009). After conducting these analyses, researchers must elucidate why certain adaptations should have produced better solutions to specific evolutionarily relevant problems than other possible adaptations, and good tests of alternative models should be performed.

These limitations might also be rectified if investigators structured more of their research around the predictions that specific evolutionary theories or models make regarding the onset, operation, and termination of specific psychological processes or mechanisms. When doing so, a clear conceptual distinction must be maintained between models of historical (evolutionary) events and the current psychological events or processes being examined (see Tinbergen, 1963). This can be achieved by organizing research questions around Buss's (1995, pp. 5–6) incisive definition of evolved psychological mechanisms:

> An evolved psychological mechanism is a set of processes inside an organism that: (1) Exists in the form it does because it (or other mechanisms that reliably produce it) solved a specific problem of individual survival or reproduction recurrently over human evolutionary history; (2) Takes only certain classes of information or input, where input (a) can be either external or internal, (b) can be actively extracted from the environment or passively received from the environment, and (c) specifies to the organism the particular adaptive problem it is facing; (3) Transforms that information into output through a procedure (e.g., decision rule) in which output (a) regulates physiological activity, provides information to other psychological mechanisms, or produces manifest action and (b) solves a particular adaptive problem.

When developing and testing the deductive logic of a theory, therefore, evolutionary scientists should: (a) articulate how and why specific selection pressures should have shaped certain psychological mechanisms or processes, (b) identify the specific environmental cues that should have activated these processes in relevant ancestral environments, (c) explain how these processes should have guided thoughts, feelings, and behavior in specific social situations, and (d) specify the cues or outcomes that should have terminated these psychological processes or mechanisms. The wider adoption of this general approach could yield several benefits. First, by clarifying and more rigorously testing the deductive logic underlying an evolutionary theory or model, investigators are in a better position to articulate how and why their theory provides a *forward-thinking* account of specific psychological processes or mechanisms rather than an ad hoc, backward-thinking explanation. Second, because subtle connections between different theoretical levels are more fully explained, the theory or model being tested should have greater explanatory coherence. Third, sounder and more extensive deductive logic will help researchers to derive more novel predictions. The most powerful theories generate new and unforeseen predictions that cannot be easily derived from alternative theories. Many novel hypotheses are likely to involve statistical interactions in which certain psychological mechanisms are activated or terminated by very specific environmental inputs. And theories that predict specific types of context-dependent statistical interactions usually have fewer alternative explanations.

ADAPTATIONS, ADAPTATIONISM, AND STANDARDS OF EVIDENCE

At a conceptual level, many evolutionary psychologists adopt a general investigative orientation known as adaptationism. Using this approach, researchers try to identify the specific selection pressures that shaped the evolution of certain traits or characteristics in our ancestral past (Thornhill, 1997; Williams, 1966). This approach asks questions of the form "What is the function or purpose of this particular structure, organ, or characteristic?" Answers to such questions have produced rapid and significant advances in many areas of science. With respect to human evolution, some adaptationist research programs have used optimization modeling (e.g., testing different formal mathematical theories of possible selection pressures in the environment of evolutionary adaptedness [EEA]; Parker & Maynard Smith, 1990) to provide evidence for certain presumed adaptations in humans. Most programs, however, have simply developed plausible, intuitive arguments regarding how a given trait or characteristic might have evolved to solve specific evolutionary problems (Williams, 1966, 1992).

The general adaptationist approach has been criticized by Gould and Lewontin (1979), who claim that most adaptationist research has used weak or inappropriate standards of evidence to identify adaptations. They argue that most adaptationist research simply demonstrates that certain outcomes are consistent with theoretical predictions without fully examining competing alternative accounts. Gould (1984) has also argued that most adaptationist research has overemphasized the importance of selection pressures and underestimated the many constraints on selection forces, leading some adaptationists to presume that adaptations exist when rigorous evidence is lacking. Gould and Lewontin (1979) maintain that many constraints—genetic, physical, and developmental—may have opposed or hindered the impact that selection pressures had on most phenotypic traits and characteristics over evolutionary time. Thus, they claim that exaptations (i.e., preexisting traits that take on new beneficial effects without being modified by new selection pressures) are numerous, making it nearly impossible to recreate the selection history of a given trait or characteristic. Most adaptations are, in fact, built on earlier adaptations, exaptations, or spandrels (i.e., by-products that happen to be associated with adapted traits). The evolutionary sciences, therefore, must use methodologies capable of documenting specific adaptations more directly (Mayr, 1983; see also Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998).

What types of evidence have been gathered to test whether certain traits or psychological attributes might be adaptations? Andrews, Gangestad, and Matthews (2003) discuss six standards of evidence: (1) *comparative standards*, which make specific phylogenetic comparisons regarding a purportedly adaptive trait across different species; (2) *fitness maximization standards*, which identify particular traits that ought to maximize fitness returns in particular environments, including current ones; (3) *beneficial effects standards*, which focus on the fitness benefits that a presumably adaptive trait could have produced in ancestral environments; (4) *optimal design standards*, which test formal mathematical simulations of how different selection pressures might have produced trade-offs in evolved features and how fitness could have been increased by trading off the features of one trait against others; (5) *tight fit standards*, which examine how closely a presumably adaptive trait's features match, and should have efficiently solved, a major evolutionary problem; and (6) *special design standards,* which identify and test the unique functional properties of a purportedly adaptive trait.

The first five standards offer indirect evidence that a given trait might be an adaptation. The sixth standard—special design—provides much more rigorous evidence (Andrews et al., 2003). *Thus, evolutionary research programs must be developed, organized, and structured around providing more firm and direct evidence for the special* *design properties of possible adaptations.* As more special design features of a hypothesized adaptation are documented, each contributing to a specific function, it becomes more plausible that the hypothesized adaptation actually evolved for that function. The best and most rigorous evolutionary research programs routinely test for special design features (also see Schmitt & Pilcher, 2004).

SPECIAL DESIGN EVIDENCE

Organisms are living historical documents (Williams, 1992). Accordingly, adaptations should reveal remnants of the selective forces that shaped them. Before a trait can be classified as an adaptation, however, its primary evolutionary function or purpose must first be ascertained (Mayr, 1983; Thornhill, 1997). To accomplish this, the specific selection pressures that most likely generated and shaped the functional design of the trait must be inferred. Functionally designed traits tend to perform a purpose "with sufficient precision, economy, efficiency, and so forth to rule out pure chance as an adequate explanation" (Williams, 1966, p. 10). Chance factors can include processes such as phylogenetic legacy, genetic drift, by-product effects, and mutations, any of which could be responsible for the development of a particular trait.

Several additional factors make it difficult to determine whether a particular trait is an adaptation. These include the potentially confounding effects of historically prior adaptations (e.g., those upon which more recent "secondary adaptations" may have been constructed), trade-offs between interacting adaptations (e.g., selection for camouflage from predators versus colorful ornamentation to attract mates), and counteradaptations (e.g., countervailing mating tactics that emerge between the sexes in a species). Further complicating matters, different traits may require different types of evidence to demonstrate their special design properties. For example, the special design features of many morphological traits (e.g., the human eye, body organs) have been demonstrated simply by showing that a particular trait has complex design and performs a specific function with a very high degree of precision, economy, and efficiency. Additional evidence, however, is often needed for complex behavioral and cognitive traits believed to be adaptations because domain-general learning processes (such as exapted learning mechanisms) can produce traits with considerable specificity, proficiency, and complexity (see Andrews et al., 2003). For these "complex traits," further evidence for their special design properties is often required.

Fortunately, several sources of evidence can increase our confidence about the "special design" of certain traits (Andrews et al., 2003). First, complex trait adaptations can be documented by showing that a trait is a biased outcome of a specific developmental or learning mechanism (Cummins & Cummins, 1999). Such traits develop or are learned very easily, quickly, and reliably, and they tend to solve specific adaptive problems with much greater proficiency than other traits that could have been produced by the same underlying mechanisms. Examples include the strong and automatic propensity to fear certain objects (e.g., snakes, Öhman & Mineka, 2001), the capacity to develop grammar and language (Pinker, 1994), the environmentally specific conditioning associated with punishment (Garcia, Hankins, & Rusiniak, 1974), and the perceptual expectations and preferences of young infants (Spelke, 1990). Second, complex adaptations can be demonstrated by showing that a trait's specially designed features would have solved major problems in ancestral environments, but tend to be dysfunctional or harmful in modern environments. One example is the strong cravings that most people—especially young children—have for foods high in fat and sugar (Drewnowski, 1997). Third, complex adaptations can be documented by revealing that alternative theories or processes do not predict or cannot explain certain outcomes (e.g., the superior spatial location memory of women, Silverman & Eals, 1992; the superior cheater detection capabilities of both sexes, Cosmides, 1989). Finally, confidence in a trait's adaptive status increases when several traits all serve the same basic function (e.g., the factors that govern shifts in women's mate preferences across the reproductive cycle; see Thornhill & Gangestad, 2008).

There are, of course, some drawbacks to using special design as the sole evidentiary criteria for adaptations. It might, for example, be difficult to provide unambiguous evidence for the special design features of certain adaptations. To guard against this possibility, investigators should test not only for the special design features of specific traits, but should provide some evidence for the other standards as well. Adaptations may also be difficult to identify because many complex traits may have mixed design (e.g., female orgasm, the development of the neocortex; see Andrews et al., 2003). If, for instance, a trait initially evolved as an adaptation for one effect, then was exapted for a different purpose, and then became a secondary adaptation for yet another purpose, the trait could serve multiple functions that were shaped by different—and perhaps even conflicting—selection pressures. This would obscure the trait's specially designed features.

VALIDITY ISSUES

Validity is generally defined as "the best available approximation to the truth or falsity of propositions" (Cook & Campbell, 1979, p. 37), so it reflects the degree of truth regarding the statements, inferences, or conclusions drawn from empirical research. Because research programs have different missions, the validity of a given study must be evaluated in the context of the broader goals, purposes, and objectives of a given research program.

A PROCESS MODEL OF VALIDITY

The procedures for establishing the validity of an operationalization or measure of a construct are similar to those for developing, testing, and confirming scientific theories (Loevinger, 1957). Since the operations and measures used in any single study are imperfect and incomplete representations of the theoretical constructs they are designed to assess, theory testing is an ongoing, cyclical process in which constructs inform research operations, which generate revised constructs, which in turn suggest new and improved operations.

Two methodological traditions have influenced how validity is defined and conceptualized. One tradition, grounded in experimental and quasi-experimental research, has focused on the validity of independent variables, particularly their conceptualization, their operationalization, and how they are perceived by participants (Cook & Campbell, 1979). A second tradition, stemming from nonexperimental research in personality and clinical psychology, has focused on the validity of dependent variables and psychological scales (Cronbach & Meehl, 1955; Loevinger, 1957).

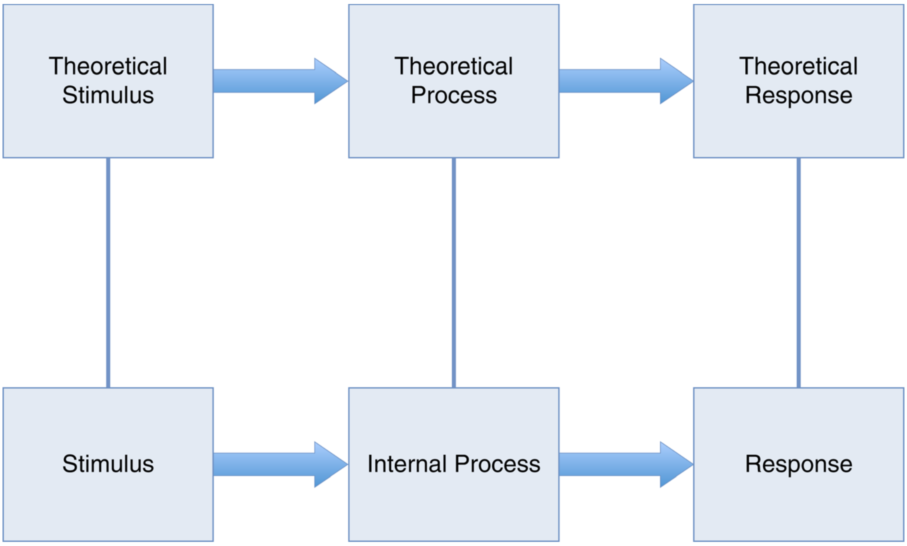

Figure 3.1 Constructs and Operationalizations. The vertical lines represent hypotheses connecting observed measures with their underlying theoretical processes/constructs. Adapted from Brewer (2000) with permission.

Bridging these traditions, Brewer (2000) proposed a three-stage process model of how hypothetical theoretical constructs are conceptually linked with three sets of measures: (1) observable stimuli (independent variables), (2) intervening physiological or cognitive processes (those occurring *within* individuals), and (3) observable responses (dependent or outcome variables). As shown in Figure 3.1, researchers need to make three inferential connections when planning and conducting studies.

On the independent variable side, they first must make important assumptions, inferences, and decisions about how the latent causal concepts specified by their theory should be operationally defined and manifested in the independent variables. If they are interested in essentialist causation, researchers must also establish solid inferential ties between the mediation processes predicted by their theory and the measures identified as possible mediators. On the dependent variable side, they must derive clear inferential connections between the effects anticipated by their theory and the responses (outcomes) that are measured. Numerous problems can undermine valid inferences from a study at each stage. To complicate matters, many areas of evolutionary science lack standardized measures, operations, or procedures that correspond closely with the latent theoretical constructs of interest. Because of this, evolutionary scientists must often make fairly large inferential leaps across each set of linkages.

These difficulties can create thorny methodological problems. For example, the validity of stimulus or response measures may be called into question if the variations (either manipulated or measured levels) in a given study do not mirror the typical levels of variation in the theoretical states that the stimuli or responses are designed to assess. Moreover, it may be difficult to predict the precise levels at which certain independent variables should (or should not) have causal effects on certain outcome measures. And it might be challenging to anticipate the range over which certain independent variables should have their strongest effects on specific outcomes.

Given the multitude of ways in which the validity of a study can be reduced, it is often difficult to determine whether null results from a single study reflect a failure of the theory, the operationalizations at one or more of Brewer's (2000) three stages, and/or the measures employed.

Validity in Experimental and Quasi-Experimental Research

There are four basic types of validity in experimental and quasi-experimental research (Cook & Campbell, 1979): (1) internal validity, (2) statistical conclusion validity, (3) external validity, and (4) construct validity.

Internal validity reflects the degree to which a researcher can be confident that a manipulated variable (X) has a causal impact on an outcome measure (Y). The internal validity of a study is high when one can confidently conclude that variations in Y were produced by manipulated changes in the level or intensity of X (i.e., the independent variable had a causal influence on the dependent variable, *independent* of other possible causal factors). If third variables correlate with X, these confounds can generate spurious effects. Fortunately, true experiments control for the deleterious influence of third variables through random assignment of participants to experimental conditions and through careful operationalizations and manipulations of the independent variables.

Moderating and mediating variables, however, can complicate causal inferences (Preacher & Hayes, 2008). Moderating effects exist when there is a true causal connection between an independent variable (X) and a dependent variable (Y), but the relation varies at different levels of some third variable (C). Evolutionary scientists, for instance, might posit that an experimental manipulation of high versus low physical threat should lead most highly threatened individuals to stand and defend themselves. This link, however, might be moderated by gender, with men being more likely to adopt the "stand and defend" response under high threat than women.

Mediating effects occur when a third variable (C) is needed to complete the causal process (pathway) between X and Y. That is, systematic changes in an independent variable (X) predict changes in the mediator (C), which then predicts changes in the dependent variable (Y), statistically controlling for X. Returning to our example, evolutionary scientists might also postulate that a high level of physical threat should lead most men to experience "challenge" physiological responses that prepare them to stand and defend. Such threats, however, might lead most women to experience "threat" physiological responses, leading them to engage in different tactics.

A second major type of validity, *statistical conclusion validity*, involves the degree to which a researcher can infer that two variables reliably covary, given a specified alpha level and the observed variances. Statistical conclusion validity is a special form of internal validity, one that addresses the effects of random error and the appropriate use of statistical tests rather than the effects of systematic error. This form of validity can be undermined by having insufficient statistical power (leading to Type II statistical errors), violating important assumptions of statistical tests (e.g., that errors are uncorrelated when they are actually correlated), suffering from inflated experiment-wise error rates (which occur when multiple statistical tests are performed without adjusting the p values for the number of tests conducted), or when measures have low reliabilities. Statistical conclusion validity can also be threatened if treatment or condition implementations are unreliably administered, if random events occur during experiments, or if respondents differ in how they interpret the meaning of treatments, independent variables, or outcome measures.

A third major form of validity, *external validity*, involves the degree to which a researcher can generalize from a study: (a) *to* particular target persons or settings, or (b) *across* different persons, settings, and times. The external validity of a study can be assessed by testing for statistical interactions (i.e., whether an effect holds across different persons, settings, or times), and it can be enhanced by conducting several heterogeneous studies. External validity is threatened when statistical interactions exist between selection and treatment (i.e., do recruitment factors make it easier for certain people to enter particular treatments or conditions?), between setting and treatment (i.e., do similar treatment or condition effects emerge across different research settings?), or between history and treatment (i.e., do effects generalize across different time periods?).

Brewer (2000) distinguishes three forms of external validity: ecological validity, relevance, and robustness. *Ecological validity* is the extent to which an effect occurs under conditions that are "typical" or "common" for a given population. *Relevance* reflects the degree to which findings are useful or applicable in solving social problems or improving the quality of life. *Robustness* (sometimes called "generalizability") has the most important implications for evolutionary research because it reflects the degree to which a finding is replicable across different settings, people, and historical contexts.

To evaluate the robustness of an effect, theorists must clearly define the populations and settings to which it should (and should not) generalize. Within the evolutionary sciences, generalizability from one prototypical participant population at one time period (e.g., Westernized college students in current environments) to target populations from other time periods (e.g., typical hunters and gathers in our ancestral past) is one of the most common external validity concerns. Similar concerns have been raised in other fields within psychology (see Arnett, 2008). Evolutionary scientists need to articulate the principle ways in which contemporary participant populations are likely to differ from more traditional hunter/gatherer "target" populations and how these differences may qualify the interpretation of certain evolutionary findings.

The fourth type of validity—*construct validity*—is the most encompassing form of validity. Construct validity reflects the degree to which operations that are intended to represent a given causal construct *or* effect construct can be explained by alternate constructs (Cronbach & Meehl, 1955). For causal constructs, construct validity addresses the question, "Does a finding reveal a causal relation between variable X and variable Y, between variable Z and variable Y (which might also correlate with variable X), or with some other outcome variable?" For effect constructs such as outcome measures, construct validity addresses the question, "From a theoretical standpoint, does this measure/scale correlate with measures with which it should covary (convergently), and does it *not* correlate with measures with which it should not correlate (discriminantly)?"

Most independent variables are complex packages of multiple and sometimes correlated variables. For example, when an experimenter tries to induce social isolation in participants, the manipulation may produce other unanticipated states, such as heightened anxiety, depressive symptoms, or negative moods. Many of the concerns about construct validity, therefore, revolve around how independent variables are (or should be) operationalized in particular studies and how they are perceived by participants. An experimental manipulation might also elicit multiple hypothetical states in the same individual, making it nearly impossible to identify the specific causal agent that is operative in a study. Cook and Campbell (1979) claim that the most serious threat to the construct validity of causal constructs is a mono-operation bias—the recurrent use of a single method or paradigm to assess a theoretical construct. *Conceptual replications that involve different operationalizations of the same construct are essential to demonstrate sufficient construct validity.*

MULTITRAIT-MULTIMETHOD APPROACHES

Gathering evidence for the construct validity of a trait or scale requires testing its convergent and discriminant validation properties. This can be accomplished using the multitrait-multimethod matrix approach (Campbell & Fiske, 1959). Measures have three sources of variance: (1) variance that a construct was intended to assess (convergent validity components), (2) variance that a construct was *not* intended to assess (systematic error variance), and (3) random error due to unreliability of the measures. All studies fall into one of four categories: (1) monotrait-monomethod (when a single trait/scale is studied using one research method), (2) monotrait-heteromethod (when a single trait/scale is studied using different methods), (3) heterotrait-monomethod (when different traits/scales are studied using one method), or (4) heterotrait-heteromethod (when multiple traits/scales are studied using multiple methods). Heterotrait-heteromethod approaches are preferable because they allow researchers to test for both the convergent and discriminant validation properties of traits/scales. Strong evidence for convergent validity exists when a trait/scale correlates with measures that tap theoretically similar constructs, even when the trait/scale is measured using different methods. Compelling evidence for discriminant validity exists when a trait/scale does *not* correlate with measures that tap theoretically independent or unrelated constructs, even when the same methods are used.

STATISTICAL POWER

Another very important issue when designing studies is statistical power, a topic that has been brought back to the forefront of discussion in recent years (e.g., Schimmack, 2012). Statistical power is the probability of rejecting the null hypothesis when it is false (Cohen, 1988), but it is more commonly discussed as the ability to detect an effect if it actually exists. Having an appropriate level of statistical power (approximately .80 or 80%), therefore, is essential to test hypotheses adequately, particularly those derived from evolutionary models that are novel or counterintuitive, such as the effects of ovulation on women's mate preferences.

The average power of most published studies in various fields is worrisomely low. Cohen (1988) has lamented the low power of most published research in psychology, and he has advocated strongly for increasing the power of studies. Despite this clarion call, little improvement in power had been achieved in the intervening years. Recently, Bakker, van Dijk, and Wicherts (2012) estimated the average power of studies in psychology to be 35%, and Button et al. (2013) estimated the average power of research in neuroscience to be even lower (21%). When the fact that over 90% of all published research reports statistically significant (non-null) findings (Sterling, Rosenbaum, & Weinkam, 1995) is combined with the low power of most studies, a non-trivial amount of published findings must be false positives (Ioannidis, 2005).

To understand how low power negatively impacts research, Button et al. (2013) identified three problems of low statistical power. First, with low power, there is a low probability of discovering true effects and, thus, a high level of false negatives. When a researcher genuinely believes that an effect exists (particularly if it has not been documented yet), it makes sense to design a well-powered study. Otherwise, a real effect may go undiscovered and the research process becomes inefficient and a waste of time for everyone involved (the researchers, ethics board evaluators, research assistants, and participants).

Second, low power combined with the prior probability of an effect being true at $p < .05$ can result in low positive predictive value (PPV), the probability that the effect found is indeed true (Ioannidis, 2005). When power is low, the probability that a set of effects are true effects decreases. Low power, in other words, makes it more difficult to find true effects (false negatives), and it can also result in discovering effects that are not true (false positives).

Third, low power can produce exaggerated estimates of the magnitude of an effect when a true effect is discovered. This phenomenon is known as the "winner's curse" (Ioannidis, 2008). Because low powered studies can detect only large effects, when a true effect is not very large, a low powered study will overestimate the size of the effect when the results happen to pass the threshold for statistical significance (i.e., capitalizing on chance in small samples). Subsequent replication studies using the same number of participants will not be likely to detect the effect, and replication attempts using sample sizes at least 2.5 times larger than the original sample are generally required to detect the effect, if it exists (Simonsohn, 2013). Additionally, when high powered replication studies do detect the effect, it is likely to be much smaller than in the original low powered study.

Schimmack (2012) has identified another problem with low power when multiple studies are reported. Specifically, when a series of low powered studies consistently reject the null hypothesis, this undermines one's ability to conclude that the effect (or effects) truly exists, given the low probability of obtaining this pattern of positive effects over multiple studies. Instead of obtaining a string of positive effects, the likelihood of finding null effects in some of these tests is actually *higher* when the power of the studies is *lower*. Schimmack proposes that fewer but more adequately powered studies provide more convincing and statistically defensible support for hypotheses.

LEVELS OF ANALYSIS AND PHYLOGENETIC APPROACHES

To marshal truly compelling and complete evidence for a purportedly evolved trait or behavior, one needs to distinguish between four distinct levels of analysis—adaptive function, ontogenetic development, proximate determinants, and evolutionary history (Tinbergen, 1963). Adaptive function (ultimate) explanations are concerned with the evolved adaptive purpose of a given trait or behavior. An adaptive function explanation, for example, might focus on associations between dominance and reproductive success in males and females in a species such as the chimpanzee, noting that dominance is more critical to the reproductive success of males than females. Developmental (ontogenetic) explanations address the lifespan-specific inputs that sensitize an organism to particular cues in the environment. A developmental explanation, for instance, might address the fact that maturing male chimpanzees experience certain hormonal changes during adolescence, making them more likely to engage in dominance-related behaviors than females. Proximate explanations focus on the immediate triggers of a given trait/behavior, including its inputs, information processing procedures, and outputs. A proximate explanation, for example, might document that displays of male dominance are typically triggered by threats from other males, and that responses to other males' displays are stronger when circulating testosterone levels are higher. Finally, historical (phylogenetic) explanations consider the ancestral roots of a given trait or behavior in relation to other species. Researchers who adopt this approach, for example, might view sex differences in chimpanzee dominance relative to other primate species or other social mammals (i.e., increasingly more distant relatives), observing that males are larger and more competitive in most mammalian species. Comparative methods that address questions at the phylogenetic level are less utilized than other methods, yet they can clarify and extend our understanding of the evolutionary history of a given trait or behavior in a given species in important ways (see Eastwick, 2009).

Phylogenetic methods typically reside in section I (field studies) of the circumplex model shown in Figure 3.2. Certain traits or behaviors can be correlated within or

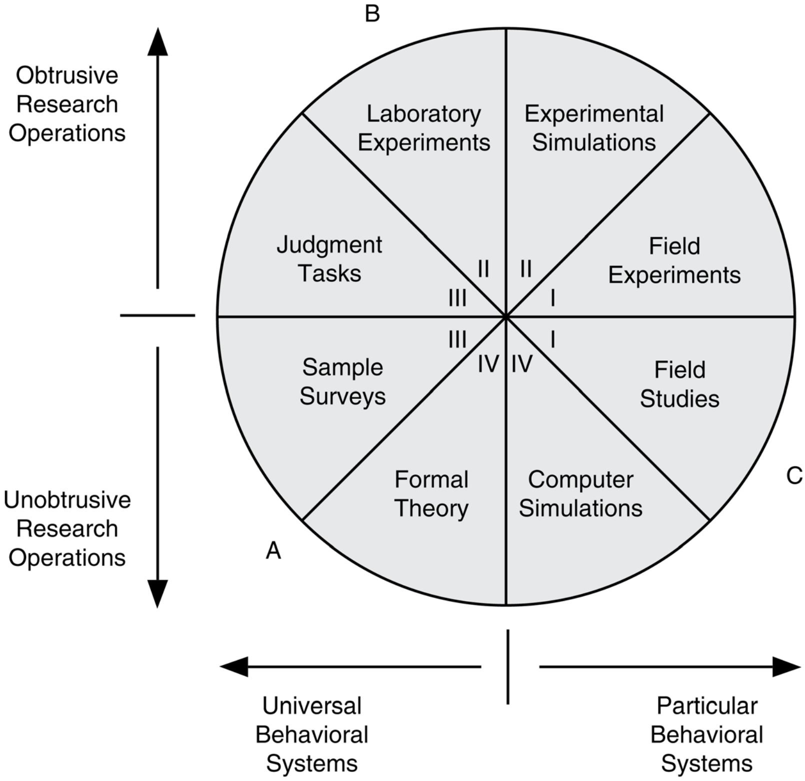

Figure 3.2 Research Strategies. A = Point of maximum concern with generality across actors; B = Point of maximum concern with precision of measurement; C = Point of maximum concern with realism of the context. *Source:* From *Research on Human Behavior: A Systematic Guide to Method* (Figure 4-1, p. 85), by P. J. Runkel and J. E. McGrath, 1972, New York, NY: Holt, Rinehart, & Winston.

between species for functional or nonfunctional reasons (Harvey & Pagel, 1991). Thus, documenting a correlation between two traits or behaviors does not mean they have evolved together between different species over evolutionary time. To fully evaluate the adaptive nature of the covariation between a pair of traits or behaviors, one must model their phylogenetic relationship between specific species over time. Phylogenetic relationships are the specific patterns of descent and ancestry over very long periods of evolutionary time, which can be summarized in phylogenetic trees.

Phylogenetic relationships are important to test and document in comparative studies because species that are more closely related phylogenetically (i.e., are closer to each other in phylogenetic trees) are often similar on many traits and behaviors (Blomberg, Garland, & Ives, 2003). Species may share similar morphologies and behaviors because they evolved from a common ancestor or because similar selection pressures generated the *independent* evolution of the traits/behaviors they have in common. Similarities among species, in other words, can be attributable to either *homology* (having a shared ancestry) or *analogy* (the independent evolution of the trait/behavior within each species, also known as convergent evolution).

Consider an example. Two traits may be highly or even perfectly correlated in two or more living species, such that trait X (e.g., high paternal investment in offspring) always co-occurs with trait Y (e.g., adult pair-bonds between mates), and the absence of trait X always co-occurs with the absence of trait Y. If there are no species in which X is present but Y is not (or vice versa), the two traits are likely to be homologous; both traits are most likely shared (or not shared) because of some earlier ancestral species from which the current species evolved. The two traits, therefore, most likely emerged at the same time for functional reasons; they did not coevolve independently within each species.

If, however, the two traits evolved together at separate points during evolutionary history, there should be multiple occasions on which changes in one trait (e.g., paternal investment) were linked with the other trait (e.g., pair-bonding). Even though the two traits are highly or even perfectly correlated in the current species, they evolved independently in different lineages and the changes in the two traits just happen to be associated. The correlation between the two traits across species, in other words, simply reflects their repeated and independent coevolution (Harvey & Pagel, 1991).

Comparative phylogenetic methods can answer important and novel questions about the evolutionary history of evolved traits/behaviors. Fraley, Brumbaugh, and Marks (2005), for instance, have used these methods to investigate patterns of pair-bonding across different species. Doing so, they have found that the connection between the provision of paternal care and pair-bonding between mates is probably due to convergent evolution, whereas connection between neoteny and pair-bonding appears to be due to homology (shared ancestry). Eastwick (2009) has suggested that evolutionary scientists should build phylogenetic relationships between humans and our hominid and pongid relatives (both living and extinct) more directly into our theorizing. He proposes that if one considers the specific timing of evolutionary events along with evolutionary constraints, phylogenetic approaches can generate novel predictions about patterns of human mating and new explanations for existing findings such as adaptive workarounds, which are more evolutionary recent adaptations in a species that “manage” the maladaptive elements of preexisting evolutionary constraints.

RESEARCH PROGRAMS PROVIDING GOOD EVIDENCE FOR PSYCHOLOGICAL ADAPTATIONS

Different traits or behaviors are likely to require different types of evidence to reveal their special design properties, but certain methodological strategies can facilitate the documentation of special design. The special design features of specific traits can be revealed by conducting research that: (a) uses multiple methods and multiple measures to assess and triangulate the major constructs, (b) tests for and systematically discounts alternative explanations for a trait's uniquely designed functional features, and (c) reveals the footprints of special design at different measurement levels (ranging from neural mechanisms, to context-specific modes of information processing, to emotional reactions, to molar behavioral responses; see Wilson, 1998). Some programs of research have documented the special design properties of certain hypothesized psychological adaptations. Examples include research on the effects of father absence/involvement on daughters' pubertal development (Ellis, McFadyen-Ketchum, Dodge, Pettit, & Bates, 1999), patterns of homicide in families with biological fathers versus stepfathers (Daly & Wilson, 1988), and mother-fetus conflict during gestation (Haig, 1993). Two particularly laudatory programs of research are highlighted next.

Snakes and an Evolved Fear Module

Öhman, Mineka, and their colleagues have offered strong, programmatic, and compelling evidence that humans and closely related primates have an evolved "fear module" for reptiles (Öhman & Mineka, 2001). What makes this program of research exemplary is the nature, quality, and type of evidence that has been gathered for the special design features of this purported adaptation. This evidence has been strengthened by the use of multiple research methods (e.g., comparative methods, interviews, field observations, experimental laboratory studies) to test carefully derived predictions, by systematically testing and ruling out alternative theories and explanations, and by documenting the unique footprints of special design at multiple levels of measurement (ranging from neural mechanisms to general cognitive expectations and behavioral reactions).

Several interlocking findings clearly indicate that higher primates possess an evolved fear module (see Öhman & Mineka, 2001, for a review). Based on interviews with humans (Agras, Sylvester, & Oliveau, 1969), comparative field data on different primate species (King, 1997), and observations of primates living in captivity versus in the wild (Mineka, Keir, & Price, 1980), research has confirmed that humans and other higher primates have an acute fear of snakes with distant evolutionary origins. Conducting well-designed experiments, researchers have also demonstrated that lab-raised monkeys learn to fear snakes very quickly just by observing fearful expressions in other monkeys (Cook & Mineka, 1990), lab-raised monkeys show preferential conditioning to toy reptiles but not to innocuous stimuli such as toy rabbits (Cook & Mineka, 1991), and humans who receive shocks in the presence of snakes show longer, stronger, and qualitatively different conditioning responses than do humans who are shocked in the presence of non-aversive stimuli such as flowers (Öhman & Mineka, 2001). This body of findings implies that the strong association between snakes and aversive unconditioned stimuli emanates from the evolutionary history of primates rather than from culturally mediated conditioning processes.

Additional lab experiments have shown that humans automatically infer illusory associations between snakes and aversive stimuli. For example, people are more likely to perceive that fearful stimuli (snakes) co-occur with painful experiences (shocks) than is true of other nonfearful stimuli, even when there is no actual association between pairings of shock and different stimuli (Tomarken, Sutton, & Mineka, 1995). People also believe that shocks are more likely to follow exposure to dangerous stimuli such as snakes and damaged electrical equipment, but illusory correlations emerge only between snakes and shock once people have been exposed to a random series of stimulus/shock trials (Kennedy, Rapee, & Mazurski, 1997). Experiments assessing visual detection latencies have confirmed that when people are shown large sets of stimulus pictures, snakes automatically capture their visual attention, regardless of how many distractor stimuli are present (Öhman, Flykt, & Esteves, 2001). These results suggest that humans are "prepared" to perceive associations and process visual information about snakes and aversive outcomes in systematically biased ways.

Experiments have also identified where in the brain the "fear circuit" might be located. Using backward masking techniques that present stimuli outside of conscious awareness, Öhman and Soares (1994, 1998) discovered that fear responses can be learned and activated, even when backward masking prevents images of snakes from reaching higher cortical processing. This indicates that fear responses reside in ancient neural circuits that evolved long before the full development of the neocortex.

Viewed together, this entire body of evidence strongly suggests that humans and higher primates have a fear module that evolved to reduce recurrent threats posed by dangerous and potentially lethal animals. This module is sensitive to, and is automatically activated by, a specific class of stimuli, it operates in specific areas of the brain (the amygdala) that evolved before the neocortex, and it has fairly specialized neural circuitry. This innovative program of research nicely illustrates how different research methods—lab and field experiments, field observations, comparative methods—can be used to provide compelling evidence for a specific, cross-species psychological adaptation whose footprints exist at different levels of analysis and measurement.

MATE PREFERENCES IN WOMEN ACROSS THE REPRODUCTIVE CYCLE

Several well-conceptualized and carefully designed studies have tested the ovulatory shift hypothesis—that women have an evolved psychological adaptation that motivates them to prefer men who have "good genes" as short-term mates, primarily when they are ovulating and could conceive a child with such men (Thornhill & Gangestad, 2008). This program of work is elegant because the predictions are carefully derived from good genes sexual selection models as well as cross-species data, the predictions are very specific (entailing specific statistical interaction patterns), the predictions and findings are difficult to derive from competing theories/models, and numerous alternative explanations have been discounted.

According to the strategic pluralism model of mating (Gangestad & Simpson, 2000), women evolved to make trade-offs between two sets of attributes when evaluating men as potential mates: men's degree of health/viability (their "good genes") and their level of commitment/investment in the relationship and subsequent offspring. Fluctuating asymmetry (FA: the extent to which individuals are bilaterally symmetrical at different locations of the body) is one good marker of health/viability

(Thornhill & Gangestad, 2008). Thus, women should find more symmetrical men more attractive than less symmetrical men in short-term mating contexts, especially when they are ovulating (and could conceivably transmit the "good genes" of these men to their offspring). This model, therefore, predicts very specific statistical interaction patterns that are neither anticipated nor easily explained by alternative perspectives.

The ovulatory shift hypothesis has been tested using a variety of research methods and techniques (see Gildersleeve, Haselton, & Fales, 2014, for a review). Self-report questionnaire studies have confirmed that more symmetrical men are more likely to engage in extra-pair sex and are more prone to be chosen by women as extra-pair partners (e.g., Gangestad & Thornhill, 1997). Self-report and interview studies have revealed that women are more likely to have extra-pair affairs when they are ovulating, but they are *not* necessarily more prone to have sex with their current romantic partners during ovulation. Moreover, women report stronger sexual attraction to and fantasies about men other than their current romantic partners when they are ovulating (Gangestad, Thornhill, & Garver, 2002), a pattern that is *not* found for current partners unless they have "good genes" characteristics (e.g., Haselton & Gangestad, 2006).

To test predictions about olfactory markers of men's FA and ovulatory shifts in women, Gangestad and Thornhill (1998) had women smell unscented T-shirts worn by different men. If women were ovulating during the study, they rated the scents of more symmetrical men as more attractive than those of less symmetrical but, as predicted, this interaction effect did not emerge in nonovulating women. Providing discriminant validity evidence for this effect, Thornhill et al. (2003) also found that even though women prefer the scent of heterozygous major histocompatibility (MHC) alleles in men (which should be valued in primary partners because mating with an individual who has more diverse MHC alleles should limit infections within families), the preference for MHC did *not* increase when women were ovulating.

In a laboratory behavioral observation study, Simpson, Gangestad, Christensen, and Leck (1999) found that more symmetrical men displayed greater social presence and more direct intrasexually competitive tactics (rated by observers) than less symmetrical men when being interviewed by an attractive woman and competing against another man for a "lunch date." When a different group of women evaluated the videotaped interviews of these men and rated how attractive they found each one as a short-term and a long-term mate, women who were ovulating were significantly more attracted to men who displayed greater social presence and direct intrasexual competitiveness—the tactics displayed by more symmetrical men—in short-term but *not* in long-term mating contexts (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004). Considered together, these findings confirm that women's mate preferences vary across the reproductive cycle in very specific and theoretically consistent ways.

SUMMARY AND CONCLUSIONS

Current research programs in the evolutionary sciences can be strengthened in several ways from a methodological standpoint. First, when feasible, researchers should use a wider range of research methods in their ongoing programs of work, especially more experimental methods and techniques. Second, a wider array of measurement and statistical techniques should be utilized. Third, sounder evidence needs to be provided regarding the validity of major manipulations, scales, and individual-item measures before they are adopted for widespread use (e.g., experimental manipulations of "social status," self-report measures of "mate value"). Fourth, greater attention should focus on deducing, modeling, and testing the features of psychological mechanisms that are believed to be evolved adaptations. Fifth, stronger and better evidence is needed to determine how well outcomes predicted by different evolutionary theories or models fit different data sets, especially relative to competing nonevolutionary theories or models. Whenever possible, alternative constructs and explanations should be carefully derived and measured to test and adjudicate between competing constructs or models. Sixth, the special design features of purported adaptations should be directly specified and tested at different levels of analysis and measurement. Seventh, evidence for possible adaptations needs to be procured for multiple evidentiary standards. Eighth, empirical evidence for specific hypotheses should be gathered in different cultures, especially those that are more similar to the environments in which ancestral humans evolved. Finally, more effort must be devoted to developing and testing novel predictions, particularly those that cannot be easily derived or explained by competing theories.

In conclusion, evolutionary scientists need to emulate the methodological breadth and creativity of Charles Darwin. This can be accomplished in part by utilizing a broader array of research methods and statistical techniques, many of which can help investigators map out and comprehend the evolved architecture of the human mind much more precisely. To convince the wider scientific community of the value as well as the predictive, explanatory, and integrative power of evolutionary approaches, evolutionary theories and models need to be developed more carefully, derived more precisely, and tested more thoroughly than theories that do not involve historical origins. Given their tremendous explanatory and integrative power, some evolutionary theories have, at times, proceeded ahead of good empirical evidence, especially with respect to humans. Recent advances in research and statistical methods are now closing this gap. However, evolutionary researchers must continue to refine the deductive logic of their theoretical models, revise or alter questionable or conflicting tenets of middle-level theories, discard or recast problematic hypotheses, and formulate more specific hypotheses that explicitly test the special design properties of presumed adaptations. If these goals are achieved, the evolutionary sciences will continue to make rapid and significant theoretical and empirical progress in the coming years.

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CHAPTER 4

Evolutionary Psychology and Its Critics

EDWARD H. HAGEN

> Given the character of the evolutionary process, it is extremely unlikely that all human beings are essentially the same, but even if we are, I fail to see why it matters.
>
> —Philosopher David Hull (1986, p. 4)

> Progress in physics depends on the ability to separate the analysis of a physical phenomenon into two parts. First, there are the initial conditions that are arbitrary, complicated, and unpredictable. Then there are the laws of nature that summarize the regularities that are independent of the initial conditions. The laws are often difficult to discover, since they can be hidden by the irregular initial conditions or by the influence of uncontrollable factors such as gravity friction or thermal fluctuations.
>
> —Physicist David Gross (1996, p. 14256)

INVARIANTS

At every spatial and temporal scale, the universe varies. It is astonishing, then, that all this variation can be explained in terms of (a) a small number of invariants, specifically, a few elementary particles that interact via a few fundamental forces subject to the laws of physics, and (b) the variable initial *state* of these particles, for example, their positions and momenta.

Like physics, most scientific disciplines seek to partition the systems they study into an invariant, or nearly invariant, part and a variable part. In chemistry, for example, a relatively few invariant elements combine to form countless distinct molecules, and in biology an invariant genetic code with but four symbols is the basis for countless genetic sequences.

Thanks to Clark Barrett, Dan Conroy-Beam, and David Buss for many helpful comments and suggestions.

Evolutionary psychology (EP) has made a bold claim: The human brain comprises a large set of complex psychological mechanisms whose *designs* are invariant, that is, universal in the species. These designs evolved by natural selection in response to a limited set of invariant properties of ancestral environments that were relevant to human reproduction, which EP dubs the environment of evolutionary adaptedness (EEA). The designs are grounded in the invariant DNA all humans share. Individuals, in contrast, are unique *states* of invariant complex designs, plus a small dollop of genetic noise (e.g., Hagen & Hammerstein, 2005; Tooby & Cosmides, 1990a).

Object recognition is an example of a psychological mechanism with an invariant complex design. Object recognition is computationally difficult: Each particular object can produce infinitely many different images on the retina due to changes in position, angle, distance, lighting, and the presence of visual clutter (e.g., background, other objects); though we see an object many times, we never see the exact same image of it twice. Yet within 300 ms, virtually all humans effortlessly identify and categorize an object from tens of thousands of possibilities. As I write, this is a feat beyond the capabilities of any computer (DiCarlo, Zoccolan, & Rust, 2012).

According to EP, much of human cognition will be similarly complex and universal, a proposition that is the brain-specific version of the more general, and much more widely accepted, claim that the human organism comprises a large set of complex evolved mechanisms, such as the heart, lungs, and kidneys, whose designs are invariant in the species.

The claim of invariant design is restricted to *complex* mechanisms (physiological or psychological), that is, those whose development involves the coordinated interactions of many loci across the genome (Tooby & Cosmides, 1990a). Whereas simple evolved mechanisms that are based on one or a few genes, such as skin color, often vary among populations, complex mechanisms generally do not, an issue to which I will return.

Bold claims rightly attract critical attention. Some of it has come from biologists, like Stephen J. Gould and Richard Lewontin, and from behavioral ecologists, like Foley (1995) and Laland and Brown (2011). Much of it, though, has come from philosophers of science, many of whom have concluded that EP is a "deeply flawed enterprise" (Downes, 2014).

I tackle criticisms of invariant evolved psychological design in the first part of this chapter. These call into question the role and importance of "design," "function," and "adaptation" in the study of life. I tackle criticisms of the EEA concept in the second part of this chapter. My responses highlight a perspective that is commonplace in EP, and among adaptationists more generally, yet which these critiques rarely acknowledge.

DESIGN

The universe is a machine. Organisms are machines. Brains are machines. If, by *machine*, we mean a system whose properties and dynamics conform to the laws of physics and chemistry, which I refer to as the *mechanical* view, then each statement is accepted by virtually all scientists today. If, instead, we mean a system that exhibits design or purpose, which I refer to as the *teleological* view, then each statement has had passionate adherents and detractors from the dawn of Western thought right up to the present. Until the Enlightenment, for instance, it was widely believed that the clocklike movement of the planets was evidence of design or purpose in nature, which then implied the existence of a Designer (God) (Ariew, 2002).

Teleological accounts of the nonliving world were defeated by the accumulating ability to explain the nonliving world in purely mechanistic terms. Examples include that the orbits of the planets are explained by the law of gravitation, that physical objects comprise atoms, and that the properties of light, electricity, and magnetism are explained by Maxwell's equations. None of these explanations implies function or purpose.

The idea that, in contrast to the cosmos and all other nonliving systems, organisms and their parts *are* designed or purposive, which I term *biological teleology*, has had a very different fate. The parts of animals, such as hearts, lungs, arteries, and nerves, have been seen as serving important functions or purposes for the organism since antiquity, and this view remains the foundation of modern medicine.

The main difference between the biological teleology of Aristotle, Galen, Paley, and many others, and that of modern biology textbooks, would seem to be the explanation of the origins of design or purpose. Prior to Darwin, the intricate designs seen in organisms were, like the clockwork motion of the heavens, taken by many to be evidence of God. After Darwin, organism design was attributed to natural selection.

Much of the controversy surrounding EP involves its explicit and enthusiastic grounding in biological teleology: The brain comprises parts that are useful, and that usefulness explains why they are there. Human cognition exhibits all the hallmarks of design: our impressive ability to identify and recognize objects, and to construct detailed 3D models of the world from 2D stimuli; to remember vast amounts of information for decades; to learn language and countless other skills; to produce impressive tools; and to use all the foregoing to make our way in the world. These abilities are all the more impressive in light of the failure to replicate most of them in artificial systems despite well-funded efforts spanning more than half a century.

Given that the usefulness of the body's other parts, and their origin by natural selection, is relatively uncontroversial, why is EP surrounded by controversy (e.g., Hagen 2005)? Many of the critics of EP are philosophers, and in philosophy, teleology has a checkered past. The philosopher Perlman (2004, pp. 3–4) explains:

> Philosophers, going back to Aristotle, used to make generous use of functions in describing objects, organisms, their interactions, and even as the basis of ethics and metaphysics. And yet, since the Enlightenment, talk of the function of natural objects, teleological function, began to be viewed with suspicion, as the mechanical model of the world replaced the old Aristotelian model. From a religious standpoint, it used to be easy to see how objects in the natural world could have natural functions, for God was said to instill functions by design throughout Creation. But philosophers became increasingly (and wisely) reluctant to invoke God to solve every difficult philosophical problem, and became unwilling to indulge in such religious explanations of teleology. It is easy to see how artifacts produced by humans would have functions, derived from the intentions of the human designers, but without God, it seemed impossible to believe that teleology has a place in Nature.
>
> By the twentieth century, analytic philosophers were positively allergic to any mention of teleology or teleological function.

The philosophers have a point. If organisms are physiochemical systems whose structure is completely independent of human agency, and if the properties of such systems are fully explained by physics and chemistry, then where does the function or purpose of their parts come from? Function and purpose seem to require intention. Without God, are these terms anything more than handy metaphors?

Functional explanations are so intrinsic to biology, however, that philosophers started taking teleology seriously again in the 1970s (Griffiths, 2011). At about the same time, a debate erupted in biology over teleological, that is, adaptationist, explanations of behavior, especially human behavior.

The Spandrels of San Marco (Gould & Lewontin, 1979) was perhaps the most influential contribution to this debate. Gould and Lewontin argued that the organism is like the great dome of Saint Mark's Cathedral in Venice, which sits atop four arches. The dome's spandrels—the triangular spaces at the intersection of two rounded arches at right angles—are, they claimed, a necessary by-product of mounting a dome on four arches.[1] The spandrels are decorated, and

> The design is so elaborate, harmonious, and purposeful that we are tempted to view it as the starting point of any analysis, as the cause in some sense of the surrounding architecture. But this would invert the proper path of analysis. The system begins with an architectural constraint: the necessary four spandrels and their tapering triangular form. (Gould & Lewontin, 1979, p. 582)

Gould and Lewontin's charge is that students of evolution regard "natural selection as so powerful and the constraints upon it so few that direct production of adaptation through its operation becomes the primary cause of nearly all organic form, function, and behavior." Instead, they rightly argue, in organisms as in buildings, constraints and by-products abound. According to them, the adaptationist program atomizes organisms into traits, each of which is assumed to be an adaptation; by-products, constraints, and other alternatives to adaptation are rarely entertained. For Gould (1997a), EP committed the sins identified in the Spandrels paper:

> I shall also take up the methodology of so-called "evolutionary psychology"—a field now in vogue as a marketplace for ultra-Darwinian explanatory doctrine. Evolutionary psychology could, in my view, become a fruitful science by replacing its current penchant for narrow, and often barren, speculation with respect for the pluralistic range of available alternatives that are just as evolutionary in status, more probable in actual occurrence, and not limited to the blinkered view that evolutionary explanations must identify adaptations produced by natural selection.

The Spandrels paper had a substantial impact on philosophers of biology, who have attempted to sort out what adaptationism is, and what role it plays in evolutionary biology, which after all, also studies genetic drift and constraints. To advance debate over adaptationism, the philosopher Godfrey-Smith (1999, p. 186) identified three possible types:

> *Empirical Adaptationism*: Natural selection is a powerful and ubiquitous force, and there are few constraints on the biological variation that fuels it. To a large degree, it is possible to predict and explain the outcome of evolutionary processes by attending only to the role played by selection. No other evolutionary factor has this degree of causal importance.

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[1] There have been many criticisms of the Spandrels paper, including that the architectural feature is actually called a *pendentive*, that pendentives play an important structural role in supporting both the arches and the dome, and that this design was chosen over others because it was better suited for displaying Christian iconography, the *raison d'être* of Saint Mark's. Hence, the spandrels of San Marcos *are* functional and the term *spandrel* is, therefore, a poor choice to refer to by-products of adaptations. See, for example, Dennett (1995); Mark (1996); Houston (2009); cf. Gould (1997b).

> *Explanatory Adaptationism*: The apparent design of organisms, and the relations of adaptedness between organisms and their environments, are the big questions, the amazing facts in biology. Explaining these phenomena is the core intellectual mission of evolutionary theory. Natural selection is the key to solving these problems—selection is the big answer. Because it answers the biggest questions, selection has unique explanatory importance among evolutionary factors.
>
> *Methodological Adaptationism*: The best way for scientists to approach biological systems is to look for features of adaptation and good design.

Empirical adaptationism is close to Gould and Lewontin's view of adaptationism, to that of some other evolutionary biologists and philosophers of biology (e.g., Orzack & Sober, 1994), and probably to that of many scholars outside evolutionary biology. This might explain their skepticism about adaptationism.

Godfrey-Smith offered this typology, however, to draw attention to explanatory adaptationism, which he identifies with adaptationist Richard Dawkins. Selection might explain only 1% of all molecular genetic change, but, Dawkins and many other adaptationists would say, that is the 1% that counts (Godfrey-Smith, 2001). According to Downes (2014), EP adopts the explanatory type of adaptationism. I largely agree (but see Tooby & Cosmides, 1997, for an appeal to methodological adaptationism).

What, then, is the *scientific* status of explanatory adaptationism? Just because Dawkins and EP find these questions to be the most important, Godfrey-Smith argues, it doesn't follow that all biologists should. Explanatory adaptationism might just reflect these scientists' personal preferences. Buller (2005, p. 472) agrees:

> Evolutionary Psychology is adaptationist in the sense that it conceives of adaptations as occupying a more central place in our psychologies than any other psychological traits—indeed, so central a place that only psychological adaptations constitute our nature.
>
> Privileging adaptations in this way, however, and viewing them as "natural" in a way that other traits are not, has no foundation in evolutionary theory proper.

According to Godfrey-Smith, one way to defend explanatory adaptation is to appeal to what natural selection does not just for biology but also for science as a whole. By destroying the Argument from Design, natural selection is an essential pin holding together the scientific/enlightenment worldview. But that means "The roots of explanatory adaptationist thinking are found not so much in biological data, but in [philosophical] views about the place of biology within science and culture as a whole" (Godfrey-Smith, 2001, p. 15). If so:

> [A]nother possible reply to explanatory adaptationism rejects the idea that the traditional problem of apparent design is a well-posed and well-motivated question, in the light of current knowledge. Rather than being a problem that has turned out to be visible and challenging from both theological and naturalistic points of view, the "problem" of design and adaptedness is itself a product of a theological view of the world. So on this view, explanatory adaptationism wrongly accepts the terms of debate favored by theological views of the world; it is the *tradition of natural theology continued.* (Godfrey-Smith, 1999, p. 190; emphasis in the original)

Buller (2005, p. 475) concurs (emphases in the original):

> The problem of complex design was actually *Paley's problem*. It was the problem that nineteenth-century theologians used to challenge naturalistic accounts of the origins and

> complexity of life, and they chose that problem because they thought it to be unsolvable by naturalistic theories. There is nothing *in the nature of things* that dictates that the problem of complex design is central to understanding life on earth.

Downes (2014) likewise agrees that EP's adaptationism does little more than distinguish it from natural theology, creationism, and intelligent design.

Explaining Explanatory Adaptationism

Organisms are physical systems that must conform to physical laws, in particular, to the laws of thermodynamics. Yet the laws of thermodynamics almost seem to rule out the existence of organisms. As Erwin Schrödinger (1944), one of the architects of quantum mechanics, explained in his classic book *What Is Life?*:

> When a system that is not alive is isolated or placed in a uniform environment, all motion usually comes to a standstill very soon as a result of various kinds of friction; differences of electric or chemical potential are equalized, substances which tend to form a chemical compound do so, temperature becomes uniform by heat conduction. After that the whole system fades away into a dead, inert lump of matter. A permanent state is reached, in which no observable events occur. The physicist calls this the state of thermodynamical equilibrium, or of "maximum entropy." . . . It is by avoiding the rapid decay into the inert state of 'equilibrium' that an organism appears so enigmatic; so much so, that from the earliest times of human thought some special non-physical or supernatural force (*vis viva*, entelechy) was claimed to be operative in the organism, and in some quarters is still claimed. (Schrödinger, 1944, pp. 69–70)

Schrödinger's physicist expects a highly structured organism to quickly decay into an inert lump of matter because the vast majority of states of the organism that are consistent with its energy and composition, and are thus physically possible states, do not preserve the macroscopic structure upon which the life of the organism depends. Hence, it would seem that there is a high probability that the system of particles that is the organism would enter states in which organism functionality is degraded. Some particles of the heart could diffuse into the lungs, for instance, and vice versa, with the effect that neither the heart nor the lungs would continue to perform their functions.[2]

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[2] It is well known that organisms do not violate thermodynamic law because they are not isolated systems; by drawing on an external source of what Schrödinger (1944) refers to as negative entropy (e.g., the sun), it is possible for a highly ordered system, like an organism, to maintain its order by increasing the disorder of the external environment. What is less widely recognized, however, is that no one knows exactly how this happens. The physics of systems at (or close to) thermodynamic equilibrium is well understood. There is no complete and unified theory of systems that are far from equilibrium, however, which includes life. As Qian (2007) remarks, "How is it possible to develop mathematical models of cellular processes such as gene regulation and signal transduction if even the underlying basic physical chemistry is still not in hand?"

Stotz and Griffiths (2003), on the other hand, criticize EP for, among other things, "redefining negentropy itself as functional design (!). . . ." But EP has done no such thing. EP, along with most evolutionary biologists, has merely claimed that *functional* organization would not arise without natural selection. That many nonliving systems exhibit order (but not functional order!) is commonplace and not disputed by EP. On the contrary, order in the nonliving world is essential to the EEA concept, discussed in the section titled The EEA.

The perspective that is missing in many criticisms of adaptationism and EP is that a functioning organism, and its persistence for even a short amount of time, appears to be a highly improbable state of affairs (e.g., Schrödinger, 1944; Tooby, Cosmides, & Barrett, 2003). Gould and Lewontin's (1979) Spandrels paper, and the many criticisms it inspired, have things backward. The question is not, Do noise and constraints play an important role in organism structure? The question is, Why don't noise and constraints *dominate* organism structure?

Even in a well-functioning organism, such as a healthy 5-year-old girl, a tiny perturbation can quickly result in Schrödinger's "dead, inert lump of matter." Only 0.00000002 grams of botulinum toxin, produced by a food-borne bacterium (Gill, 1982), is enough to divert the 20,000 gram physical system that is the girl from a trajectory that would result in her reproduction, to a second, dramatically different outcome of death.

Over the course of human evolution the latter outcome was not the exception. For most species, including humans, most individuals die before reproducing. In human populations without access to modern birth control, a woman would typically have about five to six live births, yet over the long term the average number that survive to reproduce can only be about two (the replacement rate)—the famous observation of Malthus that so inspired Darwin. Prior to the modern era, a large fraction of all humans that ever lived died in childhood. Even today, about 5%–6% of all children under the age of 5 die, and in the 48 least-developed countries approximately 13% of children die before the age of 15 (United Nations, 2011).

It is the special mechanisms—adaptations —that provide any hope of survival from one moment to the next. Interestingly, Paley (in a sermon arguing that God designed life as a state of probation, not misery) expressed a similar thought:

> In our own bodies only reflect how many thousand things must go right for us to be an hour at ease. Yet at all times multitudes are so; and are so without being sensible how great a thing it is. Too much or too little of sensibility, or of action, in any one of the almost numberless organs, or of any part of the numberless organs, by which life is sustained, may be productive of extreme anguish or of lasting infirmity. A particle, smaller than an atom in a sunbeam, may, in a wrong place, be the occasion of the loss of limbs, of senses, or of life. Yet under all this continual jeopardy, this momentary liability to danger and disorder, we are preserved. It is not possible, therefore, that this state could be designed as a state of misery, because the great tendency of the designs which we see in the universe, is to counteract, to prevent, to guard against it. (Paley & Paley, 1825, p. 43)

Drift and constraints only come into play if organisms survive and reproduce, and it is exactly this problem—survival and reproduction in a particular physical, biological, and social environment—that adaptationists are trying to solve.

The focus of Dawkins, EP, and other adaptationists on adaptation and natural selection, then, is not explained by mere personal preference or by the role that natural selection plays in supporting a scientific worldview. Instead, it is explained by the fact that it is precisely an organism's adaptations that enable, or permit, its reproduction despite all the physical processes that militate against it.[3]

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[3] Some adaptations are strictly necessary for reproduction; others simply increase the probability of reproduction.

Is explanatory adaptationism, so understood, "the tradition of natural theology continued"? Natural theology also emphasized cosmological teleology: Copernicus, Kepler, Newton, and many other founders of modern science viewed their work on, for example, the clocklike motion of the heavens, as providing evidence of a transcendent designer (Brooke, 2002). As Gillispie (1951, p. 6) argued,

> Natural philosophy and religion were not the same realm, of course, but science and theology paralleled each other in being concerned with manifestations of divinity in a universe which was assumed to be permanently divine, increasingly intelligible, and so designed that man could better his lot by improving his understanding of physical phenomena.

If adaptationism and EP are the tradition of natural theology continued, then so, too, is much of science.

Still, it is worth considering how scholars working in the tradition of natural theology could discover numerous anatomical and physiological truths. Here, the towering figure is not Paley, the 18th-century British theologian, but Galen, the second-century Roman physician and philosopher whose teachings dominated Western medicine for 1,500 years. Galen was the consummate empiricist, basing his views on countless dissections and experiments. He showed that cutting the recurrent laryngeal nerves in the pig resulted in the loss of vocalization, for example, which might have been the first experimental evidence that the brain controls behavior (Gross, 1998). Such was the quality of his work that much of it is either textbook material to this day, or was the foundation for the later advances of Vesalius, Harvey, and their scientific heirs (Pasipoularides, 2014).

Galen viewed the structure of the body as the result of, and evidence for, intelligent design by a Platonic Demiurge. Unlike the Stoics, however, who argued that each kind of organism serves a purpose external to it that is established by God—the purpose of grass is to be eaten by sheep, just as that of sheep is to be eaten by man—Galen espoused an internal teleology: The parts of organisms serve the survival and reproduction of the organism itself and not some purpose external to the organism (Schiefsky, 2007). The distinction is critical:

> While the functions of the parts of an externally teleological system depend on the purpose for which the system has been designed, the functions of the parts of an internally teleological system can be understood independently of the intentions of its designer—if there is one. The parts have functions, understood as contributions to the system's continued existence, whether or not the system was designed by an intelligent agent. (Schiefsky, 2007, pp. 396–397)

Galen's empiricism and his adherence to internal teleology—a notion very similar to the views of modern anatomy and physiology and to the view that emerges from Darwinian theory—enabled him to correctly infer much about the functional structure of the body.[4]

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[4] Although there is clear overlap between the functions of Galen and the adaptations of evolutionary biology, there are also substantial differences. For instance, Galen, like Aristotle, thought that some organs existed not simply to make life possible but to make life better—to serve well-being or the best life (Schiefsky, 2007). Adaptations have no such function. Conversely, adaptations can have properties that, for Galen and Paley, might have been inadmissible, such as trading off survival for reproduction.

THE INVARIANCE OF COMPLEX DESIGN

EP is a theory of human nature. Philosopher David Hull famously asserted that there is no such thing, specifically, that there is no set of characteristics possessed by all, and only, humans (Hull, 1978; see also Ghiselin, 1997). All humans have hearts, for instance, but so do many other animals. No nonhuman animal has language, but some people also have failed to develop language abilities, yet are still human. For Hull,

> [P]articular organisms belong in a particular species because they are part of that genealogical nexus, not because they possess any essential traits. No species has an essence in this sense. Hence there is no such thing as human nature. (Hull, 1978, p. 358)

Buller concludes his book-long critique of EP recapitulating Hull's argument (for philosophical views of human nature that are more compatible with EP, see, e.g., Machery, 2008; Samuels, 2012).

Half of Hull's argument is of little concern to EP, which does not limit itself to *uniquely* human psychological mechanisms. On the contrary, if, for example, many primate relatives had a mechanism to learn fear of snakes, that would support the hypothesis that humans do too (and EP would count it as part of human nature).

The other half of Hull's argument, though, strikes at EP's core: Many complex mechanisms are present in some humans and absent in others. Newborns cannot walk bipedally, for instance, and men lack ovaries, yet both are still human. In principle, there could even be nonsexual morphs, as there are in other species: Male side-blotched lizards, for instance, have one of three different throat colors, each of which is associated with different behavioral patterns and physiology (Wilson, 1994). Hull (1986) and Buller (2005) additionally emphasize widespread genetic polymorphisms.

These apparent exceptions to invariant complex design are not really exceptions, and instead serve to clarify the concept. First, polymorphisms at loci that vary independently of one another are simple differences that EP does not expect to be necessarily invariant but that also can't explain the complex abilities of human cognition, like object recognition. Second, infants obviously possess the complex genetic design for bipedalism, but it isn't yet fully developed.

Third, most of the genes for ovaries, testes, and other important and complex sex differences reside on autosomes (or on the X-chromosome), which, across generations, spend half their time in male bodies and half in female bodies.[5] Thus, males possess the design for ovaries (which is not expressed in males), and females possess much of the design for testes (which is not expressed in females). The difference is the presence or absence of a genetic switch, the Y-chromosome.[6] Similarly, in many polymorphic species, most of the genes for all morphs seem to occur in all individuals; the design is shared, just as it is with sexual morphs. What differs is the presence or absence of a genetic or environmental switch that determines which design is expressed.[7]

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[5] The X-chromosome spends one-third of its evolutionary history in males.

[6] The Y-chromosome is small, and because a single gene on it, SRY, initiates male sexual differentiation, it can be thought of as a genetic switch that activates one of two genetic designs, both of which are present in both sexes. Recently, though, other male-specific genes have been discovered on the Y-chromosome. This male-specific region seems to mostly involve genes that are expressed in the testes (e.g., Hughes et al., 2010).

[7] By genetic switch I mean a single locus, or a very small number of loci, that regulates expression of many loci; alleles at the switch locus then "toggle" development of different complex morphs.

The reason that complex functional differences among morphs in the same species are typically based on genetic switches, rather than large suites of interacting alleles that are unique to each morph, is that the latter genetic architecture is unstable: Sexual reproduction and recombination quickly erode associations among alleles at multiple loci, and even a small amount of migration quickly erodes genetic differences between populations.[8]

Thus, EP and other evolutionary biologists locate invariant design in the DNA-encoded developmental programs that generate complex phenotypes during ontogeny (e.g., Hagen & Hammerstein, 2005; Tooby & Cosmides, 1990a).

THE INDIVIDUAL IS A UNIQUE REALIZATION OF AN INVARIANT DESIGN

Though the design of a complex psychological mechanism—its underlying developmental program—is invariant, the neurological mechanism it generates need not be. Invariant developmental programs, typically, evolved to read environmental inputs, which can alter the assembly of the mechanisms in principled ways. The language circuitry of a native Chinese speaker might differ from those of a native English speaker, for instance (e.g., Geary & Bjorklund, 2000; Hagen & Hammerstein, 2005; Tooby & Cosmides, 1990a).

Complex functional differences among individuals, then, are probably not due to differences in design (i.e., suites of interacting alleles that are present in some individuals but not others), but to age- and sex-specific differences in the expression of a shared design during development, differences in expression due to differences in the condition of the environment or organism, differences in genetic and epigenetic switches (e.g., Haig, 2007), or perturbations due to mutations or disrupted development.

Even when there are no functional differences between individuals, invariant designs will still give rise to enormous interindividual variation because evolved mechanisms typically have multiple states. The *raison d'être* of psychological mechanisms is to read and respond to environmental input. Because no two individuals inhabit identical environments or have identical sequences of experiences, and because each individual has a unique dollop of genetic noise, the joint *state* of an individual's psychological mechanisms is unique. Each individual has been exposed to an overlapping but not identical set of objects during his or her life, for example, and thus has a unique ability to recognize a particular large set of objects. The states of invariant memory mechanisms, emotion mechanisms, hunger mechanisms, and so forth, are all contingent on individual experiences and circumstances. A hypothetical brain with but 30 independent invariant mechanisms, each of which had only two states, would have, altogether 2^{30}, or about 1 billion possible states. According to EP, the human brain comprises hundreds or thousands of evolved mechanisms, most of which can be in multiple states contingent on conditions during development and the current environment. It is obvious that, although the designs are invariant, the state of the phenotype is unique for each individual (Tooby and Cosmides, 1990a; Buss, 2009).

Hagen and Hammerstein (2005) frame this perspective in strategic terms. The genome encodes a strategy that is shared by all members of the species. During development, each individual makes a different series of "moves" that depend on

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[8] There are genetic mechanisms other than switches that might underlie complex polymorphism in some species, and if these occurred in humans they might constitute genuine exceptions to EP's claim of an invariant complex evolved design. For review, see Mckinnon and Pierotti (2010).

environmental circumstances or the inherited values of genetic and epigenetic switches. Male, female, and other morphs are such “moves,” and a phenotype is thus a state of play.

THE EEA

For a new allele to increase to high frequency in the population, it must cause some particular effects that (on average) increase the reproduction of the organism in which it resides, and it must do so for, typically, many hundreds or thousands of generations. For the allele to persistently cause these effects, the environment with which it is interacting, which can include the organism itself, must have persistent properties. This does not mean that the target environment does not vary, but rather that variation is governed by unchanging rules or statistical patterns. The varying world, in other words, is a consequence of a deeper, invariant structure.

This invariant structure includes mathematical properties, such as the rules of arithmetic; physical and chemical laws, such as the laws of optics and conservation of energy; and looser statistical regularities, such as spiders and snakes are often venomous. Invariant designs evolve to reliably manipulate the variable environment by exploiting its underlying invariant structure.

Even associative learning depends on environmental regularities: It would be pointless to learn to associate a stimulus with food today if that stimulus did not predict food tomorrow. That the world is rife with shorter-term associations is itself an invariant that underlies the evolution of associative learning mechanisms.

EP uses the term EEA in two senses: to refer to the entire set of environmental regularities that were relevant to human evolution, and, as discussed shortly, to refer to adaptation-specific regularities. It is the latter that is the basis of specific EP research programs.

EP often equates the human EEA, in its broad sense, with the Pleistocene, which began 2.6 million years ago[9] and ended about 10,000 years ago. This choice was motivated by four facts: The first members of the genus *Homo* appear in the African fossil record near the beginning of the Pleistocene; there was sufficient time during the Pleistocene for new complex adaptations to evolve; near the end of the Pleistocene modern humans had completed a global expansion out of Africa and were starting to transition to an agricultural lifestyle, which brought profound changes in, among other things, diet, disease, and settlement pattern; and new complex adaptations could not have evolved in the past 10,000 years.

I next address four common criticisms of the EEA, one of the most controversial concepts in EP.

IS THE EEA UNKNOWABLE?

> For many purposes the study of present environments as models of past environments are our best window on the past, because an enormous number of factors, from the properties

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[9] Until recently, the beginning of the Pleistocene was placed at 1.8 million years ago. However, there has long been a consensus that it should be placed at the first evidence of climatic cooling of ice-age magnitude, which is now known to have occurred earlier, c. 2.6 million years ago, perhaps triggered by the closing of the Panama isthmus (Cohen and Gibbard, 2010).

> of light to chemical laws to the existence of parasites, have stably endured. (Tooby & Cosmides, 1990b, p. 390)

Many critics have argued that we don't know, and perhaps can't know, much about how our Pleistocene ancestors lived, so the EEA concept is, at best, uninformative, and, at worst, invites groundless speculation and storytelling. Gould (1997a), for example, wrote that evolutionary psychologists "have made their enterprise even more fatuous by placing their central postulate outside the primary definition of science—for claims about an EEA usually cannot be tested in principle but only subjected to speculation." Ironically, Gould was a paleontologist whose own research involved testing claims about the distant past. Buller (2005, p. 93), another critic, says "[W]e can't specify the adaptive problems faced by our ancestors precisely enough to know what kinds of psychological mechanism would have had to evolve to solve them." Laland and Brown (2011, p. 177) similarly say, "What is wrong with the notion of the human EEA as a particular time and place? The problem is that comparatively little is known about the lifestyle of our ancestors throughout the Pleistocene. Consequently, the EEA concept has engendered a wealth of undisciplined speculation and story-telling in which virtually any attribute can be regarded as an adaptation to a bygone Stone-Age world." Richardson (2007, p. 41) says "Direct evidence concerning ancestral environments, variation, social structure, and other relevant features are often not available, though they sometimes are."

The criticism that we don't, or can't, know much about the human EEA is a strong claim with profound consequences for any evolutionary analysis of the human organism, including its cognitive functions. Adaptations evolved to manipulate aspects of the environment. If the environment is unknown, it would be difficult, and perhaps impossible, to make much sense of the adaptation. Because many EP critics accept that the functional properties of organisms evolved by natural selection, their claim that the human EEA is mostly unknown, and often unknowable, entails the claim that the evolved functions of the body, including the brain, will remain mostly unknown. These include all evolved cellular functions (including neural functions), the immune system, organs, bones, and the rest. This conclusion seems absurd. If it were true, the critics should worry much more about the billions of dollars spent every year on research to elucidate all these functions than they should about the relatively small group of evolutionary psychologists (Hagen, 2005).

How mysterious, then, is the human EEA? If the EEA were *completely* unknown, we would have to consider that it might have resembled any possible environment. Did humans evolve in a galactic dust cloud? Did they evolve on a gas giant, like Jupiter? Did they evolve in the asteroid belt, or on a planet like Mars or Venus? Did they evolve in the oceans of earth, or among the giant dragonfly-like insects of the Carboniferous, or during the time of the dinosaurs?

No, *Homo* evolved in the terrestrial environments of Africa and Eurasia during the past 2 million years, which, in evolutionary terms, is relatively recently. The giant insects of the Carboniferous were gone, the dinosaurs were gone. Many of the plant and animal taxa of the Pleistocene are similar to those that exist today. Physics and chemistry were the same—the refractive index of the atmosphere was close to 1, for example, just as it is today. Geology was the same. Much of the ecology was similar to what we see today. Our bodies were almost the same. Even the social environment was not so different: There were people of various ages and both sexes, that lived in groups, that were healthy and sick, that were of varying degrees of relatedness, and so on.

Some critics acknowledge that aspects of the environment in which humans evolved are known, but nevertheless argue that the selective pressures that acted on human cognition might never be understood well enough. Along these lines, Sterelny and Griffiths (1999) raise a "grain" problem, which is taken up by Buller: "It is true that we can always be certain that just about all sexually reproducing species face the adaptive problems of selecting mates of high reproductive value and inducing potential mates to become actual mates. These descriptions of adaptive problems are so coarse-grained, however, as to be wholly uninformative about the selection pressures that act on a species" (Buller, 2005, p. 97).

To illustrate the problem, Buller notes that although all male birds must attract mates, different species do this in very different ways: The male bowerbird must build an ornate bower, for example, whereas a male sedge warbler must sing a wide repertoire of songs. Thus, although, at a coarse grain, males of both species face the same problem, at a finer grain, the males face very different problems—building bowers versus singing—and hence different selection pressures on their cognitive evolution. Buller concludes "[S]imply knowing that Pleistocene humans needed to attract mates doesn't inform us of the subproblems that constituted that adaptive problem for Pleistocene humans. And it is those more specific subproblems that adaptations would have evolved to solve. In order to get the more fine-grained and informative description of the subproblems, however, we would need to have more detailed knowledge of the lifestyles of our ancestors. And that's knowledge we simply don't have" (Buller, 2005, p. 98).

How, then, can Buller write confidently about the evolved strategies of male bowerbirds and sedge warblers, about whom we have even *less* direct evidence of ancestral lifestyles (e.g., Naish, 2014)? Buller is inferring the mate attraction strategies of ancestral birds from the strategies of living birds, of course, but apparently is not willing to do the same with humans.

Sterelny and Griffiths (1999) and Buller (2005) both argue, in addition, that because human cognitive evolution was driven by a social arms race (they claim), there was no stable EEA to which to adapt:

> According to [the Machiavellian] hypothesis, our mental capacities evolved in an "arms race" with human populations. . . . If the selection pressures important in cognitive evolution derive from interactions within the group, then selective environment and adaptive response change together. There is no invariant environment to which the lineage is adapted. (Sterelny & Griffiths, 1999, p. 328)

Pitting the arms race concept against the EEA concept is puzzling (Machery & Barrett, 2006). First, arms races have produced some of the most spectacular and indisputable examples of adaptation known to science—the speed of cheetahs and gazelles, the jaw-dropping camouflage of leaf insects, the sophistication of the immune system and of the pathogens that evade it. Second, as such examples make clear, arms races often (though not always) produce strong *directional* selection: Fast gazelles select for faster cheetahs, which select for faster gazelles, and so forth. In these cases, the EEA is especially well defined. Third, the social arms race idea is not a core premise of EP. Instead, it is a very specific empirical claim about the human EEA, which is why the evolutionary psychologists who have developed versions of it (e.g., Flinn, Geary, & Ward, 2005; Miller, 2001) have invested considerable effort in providing the necessary theoretical and empirical support. Their main thesis is that a social arms race created strong directional selection on human intelligence, which would explain the evolution of exceptional human brain size and the corresponding cognitive abilities. Ultimately, it seems contradictory to ground one's argument that we can't know anything useful about the human EEA, or there was no stable EEA, in a claim that, actually, it was a social arms race.

Given that the critics from philosophy accept that adaptations evolve by natural selection, and that selection entails interaction with the environment, why, exactly, are they skeptical that we can study this (past) environment? Is their acceptance of evolution by natural selection merely *pro forma*?

The philosophers worry about two types of reasoning. I already discussed the first, which Machery (2011) refers to as the "forward-looking heuristic." It begins by identifying an adaptive problem in the EEA (e.g., mate attraction) and then posits a solution (e.g., a mate-attraction strategy). The grain and arms-race problems target this type.

The second line of reasoning, often described as reverse engineering, or the backward-looking heuristic (Machery, 2011), begins with some organism trait that exhibits evidence of design, and then attempts to infer the adaptive problem that it evolved to solve (e.g., human males have a propensity to take unnecessary risks; this propensity would have helped signal good genes to females). Reverse engineering is also thought to have problems. For example, the Archaeopteryx foot exhibits design for grasping, but did it evolve to grasp branches (i.e., perching), which would support the hypothesis that this species was well adapted for flight, or did it evolve to grab prey, which would support the alternative hypothesis that Archaeopteryx was a terrestrial predator (Richardson, 2007)?

Used separately, these two types of arguments each do have limitations. Used together, however, and in combination with well-tested theories from evolutionary biology, they are able to make genuine contributions to understanding human evolution. Machery (2011) points out that although EP contends that the forward-looking heuristic is useful, it does not claim that it is necessary; that EP usually posits several competing hypotheses (e.g., multiple possible mating strategies); and that EP draws on several bodies of knowledge to constrain hypotheses. In addition, the backward-looking heuristic can bootstrap the forward-looking one: The universal aspects of mate preferences of contemporary women provide a decent hypothesis for the mate preferences of ancestral women, for instance, just as those of living female bowerbirds do for ancestral ones. These hypothesized ancestral female preferences are then essential components of the EEA of male-mating strategies of humans and bower birds, respectively. Machery concludes "Although clearly fallible, the discovery heuristics and the strategies of confirmation used by evolutionary psychologists are on a firm grounding." See also Machery and Barrett (2006); Machery and Cohen (2011).

In short, the environments of the past 2 million years were highly structured and exhibited many regularities, enough to keep EP busy for a long time.

The EEA, or EEAs?

Many critics have complained that because environments always vary, especially during the Pleistocene, there was no singular EEA. At best, there were multiple EEAs (e.g., Foley, 1995; Laland & Brown, 2011; Smith, Borgerhoff Mulder, & Hill, 2001). These critics are often conflating the variable state of an environment with its invariant properties.

In addition, the EEA concept has a narrower sense that is adaptation specific or adaptation relevant (Tooby & Cosmides, 1990b, pp. 388–390). These are the environmental properties that are important to one particular adaptation's development and functioning but might be irrelevant to other adaptations. Irons (1998) developed a similar concept, using the similar term *adaptively relevant environment* (ARE).

To illustrate: To focus light on the retina, the cornea and lens must have very special shapes that depend on the refractive index of air, which is about 1. The human eye would not work well if this refractive index were much different, and indeed, humans do not see well in water, which has a refractive index of 1.3. The adaptation-relevant EEA of the human cornea and lens, therefore, includes the refractive index of air. The EEA of the cornea and lens does not include gravity, however, because it does not play a role in the refraction of light, even though it does play an essential role in, for example, human locomotor adaptations.

The distance of objects from the eye was also an "adaptation-relevant" aspect of the ancestral environment. But unlike the refractive index of air, the distance of objects from the eye obviously varied constantly. There are, however, fixed laws of optics. These permitted the evolution of a mechanism that adjusts the curvature of the lens to enable focusing on objects from a few centimeters out to infinity.

Thus, in a species, there is a separate EEA for each adaptation, which for humans number in the many thousands. Moreover, because variation in adaptation-relevant properties often has underlying regularities, mechanisms can evolve to respond to it.

EVOLUTION BEFORE THE PLEISTOCENE

Critics point out that the human EEA could not begin with the Pleistocene because many human adaptations evolved much earlier. Downes (2009, p. 250), for instance, says "Components of this account [of the evolution of the human mind] will come from various times in our evolutionary history, including the Pleistocene, but also including times long before and long after this period. . . . [T]he contribution of [EP] to understanding human evolution is limited by an adherence to the thesis that our minds are a product of the Pleistocene Epoch. Actually, more is gained by rejecting this thesis than by retaining it." Laland and Brown (2011, p. 179) similarly remark, "Comparative analyses of animal abilities suggest that many human behavioural and psychological traits have a long history. Some human behavioural adaptations, such as maternal care or a capacity to learn, may even have evolved in our invertebrate ancestors. Many perceptual preferences will be phylogenetically ancient."

EP agrees:

> To the extent that there is an ambiguity in the concept of the environment of evolutionary adaptedness, it is because of the time-dimension of the problem. Because the history of any evolving lineage extends back several billion years to the origins of life, the characterization of ancestral conditions requires a time-structured approach matching specific statistical environmental regularities against specific instances of evolutionary modification in design." (Tooby & Cosmides, 1990b, pp. 387–388)

To illustrate the "time-structured approach" with the cornea and lens: The vertebrate eye evolved in a marine environment c. 500 million years ago, in which the refractive index of water, 1.3, was an invariant, adaptation-relevant property leading to the evolution of a spherical lens in fish. With the evolution of terrestrial animals, c. 400 million years ago, the refractive index of air, about 1, was now critical, leading to the evolution of a much flatter lens. Both dates differ dramatically from the EEA for other human adaptations, like the pelvis, knee, and foot, whose morphologies in hominins evolved perhaps 3–6 million years ago, enabling bipedal locomotion.

If the purpose of the analysis is to understand why modern humans retained an adaptation inherited from nonhuman ancestors, like the lens, then its EEA—and this is what almost all critics miss—is the period of most recent *stabilizing selection* on that adaptation:

> To the extent that the adaptation has assumed an equilibrium design under stabilizing selection, the period of stabilizing selection itself becomes a primary part of the EEA. . . ." (Tooby & Cosmides, 1990b, pp. 387–388)

To a close approximation, the complex design of the human organism was either stabilized by selection during the Pleistocene, in the case of the many adaptations inherited with little modification from pre-Pleistocene ancestors; or newly evolved during the Pleistocene, in the case of human-specific adaptations like language.

RECENT HUMAN EVOLUTION

A persistent criticism of EP is that human evolution did not stop when the Pleistocene ended 10,000 years ago, as the EEA concept seems to imply. Foley notes "If the EEA is a uniform background to which all humans adapted in the past, then this of course greatly limits the scope for selection operating today. The EEA has the effect of fencing evolutionary processes firmly into the past" (Foley, 1995, p. 194). Buller argued "Thus, it is safe to conclude that radically changed environments since the Pleistocene have created strong selection pressures favoring psychological evolution" (Buller, 2005, p. 110). Moreover, "the nearly four hundred human generations since the end of the Pleistocene has certainly been sufficient time for selection-driven evolution in human psychological traits. Thus, it is overwhelmingly likely that there has been some adaptive psychological evolution since the end of the Pleistocene, which has rendered contemporary humans psychologically different from their Pleistocene ancestors" (Buller, 2005, pp. 111–112). Laland and Brown (2011, p. 181) similarly question "[a]ny assumption that natural selection on humans has stopped. . . ."

Two important factors affect the rate of adaptive evolution, and thus the likelihood of recent human cognitive evolution: environmental change and population size. If the environment has changed substantially, then new adaptive mutations can experience particularly strong selection relative to the now less-well-adapted alleles already present in the population. In larger populations, there will be a greater absolute number of mutations per generation than in smaller populations (everything else equal), and hence more adaptive mutations for selection to act on. Both these factors apply to humans.

The population of *Homo sapiens* began to grow in the late Pleistocene, c. 50 thousand years ago (kya), and this growth accelerated with the advent of agriculture at the start of the Holocene, about 10 kya. The transition to agriculture, itself probably made possible by the environmental change that marked the end of the ice age (Richerson, Boyd, & Bettinger, 2001), brought further changes in diet, population density, settlement pattern, and disease. Analyses of genetic variation in modern humans indeed reveal signatures of the recent acceleration of positive selection (Cochran & Harpending, 2009; Hawks, Wang, Cochran, Harpending, & Moyzis, 2007). Humans have evolved since the end of the Pleistocene.

EP certainly acknowledges important environmental change and population growth since the end of the Pleistocene. In fact, these are cornerstones of its argument that the EEA largely corresponds to the Pleistocene. It also agrees that recent positive selection occurred, tipping its hat to the evolution of lactase persistence and malaria resistance (Tooby & Cosmides, 1990a), classic examples of adaptive evolution during the Holocene. Why, then, would it downplay the possibility of recent adaptive evolution of cognition?

Racism and Genocide In 1975, E. O. Wilson published *Sociobiology: The New Synthesis*, which summarized recent work on social evolution by many evolutionary biologists. Wilson also briefly noted that these theories could help explain human behavior. In response, a number of academics, including Stephen J. Gould and Richard Lewontin, wrote a letter to the *New York Review of Books* with the following passage (Allen et al., 1975):

> These theories provided an important basis for the enactment of sterilization laws and restrictive immigration laws by the United States between 1910 and 1930 and also for the eugenics policies which led to the establishment of gas chambers in Nazi Germany.
>
> The latest attempt to reinvigorate these tired theories comes with the alleged creation of a new discipline, sociobiology.

This was the opening shot in the sociobiology controversy of the 1970s and 1980s, much of it driven by the fear that sociobiology, applied to humans, would justify racism and eugenics. The controversy limited sociobiology—now renamed behavioral ecology—mostly to the study of nonhuman organisms. EP, although rejecting this judgment of sociobiology, did not want to suffer the same fate.

Because racists and eugenicists typically justify discrimination (and worse) by claiming that one population is biologically superior to another, EP has taken great pains to ground itself in theory and evidence of a *universal* human nature that evolved, or was maintained by stabilizing selection, roughly during the 2.6 million years of the Pleistocene. If EP is correct, then there are no fundamental biological differences among human populations, let alone any notion of biological superiority.

Unfortunately, human migration during the late Pleistocene created conditions that were amenable to the evolution of differences among populations, potentially including cognitive differences, that could be used to justify discrimination. About 60 kya, modern humans dispersed out of Africa into somewhat geographically and genetically isolated populations in Europe, Asia, Oceania, and the Americas, each characterized by distinct environmental conditions. This population structure, combined with prolonged, exponential population growth during the past 10,000 years, was conducive to genetic divergence of populations due to selection. In humans, then, recent evolution would tend to go hand-in-hand with *population-specific* evolution.

Genetic Variation in the Human Species The human genome contains about 3 billion bases. About 1% codes for proteins and another 3%–15% is under selection, that is, serves functions such as gene regulation (a recent estimate is 8.2%; Rands et al., 2014).[10] Thus, most DNA is nonfunctional. The functional part of the genome is still very poorly understood; it is not even entirely clear which sequences in the genome are functional.

Across the entire genome, any two humans, on average, are identical at >998 of every 1000 bases (Barbujani & Colonna, 2010). In protein coding and other functional regions, they are identical at >999 of every 1000 bases, presumably due to purifying selection (Tennessen et al., 2012; Ward & Kellis, 2012). Human genetic variation is substantially lower than that seen in other primate species, probably due to an especially small ancestral population size (Marques-Bonet, Ryder, & Eichler, 2009).

Of the bases that vary, rare variants vastly outnumber common ones. Most rare variants are recent mutations that are neutral or weakly deleterious and have not yet been eliminated by purifying selection (Tennessen et al., 2012). Because most of the genome is nonfunctional, most genetic differences between individuals are nonfunctional differences.

The low levels of genetic variation across the human genome, even lower levels in functional regions, and the concentration of this variation in rare alleles, most of which are neutral or deleterious, all support the EP view that there is a set of complex human physiological and psychological adaptations that is based on a universal, genetic architecture that evolved by natural selection.

Recent Evolution and Genetic Diversification It might be the case, though, that important aspects of this universal genetic architecture evolved during the past 10,000 years. It might also be the case that the functional variation that does exist contributes to adaptive cognitive differences between populations.

Social scientists have long accepted Lewontin's argument that because there is greater genetic variation within human populations than between them, genetic differences among populations are unimportant (Lewontin, 1972).[11] Alleles do not vary independently across loci, however. By taking account of the correlation of alleles across many loci, it is possible to classify individuals into groups based on ancestry (Edwards, 2003). At the same time, group boundaries are not sharp, or even entirely consistent across studies, and some variation is better explained by clines than clusters (Barbujani & Colonna, 2010).

Analyses of genetic variation in contemporary human populations, combined with archaeological evidence, support the following scenario. Modern humans evolved in Africa by c. 200 kya. Between 200 and 100 kya, modern humans diverged into distinct subpopulations within Africa, albeit with admixture. The effective population size might have been about 7,000–15,000. Sometime between 100 and 50 kya, one or more small groups of Africans, perhaps as few as 1,000 individuals, migrated out of Africa. These migrants did not contain all the genetic diversity in the African population. Instead, they came from one or a few African subgroups. The migrant population expanded in the Middle East, interbred with local archaic human populations (e.g., Neanderthal-derived DNA accounts for an estimated 1%–4% of the Eurasian genome), and subsequently migrated to Europe, Asia, Oceania, and the Americas. With each

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[10] A large consortium claimed to have assigned biological functions for 80% of the genome (The ENCODE Project Consortium, 2012). This claim was widely criticized (Rands et al., 2014, and references therein).

[11] Ironically, Lewontin, a harsh critic of adaptationism, and EP have come to the same conclusion via very different lines of reasoning. For EP, population genetic differences are unimportant because all humans share a universal, complex, genetically specified design that evolved, or was stabilized, in an African population over the past 2 million years.

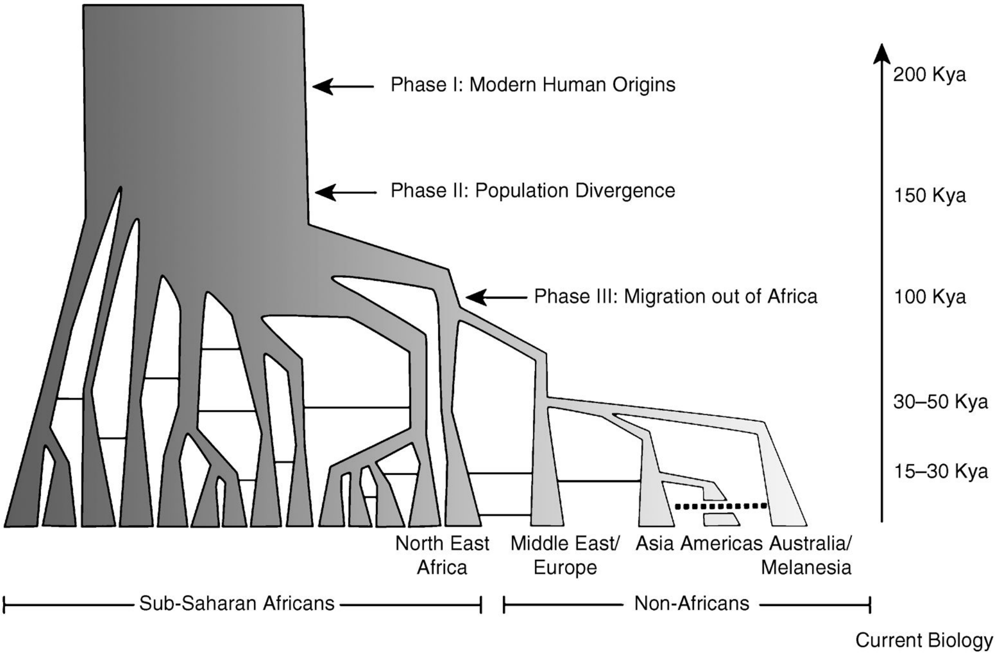

Figure 4.1 Decreasing Intensity of Color Represents the Concomitant Loss of Genetic Diversity as Populations Migrated in an Eastward Direction from Africa. Solid horizontal lines indicate gene flow between ancestral human populations and the dashed horizontal line indicates recent gene flow between Asian and Australian/Melanesian populations. *Source:* From Campbell and Tishkoff (2010).

migration, there was a loss of genetic diversity, probably due to a serial founder effect. At the end of the Pleistocene, every continent (except Antarctica) was populated and each non-African population exhibited a subset of the common genetic variants found in Africa (Barbujani & Colonna, 2010; Campbell & Tishkoff, 2010; Henn, Cavalli-Sforza, & Feldman, 2012). See Figure 4.1.

The now global human population exploded during the Holocene, almost certainly due to the transition to agriculture. This explosion generated the large number of rare variants noted earlier, most of which are of recent origin (5–10 kya) and more or less specific to the major continental populations. Thus, there has been recent genetic divergence among the continental populations, but much of this variation—perhaps 95%—is neutral or weakly deleterious (Fu et al., 2013; Fumagalli et al., 2011; Tennessen et al., 2012).

Recent Positive Selection Despite the foregoing, evidence has been accumulating for over half a century that the human species has undergone at least some recent adaptive evolution. It does not appear to have acted uniformly on the human species, however, but instead has driven divergence among the major continental human groups (though results to date might reflect methodological limitations; Lachance & Tishkoff, 2013).

Although most studies of recent positive selection in humans have focused on hard sweeps—new mutations that sweep to fixation—theory and evidence suggest that most recent positive selection has instead been on standing variation—alleles that were common prior to the onset of the new selection pressure, or simultaneous selection on multiple loci (Hernandez et al., 2011; Tennessen & Akey, 2011).

Regions of the genome that have apparently experienced recent positive selection often contain multiple genes and numerous nucleotide polymorphisms, hampering identification of the target of selection, but studies have consistently fingered climate, subsistence, sexual selection, and especially pathogens as probable selection pressures (Fu & Akey, 2013; Fumagalli et al., 2011; Lachance & Tishkoff, 2013). In only a very few cases, however, such as adaptation to high altitude, lactase persistence, and malaria resistance, have the selected variant, phenotype, and selection pressure all been pinpointed.

Regarding recent cognitive evolution, Huang et al. (2013) conducted a meta-analysis of 27 studies of positive selection across the human genome and found that genes that are highly expressed in the central nervous system are enriched in recent positive selection. Keeping in mind that false positives are common in studies of positive selection, possible examples of divergent positive selection on neural function include: opioid cis-regulatory alleles (Rockman et al., 2005); loci involved in the axon guidance pathway, which determines the direction the axon will grow, ultimately influencing the development of neuronal networks (Tennessen & Akey, 2011); genes in non-African populations in the neuregulin ERBB4 signaling pathway, which is involved in the development of the nervous system, heart, and other tissues (Pickrell et al., 2009); selection of downstream gene targets of FOXP2, which is implicated in language abilities, in a European sample but not an East Asian or African sample (but the selected downstream genes have multiple functions in neural and nonneural tissue) (Ayub et al., 2013); and alleles in Ashkenazi Jews that have been argued to increase intelligence in heterzygotes but cause severe disease in homozygotes (Cochran & Harpending, 2009).

In none of these examples are the phenotype and selection pressure well understood. It is quite possible that selection was on non-neural aspects of the phenotype (i.e., pleiotropy). It is also possible that, due to convergent evolution, population divergence in genes underlying neural pathways resulted in little divergence in neural/psychological function. Additionally, population differences in frequencies of alleles impacting neural function might be due to founder effects and drift. Such seems to be the case with the dopamine D4 alleles (Kidd, Pakstis, & Yun, 2013).[12] Finally, because exposure to neurotoxins from plants, fungi, pathogens, and the environment varied across populations, some divergent neural evolution might represent protective changes in neuroreceptors and other neural functions.

Nevertheless, despite the lack of compelling evidence to date, it would not be surprising if there were limited population divergence in some neural/psychological functions due to recent positive selection on cognition and behavior.

Recent Positive Selection and Complex Design Given the possibility of divergence in neural function, it would be unsatisfying, to say the least, if EP's claim of a universal evolved human psychological design were grounded in moral and political concerns about racism and had little basis in science. It is reassuring, then, that more than 2,000 years of research in anatomy and physiology, more than a century of research in

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[12] There also appears to be balancing selection at this locus (Ding et al., 2002).

cellular biology, and more than half a century of research in molecular biology—including all their neurospecific versions, such as neuroanatomy, neurophysiology, and neurobiology—has found profound similarities in evolved function within the human species, and even across species. The complex design that defines the human organism is, to a close approximation, universal in the species.

Known, recently evolved population differences in physiology are limited to relatively simple modifications of this universal design, often involving changes to only a single nucleotide. The sickle cell trait, for example, which protects some populations from malaria, is a point mutation in the hemoglobin gene (the protective mechanism is still uncertain). Lactase persistence in some populations is due to a point mutation in a regulatory region of the lactase enzyme. Population differences in skin color are primarily due to differences in melanin pigment production by cutaneous melanocytes (the genetic mechanisms are still not well understood).

The reason there are no complex adaptive differences between the continental human populations, despite their relative genetic isolation (but see Hellenthal et al., 2014), is simply that there hasn't been enough time for them to evolve. Physicist Greg Cochran and population geneticist Henry Harpending, who argue for the importance of recent adaptive divergence in human populations (Cochran & Harpending, 2009; Hawks et al., 2007), concede this point:

> John Tooby and Leda Cosmides (two of the founders of modern evolutionary psychology) have said that "given the long human generation time, and the fact that agriculture represents less than 1 percent of the evolutionary history of the genus *Homo*, it is unlikely that we have evolved any complex adaptations to an agricultural (or industrial) way of life." A complex adaptation is a characteristic contributing to reproductive fitness that involves coordinated actions of many genes. This means that humans could not have evolved wings, a third eye, or any new and truly complicated adaptive behavior in that time frame. Tooby and Cosmides have argued elsewhere that, therefore, deep mental differences between human populations cannot exist.
>
> We think that this argument concerning the evolution of new complex adaptations is correct, but it underestimates the importance of simple adaptations, those that involve changes in one or a few genes. (Cochran & Harpending, 2009, pp. 9–10)

For Cochran and Harpending, "importance" does not mean profound changes in design but rather profound effects on human history and prehistory, such as the spread of the Proto-Indo-Europeans (which they attribute to the evolution of lactase persistence).

In summary, the genetic evidence is consistent with the view that the evolved design of humans' psychological mechanisms are either (a) universal, (b) slightly modified versions of universal designs, or (c) new, very simple, and population specific.

CONCLUDING REMARKS

Most EP critics accept most of the major tenets of EP: the blank slate is untenable, functions evolve by natural selection, and an evolutionary perspective will consequently be important to understanding human brain function. Most critics also understand that EP is science, and that it will ultimately stand or fall on the empirical evidence. In a review of *Alas, Poor Darwin: Arguments against Evolutionary Psychology*, philosopher David Hull, himself a critic of EP, concludes,

> Rose and Rose remark that "bad theory can never be driven out solely by criticism." If so, the critics of evolutionary psychology could make better use of their time by developing these alternative theories, no matter how complicated they turn out to be. Repeating overly familiar criticisms of evolutionary psychology and sociobiology is unlikely to have much effect. For all their crudity and lack of sophistication, evolutionary psychologists keep churning out book after book, paper after paper, both popular and technical. They are not content to carp on the sidelines. (Hull, 2000, p. 125)

As this *Handbook* testifies, indeed we are not.

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CHAPTER 5

Intuitive Ontologies and Domain Specificity

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THE IDEA THAT the mind is comprised of many specialized competencies is perhaps the hallmark of evolutionary psychology. That there are specializations in so-called "peripheral" systems in the mind, such as perceptual and motor systems, is broadly accepted in psychology. However, the idea that there are specializations in higher-level thought—knowledge, reasoning, and the like—remains controversial.

Here we review theory and evidence suggesting that human expertise about the world—not just at the level of perception, but at the conceptual level as well—is best construed as consisting of many distinct, specialized competencies, organized around recurrent adaptive challenges that are in many ways functionally distinct, resulting in functionally specialized architecture. These competencies are not atomic, indivisible, unitary entities, but involve the orchestration of diverse neural structures according to particular inferential principles and functional goals. The organization of these competencies reflects certain implicit assumptions about the domains that they have involved to handle. In this sense they embody *intuitive ontologies*: implicit assumptions about how the world is organized that are in turn used to structure knowledge, inference, and decision-making.

Our strategy in this chapter is twofold. First, we present several examples of intuitive ontologies, summarizing the evidence for domain specificity in order to give the reader a sense of the empirical phenomena at hand. Then, we use these examples to extract some general theoretical points about what intuitive ontologies are and how they evolve, develop, and are organized. We begin with a brief history of early ideas of domain specificity in developmental psychology, followed by case studies showing how relatively simple views of domain specificity have had to be revised, and conclude with a summary of the contemporary picture of domain specificity in cognition.

DOMAIN SPECIFICITY: EARLY MODELS AND THEIR LIMITS

DOMAIN SPECIFICITY AS AN INTUITIVE ONTOLOGY

The notion of semantic knowledge as a suite of domains informed by different principles was first popularized by developmental psychologists (R. Gelman, 1978; R. Gelman & Baillargeon, 1983) who proposed distinctions between physical-mechanical, biological, social, and numerical competencies as based on different learning principles (Hirschfeld & Gelman, 1994). This early research emphasized two important aspects of cognitive architecture, namely (1) that early cognitive development is based on content-rich prior expectations and principles about the world, and (2) that these expectations and principles differ between large ontological domains, such as solid objects, living things, and intentional agents.

An excellent example of the first point is research on the early development of inferential physical principles, generally called an "intuitive physics" (Kaiser, Jonides, & Alexander, 1986). Infant studies (Baillargeon, Kotovsky, & Needham, 1995; Spelke, 1988; Spelke & Van de Walle, 1993) challenged the classical Piagetian assumption that the development of physical intuitions followed the development of physical competence. They documented the early appearance of systematic expectations in terms of solidity (objects collide, they do not go through one another) continuity (an object has continuous, not punctuate existence in space and time), and support (unsupported objects fall), as well as a distinction between the roles of agent and patient in causal events and surprise at apparent action at a distance (Leslie, 1984; Spelke, 1990).

The second aspect, domain specificity proper, is best illustrated by early research on the differences between living things and man-made objects. Animal species are intuitively construed in terms of species-specific "causal essences" (Atran, 1998), that is, undefined, yet causally relevant qualities particular to each kind. A cat is a cat, not by virtue of having this or that external feature—even though that is how we recognize it—but because it possesses some intrinsic and undefined quality that one only acquires by being born of cats. By contrast, man-made objects are principally construed, from infancy, in terms of their *functions* (Keil, 1986). So the fact that an object is identified as either living or man-made leads to (a) paying attention to different aspects of the object; (b) producing different inferences from similar input; (c) producing categories with different internal structures (observable features index possession of an essence [animals] or presence of a human intention [artifacts]).

In this early implementation, the notion of domain specificity in psychology was taken to imply that human minds comprised an *intuitive ontology,* that is, a set of core categories (e.g., person, object, living thing, artifact, etc.), with associated expectations and learning principles (Boyer, 2000), appearing early in development in the form of core principles or core domains of knowledge (Keil, 1989; Spelke, 1994, 2000).

DOMAIN-SPECIFIC SYSTEMS AS RESPONSES TO DISTINCT ADAPTIVE PROBLEMS

Early on, empirical evidence suggested that this ontological interpretation of domain-specificity was overly simplistic in both its central assumptions: Development of domain-specific knowledge need not occur early in infancy, and the organization of inference systems within the mind need not correspond to the way philosophers or scientists would carve the word, for example, into domains of physics, biology, and psychology.

From an evolutionary perspective, there is no reason to expect that all or most adaptively crucial capacities would be present at birth or early infancy. Instead, the idea that the products of evolution must be innate—present at birth—was imported into this literature from older philosophical traditions, leading to protracted (and in our view largely sterile) controversies about innateness. Debates around that term generally started from the assumption that human genetic nature would be manifest in early (preferably neonatal) capacities, whereas their change over the lifespan would be mostly a matter of (nongenetically driven) learning (Elman, Bates, Johnson, & Karmiloff-Smith, 1996). This is highly misleading. Indeed, evolutionary thinking would predict the opposite. Because computational capacities are expensive, organisms rarely develop them at life-stages when they are not required (and some capacities may require more time to develop than others). That is why, for instance, humans do not develop sexual motivations or mate-selection competence before puberty. Against "innateness" assumptions, many specific competences that are crucial to fitness are not rooted in infant cognition. They unfold as a result of genetically controlled, later development.

Similarly, there is no evolutionary reason to expect cognitive systems to correspond to large domains of reality, for example, with one chunk of the mind dedicated to living things (biology) and a separate chunk to social behavior (psychology). Instead, one would expect specific cognitive systems to be dedicated to distinct fitness challenges, rather than categories of objects per se. For instance, we might expect humans to have a system for handling pathogen threats, regardless of whether the danger stems from plants, nonhuman animals, or other humans, so that such a system would straddle ontological categories as a philosopher might define them (e.g., "social" versus "nonsocial"). Conversely, we would expect human reproductive competence to be activated in the presence of potential mates and turned off in encounters with other conspecifics, thereby showing that dedicated systems sometimes focus on a subset of an ontological category.

Next, we present several case studies of specialized cognitive systems, to illustrate these points and to give readers some sense of the biological reality of how specialized knowledge in the brain is organized. We then use these case studies to derive some general points about the nature of specialized, domain-specific systems in the mind.

INTUITIVE PSYCHOLOGY: FROM "THEORY OF MIND" TO SPECIALIZED DETECTION SYSTEMS

A good example of an intuitive ontology built from the interaction of many specialized systems is the set of capacities to make sense of and respond to other agents' behavior, sometimes known as mindreading, intuitive psychology, or theory of mind (Povinelli & Preuss, 1995). Mechanisms involved in responding to others' behavior are distributed widely across taxa, and human mindreading abilities appear to recruit both newer, possibly human-specific mechanisms interacting with phylogenetically older ones, with the most sophisticated of these mechanisms modeling others' behavior as a product of unobservable internal states such as intentions and beliefs (Dennett, 1987). Mindreading illustrates the two general points about domain-specific abilities made earlier: Rather than being a single, atomic skill, it involves the interaction of a hodge-podge of more specialized abilities whose boundaries do not align neatly, and whose developmental trajectories are heterogeneous as well.

In the early days of the study of intuitive psychology, it was assumed that a unified system handled mindreading, on the basis of unified theoretical principles, usually described as the child's or the adult's theory of mind (Gopnik & Wellmann, 1994). Most studies were based on one experimental protocol, the false-belief task. Also, a common pathology, autism, seemed to be largely explained by a general deficit in mindreading. Further research, however, showed that the false-belief task was a very limited and flawed protocol (Bloom & German, 2000; Leslie, Friedman, & German, 2004) and that autism was more varied and complex than a false-belief processing deficit (Chevallier, Kohls, Troiani, Brodkin, & Schultz, 2012; U. Frith, 2001; Nielsen, Slaughter, & Dissanayake, 2013). This led to an appreciation of the fact that intuitive psychology corresponds to a suite of distinct inferential capacities, the smooth coordination of which produces mindreading (Samson & Apperly, 2010).

One of the crucial systems is geared at detecting *animate motion*. This system takes as input particular patterns of motion and delivers as output an automatic interpretation of motion as animate. The system seems to develop early in infants (Baldwin, Baird, Saylor, & Clark, 2001; Rochat, Morgan, & Carpenter, 1997) and modulates activation of specific circuitry (Gao, Newman, & Scholl, 2009). Animates are also detected in another way, by tracking *distant reactivity* from infancy (Johnson, Slaughter, & Carey, 1998). Detection of reactivity modulates specific neural activity, distinct from that involved in the interpretation of intentions and beliefs (Blakemore, Boyer, Pachot-Clouard, Meltzoff, & Decety, 2003).

A related capacity is *goal ascription*. Animates act in ways that are related to particular objects and states in a principled way. For instance, their trajectories make sense in terms of *reaching* a particular object of interest and *avoiding* nonrelevant obstacles, and infants' expectations reflect these principles (Csibra, Gergely, Biró, Koós, & Brockbank, 1999). Goal ascription, distinct from animate motion, modulates specific neural circuitry (Gao, Scholl, & McCarthy, 2012; Gobbini et al., 2011; Reid, Csibra, Belsky, & Johnson, 2007; Skewes, Roepstorff, & Frith, 2011).

Successful coordination in humans also requires the coordination of attention between different agents. That is why *joint-attention* capacities are particularly sophisticated in humans (Carpenter, Nagell, & Tomasello, 1998; Tomasello & Carpenter, 2007) and develop early in infants (Butterworth, 2001; Wu, Pan, Su, & Gros-Louis, 2013). In normal adults, following gaze and attending to other agents' focus of attention are automatic and quasi-reflexive processes (Friesen & Kingstone, 2003), activating a set of dedicated neural circuits (Hooker et al., 2003; Redcay, Kleiner, & Saxe, 2012) that seem deficient in autistic infants (Pelphrey, Morris, & McCarthy, 2005).

A capacity for relating *facial cues to emotional states* also develops early and seems to achieve similar adult competence in human cultures (Ekman, 1999; Keltner et al., 2003). Five-month-old infants react differently to displays of different emotions on a familiar face (D'Entremont & Muir, 1997). It seems that specific neural circuitry is involved in the detection and recognition of specific emotion types (Kesler-West et al., 2001), distinct from the general processing of facial identity. These networks partly overlap with those activated by the emotions themselves.

Finally, *belief-ascription* inferences take as input the information delivered by the systems described earlier, and produce consciously available explanations and prediction of complex behaviors. Early studies of this process identified particular areas of the medial frontal lobes as specifically engaged in theory-of-mind tasks (Happé et al., 1996). There is also neuropsychological evidence that right-hemisphere damage to these regions results in selective impairment of this capacity (Happé, Brownell, & Winner, 1999). Note that, in both cases, the protocols consist in false-belief tasks, that is, in the *explicit* description of another agent's beliefs. In other words, the functional capacity isolated in such tasks is not intuitive psychology, but only its ultimate, verbally explicit outcome.

This survey is certainly not exhaustive but indicates the variety of systems engaged in the smooth operation of our intuitive, mentalistic understanding of behavior, which operates in remarkably similar ways in all normal human beings (Avis & Harris, 1991; Yazdi, German, Defeyter, & Siegal, 2006). In an evolutionary perspective, there is nothing surprising in the multiplicity of distinct capacities engaged. The brain structures involved in mindreading have distinct evolutionary histories, some pre-social (e.g., tracking eyes and motion is crucial in predator–prey interaction) and some more recent (e.g., joint attention facilitates cooperative contexts). The collection of neural systems that collectively support mind reading is probably the result of several distinct evolutionary paths.

LIVING THINGS VERSUS ARTIFACTS: FROM ONTOLOGICAL CATEGORIES TO GOAL-SPECIFIC SYSTEMS

The distinction between the broad domains of living things and man-made objects was a major theme in early models of domain specificity, particularly in developmental psychology. However, evolutionary considerations suggest that specificity of semantic knowledge should be found at a more specific level, corresponding to situations that carry distinct fitness consequences; different living things, like mates, predators, pathogens, and foods, are important to us for very different reasons. Also, in evolutionary terms, one should consider not just categories of objects, but also the kinds of interaction likely to impinge on the organism's fitness: The way we interact with tools, for example, is not the same way we interact with physical spaces like buildings, even though both are technically artifacts. We should expect the input format and activation cues of domain-specific inference systems to reflect this fine-grained specificity. Indeed, this hypothesis of a set of finer-grained systems receives some support from behavioral, developmental, neuroimaging, and neuropsychological evidence.

In behavioral terms, interaction with (most kinds of) nonhuman animals triggers activation of the animacy-detection and goal-detection systems described earlier, which are clearly not activated by exemplars of plant species. Also, animal and plant exemplars activate a unique categorization system, a taxonomy. Categories (e.g., snake) are embedded in other, more abstract ones (reptiles) and include more specific ones (adder); there is property inheritance from higher to lower nodes in the taxonomy, allowing for inferences about the properties of specific exemplars; and the categories are mutually exclusive and jointly exhaustive, which is not the case in other domains (Atran, 1981). Although animal and plant classifications vary between human cultures, the hierarchical ranks (e.g., varietals, genus, family, etc.) are found in all ethno-biological systems and carry rank-specific expectations about body-plan, physiology, and behavior (Astuti, Solomon, Carey, Ingold, & Miller, 2004; Atran, 1998; López, Atran, Coley, & Medin, 1997; Medin & Atran, 1999; Taverna, Waxman, Medin, & Peralta, 2012).

In development, too, one can observe principled, early-emerging domain-specific principles (beyond the ones already mentioned, in the section titled Domain

Specificity: Early Models and Their Limits). For instance, preschoolers consider the "insides" a crucial feature of identity for animals even though they of course only use the "outside" for identification criteria (S. A. Gelman & Wellman, 1991). They extend a new label to same-appearance animals and same-function artifacts, not the converse (Graham, Welder, Mernfield, & Berman, 2010). Children, like adults, spontaneously produce more inductive generalizations about animals than tools (Brandone & Gelman, 2009). Developmental schedules are different with regard to tools and animals, in terms of acquiring information about their internal versus external features (Diesendruck & Peretz, 2013). Young children clearly associate tool concepts with typical use from an early age, using socially transmitted information as well as direct observation (Casler & Kelemen, 2005; Phillips, Seston, & Kelemen, 2012). Children represent a connection between a tool concept and a privileged intentional use, which may be the first-cited use or the creator's intended use (Matan & Carey, 2001), consistent with their general teleological stance (Kelemen, 1999). Specific to the artifact domain is the expectation that such use is, in fact, consistent with observable functional affordances (Asher & Nelson, 2008). The tacit principles uncovered in these developmental studies are invariably about medium-size animals (gradually and only partly extended to bugs, plants) and manipulable tools with a direct, observable effect on objects (in contrast to such man-made objects as houses, bridges, or lamp-posts), in contrast with the broad categories of "living thing" and "artifact." Indeed, the evidence suggests that the living-thing category is certainly too broad (Waxman, 2005), whereas the man-made-object category is simply not represented as such (S. A. Gelman, 2013).

A host of early neuroimaging studies, using both PET and fMRI scans, with either word or image recognition or generation, showed that living things and artifacts triggered significantly different cortical activations. However, the results were not straightforward, or even consistent (Perani et al., 1995). This would suggest that early expectations of neural localization for different semantic categories were misguided. Face processing, which is *both* functionally specific and neurally localized, is probably an exceptional case. Also, based on the assumption of a well-organized brain ontology, these studies often used stimuli sets for "living things" and "artifacts" that straddled several important evolutionary distinctions, for example, between foodstuffs and other natural things, between plants and animals, between tools and other artifacts.

One would expect some neurocognitive differences to underpin the observed behavioral differences, for example, the different time course for thematic versus functional knowledge retrieval, for tools and animals (Kalénine, Mirman, Middleton, & Buxbaum, 2012). Most recent neuroimaging studies demonstrate such differences, in terms of the differential orchestration of shared lower-level circuitry (Zannino et al., 2010). The categories are, again, more specific than originally expected. For instance, there are specific activation patterns for medium-sized animals and for insects (Connolly et al., 2012). This narrow scope of specialized systems is more radical in the domain of artifacts. Studies that find specific activation for that domain also report that effect only applies to *manipulable* objects, familiar or not (Anzellotti, Mahon, Schwarzbach, & Caramazza, 2011; Mecklinger, Gruenewald, Besson, Magnie, & Von Cramon, 2002; Moore & Price, 1999), with clear premotor activation, in particular of areas involved in the control of grasping gestures (Chouinard & Goodale, 2012).The sparse neuropsychological evidence is congruent with these conclusions (Pillon & d'Honincthun, 2011; Sacchett & Humphreys, 1992; Sartori, Coltheart, Miozzo, & Job, 1994).

These different strands of evidence are remarkably convergent, suggesting that mental systems are not organized around strict ontological domains ("living beings" versus "artifacts") but around goal-related categories, for example, "manipulable objects that one can use to modify other objects" or "animals with which there is a potential predator/prey interaction." This would suggest that the architecture of such systems is closely aligned with fitness-relevant aspects of objects, rather than perceptible or inferred categorical differences.

DOMAIN-SPECIFIC SYSTEMS AND CULTURAL KNOWLEDGE: NUMBER

Our final example concerns psychological competences related to number. Number is a useful example because dealing with number must require some specialized psychological skills, and yet number crosscuts traditional domains. Humans can estimate the magnitude or continuous numerousness of aggregates (e.g., they prefer more sugar to less); they also estimate relative quantities of countable objects (a pile of beads is seen as "bigger" than another); they count objects (applying a verbal counting routine, with number tags and recursive rules, to evaluate the numerosity of a set); they produce numerical inferences (e.g., adding two numbers); they retrieve stored numerical facts (e.g., the fact that 2 × 6 = 12). Although it makes sense to speak of an ontology of number and numerosity, this almost certainly involves the interaction of multiple systems with distinct functions, evolutionary histories, and developmental trajectories.

One salient contrast is between numerical competences that reliably develop in all human beings, with minimal social support, and those capacities that require sustained, effortful acquisition. In the course of human history, most societies made do with rudimentary series like "singleton, pair, triplet, a few, many" (Crump, 1990; Frank, Everett, Fedorenko, & Gibson, 2008), acquired in the same effortless manner as other parts of the lexicon. More elaborated, recursive combinatorial systems that assign possible verbal descriptions to any numerosity are more rare in origin, though they easily spread between different groups, especially with the development of trade. These are the number systems we are familiar with. Finally, literacy and cognitive specialization make possible the emergence of abstract mathematical knowledge.

This variety of behaviors is reflected in a diversity of underlying processes. Against the parsimonious but misleading vision of a unitary, integrated numerical capacity, many findings in behavioral, developmental, neuropsychological, and neuroimaging studies converge to suggest a variety of representations of numbers and a variety of processes engaged in numerical inference (Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999). In particular, one must distinguish between the analogue representation of magnitude, on the one hand, and the representation of digital number concepts and associated number facts and principles, on the other hand (Gallistel & Gelman, 1992). The analogue magnitude system encodes different numerosities as different points (or, less strictly, fuzzy locations) along a "number line," an analogical and incremental representation of magnitudes. It is engaged in approximation tasks and comparisons, activating bilateral areas of the inferior parietal cortex. The digital system is activated in exact computation tasks, engaging activation of (mostly left hemisphere) inferior prefrontal cortex as well as areas typically activated in verbal tasks. The engagement of parietal networks in number estimation suggests a spatial representation of magnitudes, supported by the fact that magnitude estimation is impaired in subjects with spatial neglect, and can be disrupted by transcranial magnetic stimulation (TMS) of the angular gyrus. Magnitude estimation tasks are impaired in patients with spatial neglect (Zorzi, Priftis, & Umilta, 2002). TMS results support this link between parietal spatial networks and numbers, since stimulation of the angular gyrus seems to disrupt approximate magnitude estimations (Gobel, Walsh, & Rushworth, 2001).

The distinction between systems is also relevant to development of the domain. To produce numerical inferences, children need to integrate the representations delivered by the two different systems. The first one is the representation of numerosity provided by magnitude estimation. The second one is the representation of object identity. Individuated objects allow inferences such as $(1 - 1 = 0)$ or $(2 - 1 \neq 2)$, which are observed in infants in dishabituation studies (Wynn, 1992, 2002). The acquisition process requires a systematic mapping or correspondence between two distinct representations of the objects of a collection (Ansari, 2011; R. Gelman & Meck, 1992).

Magnitude estimation, the capacity to judge relative amounts or compare a set to some internal benchmark, and verbal counting, probably have different evolutionary histories. Experimental comparative evidence shows that magnitude estimation exists in a variety of animals, supported by a system that can (a) trigger a specific physiological event with each occurrence of an event (not necessarily linked to event-duration) and (b) store the accumulated outcome of events in some accessible register for comparisons (Meck, 1997). This accumulator would provide an analogue representation whose variance would increase with the magnitudes represented, in keeping with the available human and animal evidence (Gallistel & Gelman, 1992). There has probably been a long history of selection for refined magnitude estimation and comparison in humans, because this capacity is required in the sophisticated foraging practiced by human hunter-gatherers (Mithen, 1990). Verbal counting, on the other hand, is not only unique to humans but indeed to particular cultures, with number systems that can represent any numerosity occurring only in some, mostly modern human societies. A number system is a highly “contagious” kind of cultural system, generally triggered by sustained trade. Number systems, therefore, require cultural transmission, in the form of exposure to specific behaviors (counting, noting numbers). But cultural material is transmitted inasmuch as it “fits” the input formats of one or several evolved inference systems. So it may be relevant to see number systems, like literacy, as cultural creations that “hijack” prior cognitive dispositions by mimicking the input format of inference systems. Systematic verbal counting requires a sophisticated sense of *numerical individuation*, that is, an intuition that an object may be perfectly similar to another and yet be a different instance. This seems to develop early in human infants (Xu & Carey, 1996) and is recruited in the acquisition of the first number concepts (Carey, 2009).

GENERAL FEATURES OF INTUITIVE DOMAIN-SPECIFIC INFERENCE SYSTEMS

With these examples of domain-specific inference systems in mind, we turn to the question of what features these systems have in common, and whether we can extract some general principles concerning their evolution and organization, which can be extended to domain-specific inference systems more generally. We suggest eight relatively general features of domain-specific inference systems, though this list is not meant to be exhaustive, and, in keeping with the idea of psychological diversity, not all these points might apply equally well to all evolved systems.

SPECIALIZED INFERENCE SYSTEMS FOCUS ON RECURRENT ADAPTIVE CHALLENGES

Clearly, each of the systems previously described handles information relevant to a highly specific adaptive challenge. For instance, organisms must be able to quickly associate specific behaviors with conjectures about the agents' intentions and other representations. Organisms that make and use tools must have an easy access to the connections between affordances and functions. Organisms that acquire nutrients from a vast number of plant and animal species, which they process in complex ways, must build an efficient database of the distinct properties of these species. In the preceding sentences, the word *must* means that a certain minimal level of competence in this domain was required to support the behaviors in question, but also suggests that any increment in the efficiency of these competences may confer fitness benefits.

This implies that the domains used by the brain, as opposed to the domains that might be used by a philosopher or a scientist, are not given by reality but are cognitively delimited. As we saw earlier, there are no cognitive systems that directly map onto ontological categories like animal or man-made object. Also, many domain-specific systems focus on aspects of reality that are distinctive only given the specific evolutionary history of the species, such as human-made tools, which can be part of the environment of other species, but are not conceptualized the same way.

This also implies a distinction between the proper or evolutionary domain of a system, and its actual domain of operation (Sperber, 1994). The fact that some cognitive system is specialized for a domain *D* does not entail that it invariably or exclusively handles *D*, nor does it mean that the specialization cannot be co-opted for evolutionarily novel activities. To use an analogy from human design, just because an object has been designed for cutting bread and possesses specialized features for doing so does not mean that it is always used for this purpose, nor that it might not be well-suited for other purposes. For example, a variety of sources of evidence point to the possibility that human-made writing systems exploit object-recognition areas of the brain that treat written words and letters as physical objects (Dehaene, 2005). Because writing is relatively recent in origin, we can conclude that written words per se are not the proper domain of the visual word form area and other brain regions that develop to systematically handle them; but they are part of its actual domain, because they satisfy the input conditions of those regions due to their resemblance to three-dimensional objects. Proper and actual domains are nearly always different in some ways. Mimicry and camouflage use this noncongruence. Nonpoisonous butterflies may evolve the same bright colors as poisonous ones to avoid predation by birds. The proper (evolved) domain of the birds' bright-colored bug avoidance system is the set of poisonous insects; the actual domain is that of all insects that look like them (Sperber, 1994).

SPECIALIZATION IS FUNCTIONAL, NOT ANATOMICAL

The example of face-recognition shows how our understanding of domain specificity is crucially informed by what we know about neural structures and their functional specialization. However, the example is perhaps misleading in suggesting a straightforward, one-to-one mapping from functional specialization onto neural specialization. In practice, most cognitive domains correspond to recurrent fitness-related situations or problems (e.g., predators, competitors, tools, foraging techniques, mate selection, social exchange, interactions with kin, etc.). Should we expect to find neural structures that are specifically activated by information pertaining to one of these domains? There are empirical and theoretical reasons to expect a rather more complex picture. First, neural specificity should not be confused with easily tracked anatomical localization. Local activation differences, salient though they have become because of the (literally) spectacular progress in neuroimaging techniques, are not the only index of neural specialization. A variety of crucial differences in brain function consist in time-course differences (observed in ERPs), in neurotransmitter modulation and in spike-train patterns that are not captured by fMRI studies. Second, novel brain mapping techniques such as tractography are revealing properties of whole networks of interacting brain regions, crucial to understanding how complex cognition is achieved via computational division of labor. Although the idea of cognition in distributed networks is sometimes seen as antithetical to the kind of modular or domain-specific view of mind presented here, it is actually quite consistent, as long as a biologically appropriate view is adopted of what modularity and specialization might mean in the brain.

Much confusion has surrounded the notions of domain specificity and functional specialization because of the classical view of *modularity* in psychology, which views modules as rigid, narrow, innate, and reflex-like cognitive mechanisms. It is a mistake to equate this concept with the idea of an evolved specialization, yet it is also a mistake to discard the idea that complex cognition is carried out by the orchestrated interaction of specialized processes (H. C. Barrett & Kurzban, 2006). Indeed, data on brain networks are consistent both with the idea of a high degree of modularity and a high degree of interactivity and flexibility (Bullmore & Sporns, 2009). These are not at odds, but rather, go hand in hand. Moreover, the functionally specialized processing one sees occurs via distributed networks, not single brain regions acting alone.

One metaphor for thinking about how complex cognition might be achieved through the flexible, contingent, and parallel interaction of many specialized parts is enzymatic computation (H. C. Barrett, 2005). Enzymes are computational input-output devices that catalyze reactions. Although every single enzyme is functionally specialized, their activities are collaborative by design, often involving enzymatic cascades and contextual modulation via molecular signals. In some ways, the processing of information by intuitive ontological systems is akin to catalysis or digestion of information in this sense, with different mechanisms attacking different bits of the problem to construct novel representations that are useful for the organism. This entails not single mechanisms operating in isolation, but orchestrated suites and networks of mechanisms, often operating both in parallel and hierarchically, as occurs in vision: Meaningful higher-level representations are constructed bit by bit, adding complexity as they ascend the computational chain (Ullman, 2007). The same is likely to be true in, for example, cognition about persons, artifacts, and the like. As mentioned above, neuropsychological accounts of social cognitive processes such as mindreading are converging on the view that what appears to be a single process is actually achieved via coordinated interaction between many subsystems (C. Frith & Frith, 2007).

DOMAIN-SPECIFIC SYSTEMS COMBINE REPRESENTATION AND MOTIVATION

One of the main functions of intuitive ontologies has to do with semantics, or meaning: parsing and interpreting the world in ways that help the organism judge, decide, and act. However, it would be a mistake to assume that such systems are *solely* semantic or conceptual, because in order to inform decisions and actions, they must have a motivational component as well (Tooby, Cosmides, & Barrett, 2005). At minimum, semantic processes underlying intuitive ontologies must interface with emotional and motivational processes. However, at least some views of how information processing occurs in the brain suggest that the separation of cognitive and emotional processes is not as simple as once thought, and in the limit may not be separable at all. In other words, the very same processes that interpret the world for an organism may be, at least in part, the processes that motivate it to act.

Consider, for example, evolutionary aesthetics. The processes that cause an object to appear attractive, delicious, or repulsive are, in a certain sense, the same processes that produce motives with regard to that thing. Conventionally, the processes that make a loaf of baking bread smell good are said to be perceptual, but the percept is value-laden in a way that motivates action. Similarly, the perception of pain is what causes us to withdraw a limb from a hot stove. Unfortunate cases of brain damage illustrate that damaging the systems that add value to stimuli in this way removes the motivation to act; people who cannot perceive pain injure themselves and die much younger than people who can, a gruesome illustration of the fitness value of the perception-motivation link (Nagasako, Oaklander, & Dworkin, 2003). This relationship is true even of more complex stimuli. For example, the many facets of attractiveness in mates, including not just physical but psychological attractiveness, are what draw us to them; in evolutionary terms, these aesthetic evaluation systems would be useless if they did not motivate action. Similarly, our moral judgment systems not only deliver to us a moral interpretation of acts as right or wrong, but distinct feelings associated with them; it is not a coincidence that moral wrongdoing is often described as repugnant or disgusting (Greene & Haidt, 2002; Tybur, Lieberman, Kurzban, & DeScioli, 2013). This is probably a general feature of intuitive ontologies, if not cognition in general; systems for representing the world only evolve because they motivate decisions and action.

ORGANISMS NEED TO KNOW MORE IN ORDER TO LEARN MORE

In many popular discussions of innateness, it is assumed that organisms that acquire vast amounts of information from external environments somehow require less genetically controlled structure than those that learn less. But interspecific comparisons suggest that there is something fundamentally wrong with this idea of a zero-sum game between genetic and environmental information. Paramecia learn less than cockroaches, and mice less than chimpanzees; at each point, the organisms with more complex information-processing structure are also the ones that can (and must) extract more external information. Computational logic, too, supports this assumption. Development in any complex organism requires specific attention to particular kinds of information and systematic neglect of information that is only relevant to other species. Human capacities offer a spectacular illustration of this principle. For instance, the lexicon of a natural language (10,000 to 100,000 distinct items) is extracted during language acquisition from the utterances of other speakers. This constitutes an impressive economy for genetic transmission, as human beings can develop complete fluency without any lexical items being stored in the genome. But this external database is available only to a mind with complex linguistic predispositions (Jackendoff, 2002; Pinker & Bloom, 1990).

DEVELOPMENT REQUIRES NORMAL ENVIRONMENTS AND SUSTAINED GENETIC CONTROL

Classical confusions about learning and innateness often stem from the fact that an evolved competence depends on a highly specific environment to develop in the species-typical manner. Face recognition would probably be disrupted in individuals raised without access to different faces. Language acquisition requires people interacting with a child in a fairly normal way. Tool-making competence develops in a world furnished with some functionally specialized man-made objects. In this sense, inference systems are similar to teeth and stomachs, which need digestible foods rather than intravenous drips for normal development, or to the visual cortex that needs retinal input. What is normal about these normal features of the environment is not that they are inevitable or general (food from pills and IV drips may become common in the future) but that they were reliably present in the environment of evolution. Children a hundred thousand years ago were born in an environment that included natural language speakers, man-made tools, gender roles, predators, gravity, chewable food, and other stable factors that made certain mental dispositions useful adaptations to those environmental features.

In a related manner, discussions of innateness often imply that genetic influence on brain structures is akin to a *ballistic* process (such as kicking a ball), such that one has influence over initial conditions (e.g., direction and energy of the kick) but this influence stops there and then, as the motion is influenced only by external factors (e.g., friction). If brain development was one such ballistic system, the genome would assemble a brain with a particular structure until birth and then stop working on it, as it were. From the end of organogenesis, the only functionally relevant brain changes would be brought about by interaction with external information. But that is clearly not the case. Nongenetic environmental influence is present before birth, and conversely genetic control of organic structures, including brain function, is pervasive throughout the life span.

EACH DOMAIN-SPECIFIC SYSTEM HAS A SPECIFIC LEARNING LOGIC

Evolution results not just in a specific set of adult capacities but also in a specific set of developmental pathways (Gallistel, 1990; R. Gelman, 1998; Spelke, 1998). Also, different systems have different developmental schedules, including "windows" of development before or after which learning of a particular kind is difficult (Keil, 1990). Learning specificity is manifest in the circuitous path to adult competence that children follow in many domains. For instance, young children do not build syntactic competence in a simple-to-complex manner, starting with short sentences and gradually adding elements. They start with a one-word stage, then proceed to a two-word stage, then discard that structure to adopt their language's phrase grammar (Pinker, 1984). This is true of many other domains, as illustrated here. Development follows independent paths in the domains of intuitive biology, intuitive psychology, or numerical cognition. These empirical findings have led developmental psychologists to cast doubt on the notion of a general, all-domain “learning logic” (if such a concept was coherent) that would govern cognitive development in different domains (Tooby et al., 2005).

Domain-Specific Systems Produce Intuitions, Not Reflective Representations

The domain-specific inference systems reviewed here deliver information that either remains unconscious or is available to conscious inspection in the form of intuitions, that is, representations that direct an agent’s expectations and behaviors, although the pathways that led to holding that information are not accessible to introspection. To illustrate this contrast, consider the following situations. Humans expect a solid object on a collision course with a solid surface to bounce against it, not to fuse into it; but people can also try to explain the trajectories of tennis balls in terms of force, impetus, speed, and so on (McCloskey, 1983). People who see someone’s facial expression change, and see that person retrace her steps, will automatically infer that she remembered some information that changed her goals; but they can also talk about the “mind” and form explicit hypotheses about how memory stores images and how desires force us to behave in particular ways (Malle & Knobe, 1997). People primed with quick exposure to faces of minority men tend to misidentify pictures of tools as weapons, while they make the opposite mistake when primed with male faces from their own ethnic group; they can also produce deliberate representations of members of a particular ethnic group as lazy, aggressive, irresponsible, and so on (Payne, Lambert, & Jacoby, 2002). In each of these three domains, intuitive representations may or may not be conscious mental events, but their origin is not accessible. They just pop up, so to speak, as a largely automatic and fast result of being presented with the relevant stimuli. In contrast, reflective mental events take more time, are largely accessible, and are generally under cognitive control (Baumard & Boyer, 2013; Evans, 2003; Lieberman, 2000).

Domain-Specific Intuitions Support (and Constrain) Socially Transmitted Knowledge

Empirical evidence for domain-specific mental systems allows us to avoid the traditional and entirely sterile partitioning of human competence in two exclusive domains of natural and cultural information. The opposition was always problematic, because acquiring information from conspecifics through cultural transmission is clearly an evolved adaptation of human beings, a hallmark of human nature (Tooby & DeVore, 1987). Beyond this, is it clear that human cultural information, that is, information that is spread and communicated in a human group, is far from arbitrary, and includes many universals or variations on universal principles (Brown, 1991). That is because specific expectations make certain kinds of cultural information much more likely than others to be acquired, stored, and communicated (Sperber, 1985; Tooby & Cosmides, 1992). In the last decades, findings in cognitive anthropology have demonstrated that intuitive domain-specific expectations explain culturally recurrent themes in domains as diverse as kinship (Jones, 2003), social categorization

(Hirschfeld, 1994), narrative fiction (Boyd, 2010), folk-biological knowledge (Atran & Medin, 1999), ritual (Lienard & Boyer, 2006), religion (J. L. Barrett, 2000; Boyer, 1994), and many others (Sperber & Hirschfeld, 2004).

EPILOGUE

Obviously, the various evolved, domain-specific systems described here map the environment in a way that is strikingly different, and often incompatible with scientific ontologies. As we have shown, there are many discrepancies between the world as science or commonsense see it, and the kinds of objects in the world between which brain systems distinguish. The many specialized systems of cognitive specificity certainly do not correspond to the classical domains of domain specificity (e.g., intuitive psychology, intuitive physics).

Indeed, the domain-specific systems described earlier do not actually constitute an ontology in the standard sense of a catalogue of mutually exclusive, jointly exhaustive categories, with associated principles and expectations (Keil, 1979; Sommers, 1959). Domain-specific systems in fact do not classify things in distinct categories. Rather, they get activated by information about specific *aspects* of objects, and handle information about those aspects only. There is, for instance, a system that handles cues for animacy, but no category of animates. Indeed, any object, from geometrical shapes to humans, animals, and (occasionally) machines, can activate the animacy-detection and goal-inference systems, if its motion fits the relevant input conditions. Even these aspects of objects are not processed in a manner that either commonsense or science would predict. For instance, the concept of number is not handled as a simple property of sets, but as a juxtaposition of different aspects (numerosity, object files, number tags) handled by distinct neurocognitive systems. Most important, the menagerie of domain-specific cognitive systems diverges from standard ontologies in its combination of "is" and "ought." The information that motivates an animal to court a particular mate is the same information that constitutes the potential-mate category. The adapted mind is, to coin a phrase, not "philosophically correct."

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PART II

SURVIVAL

DAVID M. BUSS

Charles Darwin coined the apt phrase "the hostile forces of nature" to describe the elements that impede an organism's survival. He described three fundamental classes of hostile forces. The first involves *struggles with the physical environment*, such as extremes of climate and weather, falling from dangerous heights, or being swept away by landslides or tsunamis. The second involves *struggles with other species*, such as predators, parasites, and prey. The third involves *struggles with conspecifics*. To some extent, this tripartite scheme oversimplifies, since adaptive problems obviously cut across classes. Finding prey for food, for example, requires navigating the physical environment, dealing with the evolved psychology of prey animals, and sometimes out-competing conspecifics. Nonetheless, Darwin's "hostile forces of nature" provide a natural starting point for the adaptive problems of survival that humans recurrently confronted.

Chapter 6 provides an entirely new chapter on the evolutionary psychology of *food* and *food choice*, by Paul Rozin and Peter Todd. Although many modern humans take food abundance for granted, human ancestors spent considerable time obtaining and processing the food on which their survival depended. Rozin and Todd explore what we know about how humans find and exploit possible food sources; how people decide what to eat; describe adaptations for neophobia and neophilia; explore the consequences of evolved preferences for sweet and fatty foods; explore cultural adaptations for processing foods such as corn and manioc; describe the fascinating origins of milk and other forms of dairy consumption, a classic case of gene-culture coevolution; articulate the importance of meat as a source of vital nutrients but also a vector of microbes; and end with the future of food and how evolved adaptations play out in modern cultural contexts.

Mark Schaller provides an entirely new chapter on *the behavioral immune system* (Chapter 7). Most are familiar with our physiological immune system, but fewer are aware of the growing evidence for an analogous behavioral immune system, a key element of which is the emotion of *disgust*. The behavioral immune system, Schaller argues, helps humans to prevent infection to begin with—a proactive defense rather than a reactive defense after pathogens have intruded. It has unique implications not just for avoiding dangerous foods, but also for social phenomena, since other humans are disease vectors. Hence, the behavioral immune system has profound implications for interpersonal attraction and repulsion, stigma and prejudice, conformity, and even culture. This chapter highlights the dramatic explosion of evolutionary psychological research in a domain that was almost entirely absent a decade ago.

Chapter 8, by Irvin Silverman and Jean Choi, describes theory and research on human spatial navigation and landscape preferences. These features of human evolutionary psychology are critical for a host of adaptive problems. Adaptive challenges include finding shelter that offers protection from hazardous elements, locating water sources, and finding food that can be gathered or hunted. Silverman and Choi describe important discoveries about spatial abilities, such as female superiority in spatial location memory, that were entirely missed by previous generations of psychologists who lacked the lens of evolutionary psychology.

Chapter 9, by Clark Barrett, provides a groundbreaking theoretical analysis and relevant empirical studies on human interactions with two classes of species—predators and prey. He furnishes evidence for specialized psychological adaptations attuned to unique design features of predators and prey, such as self-propelled motion, morphology, contingency, and directed gaze. Although this line of research is relatively new, Barrett elucidates the exciting discoveries already made and the promise of many more to come.

Joshua Duntley devotes Chapter 10 to other humans as one of the most important "hostile forces of nature." He describes recurrent arenas of human conflict, and argues that humans have adaptations both to inflict costs on other humans and to defend against having costs inflicted on them. Duntley then elucidates an exciting new co-evolutionary theory of the evolutionary psychology of homicide and homicide defenses—manifestations of human conflict with the most dramatic fitness consequences.

Modern introductory textbooks in psychology are notable for their absence of attention to problems of survival. Perhaps because most view evolutionary theory as optional, they fail to offer coverage of the rich psychology of human survival adaptations. Taken together, the five chapters in this section showcase the scientific gains already made by exploring psychological adaptations to the hostile forces of nature, and offer the exciting promise of many more to come.

CHAPTER 6

The Evolutionary Psychology of Food Intake and Choice

PAUL ROZIN and PETER M. TODD

INTRODUCTION

The authors of this chapter and, presumably, all its readers are classified as vertebrates, in the class *Mammalia*. This class is a major group of vertebrates and includes those of greatest concern to all of psychology. The class is named and defined in terms of its mode of *feeding* infants. Among the mammals, two major orders, the *Carnivora* and the *Insectivora*, are named for their *feeding* habits. Many important taxa of nonmammals can also be distinguished by their feeding habits. Evolutionary biologists generally hold that the three most important pieces of information about an unknown animal are its taxonomic position, its feeding habits, and the ecological setting in which it lives. The three are closely related, especially ecology and food. Food choice coupled with ecology almost certainly are the major forces directing the evolution of animals. And the *defining* feature of animals is that they have to obtain food from living organisms in the external world.

Food (including water) holds a special place for biology and for psychology. Obtaining food is one of the six basic biological functions that engage behavior: breathing, excretion, sleeping, protection (avoiding harm), mating, and feeding. Breathing and excretion do not play a major role in psychology (*pace* Freud) because the behaviors, though frequent, are very basic and not very different between humans and nonhumans, and they do not vary across individuals in interesting ways. Sleeping, which is surely a boring behavior, has fascinated psychologists and often gets its own chapter in introductory psychology texts. Protection (avoiding predators, building nests, finding safe places to sleep, parasite avoidance) receives little attention in psychology though these behaviors are often quite elaborate (although see Barrett, Chapter 9, this volume; Duntley, Chapter 10, this volume; Schaller, Chapter 7, this volume; Silverman & Choi, Chapter 8, this volume). Parasite avoidance in particular has recently come to the attention of psychologists as a result of a renewed interest in disgust, driven in substantial part by the work of evolutionary psychologists (e.g., Curtis, 2013; Tybur, Lieberman, Kurzban, & DeScioli, 2013). A, if not *the*, major source of parasites comes through ingestion, that is, food and eating.

Eating occupies more time and thought than most of these other activities and plays a crucial role in biological and cultural evolution. And yet eating and food choice, other than abnormalities therein (obesity, eating disorders) and regulation of food intake (hunger, thirst), gets little or no attention in introductory psychology texts.

Food selection is performed very frequently in animals, including humans, and varies widely across species and within our special favorite species, *Homo sapiens*. In terms of both survival and elaboration, it is probably the most important psychologically relevant biological function. Although psychologists show almost no interest in food choice, it is food and water that were the core of the behaviorist enterprise that dominated American psychology in the mid-20th century. This was simply because they were convenient: An animal can work for hundreds of small food and water reinforcements a day.

Food choice and accompanying changes in the environment, probably co-occurring, are generally cited as the most important forces in human biological and cultural evolution. The invasion of the savannah niche by previously forest-dwelling hominids is a major step in the evolution of humans and their big brains. Among the most profound changes and advances that have caused the great elaborations of modern human life, through biological and cultural evolution, are meat consumption and hunting, the discovery and harnessing of fire for cooking (Wrangham, 2009), and the domestication of plants and animals (Diamond, 1997). All these are about food.

We claim that what has made humans so special is a combination of changes in food choice (P. Rozin, 1976) and accompanying changes in sociality (Humphrey, 1976). Two great problems humans have faced in their evolution and brain expansion are how to figure out, from an enormous number of options, what is toxic and what is nutritive—the omnivore's dilemma—and how to coordinate the activities of multiple individuals to satisfy the needs of an omnivorous food-selection pattern.

The enterprises of both evolutionary biology and psychology have two explanatory components (P. Rozin & Schull, 1988). One is to determine the adaptive value of a current behavior, in terms of the ancestral environment in which it evolved. The second is actually tracing out over time how something came to appear in our species. This is particularly challenging for evolutionary psychology, because unlike the skeleton, behavior leaves few fossilized traces.

The concept of preadaptation (also called co-optation and exaptation; Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; Gould, 1991) figures centrally in trying to account for the food world of contemporary human beings in terms of its evolved biological and cultural history. Mayr (1960) proposed that *the* major source of evolutionary "novelties" is the co-opting of an existing system for a new function, or preadaptation. Preadaptation can either replace an original function or add new functions to an existing system. A food-relevant example is the human mouth. The teeth and tongue evolved for food handling. However, by a process of preadaptation, they are now shared by the language expression system. Teeth and tongue are critical in pronunciation, but they did not evolve for that purpose. A process like preadaptation can be seen in both individual development and cultural evolution; in development it can be described as the accessing of previously inaccessible systems for a wider range of activities, functions, or elicitors (P. Rozin, 1976), whereas in cultural evolution, a new discovery can be leveraged quickly to new applications without having to wait for a genetic change.

Food itself has come to serve many functions—aesthetic, social, and moral—in addition to its original nutritive function (Kass, 1994; P. Rozin, 2007). The food vocabulary has expanded to encompass metaphorical functions, again by a process of preadaptation. The words *taste* and *distaste* indicate general aesthetic judgments. In Hindu India, food and eating are deeply social and moral activities (Appadurai, 1981).

THE FOOD CYCLE

The food cycle is a description of a sequence of activities that usually terminates in the consumption of food. For most animals, it begins with arousal, a motive for searching for an appropriate food item. This is the part of the cycle that has been of most interest to psychologists, in the form of two motivational systems—hunger and thirst. Hunger is principally activated by a shortage (or anticipated shortage) of energy. Thirst is activated by a shortage of water, the most fundamental nutrient. A possible third system, sodium appetite, clearly exists in rats and some other animals (Schulkin, 1991) and may exist in humans.

The second phase of the food cycle is *search*. Search has two very important psychological components. One has to do with *what to search for*, that is, the identification of good candidates for ingestion. This is particularly important for a generalist (omnivorous) animal, such as humans. The second has to do with the *pattern of search*—where to look and when to shift from one foraging area to another to maximize energy input with respect to energy expenditure. This aspect of behavior has been well studied in animal behavior in the framework of optimal foraging theory.

The third stage of the food cycle involves the *capture* of food, once it is identified. This may be trivially easy for some grazing animals, but for others, plant foods may be difficult to access and require specific adaptations, witness the giraffe. For animals that consume some animal life (carnivores and omnivores), the capture phase may be by far the most challenging in the food cycle. A wolf pack capturing an antelope involves many highly honed skills including social skills. The speed of a cheetah is clearly an adaptation to capturing swift prey, as is the sonar system of some types of bats, used to both detect and capture insects. Some of the best and most exciting examples of "arms races" occur in this area, such as the coevolution of bat predatory abilities (e.g., sonar) and moth protective predator detection abilities (Roeder, 1998).

The fourth stage is preparation of food for consumption, subsequent to capture. Again, for grazing animals or insect eaters, this phase is absent or minimal, but for some animals, access is a critical challenge. Oyster drills have to make holes in the oyster shell to obtain the meat inside, and many mammals and some birds have to crack nuts or shells. Food storage is also a part of this stage. Preparation becomes a major aspect of the relation of modern humans to food.

The fifth stage, *consumption*, is vitally important but usually less interesting. Of course, for humans, the meal is quite an elaborate and social consumption activity.

Depending on its type of food, an animal's adaptations to its food world will elaborate different phases of the food cycle. For the specialist, an animal that eats one relatively small class of foods, the identification of food (e.g., bamboo leaves for a panda) can be innate, and preparation and consumption is straightforward. Carnivores eat a wider class of foods, but they can often be encoded in a rather simple way, so that the detection of food is not problematic. For some species of frogs, if it is small and moving, it is food. There are adaptations needed for capturing prey (such as the speed of the cheetah), identifying vulnerable prey, and deciding where to forage.

The same considerations hold in general for other animals with limited classes of food, such as exclusive leaf or exclusive fruit eaters.

The generalist eats a wide range of different foods. One subset of generalists, omnivores, consumes both animal and plant foods. For the generalist, there is no way to prespecify what is edible and what is not, or what is toxic, from the enormous set of food possibilities. This requires learning, but with some biological predispositions. Unlike plant generalists, omnivores have two more problems. First, it is usually more challenging for them to find and capture their animal foods. Second, animal foods are more likely to harbor dangerous pathogens, so the omnivore must manage to avoid both plant poisons *and* harmful micro-organisms contained in animal flesh. The latter is a special problem for modern humans because, for the past 8,000 years or so, they have lived close to domestic animals. But there is one major advantage that a carnivore or omnivore has: The animals they eat are much more like them, biochemically, than are plants. As a result, diets high in meat are nutritionally complete. The plant generalist faces the additional problem of establishing a repertoire of consumable species that together, but not separately, meet all nutritional needs. Mayr (1974) has identified mate choice as a closed system, meaning the target can be substantially prespecified in the genetic program, and food selection for generalists as an open system, meaning that the category of food is not well specified in advance, and much acquisition is involved.

Thus, it is the omnivores that face the greatest psychological food challenges. The return for this is an ability to live almost anywhere. It is no accident that three of the great omnivores, humans, rats, and cockroaches, are found all over the world. The demands of omnivore (and generalist) food identification establish a selection pressure for bigger and more computationally sophisticated brains (Milton, 1981).

Specialists have one system indicating a need for food and another for identifying the specific food. Humans and other generalists have at least two motivation systems, hunger and thirst, but for both, there is a major problem in identifying and innately specifying what entities in the world satisfy each motive. Thus, they also have a bit of the prewired specialist in them, that is, subsystems with specific arousal and motivation mechanisms (e.g., thirst) and relatively well-defined target entities (e.g., water) that can satisfy the motive.

FINDING POSSIBLE FOOD SOURCES

For humans and other mobile species, finding food involves two primary steps: exploring for a new food source or returning to a previously encountered one, and exploiting (consuming or harvesting) that resource until the decision to leave that resource (and possibly return to exploring for another). The ways that other animals solve the problem of sufficient energy and nutrient intake have been widely investigated in behavioral ecology, including the framework of optimal foraging theory (Stephens & Krebs, 1986). For example, shore crabs preying on mussels will preferentially work to open mussels from which they can get the highest net energy gain: Larger mussels have more meat but it takes more time to open them (Elner & Hughes, 1978). The same theoretical approach has been combined with the tools of ethnography and archaeology to study human foraging behavior in the field of human behavioral ecology (Hawkes, O'Connell, & Rogers, 1997; Winterhalder & Smith, 2000). Two important threads of research on optimal foraging are the efficacy of foraging behaviors and the mechanisms driving those behaviors. The data on how precisely foraging is tuned to energy and nutrient needs are impressive, encompassing many species including humans. Less is known about the mechanisms that account for the finely tuned behavior, which involve biologically evolved tuning systems using acquired input from the environment for purposes of calibration.

Exploring and Returning When seeking food, an organism can search until a possible food resource is found, then assess the resource and decide whether it is edible and worth eating or collecting, and repeat this process until the decision is positive. Such exploration for new resources can follow trajectories that are shaped to cover the region to be searched without revisiting previously seen locations (Bell, 1991). It is also typically guided by the use of distal cues indicating the presence of those resources. For humans, the cues used are primarily visual, including the presence of other species seeking the same resource or the number of people around a resource as an indication of how rich it might be (Goldstone & Ashpole, 2004), as well as the communication signals of other conspecifics when foraging socially in groups. Silverman and Eals (1992) proposed that men and women would have different evolved exploration abilities stemming from sex differences in Pleistocene foraging roles, with men using more orientation-based navigation appropriate for pursuing and bringing home wide-ranging mobile prey, and women using more landmark-based searching appropriate for finding and returning to local plant-based foods. A variety of sources of evidence supports this hunter-gatherer theory of sex differences in spatial abilities (Silverman, Choi, & Peters, 2007), though much of it has been from laboratory studies with low ecological validity (but see Pacheco-Cobos, Rosetti, Cuatianquiz, & Hudson, 2010, for a field study). Men are also predicted to be better at finding an efficient path home after a foraging trip (e.g., to bring captured prey back quickly), in terms of minimizing distance traveled, as Silverman et al. (2000) found in an exploration task set in the woods.

If individuals have previously encountered a renewable resource (or it was not fully depleted when they left), then it could be profitable to return to it, depending on the other options available. In this case, memory for the location of the resource will be useful. Assuming the same evolved sex differences in foraging just mentioned, New, Krasnow, Truxaw, and Gaulin (2007) predicted that women would be better than men at recalling the spatial locations of plant-based foods. To test this, they took people around a farmers market to sample the foods at different stalls, and then they gave them a surprise memory task, asking them to point in the direction of the stall for each food they had tried. Women were indeed more accurate than men, by 7 degrees on average. But men and women were both better at remembering the locations of calorie-dense foods (such as almonds and olive oil) than calorie-sparse ones (lettuce, cucumber), indicating foraging behavior designed to promote return to the most profitable food resources.

Exploiting and Leaving Once a food resource has been found, the forager can decide how long to exploit that resource (e.g., consuming or harvesting it). If the resource is a single item, the decision can be about how much to consume (e.g., of a meal) or how to share it with others (e.g., for a hunted animal). The former is controlled in part by well-studied satiety mechanisms that can be strongly affected by top-down visually driven influences (as shown by people trying to eat until all the soup is gone in "bottomless bowls" (Wansink, Painter, & North, 2005) and reduced regulation of amount eaten in "dark restaurants" (Scheibehenne, Todd, & Wansink, 2010). Memory of amount recently consumed can also determine satiety: Amnesic patients will consume two or three consecutive lunches, because they do not remember having just consumed a culturally appropriate amount for a meal (P. Rozin, Dow, Moscovitch, & Rajaram, 1998). How much to eat is also influenced by social norms for consumption (including eating more when in groups—de Castro & de Castro, 1989), copying the amount eaten by other positively valued models (but not by negative, e.g., obese, models—McFerran, Dahl, Fitzsimons, & Morales, 2010), and environmental cues that are predominantly cultural (e.g., bowl or utensil size—see Wansink, 2006). Food sharing may be the outcome of multiple possible selective forces (Winterhalder & Smith, 2000), including exchange of uncertain large prey resources to minimize risk of insufficient calories for one's family or to show off hunting skills that may garner status or mating opportunities, and provisioning kin with steadier food sources such as tubers that take skill to process (the grandmother hypothesis for extended postmenopausal female life span—Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998).

Food resources can also take the form of patches of individual items concentrated in a local area, such as berries on a bush or fish in a pond. In this case, the forager must decide how long to exploit the patch—when to stop looking for more items in this patch and leave to either explore for another patch or engage in another activity. Typically, as a patch is exploited, there will be fewer items to find, so that the rate of return will fall over time, and at some point it will be better to leave the patch than to stay and try to find more in it. Such patch-leaving decisions have been studied in terms of optimal foraging theory, with the optimal strategy (under some assumptions) being to leave a patch when its current rate of return falls below the mean rate of return from optimally exploring and exploiting the whole distribution of patches in the environment (the marginal value theorem—Charnov, 1976). A forager should leave the current patch when it could do better by going elsewhere, including the costs of traveling to the next patch. Many species have been found to come close to the predictions of the marginal value theorem while foraging (Stephens & Krebs, 1986), typically by employing simple patch-leaving heuristics that approximate the optimal strategy (Bell, 1991).

Humans also appear to have a general expectation that resources will appear in patches or clumps (Wilke & Barrett, 2009), which in turn calls for psychological mechanisms to decide when to leave them. These mechanisms have been studied in lab tasks such as simulated fishing in a sequence of ponds (the patches), where participants foraged in each pond before deciding when to leave it and travel to the next one (Hutchinson, Wilke, & Todd, 2008), and a visual search task where participants had to find ripe berries in patches (Wolfe, 2013). People stayed longer in patches as the travel time between them increased and overall used patch-leaving mechanisms (including time elapsed between successive items) that produced near-optimal rates of finding resources in typical environments.

DECIDING WHAT TO EAT

When an item that may potentially be food is encountered, the individual must decide whether to consume it. A variety of evolved mechanisms contribute to the ability of humans to assess edibility and learn about appropriate foods, both individually and socially.

Innate Predispositions for Identifying Food The identification of foods is facilitated by some built-in sensory biases. Humans (and rats) at birth have an immediate acceptance of sweet-tasting fluids (Steiner, 1979). This is highly adaptive, since sweetness is most associated, in the environment, with fruits, a major source of nutrition. Human infants also show an innate aversion to bitter and sour tastes (Steiner, 1979). The bitter avoidance is clearly adaptive, since many common plant poisons are bitter. There is probably a genetically programmed preference for moderate levels of salt (sodium), a vital nutrient that is in short supply in many environments, but it emerges well after birth (Beauchamp, Cowart, & Moran, 1986). Finally, although there is no definitive data from newborn infants, there is probably a genetically programmed positive response to fatty textures (corresponding to the presence of fat, one of the three major macronutrients), and a genetically programmed aversion to oral irritants, such as chili pepper. It is not clear why humans have an irritant aversion. Many irritants in the environment are nutritive and have become major parts of human cuisines. All these evolved taste biases have been demonstrated in rats (*Rattus norevegicus*) and in a range of primates. More recent research on a number of mammals, including humans, has established the existence of a fifth basic taste, umami. This taste is elicited by many amino acids and thus constitutes a form of protein detector. At modest concentrations, it is attractive to many mammalian species, including humans (Galindo, Schneider, Stáhler, Tòle, & Meyerhof, 2012). Through a mixture of genetically programmed taste preferences and aversions, either present at birth or maturing during infancy, by the time of weaning human infants have a suite of taste preferences and aversions that help them negotiate the complex world of foods that they will experience.

Neophobia and Neophilia A new food has the potential to be an addition to the diet, but it also has the potential to be toxic. Thus, as studied primarily in the rat, there is a clear conflict about sampling a new food. When facing a new food, rats consume small amounts, in isolation, allowing for the assessment of the effects of the food (P. Rozin, 1969). In humans, there is a great deal of ambivalence about new foods, and a very wide range of tendencies related to sampling or avoiding them. The individual difference in avoidance tendency is called neophobia and is measured with a standard neophobia scale (Pliner & Hobden, 1992). Neophilia is the opposite tendency to approach new foods. The cause of the wide variation in individual levels of neophobia (and neophilia) is unknown, but it has a significant heritability (as does the related behavior of food variety seeking; Scheibehenne et al., 2014).

Learning What Is Edible and What Is Not There is a big problem in learning about the effects of foods. The ingestion event often precedes the consequences by hours, but basic Pavlovian conditioning was believed not to support conditioning with such long time intervals. The discovery in the 1960s of the adaptive specializations of learning about foods and their effects was a major event in the psychology of learning, which brought the evolutionary-adaptive approach to the fore and certainly constituted one of the major steps that set the stage for a flourishing evolutionary psychology. Work on specific hungers was pointing to special learning mechanisms (P. Rozin & Kalat, 1971), but the needed adaptive learning mechanisms were dramatically demonstrated by two classic experimental studies by John Garcia and his colleagues, in 1966 (summarized in Garcia, Hankins, & Rusiniak, 1974). This work, and its sequelae, broke the hegemony of the belief in one set of learning laws operative in many different situations. Long-delay learning, and the filtering of "relevant" stimuli (tastes) for ready association with negative gastrointestinal effects, explained effective poison avoidance in rats, and subsequently, specific hungers. Later work (e.g., Sclafani, 1999; Yeomans, 2010) documented long-delay learning in animals for positive events, like increases in the availability of energy some time after consumption. This work showed how the delay between the experience of food and its effects was bridged by special food-related learning mechanisms, including filtering out biologically irrelevant stimuli such as sights and sounds. For both rats and humans, upper gastrointestinal events, particularly nausea, seem to be the critical consequences that produce learned taste aversions (Pelchat & Rozin, 1982). Nausea following food ingestion, even after a delay, results in a dislike for the relevant food, whereas other negative visceral events (such as pain or allergy symptoms) following ingestion typically do not lead to a dislike but may lead to an instrumental, rationally discovered food avoidance.

As dietary generalists able to adapt to changing food environments, humans must also learn what is appropriate to eat in their particular locale. Some of this learning is the result of individual exploration, which may in some cases be guided by broadly useful innate biases. Adults and children (and macaques) learn about new foods and generalize that knowledge based on intrinsic features including color, texture, taste, and odor, but they use shape cues when learning and generalizing about useful artifacts. There is, however, evidence that this distinction may be absent in infants, leading some to question the status of food as a core domain of knowledge (Shutts, Condry, Santos, & Spelke, 2009), though it may be one that comes online only when it is needed after weaning.

Much of food learning follows what others are already successfully eating (Todd & Minard, 2014). This appears to begin in infancy, with 12-month-olds preferring to eat what adults from their own culture model eating with positive affect (Shutts, Kinzler, McKee, & Spelke, 2009). Wertz and Wynn (2014) found that 18-month-olds bias their learning about what others are eating toward plant sources over artifact sources, suggesting specialized responses to plants as potential foods. Consistent with an adaptive advantage of copying older individuals with greater knowledge of the local environment, Birch (1980) found that younger children (around ages 3–5 years) copied the food choices of (on average older) peers significantly more than the reverse, and Addessi, Galloway, Visalberghi, and Birch (2005) showed that young children would copy the specific novel food choices of familiar adults (but cf. P. Rozin, 1991, on limits of parental influence).

Like rats, humans show individual learning in the form of one-trial food avoidance, often being repelled for a lifetime from a food that they have been sickened by once (P. Rozin & Kalat, 1971). But although rats only socially learn food *preferences* (Galef, 2012), humans also learn what to *avoid* based on socially transmitted cues of disgust—seeing another person make a disgust face in response to a food may lead to an unwillingness to try that food oneself (Baeyens, Kaes, Eelen, & Silverans, 1996).

Making a Decision Given all these evolutionarily relevant cues that could possibly go into deciding what to eat—including sensory aspects, disgust, learned aversions, familiarity, handling time, cultural norms, family background, what others are eating—how is a decision ultimately made? Some factors (culture, disgust, and aversions) serve to narrow the range of items that would even be considered for consumption. To select from the remaining set of edible items, there is evidence that choices are not made by weighing and combining all the available information about each current option but rather are based on just a small set of cues processed in a quick heuristic manner (Scheibehenne, Miesler, & Todd, 2007; Schulte-Mecklenbeck, Sohn, De Bellis, Martin, Hertwig, 2013; Todd, Hertwig, & Hoffrage, Chapter 37, this *Handbook*, Volume 2). The most-used cues found in such studies of Western food choices are palatability and healthfulness (reflecting energy and nutrition content of the food) and price and convenience (reflecting opportunity costs and handling time).

THE FUNDAMENTAL RICH AND COMPLEX RELATION BETWEEN HUMANS AND THEIR FOOD

There are several universals of the way humans deal with food, such as meals, social gatherings around food, processing of food in some ways, and the development of culture-specific cuisines. Cuisines can be described in terms of staple foods, flavorings, and preparation methods (E. Rozin, 1982), supplemented by a variety of rules about who eats with whom and how to consume food. There is a mapping of food onto other domains of life, including the social world and social status, the sharing of food as a bonding activity, and the emergence of food as a moral substance. All this can be described in terms of preadaptations. Food and eating have been transformed into a distinctively human activity, as a sign and expression of our civilization and our distance from animals: We eat in a mannered way, with implements, bringing food to our mouth (as opposed to the animal way of bringing the mouth to food). Leon Kass (1994) has described this elegantly in *The Hungry Soul*, pointing out that "We eat as if we don't have to, we exploit an animal necessity, as a ballerina exploits gravity" (p. 158).

Humans have developed adaptations with respect to food, many consequent on the crowded living and work specialization afforded by domestication (Wolfe, Dunavan, & Diamond, 2007). Some, like bitter avoidance or sweet preference, have clear evolutionary roots. Others, like cooking and other forms of food sterilization, are clearly cultural acquisitions, but their acceptance is driven by biologically evolved motives such as parasite avoidance. Though it is important to understand the adaptive value of culinary practices, such as the corn and bean staples of Mesoamerica that together provide an adequate mixture of amino acids, or the possible antimicrobial properties of garlic and some other spices (Billing & Sherman, 1998), the existence of such links does not itself tell us whether they have a genetic component. A challenge for evolutionary psychology is to define the interplay of evolved and cultural forces in these and many other food areas, as we outline in the following examples.

There are two very general ways in which evolutionary forces have affected food eaten by contemporary humans. The first route is only indirectly psychological. The human gut and dentition is adapted to a mixed animal and plant diet. The human inability to digest cellulose sharply limits the types of plant foods that can be nutritive. Second, the large human brain, itself partly a function of the challenges of an omnivorous diet and the sociality encouraged by that, becomes deeply involved in the elaboration of the human food world, including such culinary leaps as the invention of milk chocolate, or food preservatives, or the various combinations of flavors that characterize most of the world's cuisines. We next focus on more specific links between biological and cultural evolution in the food and food habits of humans.

THE CONSEQUENCES OF INNATE PREFERENCES FOR SWEET TASTES AND FATTY TEXTURES

The presence of sweet and fat preferences in rats and nonhuman primates, the presence of sweet (and probably fat) preferences at birth in humans, and the fact that mother's milk is both fatty and sweet make a very strong case for sweet/fat preference as biologically evolved in humans. It is clear that these two indicators of energy content have evolved to become pleasant sought-after tastes. By themselves these innate preferences would account for a well-documented ripe food preference (sweet) and meat (fat) preference in humans. However, their impact on the contemporary human food world has been much more massive than that.

Consider just sweet preference (P. Rozin, 1982). With domestication of plants, this led to the cultivation of sweet foods, including fruits, sugar beets, and sugar cane. The search for sweeter and sweeter tastes motivated the extraction, through a series of technical advances, of the source of the sweetness, sugars. Here, cultural innovations were motivated by evolved urges. With sugars available and plentiful (Mintz, 1985), added sweetness became affordable and common: Cane sugar is much cheaper than honey. This availability led to the widespread adoption of two of the favorite foods of humans, chocolate and coffee, which,without sugar, are often perceived as unpleasantly bitter. (Chocolate quintessentially combines the human desires for sweet *and* fat; its sweetness and melt-in-the-mouth fatty texture emerge through an elaborate set of processing techniques.) The colonization of the tropical Americas by Western Europeans was partly motivated by the availability of land there for the cultivation of sugar cane. And within the past half-century or so, with a surfeit of calories in the developed world and a growing obesity problem, we face a battle between our desire for sweet and fat and the excess calories that this motive causes us to ingest. This is a commonly cited case of evolutionary mismatch between our evolved psychology (and physiology) and our current environments (Nesse & Williams, 1995; Cordain et al., 2005). But the big brain that gave us domestication and sugar extraction, motivated by our evolved urge for sweet tastes, has now brought us artificial sweeteners, which seem to uncouple sweet tastes and calorie consumption (with possible behavioral consequences—see Wang & Dvorak, 2010).

THE REVERSAL OF INNATE AVERSIONS

Humans innately avoid bitter and irritant oral experiences. A casual examination of the contemporary human diet shows that we often overcome these innate aversions. Chili pepper, black pepper, and ginger, all producing innately aversive oral irritation, are among the most popular spices in the world. Chili pepper alone is consumed daily by over 2 billion humans (Rozin, 1990). The irritant property is probably an adaptation by plants to deter consumption by mammals. Birds, which effectively spread the seeds of these plants, do not show an irritant aversion.

The human culinary landscape contains many very popular bitter foods, including alcohol (ethanol), tobacco, chocolate, coffee, and a variety of vegetables. Generally, the bitter and irritant substances are consumed because they are liked: They illustrate a major inversion of innate preferences, or hedonic reversals. This looks like an antievolutionary turn in the modern culinary world, dating back thousands of years in culinary history. There are ancestral-adaptive accounts for some of these reversals. For example, there is evidence that some spices have antibacterial properties, and that in tropical cultures like India, meat dishes, which are more likely to harbor pathogens, are more highly spiced (Billing & Sherman, 1998), though this and other possible adaptive reasons for using spices, such as masking spoilage, are debated (McGee, 1998; Rozin, 1990).

There are many correlations between culinary practices and enhanced nutrition, but these only hint at evolutionary origins. Chili pepper, in particular, has many nutritive and culinary advantages (Rozin, 1990). Some of its effects, such as relieving vitamin A deficiency, may be subtle and slow to manifest themselves; others, like the facilitation of chewing of mealy diets through salivation, are readily apparent and easily learned. But none of these adaptive/selective effects of chili ingestion would explain why people come to *like* the burn of chili pepper or other irritants, as opposed to simply consuming more because it functions as a "medicine."

We do not yet have an adequate theory about how this pervasive feature of human eating occurs. Exposure is necessary, of course, and the social context of consumption, particularly the presence of those who already enjoy the food in question, is probably critical. There are two theories that interestingly invoke some feature of human evolution (Rozin, 1990). One involves a normally adaptive, biologically programmed opponent process that produces a compensatory reaction to a negative stimulus (Solomon & Corbit, 1974). If this process is pushed further than it normally would be by cultural forces (e.g., when children copy others and consume chili pepper or tobacco that they normally find aversive), the compensation could grow to be greater than the sensation it is designed to neutralize, which could be a way of turning a pain into a pleasure.

A second theory of hedonic reversal attributes it to a characteristic of the evolved big brain. The theory, which can be described as "benign masochism" (Rozin, 1990; Rozin, Guillot, Fincher, Rozin, & Tsukayama, 2013), argues that humans get pleasure when they discover that their body is signaling danger, but they cognitively realize that they are not really in danger. It is the pleasure of mind over body and is illustrated not only by hedonic reversals in foods, but also by enjoyment of fear from roller coasters or scary movies and enjoyment of induced sadness from fictional portrayals, such as movies and plays, sad paintings, or music. Hedonic reversals seem to be uniquely human (unlike a prediction from opponent theories, which call on a mechanism widespread at least in mammals). Notably, Mexican pigs and dogs, which eat garbage including leftover Mexican food with chili sauce daily, do not develop a preference for chili pepper, a preference present in every person over five years old living in the same Mexican context (reviewed in Rozin, 1990).

Clearly, hedonic reversals involve strong cultural forces that can reverse innate tendencies, but accounts of these reversals engage the operation of biologically evolved systems. We do not, at this time, understand how the first adoptions of chili pepper into the human diet actually occurred, but we do know that tens of millions of humans in the contemporary world become chili likers every year.

Corn and Manioc: Different Problems in Explaining the Adoption of Food-Processing Technologies

As a result of practices by pre-Columbian Mesoamericans, the small and unpromising *teosinte* plant was selectively bred into corn (maize), a highly nutritive carbohydrate staple, which became the cornerstone of much of the pre-Columbian American diet. The seed stalk of corn is much larger than that of *teosinte*, the seeds on the cob are much larger and much more numerous, and unlike *teosinte*, they remain on the cob, convenient for harvesting. Much later in time, as a consequence of the green revolution and genetic engineering, corn emerged as the most efficient crop in the world in terms of calorie yield per acre, a staple for humans in parts of Africa as well as the Americas, and a major source of animal feed.

The traditional Mexican recipe for preparing corn is the tortilla. Corn is ground into a powder and mixed with "cal" (calcium hydroxide), ground seashells, and water to form dough cooked into tortillas. It was consumed by Cortez and his company. This tortilla technology has many nutritional adaptive values (Katz, Hediger, & Valleroy, 1974). The cal adds calcium to the mix, a mineral often in short supply in the Mesoamerican diet; it makes available the critical vitamin niacin and some essential amino acids from their bound, unusable state in corn. This is a classic case of a cuisine being adapted to optimize nutritional quality, in what Katz (1982) calls biocultural evolution.

But how were the nutritional advantages of tortillas discovered? The nutritional consequences are generally not salient upon ingestion and exert their effects primarily over days or weeks. What would cause people to experiment with adding things like seashells to corn, and what outcomes would encourage this enterprise, once it had been introduced? The tortilla technology makes it much easier to roll out a tortilla (P. Rozin, 1982), which may have been a palpable factor supporting the initial development of the technology. The failure of the Europeans to adopt corn may result from a simple fact: Although Cortez and later explorers brought corn back to Europe, they did not bring the tortilla technology, perhaps because only Mexican women make tortillas and the explorer parties included no Spanish women (P. Rozin, 1982).

The process of adoption of a particular culinary technology is clearer for manioc (cassava), another starch staple imported from the Americas (Brazil), primarily to Africa. Manioc is resistant to pests and easy to grow, but some varieties contain a deadly toxin, cyanide (reviewed in P. Rozin, 1982). Brazilian tradition treats manioc by grinding it and repeatedly rinsing it to remove the water-soluble cyanide. Although we do not know exactly how this procedure was invented, it is easy to imagine that the effectiveness of the procedure was highly salient given that the effects of cyanide are rapid and often deadly, and that the practice of rinsing food with water was previously established. Unlike the case of corn, the Brazilian culinary (detoxification) procedure was imported to Africa along with the manioc.

MILK: BIOLOGICAL AND CULTURAL COEVOLUTION OF METABOLIC ADAPTATIONS AND CULTURAL ADVANCES

Milk is the first food of all newborn mammals, who are biologically adapted to nurse, as are their mothers (Simoons, 1982; reviewed in Rozin & Pelchat, 1988; Durham, 1991). The infant gut contains the enzyme lactase that splits the unique milk sugar, lactose, into its two nutritive and digestible components, glucose and galactose. Milk is only available to mammal infants: Mothers cease to produce it as the process of weaning occurs. The weaning period is especially critical as the transition away from the milk superfood and toward exposure to the abundance of potential food alternatives in the world. There are three adaptations that may facilitate weaning from milk, a never-again-to-be-available food. One is induced familiarity with a range of new foods from (a) the presence of food residues (e.g., odorants, as for garlic) in mother's milk, which facilitate acceptance of these foods in the weaning transition (see Mennella & Trabulsi, 2012, for humans; Galef, 2012, for rats) and (b) exposure to maternally consumed foods through odorants on her surface in conjunction with exhaled carbon disulfide in her breath (based on rat research, Galef, 2012). Second, movement away from milk may be encouraged by developing lactose intolerance, which would cause gastric discomfort from consuming large amounts of milk in the later nursing period (Rozin & Pelchat, 1988). Third, among the sugars, lactose is relatively low in sweetness. Given that milk has to be abandoned and ideally not strongly desired postweaning, it may be easier to wean away from a less sweet fluid (Rozin & Pelchat, 1988).

Milk could be a highly nutritive food for adults, if they could procure it, except for the fact that lactase is biologically programmed to gradually disappear from the gut at around the time of weaning. The normal adult mammal is lactose intolerant, because it cannot digest lactose, and its presence in the hind gut produces diarrhea and bloating, including gas pains (Simoons, 1970, 1982; Rozin & Pelchat, 1988). How is it then that a majority of the adults in the world consume dairy products, and in some cultures, as different as India, Denmark, and Canada, they form a major part of the diet? There were two main events leading to this consumption once animal domestication occurred, one cultural and the other biological (Durham, 1991; P. Rozin, 1982; P. Rozin & Pelchat, 1988; Simoons, 1970, 1982).

On the cultural side, humans discovered that they could "culture" milk, that is, let it ferment. Under commonly occurring situations, one of the main effects of this is that bacteria break down the lactose in milk to its digestible component sugars, leading to familiar products such as yogurt and cheese. These products contain lactose, but at substantially lower levels than raw milk, and they also can be stored much more conveniently and successfully than raw milk. These cultured milk products are the principal way that dairy products are consumed today in the Mediterranean and South Asia.

But a remarkable biological adaptation also occurred in some cultures (Simoons, 1970, 1982). These were pastoral groups, primarily in Northern Europe but some in Africa, as well. There is reason to believe that the single gene mutation that blocks the deprogramming of the lactase gene at weaning time was not uncommon. Individuals who possessed it would have had the additional advantage of being able to consume milk as adults. This advantage was almost certainly the selective force for an increasing presence of this gene, which by now is prevalent in Northern Europeans and some African pastoralists. So a human domestication activity, that is, a cultural event, set up a biological selection pressure, leading to gene change for these groups, whereas the great majority of humans on Earth remain in the original state of lactose intolerance, like the rest of mammals. In our present state of knowledge, we cannot describe the actual process through which either cultured milk or raw milk actually became part of the human diet.

MEAT: A GREAT FOOD FOR HUMANS, BUT A SOURCE OF PARASITES AND FOCUS OF AMBIVALENCE

Meat is a natural food for the human omnivore (Fiddes, 1991; Rozin, 2004). It is a nutritionally complete and calorically rich food and ranks among the most appealing foods for most contemporary human beings. But the story of meat as an ideal human food has two blots against it. First, it is hard to obtain meat: Animal food sources move, so the capture phase is challenging and often involves considerable energy expenditure and social cooperation. Second, partly because animal food is so biochemically similar to the human biochemical profile, parasitic organisms that can live in animals can often live and reproduce in humans (Curtis, 2013).

The two major meat problems were dealt with rather effectively in human history. At a historical time still in dispute (Wrangham, 2009), humans were able to harness fire and use it to cook animal foods. Cooking kills virtually all parasites, though of course they can reinfect food that is left uneaten after cooking. Animal domestication reduced the skill and energy expenditure needed to obtain animal food, but it also increased parasite risks, because, postdomestication, humans lived in much closer proximity to large animals than they ever had previously. Many parasites find friendly homes in both domesticated animals and humans. In contemporary cultures, we see the expression of the high benefits but significant risks of meat consumption. Meat is at once the favored food of humans, and the most tabooed (Fessler & Navarette, 2003). Although some animal taboos are complete, applying to all members of a group (e.g., Hebrew dietary laws), many are conditional, saying that some meats cannot be consumed by some categories of individuals or at some times. The favored status of meat is clearly illustrated by conditional taboos, because they usually restrict access to favored animal parts (usually muscle) to adult males, the most powerful individuals in traditional cultures.

The complexities of response to meat, and, in particular, the negative side, has been enhanced over the past thousands of years of human cultural evolution, through the development of religions and ideas about human nature, origins, and fates. Ideas about souls, considered as the spiritual links between humans and animals, modulate human reactions to meat. Furthermore, after domestication, with the decline in hunting and the specialization of individuals into different roles, including pasturing and butchering (Diamond, 1997), the distance between many individuals and the origins of their animal foods increased. As a result, concerns about killing animals became less salient for many meat eaters in the modern world. And with increased accessibility to foods, humans became more selective about what animals they would eat (only the muscle of three mammal species, out of several thousand, for most American adults). Religious and perhaps empathic concerns led to the rejection of all animal foods by many humans (e.g., the "ahimsa" no-killing-of-animals principle followed by many Hindus). Deep sensibilities about ancestors and descendants, including beliefs about reincarnation, may have imbued animals with symbolic values (e.g., Fiddes, 1991; Twigg, 1983). Modern concerns cover not only killing or maltreating animals but also the high environmental cost of rearing and consuming them, as opposed to plants. For many adults in the developed world now, both liberal sentiment and long-term health concerns have replaced parasite avoidance as the major deterrent to meat consumption. However, in spite of the biological risks and symbolic and empathic concerns, the strong biological appeal of meat and other animal products remains.

DISGUST

It is a short step from meat as a human food to the emotion of disgust. In the last decade, disgust has become the focus of a great deal of attention from evolutionary psychologists. The striking thing about disgust is that almost all foods that some people find disgusting are of animal origin (Angyal, 1941; P. Rozin & Fallon, 1987). So the strongest negative reactions that humans have to food are focused on the favorite food category! The ambivalence toward meat appears again.

There is little doubt that, in its origin, disgust is a food-rejection system. In English, *dis-gust* means bad taste, and the semantics are similar in French. One of the two most frequent facial expressions associated with disgust involves a gape and tongue extension. Both of these serve to expel substances from the mouth. And perhaps most critically, the physiological signature of disgust is nausea, a sensation that inhibits ingestion and often precedes vomiting, the ultimate form of food rejection. A fundamental question is what triggers food-rejection disgust (called pathogen avoidance disgust by many evolutionary psychologists).

Following on classic work on disgust by Darwin (1872/1965), Angyal (1941) defined disgust as "revulsion at the prospect of oral incorporation of an offensive object." Angyal considered body waste products as a focus of disgust. P. Rozin and Fallon (1987, p. 23) added to Angyal's definition: "The offensive objects are contaminants; that is, if they even briefly contact an acceptable food, they tend to render that food unacceptable." Disgust that is related to body substances and some foods, considered the original elicitors, is sometimes called "core" disgust. Given that the core disgust elicitors are animal products, including body wastes, and that contamination sensitivity characterizes the response to these elicitors, it is very reasonable to presume that parasite avoidance is the basic motivation for core disgust. Originally expressed as the disease avoidance model of disgust (Matchett & Davey, 1991), this view developed substantially from work identifying many characteristics of disgust that fit a parasite avoidance interpretation (Curtis, Aunger, & Rabie, 2004; Oaten, Stevenson, & Case, 2009; Tybur et al., 2013). The two strongest arguments for this view are (1) that humans have contamination sensitivity, which is a part of food rejection that only makes sense for microbes, for which tiny doses can multiply in the body (unlike toxins), and (2) that core disgust elicitors center on potential foods that are vehicles for harmful microbes: meat and body products.

It is important to separate this question of whether disgust is a parasite avoidance system (for which the evidence is strong) from a second question, assuming the parasite avoidance function: Is parasite avoidance disgust biologically evolved or learned? Other behaviors such as cooking, administration of antibiotics, and water purification are also very effective uniquely human means of protection against parasites but clearly are explained through cultural learning rather than biological evolution. There is abundant evidence (e.g., Curtis, 2013; Hart, 2011) that parasite avoidance is a fundamental challenge for mammals and many other species, engendering a widespread suite of behaviors (e.g., grooming) to reduce parasite risk (see Schaller, Chapter 7, this volume). So is disgust an inherited system ("emotion") that fits in with these other evolved parasite avoidance behaviors? This has been widely assumed, but since disgust is not found in other animals and not present at birth in humans, two of the most convincing arguments for a genetic origin are not present. On the other hand, disgust (and contamination sensitivity) may be culturally universal in humans from about age 4 or 5 years onward (Hejmadi, Rozin, & Siegal, 2004). At this time, the most reasonable account of parasite avoidance disgust is that it is biologically evolved.

Another fundamental question regards the sequence of historical events that produced the widespread domain of disgust: How did a food-related emotion come to be applied to a very wide range of entities and situations, including contact with death or strangers, a variety of sexual acts (e.g., incest), and some moral violations? The process almost certainly involved preadaptation. The gape typically found in facial expressions of core disgust is part of an inherited response to bitter tastes (Grill & Norgren, 1978; Steiner, 1979); it is present at birth in humans and present in rats, primates, and other mammals. It is almost certainly true that the bitter face, which functionally rejects foods and signals this rejection, was preadapted for a new rejection function for spoiled and otherwise parasite-affected items, but it is not clear how or when this new function arose. In his analysis of disgust, Kelly (2011) highlighted this problem and postulated disgust as a combination (by preadaptation) of the innate poison (bitter) rejection and the innate parasite avoidance system (his "entanglement hypothesis").

Disgust may be the quintessential example of how the food system serves as the foundation for other systems that share its properties. The first theory of the expansion of disgust (P. Rozin, Haidt, & McCauley, 2008) proposed four historical stages, beginning with core (food-related) disgust, expanding to reminders of humans' animal nature (e.g., sex, viscera, and most critically, death), then to a subset of interpersonal contacts, and finally to a subset of moral violations characterized as divinity violations (P. Rozin, Lowery, Imada, & Haidt, 1999, using the taxonomy of Shweder, Much, Mahapatra, & Park, 1997). Preadaptation is explicitly invoked as the mechanism for expansion, and the emphasis is on cultural evolution, with the possibility open that core disgust is biologically evolved. The animal reminder phase is postulated to center on avoidance of reminders of mortality, a major problem and threat faced uniquely by humans (Becker, 1973; Goldenberg et al., 2001). Tybur et al. (2013) proposed that parasite avoidance, by itself, can encompass animal-reminder disgust, since death, deformity, and visceral exposure are all signs of infection, as well as interpersonal disgust, since strangers are more likely sources of dangerous pathogens; then they postulated two other domains of disgust: sexual and moral. Crucially, both views (and that of Kelly, 2011) ground moral disgust in terms of its origin in a food-related system.

THE TRANSMISSION OF FOOD PREFERENCES

We must clearly distinguish between a genetic basis for a species-wide tendency and a genetic basis for individual differences on the trait in question. For example, it is clear that reading/writing is a cultural invention, but differences in reading ability have a substantial heritability. On the other hand, for the food domain, the basic preference for sweet tastes is clearly based on genetics, but individual differences in the manifestation of that preference, so far as we currently understand them, have a strong acquired component, via either cultural or individually experienced causes.

One potential biological component of individual differences in food preferences is genetically based sensory differences. There are many different bitter receptors, and genetic analysis has identified specific genetic bases for many of these. One of these loci is measured by the rated bitterness of phenylthiocarbamide (PTC) or the related chemical propylthiouracil (PROP; Bartoshuk, Duffy, & Miller, 1994; Tepper, 1998). There is some modest evidence for lower preferences for foods with a bitter component (e.g., coffee, beer, and many vegetables) among people with greater PROP sensitivity (Tepper, 1998). As taste genetics develops, there will be more opportunities to examine mappings between taste and preferences.

The few existing twin studies on genetics of food preferences provide modest and mixed results including very modest heritability for specific food preferences, but perhaps higher heritability for some categories of foods such as high-fat foods or fruits (Reed, Bachmanov, Beauchamp, Tordoff, & Price, 1997). A major role for genes as contributors to the very substantial within-culture variation in food preferences is, however, challenged by data for family resemblance in food preferences. Family resemblance, usually measured as similarity in preferences or preference patterns between adult (college student) children and their parents, confounds genetics and parental influence. Therefore, family resemblance correlations can only establish upper limits for genetic contributions. The literature on family resemblance for food (and music) preferences reports surprisingly low correlations averaging about $r = 0.15$ (P. Rozin, 1991).

A problem of particular interest in the context of evolution is reliable changes in food preferences across the life span. Some short-term changes in food choice of women in the first trimester of pregnancy may be related to the vulnerability of the fetus and immune suppression in the female (Fessler, Eng, & Navarette, 2005). In bees, workers may shift during their lifetime from foraging for pollen to foraging for nectar, or the reverse. This depends on whether a particular bee is engaged in brood care (pollen preference) or supplying the hive with energy (nectar preference) and appears to be regulated epigenetically (Amdam, Norberg, Fondrk, & Page, 2004). The roles that epigenetics and the gut microbiome may play in lifetime and evolutionary changes in food preferences remain to be explored (Alcock, Maley, & Aktipis, 2014).

THE FUTURE

Food has been mostly absent for too long from the table of evolutionary psychology. This major part of human life, with its crucial connection to and influence on animal evolution, needs much more attention. Together with evolutionary selective forces, we must acknowledge the powerful role of culture in determining food choice, food habits, and the meaning of food. Just as the most informative piece of information about an animal's behavior may be what it eats, probably the most informative cue to a person's culture is what he or she eats. As we have shown throughout this chapter, the two factors, biology and culture, are inseparably intertwined: Cultural traditions are influenced both by general human metabolic and behavioral/cognitive capacities and by predispositions, and specific cultural differences in taste genetics and metabolic capacities have coevolved with cultural changes. The present is a particularly important and exciting time to study the interactions of evolution and culture in food behavior. For the first time in human history on Earth, billions of humans can sample the staple foods and cuisines from cultures across the globe. The homogenization of the world's diet may actually amplify the percentage of individual differences in food choice that can be attributed to genetics, as environmental variation is reduced. Furthermore, especially in the enlarging developed world, global perspectives about reducing pollution, food waste, and water use, saving the remaining unspoiled land on the planet, protecting animal rights, and "meddling" with nature via genetic engineering of foods add new dimensions to human food choice. All this is part of the immense future of the evolutionarily informed study of human food choice and eating behavior.

Another pressing research challenge for this field is to address increasing and changing food-related health concerns. It is ironic that two major genetically determined traits that were adaptive in the human ancestral environment, liking for sweet tastes and fatty textures, have become major suspects for a maladaptive outcome in modern cultures, namely obesity (Nesse & Williams, 1995; Speakman, 2013). The civilized environment may have inverted some of the basic selection pressures that were important in early human evolution: from food scarcity to food abundance, from low to very high caloric density foods, and from appreciable short-term consequences of food toxins and microbes to much more subtle long-term negative consequences of diet on degenerative diseases. Moreover, in the modern developed world, selection pressures operating on poor diet choice and obesity are often low (e.g., predation risk is not important in most modern settings) or occur at a range of ages that were rarely achieved in the ancestral environment (e.g., degenerative diseases). The increase in obesity and other food-related health challenges calls for study from a variety of perspectives, including two new approaches with strong evolutionary connections: epigenetics and analysis of the human microbiome.

Given that food acquisition behaviors have been fundamental to survival throughout the history of animal life, it is reasonable to expect that some of the mechanisms underlying these behaviors may have been appropriated and repurposed (as preadaptations, or exaptations) for other functions over the course of evolution. Hills (2006) argued that dopamine-driven food-search mechanisms formed the evolutionary basis of mechanisms controlling the search for other resources, including attentional control of search for information in the external environment (including visual search; Wolfe, 2013) and executive control of internal goal-driven cognition (see Todd, Hills, & Robbins, 2012 for an overview). For example, humans recalling concepts in memory (e.g., "name all the types of animals you can think of") switch between patches of related concepts (e.g., from farm animals, to pets, to insects) in a way that maximizes their success as predicted by the marginal value theorem in optimal foraging theory (Hills, Jones, & Todd, 2012). Similarly, people search the web using "information-foraging" strategies akin to those appropriate for patchy food sources (Pirolli, 2007). As already noted, preadaptation has resulted in expansion of food systems into the aesthetic domain (e.g., haute cuisine), the moral world (e.g., food in Hindu India as a biomoral substance; Appadurai, 1981), and the domain of language and metaphor, as when we say Linda is sweet, or let's get to the meat of the argument (Chan, Tong, Tan, & Koh, 2013).

We close with an example from Leon Kass's *The Hungry Soul* (1994), edited here to make a particular point. In his discussion of eating in the modern world as a statement of being civilized and not animals (the theme of his book), Kass asks us to imagine a dining scene in the Western developed world. Two adults are eating dinner, sitting opposite each other. Each spears food with a fork and conveys it into the mouth, where it is chewed and swallowed. The act of eating is done with delicacy and with great skill. Food does not fall off the fork or out of the mouth. The mass of food in the mouth is disgusting: moist, mixed with saliva, and a potential vector for germs. Each eater manages to chew the food without displaying any of the product of mastication. This is remarkable especially since the conversation at dinner is produced by sounds emanating from the same hole (mouth) that is incorporating food. So a deeply biological act, acquiring nutrients, is carried out with skill acquired through practice from early in life. We are still doing the evolved biological thing, eating, based on a biological motive, hunger, intertwined with an emotion with biological roots, disgust, in order to satisfy a basic biological necessity, but with such learned cultural skill that an innocent observer might not realize that the situation is basically about acquiring nutrients. And this whole intricate experience goes on tens of billions of times every day for contemporary *Homo sapiens*. Whether we like it or not, we are animals, and though we have largely managed, through civilized eating, to hide the evolved biological forces just below the surface, we still love sweet and fatty food.

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CHAPTER 7

The Behavioral Immune System

MARK SCHALLER

Many animals engage in many behaviors that reduce their exposure to pathogens. Ants line their nests with resins that inhibit the growth of fungi and bacteria (Chapuisat, Oppliger, Magliano, & Christe, 2007). Mice avoid mating with other mice that are infected with parasitic protozoa (Kavaliers & Colwell, 1995). Animals of many kinds—from physiologically primitive nematode worms to neurologically sophisticated chimpanzees—strategically avoid physical contact with specific things (including their own conspecifics) that, on the basis of superficial sensory cues, appear to pose some sort of infection risk (Goodall, 1986; Kiesecker, Skelly, Beard, & Preisser, 1999; Schulenburg & Müller, 2004).

Humans, too, engage in a wide variety of behaviors that provide prophylactic protection against pathogen infection. Some—such as condom use and vaccination—are modern artifacts of recently evolved neocortical processes that allow people to engage in rational decision-making of many kinds. Many other behaviors—some obvious and some not—appear to be governed by a suite of more ancient and functionally specific stimulus-response mechanisms that comprise a sort of "behavioral immune system" (Schaller, 2011; Schaller & Park, 2011). This chapter provides an overview of research on the behavioral immune system by highlighting, and elaborating upon, 12 key points. Collectively, these 12 "things you need to know" summarize the scope of this research, and provide a foundation for thinking critically about it.

THE BEHAVIORAL IMMUNE SYSTEM IS ADAPTED TO A FUNCTIONALLY UNIQUE FITNESS PROBLEM

Before discussing what we know in regard to the *how* and the *what* of the behavioral immune system (how it operates and what its implications are for psychological phenomena), it is important to address the question of *why*: Why is it even plausible that there evolved a specific set of psychological mechanisms devoted to behavioral prophylaxis against infection?

The conceptual argument for the evolution of the behavioral immune system begins with an assumption that infectious diseases imposed selection pressures on ancestral populations. The veracity of this assumption is not in doubt. Pathogens have been a presence in human and prehuman ecologies for many millions of years (Ewald, 1993; Wolfe, Dunavon, & Diamond, 2007). Their presence has not been benign. It has been estimated that infectious diseases have been responsible for more human deaths than all other causes of death combined (Inhorn & Brown, 1990). Selection pressures imposed by pathogens are sufficiently strong that genetic mutations conferring resistance to specific diseases can become widespread with unusual rapidity (Barreiro & Quintana-Murci, 2010). Over the course of human evolutionary history, these selection pressures resulted in many adaptations that are fundamental to human nature—including, most obviously, sophisticated immunological defenses.

If the existence of the immune system testifies to the selection pressures imposed by infectious diseases, it also raises an important issue that must be addressed when considering whether a *behavioral* immune system might also have evolved. Nothing evolves for free. No matter how intense the selection pressures associated with infectious diseases were, it is unlikely that a separate set of defense mechanisms would evolve unless these mechanisms were associated with a separate set of adaptive benefits. Is it plausible that, in addition to immunological defenses, there also evolved an additional set of psychological mechanisms facilitating *behavioral* defenses against infection?

Yes, and the reasons pertain to several shortcomings associated with immunological mechanisms. First, immunological responses are costly. For example: An immune response to bacterial infection typically involves some increase in body heat (local inflammation, systemic fever), and this response consumes substantial metabolic resources. (By one estimate, a 13% increase in metabolic activity is required to increase human body temperature by just 1°C; Dantzer, Kent, Bluth, & Kelley, 1991.) Second, immunological responses can be temporarily debilitating. Many symptoms of infection, such as fever and fatigue, are not directly caused by the invading pathogen itself; they are consequences of the immune system's means for combating that infection. Many of these symptoms inhibit individuals' ability to engage in various other forms of fitness-enhancing activity (mating, parental care for offspring, etc.). Third, immunological defenses are merely reactive, occurring only *after* pathogenic intruders have already entered the body and begun to do their damage. Because of the costs and limitations associated with immunological defenses, there would have been unique adaptive benefits associated with *proactive* defense: the behavioral prevention of infection in the first place.

But even this further consideration provides insufficient rationale for the evolution of psychological mechanisms devoted specifically to the problem of disease avoidance. Again, nothing evolves for free. It is unlikely that any functionally unique behavioral immune system would have evolved if, within ancestral ecologies, equally effective prophylaxis was facilitated by other (less functionally specific) psychological mechanisms. Disease-causing pathogens might sensibly be characterized as "small predators" (Kurzban & Leary, 2001, p. 197), and so one must consider the possibility that behavioral avoidance of pathogens has been governed by evolutionarily ancient psychological mechanisms that protect against predation more generally (Barrett, 2005). This fear-based predation-avoidance system governs responses to a wide range of bodily threats (including some that objectively aren't even predators at all, such as forest fires and floods). Is it plausible that there evolved a set of psychological mechanisms designed *specifically* to promote behavioral defense against infection?

Yes, and the reason is this: Even though disease-causing pathogens might logically be small predators, they are *functionally* different from other predatory threats (Tybur, Lieberman, Kurzban, & DeScioli, 2013). These functional differences arise from the fact that pathogens are not merely small; they are vanishingly small—too tiny to be perceived. Most other threats to human health and welfare (including objectively predatory threats such as snarling beasts and men with weapons, as well as things like fires and floods) are sizeable enough to be appraised as threats on the basis of sensory cues indicating size, location, movement, and sometimes even intent. By contrast, the organisms that cause infectious diseases (e.g., bacteria, viruses, helminths) are so tiny as to be imperceptible to human sensory systems. At best, their presence may sometimes be diagnosed only indirectly (e.g., the smell of organic matter that has been consumed by bacteria, or the appearance of a person suffering from infection). The imperceptibility of pathogens not only has unique implications for detection; it also has unique implications for behaviors that might mitigate their threat. Different species of pathogens are transmitted in different ways and, until very recently in human history, those modes of transmission remained outside the realm of human comprehension. (In fact, until the emergence of modern medicine and public health practices, infectious diseases were not just deeply mysterious but also uniquely diabolical: Many rewarding behaviors that served to fulfill the most basic biological needs—such as eating, drinking, and sexual intercourse—also increased the risk of exposure to disease-causing pathogens.) Behavioral strategies that were effective in mitigating exposure to other threats may have been useless, or worse, as protection against infectious diseases. For example, grouping behavior may provide protection against predatory attacks, but it facilitates transmission of many disease-causing parasites. The upshot is that psychological mechanisms facilitating adaptive behavioral responses to other forms of threat were unlikely to have provided effective prophylaxis against pathogens. There would have been unique adaptive benefits associated with an additional set of mechanisms that did, namely the behavioral immune system.

ITS ACTIVATION IS ASSOCIATED WITH DISGUST

If the behavioral immune system evolved as a means of facilitating functionally specific behavioral responses, it might be considered to be a psychologically unique motivational system (Aunger & Curtis, 2013; Bernard, 2012; Neuberg, Kenrick, & Schaller, 2011). Distinct motivational systems are typically associated with characteristic affective experiences—thirst, hunger, fear, jealousy, and so on. The affective experience associated with the behavioral immune system is disgust.

It has been argued that disgust evolved from a more primitive affective response that served the function of expelling harmful foodstuffs—which may be contaminated with poisons as well as pathogens—from entering an organism's oral cavity (Rozin, Haidt, & McCauley, 2008). In contemporary human populations, disgust is elicited not just by the taste of contaminated food, but also by the perception (via the full range of sensory and inferential organs) of many different kinds of stimuli that, throughout long stretches of human evolutionary history, were diagnostic of the presence of pathogens. Among the more obvious, such elicitors are body products that typically contain pathogens (e.g., feces), animal vectors through which pathogens may be transmitted (e.g., rats), and physical symptoms exhibited by individuals who are already infected (e.g., the sight of oozing sores, the sound of a sneeze).

Affective responses to these kinds of stimuli lie at the heart of empirical evidence attesting to the integral role of disgust in the behavioral immune system (Curtis, DeBarra, & Aunger, 2011; Oaten, Stevenson, & Case, 2009). Three kinds of evidence are especially compelling. First, disgust is elicited more strongly by these stimuli than by perceptually similar stimuli that are less likely to connote infection risk. For example, people are more disgusted by a yellowish liquid—which mimics the appearance of body products such as pus—than by an otherwise identical liquid that is blue (Curtis, Aunger, & Rabie, 2004). Second, pathogen-connoting stimuli elicit high levels of disgust but do not elicit high levels of other negative emotions, whereas functionally distinct forms of threat—such as predatory threats—elicit high levels of other negative emotions, such as fear, but do not elicit much disgust (Bradley, Codispotti, Sabatinelli, & Lang, 2001). These results implicate a functionally specific linkage between disgust and the threat posed by pathogen infection. Third, the tendency for pathogen-connoting stimuli to elicit disgust is exaggerated under circumstances in which the functional benefits of pathogen-avoidance are especially great, such as when individuals are especially vulnerable to infection. For example, immunological defenses are suppressed during the early stages of pregnancy (rendering the pregnant woman, and the developing fetus, more vulnerable to the fitness costs associated with pathogen infection). Coincident with this natural vulnerability, women in the early stages of pregnancy also exhibit stronger disgust responses to pathogen-connoting stimuli (Fessler, Eng, & Navarette, 2005).

Disgust is elicited not just by objects that overtly connote the immediate presence of pathogens; it is also elicited by specific forms of social behavior—including unusual sexual acts and actions of other kinds that violate moral codes of conduct (Haidt, McCauley, & Rozin, 1994; Tybur et al., 2013). Although there are additional functional considerations specific to the domains of mating and morality (Tybur et al., 2013), both sexual and moral behaviors also have implications for pathogen transmission. Sexual contact puts people at risk of infection, and so sexual behavior has historically been governed by cultural norms that (imperfectly) distinguish between ostensibly safe and unsafe sex acts. Consequently, as a result of cultural learning processes, sexual behaviors perceived to be non-normative within an individual's local cultural context may also come to be intuitively associated with increased infection risk. In fact, norm violations of all kinds may have this intuitive connotation. In preindustrial societies, "most conventions pertaining to subsistence and social behavior operate as prescriptions to avoid illness; almost all rules have health implications" (Fabrega, 1997, p. 36). Consequently, many transgressions against normative codes of conduct in many other behavioral domains may also come to be intuitively associated with increased infection risk. Thus, along with disgust responses to more obvious pathogen-connoting stimuli, many disgust responses in the sexual and moral domains may be indirect manifestations of the behavioral immune system.

IT INFLUENCES RESPONSES TO THINGS THAT POSE NO REAL THREAT OF INFECTION

The behavioral immune system governs responses not only to perceptual objects and actions that are truly diagnostic of increased infection risk, but also to many objects and actions that, objectively, pose no risk at all. The reasons for this overgeneralization lie partially in the common tendency for evolved cognitive mechanisms to operate on an "actual domain" of stimuli that is broader than the "proper domain" of fitness-relevant perceptual input (Sperber & Hirschfeld, 2004). But there is more to it than just that. Overgeneralization also follows from the adaptive principles articulated within *error management theory* (Haselton & Buss, 2000; Haselton, Nettle, & Andrews, 2005). Because perceptual cues connoting potential infection risk are only imperfectly diagnostic of actual infection risk, the appraisal of risk must inevitably produce errors. Two kinds of errors are possible: False-positive errors (inferring infection risk when there is none), and false-negative errors (failing to infer infection risk when, in fact, some risk exists). Both types of error are equally erroneous in a strictly logical sense; but they have different behavioral consequences, and these different behavioral consequences are likely to have had different implications for health and reproductive fitness within ancestral populations. Whereas false-positive errors would have resulted in (objectively unnecessary) avoidance of benign objects, false-negative errors would have resulted in (sometimes fatal) contact with infectious objects. The evolutionary consequence is that the appraisal mechanisms that trigger the behavioral immune system are calibrated to avoid highly costly false-negative errors. This adaptive cognitive bias inevitably produces many false-positive errors instead.

So, from the subjective perspective of the perceiver, infection risk may be connoted not just by the subset of body products that might actually be diagnostic of pathogen infection (e.g., feces, pus), but also by objectively benign body products (such as urine). Infection risk may be connoted not just by the actual physical symptoms that people exhibit when infected, but also by morphological or behavioral anomalies more generally, even those that are objectively unrelated to infection status. Infection risk may be implied not just by norm violations in behavioral domains most relevant to pathogen transmission (e.g., food, hygiene, mating) but also by norm violations more generally. These false positive errors may offer no immediate functional benefits (and may even be costly); but they are manifestations of an underlying cognitive bias that, within ancestral ecologies, evolved as an adaptive means of avoiding even more substantially costly errors.

ITS EFFECTS ARE FLEXIBLE AND CONTEXT-CONTINGENT

Even functionally beneficial mechanisms also have costs. The development, and later deployment, of any bodily system consumes resources (which then cannot be expended on the development or deployment of other bodily systems). One means of adaptively managing these cost–benefit trade-offs manifests as developmental plasticity. During the course of an organism's development, genes produce different phenotypic outcomes depending on informational inputs from the local ecology, so that mechanisms that are more functionally beneficial within that ecology become more fully developed, at the expense of less immediately relevant mechanisms. Immunological defenses are characterized by developmental plasticity (Curno, Behnke, McElligott, Reader, & Barnard, 2009). Analogously, development of the behavioral immune system is likely to be responsive to informational inputs indicating the chronic risk of infection in the local ecology, and this may contribute to chronic differences among individuals.

This developmental process is just one relatively blunt instrument for solving the cost–benefit problem. Among primates and other big-brained animals, the cost–benefit problem is also substantially solved by neurocognitive and behavioral flexibility (van Schaik, 2013). The strength of any psychological response to a stimulus is variable from moment to moment, depending on additional information conveying the extent to which the functional benefits of the response might outweigh its costs within that particular circumstance. For example, cues connoting the presence of a predatory threat elicit greater fear and stronger activation of danger-connoting cognitions under conditions in which, on the basis of additional contextual information, perceivers feel more vulnerable to predation (Grillon, Pellowski, Merikangas, & Davis, 1997; Schaller, Park, & Mueller, 2003). The same principle applies to the behavioral immune system. Under conditions in which context-specific information makes a person's vulnerability to infection psychologically salient, people are more likely to appraise perceptually ambiguous stimuli as connoting an infection risk (Miller & Maner, 2012), and they are likely to exhibit more pronounced affective, cognitive, and behavioral responses to those infection-connoting stimuli.

This *functional flexibility* principle (Schaller & Park, 2011) has informed much research on the cognitive and behavioral implications of the behavioral immune system. The utility of this principle lies not so much in the (intuitively obvious) observation that disease-avoidant psychological responses are likely to be variable across circumstances. Rather, the value lies in its specific implications for scientific inference and discovery. By employing research methods that experimentally manipulate the salience of individuals' vulnerability to infectious diseases, and that then measure some specific cognitive or behavioral outcome, one can test the extent to which there is a causal influence of perceived vulnerability on that outcome. If it is, and if that effect is *specific* to infection-vulnerability (compared to control conditions that make individuals feel vulnerable to equally dangerous but conceptually distinct forms of threat), it implies that the behavioral immune system has some psychologically *unique* influence on that outcome.

Dozens of psychological experiments have been conducted that apply these basic logical principles to a variety of psychological phenomena. The following four sections identify four broad domains of phenomena for which there is experimental evidence attesting to the unique implications of the behavioral immune system.

IT HAS UNIQUE IMPLICATIONS FOR INTERPERSONAL ATTRACTION

Many infectious diseases manifest in symptoms that affect a person's facial appearance—making it less symmetrical, less prototypical. Given the adaptive tendency for risk-averse and overgeneralized appraisal, even subtle nonsymptomatic deviations from facial symmetry or prototypicality may be intuitively interpreted by perceivers as indicating some infection risk. This is likely to manifest in subjective judgments of attractiveness, which may help explain why faces that are less symmetrical and less prototypical are also judged to be less attractive (Rhodes, 2006). If so—if the subjective assessment of facial attractiveness reflects the underlying means of identifying, and avoiding, sources of infection—then the relative unattractiveness of asymmetrical and nonprototypical faces may be exaggerated when perceivers temporarily feel more vulnerable to infection.

Exactly this effect was reported by Young, Sacco, and Hugenberg (2011). They experimentally manipulated whether the risk of pathogen infection was temporarily salient or (in a control condition) whether a different kind of threat was salient. They then assessed subjective preferences for faces varying in bilateral symmetry, as well as preferences for other (nonsocial) objects that also varied in symmetry. Results revealed that the typical preference for symmetrical faces was exaggerated when the threat of infection was salient. Preference for symmetrical objects of other kinds was not exaggerated. Thus, not only was the effect specific to circumstances that made perceivers feel vulnerable to infection, it was also specific to the perception of faces.

The results of Young et al. (2011) were obtained on judgments of both same-sex and opposite-sex faces. Other research using similar methods indicates that the effect may be especially pronounced in perceptions of *opposite-sex* faces (Little, DeBruine, & Jones, 2011). This result implies that the exaggerated preference for symmetrical faces (and perhaps for more subjectively attractive faces in general) is especially likely to occur in mating contexts. There are many possible reasons (Tybur & Gangestad, 2011). Some follow straightforwardly from the functional logic of behavioral prophylaxis against infection: Because sexual behavior puts individuals in especially intimate (and sometimes especially enduring) physical contact with other individuals, the mating domain is one in which individuals may be especially vigilant for cues indicating possible infection, and may be especially discriminating in their responses when any such cues are perceived. Other reasons go beyond the simple avoidance of sexual contact, and pertain to the genetic fitness of offspring that might result from sexual contact. For example, bilateral symmetry and other subjectively attractive features may not only be diagnostic of an individuals' current health, they may also be diagnostic of the extent to which that individuals' genes provide a basis for effective immunological defenses against infection—genes that are likely to be passed on to offspring who, in turn, are likely to have better immunological defenses and to be more reproductively fit themselves.

Even if the behavioral immune system does have implications for attraction that manifest especially strongly in mating contexts, its implications for attraction are not limited just to mating contexts. Several experiments show that, compared to conditions in which people feel vulnerable to other forms of threat, when people temporarily feel vulnerable to infection, they express stronger preferences for physically attractive political candidates and more highly prioritize physical attractiveness when selecting group leaders (White, Kenrick, & Neuberg, 2013). The latter effect was specific to the selection of *leaders*, and did not emerge on preferences for group members more generally.

Overall, it appears that activation of the behavioral immune system has unique consequences for the subjective appeal of attractive people, and that these consequences may occur especially strongly within behavioral domains (such as mate choice and leader selection) that have especially important implications for individuals' own immediate or long-term outcomes.

IT HAS UNIQUE IMPLICATIONS FOR STIGMA AND PREJUDICE

Much evidence implicates the behavioral immune system in the stigmatization of, and prejudice against, different categories of people (Kurzban & Leary, 2001; Oaten, Stevenson, & Case, 2011; Schaller & Neuberg, 2012). The most obvious implications are for prejudices toward people who actually are suffering from infectious diseases. But perhaps the most striking implications—which follow from the principles of error-management theory (discussed earlier)—are found in prejudicial responses to people who, objectively, pose no infection risk at all.

Among these targets of prejudice are people whose appearance is characterized by superficial morphological anomalies, such as facial birthmarks (Ryan, Oaten, Stevenson, & Case, 2012). Results from one study revealed that the semantic concept "disease" was implicitly activated into working memory by the perception of a facially disfigured man even when perceivers *knew* that the disfigurement was merely a superficial birthmark and that the man was healthy (Schaller & Duncan, 2007). In fact, "disease" was implicitly associated more strongly with the superficially disfigured man than it was with a man who was known to suffer from an infectious disease but who appeared superficially normal.

These implicit prejudicial responses are elicited by the perceptions of people who appear morphologically anomalous in other ways too. Consistent with the logic of functional flexibility, these prejudices emerge most strongly under conditions in which perceivers feel more vulnerable to infection. Compared to control conditions in which other threats are salient, when the threat posed by infectious disease is temporarily salient, people exhibit stronger implicit prejudices against people who are physically disabled, elderly, or obese (Duncan & Schaller, 2009; Park, Faulkner, & Schaller, 2003; Park, Schaller, & Crandall, 2007). Prejudice against obese people is particularly revealing. Obesity was unlikely to have been prevalent in the ancestral populations in which the behavioral immune system evolved; even in contemporary ecologies, obesity is unlikely to be objectively diagnostic of pathogen infection (if anything, infection is more likely to cause weight loss than weight gain). The findings, therefore, highlight the logical implications of error management theory (Haselton et al., 2005): The behavioral immune system can be tricked by novel and objectively irrelevant stimuli, and it produces prejudice accordingly.

The behavioral immune system appears also to have implications for xenophobia. There are many conceptually distinct psychological causes of xenophobia, some of which are linked to other threats implicitly associated with members of coalitional outgroups (including threats to economic resources and the threat of interpersonal violence; e.g., Esses, Dovidio, Jackson, & Armstrong, 2002; Schaller et al., 2003). In addition to those other threats, there are several reasons why outgroup members—especially those who are perceived subjectively to be "foreign"—might also be intuitively associated with infection risk. Some foreign peoples have physical appearances that may be subjectively appraised as anomalous, and so may trigger the behavioral immune system for the same reason that obese people do. A second possibility lies in the potential for exotic peoples to be sources of exotic pathogens (which may be especially virulent when introduced into local populations). A third reason is perhaps less obvious but also of potentially greater evolutionary importance: Outsiders may be ignorant of, or less personally invested in complying with, local cultural norms; and so are more likely to violate those norms. Because many local norms historically served as barriers to pathogen transmission, the presence of outsiders within one's local community may have increased the infection risk to everyone within that community. The implication is that when people are subjectively perceived to be foreigners, they are likely to elicit the psychologically unique form of prejudice associated with the behavioral immune system. This is especially likely when perceivers are—or simply perceive themselves to be—especially vulnerable to infection. Consistent with this hypothesis, women in their first trimester of pregnancy (whose immunological defenses are temporarily suppressed) exhibit exaggerated ethnocentrism and xenophobia (Navarette, Fessler, & Eng, 2007). Also, compared to control conditions in which other threats are salient, when the threat of infection is temporarily salient, people exhibit more exaggerated prejudice against immigrants from subjectively foreign places (Faulkner, Schaller, Park, & Duncan, 2004).

These finding not only have unique conceptual implications, they also have practical implications for the design of intervention strategies that might reduce prejudices (Schaller & Neuberg, 2012). One set of experiments reveals that, among people who chronically perceive themselves to be vulnerable to pathogen infection, prejudice can be reduced by interventions that specifically target these perceptions of vulnerability and bolster feelings of immunity or invulnerability instead (Huang, Sedlovskaya, Ackerman, & Bargh, 2011).

IT HAS UNIQUE IMPLICATIONS FOR CONFORMITY AND REACTIONS TO NONCONFORMITY

If cultural rituals and traditions and norms historically helped to inhibit pathogen transmission (Fabrega, 1997), it follows that activation of the behavioral immune system may lead people to be especially observant of norms, and to respond especially harshly to norm violations. These effects may manifest in a variety of specific psychological phenomena, including conformity, political conservatism, and moral judgment.

Effects on conformity are documented by recent experiments showing consistent findings across multiple measures, and across multiple cultural contexts: Compared to control conditions in which other forms of threat are salient, when people feel temporarily vulnerable to the threat posed by infectious diseases, they express greater liking for people with conformist traits, endorse more conformist attitudes, and are more likely to behaviorally conform with majority opinion (Murray & Schaller, 2012; Wu & Chang, 2012). Thus, while other self-protective motives may also lead to increased conformity (Griskevicius, Goldstein, Mortensen, Cialdini, & Kenrick, 2006), the behavioral immune system appears to have implications for conformity that are uniquely powerful.

The same rationale implies further implications for conservative political attitudes (which are characterized by attitudinal defense of long-standing cultural traditions, and by intolerant responses to individuals who deviate from those traditions). Many studies, using both correlational and experimental methods and employing both indirect and direct indicators of conservatism, indicate that when the behavioral immune system is activated more strongly, people are more conservative (Terrizzi, Shook, & McDaniel, 2013). In one illustrative experiment, Helzer and Pizarro (2011) asked people to complete a measure of political attitudes in the hallway of a public building. In one condition they did so while standing next to an antibacterial hand-sanitizer dispenser—a perceptual cue that makes the threat of infection temporarily salient. In that condition (compared to a control condition), people endorsed more politically conservative attitudes.

This conceptual framework may help explain why disgust has a carry-over effect on moral judgments (e.g., Erskine, Kacinik, & Prinz, 2011; Horberg, Oveis, Keltner, &

Cohen, 2009; Schnall, Haidt, Clore, & Jordan, 2008; Wheatley & Haidt, 2005). Given that the appraisal of infection risk often triggers disgust, the emotional experience of disgust may serve as a signal indicating vulnerability of pathogen infection. Consequently, people are more likely to morally condemn actions that violate cultural codes of conduct and other social norms.

IT MAY HAVE IMPLICATIONS FOR BEHAVIORAL DISPOSITIONS MORE BROADLY

Several studies suggest that the behavioral immune system may influence general behavioral tendencies of the sort typically measured as personality traits. For example, in the domain of sexual behavior, people differ in their dispositional tendency toward restricted versus unrestricted (e.g., promiscuous) mating strategies (Jackson & Kirkpatrick, 2007; Simpson & Gangestad, 1991). Results from one study revealed that women (but not men) who perceived themselves to be more chronically vulnerable to infection reported more restricted mating dispositions, and these effects emerged primarily when the threat of infectious diseases was temporarily salient (Murray, Jones, & Schaller, 2013). Why was this effect specific to women? It may reflect the historically adaptive tendency for women, more than men, to be risk-averse in the mating domain (Haselton & Buss, 2000). Consequently, women may be especially sensitive to the costs associated with unrestricted mating strategies—including the increased risk of contracting infectious diseases.

For both men and women, social interactions of any kind may facilitate pathogen transmission. Consequently, people who are more socially gregarious may be more susceptible to infection (Nettle, 2005). Activation of the behavioral immune system might, therefore, be expected to inhibit socially gregarious dispositional tendencies. There is some support for this hypothesis: When the threat of infection was made temporarily salient, people expressed reduced dispositional tendencies toward extraversion and agreeableness; and these effects emerged most strongly among people who chronically felt most vulnerable to infection (Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010).

Even beyond the domain of social interaction, any kind of approach-oriented, risk-tolerant, or exploratory behavioral style may increase individuals' risk of coming into contact with pathogens within their natural environment—and so may be inhibited when the behavioral immune system is activated. Some support for this hypothesis is found in additional results reported by Mortensen et al. (2010). When the threat of infection was temporarily salient, people reported lower levels on the trait "openness to experience," and this effect, too, occurred primarily among people who chronically felt most vulnerable to infection.

Compared to the other lines of work reviewed earlier, these findings on dispositional traits probably need to be interpreted more cautiously. The experimental design employed by Mortensen et al. (2010) did not include a control condition in which other kinds of threat were made salient, and so it is difficult to confidently conclude that the effects were unique to the perceived threat of infection. These results, along with those of Murray et al. (2013), are also complicated by interactions between experimental manipulations and chronic individual differences. Still, bearing these caveats in mind, the results do provide preliminary evidence that the behavioral immune system may lead to risk-averse behavioral dispositions in general.

IT MAY HELP TO EXPLAIN CROSS-CULTURAL DIFFERENCES

The functionally flexible psychological mechanisms that define the behavioral immune system have implications that manifest most immediately in individuals' feelings, cognitions, and actions. Hence, the most inferentially relevant research focuses on individual-level psychological outcomes. But these individual-level psychological phenomena may have further implications that manifest at the level of entire human populations. If the behavioral immune system is activated especially frequently or especially strongly among individuals who comprise a particular population, then those individuals are likely, on average, to exhibit somewhat different psychological tendencies compared to individuals who comprise a different population. What might lead to population-level variability in the extent to which the behavioral immune system is activated? Ecological variability in the actual prevalence of disease-causing pathogens. This implies that worldwide cross-cultural differences may be partially attributable to ecological differences in pathogen prevalence.

Building on pioneering research on the population-level correlates of pathogen prevalence (Gangestand & Buss, 1993; Low, 1990), there is now a substantial body of evidence documenting relations between pathogen prevalence and the psychological profiles of different populations worldwide. Most of this work focuses on cross-national comparisons, and many of the results conceptually mimic findings from the psychological experiments reviewed earlier. In countries characterized by higher levels of pathogen prevalence, the people inhabiting those countries place a higher value on physical attractiveness, and exhibit more xenophobic attitudes toward ethnic outgroups (Gangestad, Haselton, & Buss, 2006; Schaller & Murray, 2010). They also conform more strongly to majority opinion, exert stronger conformity pressures on others, express more highly authoritarian attitudes, more strongly endorse moral values pertaining to group loyalty and purity, and more strongly endorse collectivistic cultural values (Fincher, Thornhill, Murray, & Schaller, 2008; Murray, Schaller, & Suedfeld, 2013; Murray, Trudeau, & Schaller, 2011; Van Leeuwen, Park, Koenig, & Graham, 2012). On measures of personality traits, they have lower scores on both extraversion and openness to experience, and women within those countries report more restricted mating strategies (Schaller & Murray, 2008).

Ecological variation in pathogen prevalence also predicts additional societal outcomes that may be emergent consequences of individual-level attitudes and actions. In places where pathogens are more highly prevalent, there is more frequent ethnic conflict, governments are more authoritarian in their policies, and there are lower levels of scientific and technological innovation (Letendre, Fincher, & Thornhill, 2010; Murray, 2014; Thornhill, Fincher, & Aran, 2009). These and other conceptually related findings (e.g., Fincher & Thornhill, 2012) suggest that the functionally flexible implications of the behavioral immune system may help explain many worldwide cross-cultural differences.

The findings are provocative; but because of inferential limitations that accompany the underlying methods, one must be cautious in drawing conclusions (Pollet, Tybur, Frankenhuis, & Rickard, 2014; Schaller & Murray, 2011). These methods are necessarily correlational, and pathogen prevalence naturally correlates with other variables—including other threats to human welfare as well as societal structures that mitigate those threats—that may have conceptually independent implications for cultural norms (e.g., Hruschka & Henrich, 2013; Van de Vliert, 2013). The most inferentially compelling results are those in which pathogen prevalence remains a unique predictor of cultural differences even when statistically controlling for such variables. Some of the cross-national findings do meet this stricter standard of evidence. For instance, even when controlling for plausible demographic and economic confounds and for other threats to human life, ecological variation in pathogen prevalence still predicts cross-cultural variation in extraversion, openness, conformity, and collectivism (Fincher et al., 2008; Murray et al., 2011; Schaller & Murray, 2008).

Another thorny inferential issue arises within any analysis that treats contemporary geopolitical entities as units of analyses. Countries are not conceptually equivalent to cultures; the societal structures and popular norms observed in one country are rarely independent of those in other countries (Nettle, 2009). Relations between pathogen prevalence and cultural differences are more compelling when observed not only in analyses of contemporary geopolitical entities but also in analyses of small-scale societies that more closely approximate distinct cultural entities. Several results provide this sort of replication, and further support hypotheses linking pathogen prevalence to cultural differences in collectivistic attitudes and authoritarian governance (Cashdan & Steele, 2013; Murray, Schaller, & Suedfeld, 2013).

Finally, even if pathogen prevalence does play some unique role in creating cultural differences, there are multiple conceptually distinct explanatory processes through which this effect might occur. The functionally flexible individual-level psychological mechanisms that govern individuals' cognitions and actions offer one plausible explanation. But other conceptually distinct processes may contribute as well. These include developmental processes that manifest as phenotypic plasticity, as well as additional population-level processes (including genetic evolution) that transcend a psychological level of analysis entirely. (For a more detailed discussion of these different processes, see Schaller & Murray, 2011).

IT HAS BOTH OBVIOUS AND NONOBVIOUS HEALTH IMPLICATIONS

Because of its implications for the reduction of infection risk, the behavioral immune system almost certainly had positive implications for human health through much of human evolutionary history. It is likely that some of these same health benefits continue in contemporary human contexts too. These infection-buffering benefits may be more fully realized by interventions that target the psychological mechanisms that characterize the system. Education-based interventions that focus on rational decision-making processes often prove to be only modestly successful means of changing prophylactic behavior; in contrast, interventions that activate the behavioral immune system may be more effective in promoting safe-sex practices, hand-washing, and other infection-reducing behaviors (Porzig-Drummond, Stevenson, Case, & Oaten, 2009; Tybur, Bryan, Magnan, & Caldwell Hooper, 2011).

The individual-level manifestations of the behavioral immune system may have population-wide epidemiological implications. The speed and scope of epidemic outbreaks within a population are influenced by the behavioral tendencies of individuals within that population—tendencies regarding sexual promiscuity, social gregariousness, conformity to hygiene-relevant norms, and so on. One interesting implication is that, because different contemporary cultural populations differ in these behavioral dispositions, the dynamics of disease epidemics may also differ predictably within different cultures.

Ironically, some behavioral consequences of the system may, indirectly, have *negative* health implications too (perhaps especially in modern societies characterized by long life expectancies). If activation of the behavioral immune system inhibits extraversion, as some evidence suggests, then chronic activation may inhibit the development and maintenance of social relationships. This may put people at greater risk of loneliness and insufficient social support, which are associated with poorer long-term health outcomes (Cacioppo, Hawkley, & Berntson, 2003; Cohen, 2004). Under circumstances in which infectious diseases pose a substantial threat of health outcomes, these long-term costs—if they occur—are likely to be outweighed by the health benefits conferred by reduced infection risk. But, in modern societies in which the health threat posed by infectious diseases is minimal, or is effectively managed by technological innovations, any such long-term costs may represent a more troubling consequence.

There may also be implications for some psychopathologies. One type of obsessive compulsive disorder, as well as other specific phobias, may result in part from abnormal hyperactivity in appraisal or response mechanisms associated with the behavioral immune system (Cisler, Olatunji, & Lohr, 2009; Marks & Nesse, 1994). If so, research on these mechanisms may help illuminate the etiology of these psychopathologies, and perhaps have practical implications for effective treatment.

One additional implication is especially provocative: The perceptual mechanisms through which people appraise infection risk (and which facilitate behavioral prophylaxis against infection) may also affect actual immunological responses. Results from recent experiments show that exposure to disgust-eliciting stimuli in turn stimulates oral immune function (Stevenson, Hodgson, Oaten, Barouei, & Case, 2011; Stevenson et al., 2012). Of course, immunological responses can be affected by stressful psychological experiences of many different kinds; so it is important to test whether any such effects are *unique* to the perceptual appraisal of infection risk. Results from one experiment did so (Schaller, Miller, Gervais, Yager, & Chen, 2010). Participants were exposed to visual images connoting the risk of either pathogen infection or (in a control condition) interpersonal violence, and measures were taken of their white blood cells' production of proinflammatory cytokines in response to a bacterial stimulus. Results revealed that, even in comparison to the control condition, the perception of infection risk was associated with a more aggressive immune response.

THERE IS STILL A LOT THAT WE DO *NOT* KNOW

There is a lot that we do not yet know about the behavioral immune system. It may be worthwhile, for instance, to explore more fully the extent to which the behavioral immune system contributes to the development, and content, of individuals' intuitive theories about contagion (Rozin, Millman, & Nemeroff, 1986). Another potentially interesting connection is to the literature on self-medication. Many animal species—including humans and other primates—strategically ingest nonnutritional botanical substances that aid in antipathogen defense (Huffman, 2003). Although most of this research focuses on the benefits of self-medication for controlling infections that have already occurred, some forms of self-medication may serve a prophylactic function too. Other potential implications may also arise from close examination of other animal species. For instance, chimpanzees have been observed to act aggressively toward diseased conspecifics (Goodall, 1986). This may seem counterintuitive and maladaptive, given that acts of aggression typically involve close interpersonal contact. And yet, if aggression isolates (or kills) the victim, then its short-term risks may be outweighed by long-term fitness benefits—realized not only by the aggressor but by others too.

It will also be important to examine more closely the interrelations between affective, cognitive, and behavioral responses that characterize the behavioral immune system. The study of specific cognitive and behavioral responses has often proceeded independently of research on disgust, and vice versa. It remains unclear what the exact role of disgust is in producing the various cognitive and behavioral manifestations of the system, or if some of these additional manifestations occur even in the absence of a disgust response. It seems likely that some level of disgust accompanies certain kinds of cognitive and/or behavioral responses (e.g., xenophobic responses to foreigners), but disgust may be a mere concomitant of these responses rather than a necessary causal antecedent. In contrast, other prophylactic behaviors—such as conformity and moral condemnation of nonconformity—may be unaccompanied by the immediate arousal disgust; but this does not mean that disgust has no causal implications for these behaviors. In fact, because of its effects on memory, attitude formation, and interpersonal communication, the experience of disgust at any one moment in time may have important causal consequences for the effective long-term deployment of these behavioral strategies (Schaller, 2014).

There is also much to be learned about the *appraisal* of infection risk. Whereas lots of research has examined responses to stimuli that have been intuitively appraised as connoting an infection risk, less research has examined the appraisal process itself. Many inferential inputs that trigger the behavioral immune system may be outputs of an appraisal system that evolved separately and that operates on a wider domain of sensory signals (Woody & Szechtman, 2011). But there may also be unique appraisal mechanisms that evolved to serve the specific function of identifying pathogen-connoting cues. If so, such mechanisms may operate within specific sensory modalities, such as olfaction (Kavaliers, Choleris, & Pfaff, 2005; Olsson et al., 2014).

Finally, it will be useful to know the biological substrates of the behavioral immune system. Research on the physiological correlates of emotional experiences reveals that disgust—aroused in response to pathogen-connoting stimuli—is associated with unique patterns of autonomic nervous system activity and neurological activity (Kreibig, 2010; Vytal & Hamann, 2010). But not much is known about the functional connections between anatomical structures, neurochemical processes, and the various cognitive and behavioral phenomena that are manifestations of the behavioral immune system. Even less is known about *genetic* substrates. Research has begun to document genetic correlates of disgust sensitivity and other potentially relevant variables (e.g., Kang, Kim, Namkoong, & An, 2010; Kavaliers et al., 2005; MacMurray, Comings, & Napolioni, 2014), but we still know next to nothing about the genetic bases of the system. It is not necessary to have this knowledge in order to make discoveries about psychological phenomena. But in order to most firmly locate these phenomena within the context of human evolution, it will be useful to know more about the specific bits of genetic information that (within ancestral populations) evolved in response to the unique selection pressures imposed by infectious diseases and that (within individual organisms) construct the unique elements of human physiology that facilitate the behavioral avoidance of infection.

IT IS AN EVOLUTIONARY PSYCHOLOGY SUCCESS STORY

Research on the behavioral immune system provides a prototypic example of the scientific benefits that can accrue from the application of an evolutionary approach to psychological questions. Most psychological scientists are compelled, by either internal inclinations or external incentives, to study topics that matter in the here and now. And for most psychological scientists, the "here and now" includes obvious cognitive and technological innovations that provide modern solutions to pathogen transmission. This makes it easy to disregard the historically potent problem posed by infectious diseases, to overlook the behavioral means through which the problem might plausibly have been solved in ancient ecologies, and to be blinded to the enduring implications for psychological phenomena. Specialized tools are sometimes necessary to transcend this kind of scientific myopia. The logical principles of evolutionary psychology provide such tools.

Despite the long history of inquiry into human motivation, it is only more recently that behavioral scientists, explicitly informed by the logical principles of evolutionary psychology, have identified a psychologically unique motivational system facilitating behavioral avoidance of pathogen infection (Aunger & Curtis, 2013; Bernard, 2012; Neuberg et al., 2011). Similarly, psychologists have been studying xenophobia and conformity and interpersonal attraction for decades and decades and decades; but it is only in the past few years—aided by the toolkit of evolutionary psychology—that the motivational psychology of disease avoidance has been implicated as an important influence on these and other psychological phenomena.

Evolutionary psychology not only provides a logical basis for deducing that a behavioral immune system is likely to exist, but also additional logical tools that help to articulate how it works and what the specific consequences might be. Especially useful are evolutionary cost/benefit analyses (in which costs and benefits of psychological responses are defined by their repercussions for reproductive fitness). These cost/benefit analyses provide the logical basis for deductive principles regarding the stimuli to which the behavioral immune system responds, and the contexts within which those responses are especially likely or unlikely to occur. These logical principles have yielded dozens of hypotheses, which have been tested by empirical data, and have produced many novel discoveries. It would be wrong to assert that these conceptual insights and empirical findings *could not* have occurred in the absence of the analytic tools associated with evolutionary psychology. But it is not wrong to observe that, for the most part, they *did not*. If the scientific value of any metatheoretical perspective is measured by its demonstrated utility in generating new hypotheses and empirical discoveries, then research on the behavioral immune system testifies convincingly to the success of evolutionary psychology.

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CHAPTER 8

Spatial Navigation and Landscape Preferences

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CONSIDERATIONS OF SPACE impact virtually every aspect of the organism's adaptive behavior, including the search for food, water, and shelter; predator avoidance; mating strategies; social structure; and parenting. In this chapter, we focus on the evolutionary approach to two aspects of spatial behavior in humans and nonhuman species. The first is navigation: How do individual travels systematically from place to place? The other is landscape preference: the kinds of places in which the individual chooses to live or visit.

NAVIGATION

Watch a dog leap over a fence leaving barely enough room to clear, a child throw a ball on a near perfect arc to a target, a honeybee return directly to its hive after a meandering search for food. Ponder the physical laws of space and motion inherent in all these abilities. In no case are the subjects aware of these laws or capable of generalizing from them, yet the actions are performed with ease.

This is illustrative of the prevailing paradigm of evolutionary psychology, which seeks to replace the traditional social science model of mind as primarily consisting of *general purpose learning mechanisms*. The evolutionary-based perspective is that mind is comprised of functionally independent or semi-independent *domain-specific cognitive mechanisms* (Cosmides & Tooby, 1992), which evolved in response to specific problems for adaptation and survival in the organism's evolutionary history.

The areas of spatial perception and behavior afford excellent examples of this model. The honeybee's navigational skills enabled it to forage over a relatively large area. The canine's ability to leap over a barrier facilitated both hunting and escape from predators. The human's capacity to accurately throw a projectile also aided in hunting and in agonistic encounters with conspecifics.

GALLISTEL'S DOMAIN GENERAL VIEW

Though the concept of domain specificity may ultimately revolutionize our views of mind, contemporary theories of cognitive psychology still remain largely domain general.

Gallistel's (1990) model, frequently cited in the spatial navigation literature, provides a case in point. Gallistel contends that the representational and computational rules presumed to underlie learning and problem solving in adult humans can be applied to all cognitive capacities of all animal species. In regard to spatial navigation, he says:

> The fact that dead reckoning computations for unrestricted courses are sufficiently complex to have imposed restrictions on the courses human navigators followed would seem an intuitive argument against the hypothesis that the nervous system of infrahuman animals like the ant routinely and accurately perform such computations. I raise this point to argue specifically against such intuitions, which I believe have been an obstacle to the acceptance of computational-representational theories of brain function. Symbolic manipulations that seem complex, hard to learn and difficult to carry out by human beings often have simple physical realizations. Integrating a variable with respect to time sounds like an impressive operation, yet a bucket receiving a flow of water integrates that flow with respect to time. The filling of a bucket strikes most people as a simple physical operation. A symbolic (mathematical) presentation of the trigonometric and integrative operations involved in dead reckoning computations makes them sound forbidding, but the dead reckoning device on a ship is not complex. The trigonometric, decomposition operations it performs are easily simulated with plausible neural circuits. (1990, pp. 38–39)

What are the essential differences between models?

The domain-specificity approach of evolutionary psychology focuses on ecological requirements that could account for the evolution of a given attribute, navigational skill, or otherwise, in a given species. The goal is to uncover the evolved cognitive mechanisms mediating the behavior, however these are best described. In contrast, Gallistel's (1990) approach has taken cognitive psychologists in a different direction, the search for the expression of a general set of representational and computational rules for navigational behaviors across situations and species.

In this respect, the concept of representational/computational rules seems reminiscent of *equipotentiality*, a core principle of behaviorism that maintained that all reinforcers were equally effective for all behaviors of all species. Garcia and colleagues (Garcia, Ervin, & Koelling, 1966; Garcia & Koelling, 1966) discredited that notion in a series of studies on taste avoidance in rats that were seminal to the concept of domain specificity. They demonstrated that organisms were genetically programmed in an evolutionarily adaptive manner, such that particular behaviors conditioned only to particular reinforcers in particular species. Rats, scavengers by nature, could only be conditioned to avoid a particular flavor by the negative reinforcer of induced nausea.

A model that seeks to apply a single set of rules to navigational behavior across species will also be misled by unique, species-specific mechanisms. Bees and some other insects seem to navigate by using the sun as a compass, but are actually following planes of polarized light (von Frisch, 1967). Migrating locusts would appear to defy representational/computational analysis in that individuals are seen flying in different directions within the swarm, but this is the locusts' way of keeping the group on course, despite wind shifts (Rainey, 1962).

Finally, it is reasonable to assume that the evolutionary development of animal and human navigational abilities began with simpler mechanisms than are described in a representational/computational analyses. This does not exclude from consideration the higher order abstractions unique to humans that have enhanced our navigational capacities to the point where we can travel to space and back, but these were derived in relatively recent evolutionary time, as a function of our emergent general analytical abilities. It does not follow that these analyses are somehow embedded in mechanisms that have worked effectively from prehistory.

OPTIMIZATION IN ANIMAL MOVEMENT

Navigation is the process by which an animal uses available cues to travel to predetermined locations. The nature and extent of travel, however, varies greatly among species. Some cover relatively short distances in their lifetimes, whereas others migrate halfway around the world. Attempts to explain these differences in terms of fitness requirements have generally resided in the domain general principle of *optimization*; that is, the presumption that evolved behavioral characteristics reflect optimal trade-offs between costs and benefits to the animal's fitness.

Alcock (1984, pp. 199–203), however, has pointed out an essential problem with optimization theory; it is usually impossible to measure evolutionary costs and benefits in the same units. For example, the benefits of migrations include greater availability of food sources and facilitation of breeding, whereas the costs include expenditure of energy and danger from predators along the way. Thus, the only means by which we can conclude that the positive value of the benefits exceeds the negative value of the costs is by the fact that migratory behavior has selected in for the animal. This, of course, is a textbook example of circular reasoning.

In fact, Alcock expresses skepticism about the cost–benefit explanations of long-range migrations (pp. 241–244), and regards the phenomenon as a continuing theoretical challenge. In general, Alcock prefers a "qualitative" approach to evolutionary analyses, whereby correspondence is established for a particular species between a particular behavioral trait and particular aspect of its adaptation. Within Cosmides & Tooby's (1992) domain-specificity model, this would be phrased in terms of the correspondence of the *design features* of a specific cognitive mechanism and the *task requirements* of a specific adaptive problem.

Alcock does concede that quantitative analyses based on optimization may have utility for more circumscribed areas of behavior, where costs and benefits may be measured in the same currency—for example, calories lost and gained in foraging strategies. Janson (2000), however, has described some of the constraints of quantitatively based laboratory research on optimization of foraging behavior that limits its ability to generalize to behavior *in vivo*. He points out that laboratory experiments usually expose the animal to a single cluster of food sites that can be visited during a limited time interval; thus the only available adaptive responses for the animal are to eat at all sites and minimize travel distances between them. Janson's (1998) own studies of brown capuchin monkeys showed that the foraging behavior of these animals in their own habitat were quite different than in the laboratory. Capuchins in the wild use a variety of foraging strategies, dictated by the longer-term goal of consuming a fixed daily food requirement with the shortest required overall travel distance. Furthermore, they alter their strategies as distributions of food resources change, and they do not consume what cannot be digested during the course of the day. According to Janson, capuchin monkeys and many other species can find and ingest food faster than they can digest it; hence, there are minimal fitness returns in increasing food intake beyond that which can be digested within a limited time period.

Janson (1998) concluded that in order to devise a model to predict how an animal will forage, one must first determine what the animal knows about its environment. Most researchers implicitly assume that it is very little, but some food storing birds seem to remember hundreds of seed caches (Balda & Kamil, 1988; Hilton & Krebs, 1990) and many primate species, as well, show precise recall of specific resources (Janson, 1998; Menzel, 1991). Janson also concludes that evolutionary hypotheses should be conceptualized in the context of the animal's unique attributes and requirements, an approach compatible to both Alcock's and the domain specificity perspectives.

A MAP AND A COMPASS

As frequently noted, in order to navigate, you must have a map and a compass. The map, physical or mental, indicates where you are in relation to your goal. The compass refers, figuratively, to the cues you will use to get there. Generally speaking, we know more about compasses than maps; that is, there are much data about the cues animals use to reach a goal, but less about how they decide where the goal is.

Navigational cues fall into two distinct strategies, which we will call *orientation versus landmark* but which have also been referred to as *Euclidean* or *geometric versus topographic*, *dead reckoning versus episodic*, and *allocentric versus egocentric*. The orientation strategy, most effective for journeys over long distances, requires the animal to maintain a sense of its own position in relation to various global markers. These include the sun, the stars, wind direction, the earth's magnetic field and barometric changes, and usually involve the individual's proprioceptive bodily cues and biological clock. When navigating indoors by an orientation strategy, the subject uses the configuration of the structure. In contrast, the landmark strategy involves the learning and recall of visual markers and their relationships to each other along the route, including objects, turning points, and details of the terrain.

Many species possess the capacity for both strategies, but the one that is best developed and most frequently used depends on the animal's ecological requirements (Alcock, 1984; Drickamer & Vessey, 1986). Thus, migratory and homing animals primarily use an orientation strategy, whereas animals that stay closer to home generally use a landmark strategy. Strategy is also a function of the greater availability of landmark or global cues, as illustrated in the differential navigational processes of tropical forest versus desert-dwelling ants. The former use a landmark strategy for foraging, whereby the ants learn and follow the markings on the forest canopy above them. The latter utilize their sustained access to the sun by deriving compass information from its position. We know that these species are using these strategies by studies showing that if a forest ant is experimentally displaced to a point that it has not previous traveled, it will not be able to readily find its way back, whereas a desert ant will proceed directly on the correct path (Holldobler, 1980).

Animals that primarily use an orienting strategy often have more than one method at their disposal and use these interchangeably, in an adaptive manner. Thus, honeybees and homing pigeons orient by the sun when it is visible, but during overcast days or nights will revert to methods that utilize the magnetic fields of the earth. Migrating birds generally use a sun-based orientation strategy for most of their journey, but they revert to a landmark strategy when approaching home. The orienting strategy enables them to navigate across long distances where landmarks are not available, such as over the sea, or where frequencies of landmarks along the way are too copious to recall. The landmark strategy enables them to hone in on their precise destination when approaching the completion of their journey

Humans are, historically and prehistorically, foragers, hunters, and colonizers. Thus, we engage in short, intermediate, and long forays, thus using both orientation and landmark strategies.

To demonstrate this to yourself, point to some other state or country, far from your own. Now point to a place close to home, where you go on a regular basis, such as a grocery or a friend's residence. You will probably use an orientation strategy for the first task, by constructing a mental image of a map that includes your own and the target's location and taking an estimate of your current compass bearing in relation to the target. On the other hand, you will most likely use a landmark strategy for the second task, based on the landmarks on the route you customarily take to your target (adapted from Thorndike and Hayes-Roth, 1980).

Genetic, Neurological, and Developmental Bases of Navigational Strategies

Across studies and measures, the heritability of spatial abilities, including those directly involved in navigation, ranges at about 0.50 (Bouchard, Segal, & Lykken, 1990; Defries et al., 1976; Plomin, Pederson, Lichtenstein, & McClearn, 1994; Tambs, Sundet, & Magnus, 1984; Vandenberg, 1969).

Regarding neural mechanisms, studies with humans (e.g., Maguire et al., 1998; Maguire, Frackowiak, & Frith, 1996; Maguire, Woollett, & Spiers, 2006), monkeys (Ono & Nishijo, 1999; Rolls, Robertson, & Georges-Francois, 1997), and rats (e.g., Eichenbaum, Stewart, & Morrisa, 1990; Thinus Blanc, Save, Pucet, & Buhot, 1991), have shown that navigational processes in general are associated with the functions of the hippocampal formation, which includes the hippocampus and the adjacent cortex in the most medial area of the temporal lobe. Other studies have shown different neurological processes within the hippocampus for tasks involving orientation and landmark strategies, which supports the notion that these evolved in a domain-specific manner. O'Keefe and Nadel (1978) first demonstrated that navigation by rats in an environment that is defined only by the shape of the enclosure, thereby requiring an orientation strategy, activates different types of neurons than those involved in landmark-based tasks. The former are called *place cells*, and include neurons that encode the animal's location and specific bodily movements in relation to the geometric properties of the environment (Muller, Bostock, Taube, & Kubie, 1994; Taube 1995, 1998; Taube, Muller, & Ranck, 1990).

Pizzamiglio, Guariglia, and Cosentino (1998) presented clinical data in humans that also demonstrated the dual neurological bases of orientation and landmark strategies. Two right-hemisphere-damaged subjects were unable to orient themselves to an enclosure when its shape was the only information available, but improved considerably when a visual object was added as a cue. Two other subjects, with a different lesion site in the right hemisphere than the first two, could orient themselves using only the shape of the enclosure. Unlike right-brained-intact controls, however, these subjects did not increase their performance with the addition of the cue.

Domain specificity can also be inferred from differences in the developmental stages when the two navigational strategies emerge. Children from about 2 years of age use landmark strategies, whereas rudimentary orientation strategies do not appear until about the age of 8 (Anooshian & Young, 1981; Blades & Medllicott, 1992; Scholnick, Fein, & Campbell, 1990). Landau & Gleitman (1985), however, performed a study with a congenitally blind girl of 31 months, in which she was led to various landmarks in a room and back again, each time, to a starting point, and then asked to navigate from landmark to landmark. Gallistel (1990, pp. 99–100) interpreted her success, despite her inability to see the landmarks in relation to each other, as demonstration of orientating behavior in a very young child. As previously defined, however, the landmark strategy does not necessarily require visual contact with markers. It does require prior knowledge of their positions in relation to each other, which can come from a map, or virtual travel, or, apparently, from a guided, tactual tour.

SPATIALLY RELATED SEX DIFFERENCES

Though evolutionary theorists are primarily interested in universals, group differences often provide the first clues about these. Thus, the theory of evolution by natural selection began with Darwin's observations of subgroup differences within bird and amphibian populations in the Galapagos Islands.

Generally, the focus is on interspecies differences, but any ubiquitous group difference amenable to explanation in terms of natural selection may be relevant. Thus, the pervasive bias favoring males in spatially related tasks, both in humans and infrahuman species, ultimately led to evolutionary based theory and data on the nature of human navigational processes.

Studies of human spatial sex differences have shown a male advantage across a variety of measures, including field dependence, mental rotations, embedded figures, map reading, maze learning, and estimating the speed of a moving object. The magnitude of the sex difference varies among measures, with three-dimensional tasks showing greater differences than two-dimensional tasks and three-dimensional mental rotations tests yielding the largest and most reliable differences (Halpern, 1992; Linn and Peterson, 1985; McGee, 1979; Phillips and Silverman, 1997; Rahman and Koerting, 2008; Saucier et al., 2002; Saucier, Lisoway, Green, & Elias, 2007). Meta-analysis (Voyer, Voyer, & Bryden, 1995) has shown that the average difference between sexes for three-dimensional mental rotations, across dozens of studies, is a robust 0.94 by Cohen's *d*, indicating that the mean performance of males is nearly one standard deviation above that of females.

The male advantage in spatial tasks is highly consistent across human geographic populations. Though most studies have been conducted in North America, the sex difference across various tests has been replicated in Japan (Mann, Sasanuma, Sakuma, & Masaki, 1990; Silverman, Phillips, & Silverman, 1996), England (Lynn, 1992); Scotland (Berry, 1966; Jahoda, 1980); Ghana (Jahoda, 1980); Sierra Leone (Berry, 1966); India, South Africa, and Australia (Porteus, 1965). A more recent set of studies, demonstrating the universality of sex differences across dozens of diverse cultures, will be described in a later section.

Although the sex difference has been reported in children as young as preschoolers (McGuinness & Morley, 1991), the consensus is that it does not appear reliably across tasks until early adolescence, which is generally attributed to accelerated hormonal differentiation (Burstein, Bank, & Jarvik, 1980; Johnson & Meade, 1987). One study (Willis & Schaie, 1988) has shown that from this age, the magnitude of the difference tends to be constant throughout the lifespan.

The sex difference extends also across species. Studies with wild and laboratory rodents have shown that males consistently outperform females in maze learning tasks (Barrett & Ray, 1970; Binnie-Dawson & Cheung, 1982; Gaulin & FitzGerald, 1986; Joseph, Hess, & Birecree, 1978; Williams & Meck, 1991).

Sex hormones, in terms of both organizational and activational effects, have been implicated in spatial sex differences in humans and animals (Choi & Silverman, 2002; Gouchie & Kimura, 1991; Hampson & Kimura, 1992; Janowsky, Oviatt, & Orwoll, 1994; Kimura, 1999; Kimura & Hampson, 1993; Nyborg, 1983, 1984; Phillips & Silverman, 1997; Puts et al., 2010; Reinisch, Ziemba-Davis, & Saunders, 1991; Silverman & Phillips, 1993; Silverman, Kastuk, Choi, & Phillips, 1999; Williams & Meck, 1991). Studies have shown a decrease in spatial abilities with increased estrogen levels, consistent with the direction of the sex difference. Corresponding increases in spatial performance with increased testosterone levels, however, occur reliably for females, but not males. Males have shown direct, inverse, and nil effects across studies. Nyborg (1983) attempted to explain this paradox in terms of the fact that plasma testosterone is, under some circumstances, converted to brain estrogen. Silverman et al. (1999) explained the differences in results in terms of the difficulty levels of the tasks used. Puts et al. (2010) concluded that hormonal influences in males are limited to organizational effects.

Evolutionary Theories of Spatial Sex Differences

The first systematic, evolutionary based theory of spatial sex differences was by Gaulin and FitzGerald (1986). The core of the theory was that spatial abilities were more strongly selected for in males than females in polygynous species, for the reason that polygynous males require navigational skills to maintain large home ranges (the area within which an animal freely travels on a regular basis), in which to seek potential mates and resources to attract mates.

The investigators tested their theory with two species of voles; one, meadow voles, which are polygynous, and the other, pine voles, which feature an open promiscuous style. Findings were consistent with predictions; sex differences both in the direction of larger home ranges and superior maze learning ability for males occurred solely for meadow voles. Jacobs, Gaulin, Sherry, & Hoffman (1990) compared sex differences in size of hippocampus between these species and found, again as expected, proportionally larger male hippocampi in meadow voles but no sex difference in pine voles.

Does Gaulin and FitzGerald's mating strategy theory pertain to humans? Moderate polygyny is characteristic of our species (Symons, 1979) and a review of the cross-cultural literature on sex differences in home range size showed a near universal male bias beginning at the toddler stage (Gaulin & Hoffman, 1988). Additional support comes from Ecuyer-Dab & Robert's (2004a) finding that men tended to possess larger home ranges than women, as measured by retrospective and direct accounts of their comings and goings over extended time periods. Ecuyer-Dab and Robert posited also that if there was a "functional relation" between spatial abilities and home range size in males but not females, as inferred from Gaulin and FitzGerald's model, correlations between the two variables should be found only in the male. This was demonstrated in their study and also in earlier studies of African children (Munroe & Munroe, 1971; Nerlove, Munroe & Munroe, 1971).

Silverman and Eals (1992) questioned, however, whether the relationship between home range size and reproductive success applied to the human case. The only data that pertain to the question has shown that females exhibit greater *natal dispersal* (the distance travelled by an individual from natal site to first place of breeding) than their male counterparts (Koenig, 1989), which would contradict Gaulin and FitzGerald's theory.

Silverman and Eals (1992; Eals & Silverman, 1994) posed an alternative theory, in which the critical factor in selection for human spatial sex differences was division of labor during the Pleistocene. During that era, considered to be the most significant in human evolution, males primarily hunted, whereas females functioned as plant food gatherers, keepers of the habitat, and caretakers of the young (Tooby & Devore, 1987).

Silverman and Eals noted that the various spatial tests showing the strongest male bias (e.g., field independence, mental rotations, maze learning) corresponded to attributes that would enable navigation by orientation. This would be essential for successful hunting, which requires the pursuit of prey animals across unfamiliar territory and the capacity to return by a fairly direct route. They contended further that, if spatial attributes associated with hunting evolved in males, it is feasible that spatial specializations that would have facilitated their own roles in the division of labor would have evolved in females.

For food gathering, success would have required finding edible plants within diverse configurations of vegetation and locating them again in ensuing growing seasons; that is, the capacity to rapidly learn and remember the contents of object arrays and the relationships of objects to one another within these arrays. Success in gathering would also be increased by peripheral perception and incidental memory for objects and their locations, inasmuch as this would allow one to assimilate such information nonpurposively, while attending to other matters. Incidental object-location memory would also be useful in tending to the domicile and offspring.

There is supporting physical evidence for this analysis. Women have larger visual fields than do men; that is, they can see farther out on the periphery while fixating on a central point (Burg, 1968). They are also better than men at scanning, excelling in various tests of perceptual speed (Kimura, 1999, pp. 87–88).

Silverman and Eals (1992; Eals & Silverman, 1994) developed several methods to compare sexes on their ability to learn spatial configurations of object arrays, all of which generally supported the hypothesized female advantage. These findings have been partially or fully replicated in multiple laboratories and with diverse research designs (e.g., Choi & Silverman 1996; Dabbs, Chang, Strong, & Milun, 1998; Eals & Silverman, 1994; Gaulin, Silverman, Phillips, & Reiber, 1997; Hassan & Rahman, 2007; James & Kimura, 1997; McBurney, Gaulin, Devineni, & Adams, 1997; McGivern et al., 1997; Neave, Hamilton, Hutton, Tildesley, & Pickering, 2005; Spiers, Sakamoto, Elliot, & Bauman, 2008) with the most consistent differences occurring for incidental location recall.

Comparing the two theories of spatial sex differences, Gaulin and FitzGerald's (1986) has an advantage in that it applies to both humans and nonhuman species. Silverman and Eals' (1992), however, provide testable hypotheses about female spatial specializations. Silverman and Eals suggested that the theories may be reconciled if it is presumed that in a given species or subspecies, any difference in selection pressures between sexes related to spatial behavior may result in an evolved dimorphism. Ecuyer-Dab and Robert (2004b), however, presented a more precise means of integrating the theories, described in a later section.

Sexual Dimorphism in Navigational Strategies

Numerous studies have shown that males tend to use an orientation strategy in navigational tasks, whereas women use a landmark strategy (e.g., Bever, 1992; Choi & Silverman, 1996, 2003; Dabbs et al., 1998; Galea & Kimura, 1993; Holding & Holding, 1989; Joshi, MacLean & Carter, 1999; Lawton, 1994, 1996, 2001; Lawton & Kallai, 2002; McGuinness & Sparks, 1983; Miller & Santoni, 1986; Moffat, Hampson, & Hatzipantelis, 1998; Schmitz, 1997; Ward, Newcombe, & Overton, 1986). Specifically, males use distances and cardinal directions; that is, north, south, east, and west, whereas females rely more on landmarks and relative directions, such as right, left, in front of, and behind. These differences have been demonstrated with a variety of methods, including learning routes from maps or photographs, walking through mazes, retracing computer simulated routes on virtual mazes, drawing maps, giving directions, and finding one's way back after being led along an unfamiliar indoor or outdoor route.

Identifying Evolved Mechanisms

Evolved mechanisms tend to remain quite broadly defined at this early stage of theoretical development, and more exact definitions will entail a long-term, continuing process of theoretical refinement and data gathering. Some recent research by the present authors and their colleagues, however, may provide a first approximation of an evolved mechanism for navigation by orientation.

Silverman et al. (2000) conducted a study in which subjects were led, individually, on a circuitous route through a heavily wooded area. During the walk, they were stopped periodically and required to set an arrow pointing to the place from which they began. Eventually, they were asked to lead the experimenters back to the starting point by the most direct route. Men's performances surpassed women's on all of these measures, and overall performance scores were significantly related across sexes to three-dimensional mental rotations scores, but not to nonrotational spatial abilities nor to general intelligence. Moreover, mental rotations scores emerged as the sole significant predictor in a multiple regression analysis that included sex as an antecedent variable, suggesting that the variance in orientation ability associated with sex appears wholly attributable to mental rotations abilities.

What do mental rotations tests measure that may function as an evolved mechanism for navigation by orientation? According to the investigators, both mental rotations and navigation by orientation require that the individual maintain the integrity of a space while exposed to it from various viewpoints. A number of studies (Cochran & Wheatley, 1989; Freedman & Rovagno, 1981; Schulz, 1991) have shown that the sole method for solving mental rotations problems with any degree of efficacy is by visualizing the rotation in three-dimensional space of one object while comparing it to another. In this manner, the subject mentally peruses the periphery of the object from various perspectives while maintaining a mental representation of its whole. Silverman et al. (2000) suggested that this is comparable, in terms of the processes involved, to searching for or following a prey while maintaining a mental representation of the boundaries of one's route.

Based on this explanation, Silverman et al. (2000) considered that the evolved mechanism at the core of the relationship between mental rotations and navigation by orientation appeared to be *space constancy*, whereby, "the properties of objects tend to remain constant in consciousness although our perception of the viewing conditions may change" (Coren & Ward, 1989, p. 406). (See also Bisiach, Pattini, Rusconi, Ricci, & Bernardini, 1997; Niemann & Hoffmann, 1997; Probst, Brandt, & Degner, 1986).

Further refinements of the role of space constancy in navigation by orientation may be informed by perceptual and neuropsychological studies. A complete explanation of the evolved mechanism, however, will also require consideration of environmental interactions, inasmuch as innately based behaviors are always expressed in an environmental context. In this vein, there is evidence that exposure to lines and angles during an early critical period is salient to the development of shape constancy (Allport & Pettigrew, 1957).

ONE MECHANISM OR TWO?

The question arises about whether the diverse navigational strategies of men and women represent one mechanism or two; that is, does the females' use of a landmark strategy represent an attempt to compensate for less-developed orientation abilities, or is it part of a separate evolved mechanism related to greater proficiency in recalling object locations. The latter view would apply both to the female's greater use of landmarks than distances and to their greater use of relative rather than cardinal directions. Relative directions are more efficacious for recalling and describing the locations of objects in relation to one another within a relatively small space, whereas cardinal directions are more suitable for processing and describing the vectors denoting longer distances.

Many investigators accept the compensation interpretation (e.g., Galea & Kimura, 1993; Lawton, 1994; Miller & Santoni, 1986; Moffat et al., 1998). Silverman and Eals' hunter-gatherer theory, however, would suggest dual mechanisms. So, also, do the prior cited neurophysiological studies demonstrating different neural processes underlying orientation and landmark strategies. As well, Gur et al. (2000) has shown differential brain site activation between men and women engaged in a spatial task.

Additionally, Choi and Silverman (1996) found that in a route-learning task in which the sexes performed equally well, success was predicted by preferences for landmarks and relative directions for females only, and preferences for distances and cardinal directions for males only. Similarly, Saucier et al. (2002) administered laboratory and field navigational tasks in which participants were required, at the direction of the experimenter, to use either an orientation or a landmark strategy. The sexes did not differ in performance, but males did better when using an orientation strategy, whereas females had higher scores with a landmark strategy. In both these studies, the observation that sexes performed equally well when using their own strategies of choice suggests that the use of landmarks is not a default strategy, but an expression of a well-developed mechanism in itself.

What would be the nature of a separate evolved mechanism mediating the unique spatial attributes of women? Silverman and Phillips (1998, p. 603) suggest that it entails "a more inclusive attentional style," whereas Kimura (1999, p. 15) uses the term "efficient perceptual discriminations." There is an alternative view, however, that involves imagery rather than attention or perception. Eals and Silverman (1994) found that the markedly greater abilities of females to recall object locations within arrays pertained also to unfamiliar objects, for which they did not have verbal referents. This may suggest that females have the ability to encode and recall entire scenes, in detail, by a process akin to eidetic imagery. Data purporting to show a greater "power of visualizing" for females were first reported more than a century ago by Galton (1883), and similar reports have appeared through the years (e.g., Anastasi, 1958; Sheehan, 1967).

Thus, whereby the navigational mechanism for males enables them to create mental maps of extended spaces, to which they had never been directly exposed, the corresponding mechanism for females gives them the ability to mentally construct and recreate detailed maps of smaller, previously observed spaces. This would appear to represent a highly adaptive dimorphism for the evolution of hunters and gatherers, favoring Silverman and Eals' theory, but there is a complicating factor. Rats, who are not hunters and gatherers, also feature the sex difference in navigational strategy. When navigating in radial-arm mazes, males are capable of using distal cues such as the shape of the room, whereas females require landmarks (Williams, Barnett, & Meck, 1990; Williams & Meck, 1991).

Ecuyer-Dab and Robert (2004b) presented a revised theory, emanating from both Gaulin and FitzGerald's and Silverman and Eals's, which may account for cross-species parallels. They proposed a *twofold selection process* underlying spatial sexual dimorphisms. For males, the critical selection factor is male-male reproductive competition, which tends to be more intense in polygynous societies and which would have favored the evolution of spatial abilities essential for both orientation-type navigational strategies and the effective use of projectiles. These skills would have enabled resource provision of mates and offspring by means of hunting and also aided in agonistic encounters between males competing for reproductive opportunities.

For females, on the other hand, the paramount selection factor for the evolution of a landmark strategy is the need for physical security for themselves and their offspring. The greater capacity to learn and recall details of the proximate environment, which is the basis of a landmark strategy, would have facilitated navigation within a relatively narrow home range and keener attention to cues regarding the presence of predators and other dangers. Such attributes would have also aided in finding and recalling possible hiding places or escape routes, which would have been particularly important when pregnant or tending small children. In this model, the greater capacity for food gathering of the female is a by-product, rather than the essential selection factor, in the evolution of her spatial specializations.

Ecuyer-Dab and Robert provide examples of sex-specific spatial strategies that appear to operate for these purposes in various nonhuman species, and contend that these observations probably generalize to most mammals. Thus, they have provided a theory that can encompass the findings from both Gaulin and FitzGerald's and Silverman and Eals's, and would appear to offer the most productive venue for further research.

THE UNIVERSALITY OF SEX-SPECIFIC SPATIAL SPECIALIZATIONS

A prime indicator of the evolutionary origins of a human trait is its generality across countries and cultures. In 2005, the British Broadcasting Company (BBC), gathering information for a documentary, administered a series of psychological tests via the Internet to more than a quarter of a million participants in 226 countries throughout the world. Included in the test battery was a brief version of a standard measure of three-dimensional mental rotations, which yields the strongest and most reliable male advantage, and a test developed for group administration of object location memory developed by Silverman and Eals (1992), which consistently favors females. For the latter, the individual observed a drawing of an array of objects for a specified time; then was presented with a drawing containing the same objects, but with half in different locations, and asked to circle the objects that have been moved.

Participants in the BBC study identified their genders and their ethnic groups from seven ethnic categories listed. Thus, the opportunity was available to assess the generality of the hunter-gatherer theory of spatial sex differences across countries and ethnic groups throughout the planet.

Silverman, Choi, and Peters (2007) performed this study using the data of 40 countries; those with a minimum of 100 each of males and females partaking in both tests. For mental rotations, significant differences (at $p < .05$) favoring males were found for all of the seven ethnic groups and 40 countries. For object location memory, significant differences favoring females were found for all of the seven ethnic groups and 35 of the 40 countries. The five remaining countries showed trends in the predicted direction, with one approaching significance at $p = .07$.

THE EFFECTS OF SOCIALIZATION: A PARADOX

Evolutionary psychologists do not eschew the role of socialization in behavioral development, acknowledging that genetic effects are always manifested in environmental contexts. Thus, Lippa, Collear, and Peters (2010), using the BBC data from 53 countries for mental rotations and line angle judgment (another visuospatial test showing a male advantage), explored the question of whether spatial sex differences could be attributed, at least in part, to stereotypic sex roles. The latter was assessed from the United Nations gender-related development index, which rates countries on gender equity across three dimensions: health and longevity, standard of living, and knowledge and education.

Male scores were significantly higher for both tests in all countries. Regarding the effect of gender equity, however, results were in the opposite direction to the hypothesis; sex differences were significantly greater, rather than smaller, in countries with higher equity ratings.

The authors offered the possible explanation that women in highly developed, gender-egalitarian societies may be exposed more to evidence of spatial sex differences, leading to more pervasive stereotypes that could be debilitating in their effects on performance. An alternative explanation, however, is that inadequate educational systems in less-developed countries may not afford the environmental supports necessary in either gender for the sufficient development of adaptive, sex specific, spatial specializations.

LANDSCAPE PREFERENCE

Having considered the mechanisms of navigation, we turn now to a related issue; the choice of where to go. Questions about landscape preference have traditionally come from the study of aesthetics, but evolutionary based theories and data suggest that this was also a critical aspect of survival for both human and animal life.

HABITAT SELECTION

Deer mice, a common North American rodent, can be divided into two types according to whether they inhabit grasslands or forests. Wecker (1963) built an outdoor enclosure, half consisting of a grassland and half a forest environment. He released two samples of grassland deer mice into the center of the enclosure, one a group of wild-caught mice and the other their laboratory-reared offspring, to see which environment they would prefer. Both groups showed strong affinities for the grasslands.

These findings and similar others (Klopfer, 1963; Thorpe, 1945) may suggest that landscape preferences are manifestations of a species' habitat selection, which would depend on ecological conditions such as availability of food and water, shelter, weather, and protection from predators.

This analysis can be extended to our own species. Human reactions to landscapes, positive or otherwise, tend to be immediate, unequivocal, and emotional, a response pattern that is presumed to have evolved from the needs of our forbearers to make rapid decisions regarding the benefits versus dangers of potential new habitats (Orians & Heerwagen, 1992). The capacity of favored landscapes to evoke positive emotions is well recognized in the conventional wisdom and has been well documented in research. For example, heart rates have been shown to decrease during the viewing of video clips of natural, but not urban scenes (Laumann, Garling, & Stormark, 2003). Postoperative patients in recovery rooms with pleasant, natural views have speedier and more positive recoveries than patients without such views (Ulrich, 1984), and numerous other studies demonstrate the psychological and physiological restorative influences of exposure to natural landscapes (e.g., Fuller, Irvine, Devine-Wright, Warren, & Gaston, 2007; Grahn & Sigsdotter, 2003; Kaplan, 1995; Parsons, Tassinary, Ulrich, Hebl, & Grossman-Alexander, 1998; Rappe & Kivelä, 2005; Ulrich, 1983;)

HUMAN LANDSCAPE PREFERENCES: THE SAVANNA THEORY

Although the task of identifying the habitats and consequent landscape preferences of deer mice and most other animal species seems relatively straightforward, humans have been unique in their ability to colonize a diverse range of environments. One approach to this problem, taken by Orians (1980) is to posit that human landscape preferences evolved in the habitat where the species presumably originated, the African savanna. The savanna biome features clumps of acacia trees scattered across wide grassy plains. This would have provided the human inhabitant with a readily identifiable and accessible place for the gatherer to acquire quality food; the fruits of the trees. Trees could also be used to keep watch for both prey and predators, and escape from the latter. They also serve as protection from the sun. Furthermore, the plains are suitable for grazing animals, which provide opportunity for the hunter (Orians & Heerwagon, 1992).

Orians and Heerwagon (1992) had subjects in the United States, Argentina, and Australia rate the attractiveness of acacia trees, which varied in terms of trunk height, branching pattern, and canopy density and shape. Acacia trees rated most attractive by all samples were those from areas of the savanna considered to be *high quality* in their general adaptive value for humans. These were characterized by moderately dense canopies and trunks which bifurcated near the ground, which would contribute both to ease of climbing and concealment.

Orians and Heerwagon also pointed to the recurrent nature of tropical savanna themes in landscape art. They quoted Humphrey Repton (1907, p. 105), a 19th-century pioneer of landscape architecture, who stated: "Those pleasing combinations of trees which we admire in forest scenery will often be found to consist of forked trees, or at least trees placed so near each other that the branches intermix. . . ."

Balling and Falk (1982) provided further supporting data for the savanna hypothesis, albeit equivocal. They used a series of 20 slides, encompassing five biomes; savanna, desert, and deciduous, tropical rain, and coniferous forest. Subject groups ranging in age from 8 to 70 rated each for desirability, both as a place to live and to visit. Overall, the slides of the savanna were rated significantly higher on both criteria, but beginning at age 15, savanna, deciduous, and coniferous forest landscapes were virtually tied for highest preference scores. Balling and Falk interpreted their data as supporting an innately based preference for the savanna, but one that may be altered by experience over the life span.

PROSPECT-REFUGE THEORY

Appleton (1975) proposed an alternative theory concerning the adaptive basis of landscape preferences. Based on his analyses of landscape paintings, Appleton concluded that those with high attraction value contained a balance between *prospect* and *refuge* features. Prospect features, such as elevated landforms, provide an overall view of the landscape and facilitate the search for food, water, and prey. Refuge features, such as groupings of trees, permit the individual to see without being seen and function mainly in the interests of security. In this theory, the most important aspect of the habitat is the spatial arrangement of environmental attributes; that is, landforms, trees, open spaces, and water, inasmuch as their arrangement determines whether prospect and refuge opportunities can be effectively utilized.

Attempts to test Appleton's theory by means of comparative landscape judgments have yielded equivocal results (e.g., Clamp & Powell, 1982; Heyligers, 1981), which is possibly a function of variation in spatial arrangements of prospect and refuge features (Appleton, 1988). Supporting data for the theory were obtained by Mealey and Theis (1995), however, based on their contention that the relative attraction value of prospect and refuge should vary within individuals in accordance with their moods. Positive moods, they maintained, would induce a need to explore and take risks for the sake of future benefits, and would thus be associated with prospect. Negative moods, conversely, would give rise to a need for security and rest, and would thereby be associated with refuge. As predicted, subjects reporting positive moods preferred landscapes with vast expanses and overviews, whereas subjects reporting mood dysphoria preferred landscapes with enclosed, protected spaces.

MYSTERY AND COMPLEXITY

Kaplan and Kaplan's (1982) notions stand in contrast to the emphasis on both security and simplicity in the theories described earlier. In addition to *coherence*, referring to organization of the scene, and *legibility*, meaning how easily one can navigate within the landscape depicted, the authors included *mystery* and *complexity* as key, evolutionary-based elements of attraction in human landscape preference. Their reasoning was based on the adaptive function of curiosity for the species, particularly the predisposition to seek new information about the environment that can facilitate its mastery, and the greater likelihood of finding new information in complex designs.

Some studies based on Kaplan and Kaplan's notions have revealed preferences for "mystery," as represented by winding forest paths or obscure coves (Herzog, 1988; Kaplan, 1992). As for complexity, moderate levels appear to evoke the strongest preference levels (see Ulrich, 1983).

FUTURE DIRECTIONS

As in the case of spatial navigation, the ultimate issue for an evolutionary theory of landscape preferences is how best to conceptualize the evolved cognitive mechanisms that mediate these. All theories seem to imply a mechanism similar to the ethological construct of *innate schemata*; that is, a mental image of an ideal landscape that serves as standard for judgment. The theories differ, however, in the substance of this image. Orians maintains that it is a copy of the specific landscape in which humans evolved, whereas both Appleton's and Kaplan and Kaplan's imply that it can be any landscape type that contains features that signal fitness-related opportunities. Modern measures of brain site activation may provide a more precise methodology for the comparison of emotional responses to landscapes, and thereby help resolve this issue.

There is also a general methodological problem that needs to be addressed. Wilson, Robertson, Daly, and Wilson (1995) point to the confounds that may readily attend any attempt to compare the preference values of specific features between scenes, which has been the customary method of testing hypotheses derived from both Appleton's and Kaplan and Kaplan's theories. For example, scenes considered be high in mystery by the experimenter may simply have lower and more pleasing brightness levels.

Wilson et al. (1995) suggest a methodology whereby the same scene is manipulated so that just one feature is modified at a time, thereby allowing greater control of potential confounds. By this means, they were able to establish that small and subtle cues as to the water quality of seascapes have a marked effect on attraction value.

Finally, it is worth noting that landscape preference studies that have included urban landscapes (Kaplan, Kaplan, & Wendt, 1972; Laumann et al., 2003; Parsons et al., 1998; Purcell, Lamb, Peron, & Falchero, 1994; Ulrich, 1981, 1983) have universally found strong preferences favoring rural scenes of any type, by both urban and rural dwellers. Ulrich (1983) concluded that the distributions of preference ratings between rural and urban scenes barely overlap, even when ordinary rural scenes are compared to urban scenes that are particularly picturesque.

This, in itself, provides broad support for an evolutionary perspective on landscape aesthetics in that it suggests the profound influence of prehistoric origins, even when pitted directly against life experiences. It points, also, to the potential adverse effects of living in the "unnatural" environment of high-density urban centers, particularly in light of the previously described data on the effects of landscape exposure on psychological and physical well-being.

IN SUM

The application of the evolutionary model to human navigation and landscape preference represents a relatively recent movement in the behavioral sciences, though the burgeoning theory and data reviewed in this chapter is testimony to its relevance. This review has also highlighted two major aspects of the movement. One is the salience of an ethological approach, which has provided compelling insights about analogous processes mediating human and animal adaptations in these areas. The second is the conceptual utility of evolutionary psychology's model of mind as comprised of evolved, domain-specific mechanisms.

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CHAPTER 9

Adaptations to Predators and Prey

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How have interactions with predators and prey shaped human evolution? That they must have done so, at some point in the past, probably seems plausible to most of us. After all, we understand that the comforts and protections of contemporary urban and suburban environments are of relatively recent historical origin. The vast majority of us are no longer predators; when we do eat meat, it is delivered to us in shrink-wrapped packages. Nor will most of us end up becoming prey; only in some parts of the world does death by animal attack pose anything but the most negligible risk. And yet we all know that for most of our evolutionary history, such comforts did not exist. Our ancestors faced the risk of predator attack since well before they were human, stretching back to our most ancient mammalian ancestors. Pursuit of prey, too, stretches back to the earliest insectivorous primates and crescendos in the big game hunting of our own hominin lineage. Few things seem more Darwinian than predator-prey interactions, so it is hard to imagine such encounters *not* shaping our evolution.

And yet, most of us are probably unaware of just how deeply predator-prey interactions, looped over for vast stretches of evolutionary time, might have made us who we are. Indeed, even though there is good evidence for the influence of predator-prey interactions on many aspects of our bodies and minds, we still do not (and may never) know the full scope of that influence. It's possible, for example, that some of the most fundamental features of human nature—from big brains, to sociality, to long lifespans, to our heavy reliance on social learning and cultural transmission—were selected for, in part, because of their benefits for avoiding predation, and because of the increasing reliance of ancestral hominins on a hunting way of life. If predator-prey interactions were partly responsible for setting us on the evolutionary path that has brought us to where we are today, the scope and depth of their effects on human psychology and physiology might be hard to overestimate.

In this chapter I sketch the various ways in which predators and prey have shaped, or might have shaped, us. Although I focus on psychological adaptations, it is impossible to understand these adaptations without also understanding changes in our ecologies and in our bodies, because it is through interactions with the world that our psychological mechanisms evolve. Thus, where possible, I attempt to highlight how predator-prey interactions have shaped human bodies and minds as systems of interacting parts.

PREDATORS AND PREY AS AGENTS OF SELECTION

Evolution is a path-dependent process. The variation within a population that natural selection operates on at any given time is the product of all of the prior events and changes that have brought the population to that point. Because there is no start date for interactions with predators in the evolutionary lineage that has led to us, the effects of predators on our evolution are ancient, and might have shaped the evolution of many traits in ways that are not at all obvious now. For example, it's possible that vision itself—what many would consider to be a paradigm case of a domain-general ability—originally got its jump-start because of predator-prey interactions, which created an arms race to both see and not be seen, and possibly drove the diversification of animal species during the Cambrian, half a billion years ago (Parker, 2003). More recently, many paleontologists believe that we mammals owe our success to the extinction of the dinosaurs at the end of the Cretaceous period around 65 mya, removing the predators and competitors that had restricted our ancestors to a tree-dwelling, largely nocturnal niche (Meredith et al., 2011).

Interactions with predators and prey create a variety of adaptive problems that can have effects on nearly all aspects of organismal function and design, from life histories, to morphology, physiology, and cognition. Unlike other aspects of the environment, which are either static or changing independently of the species that inhabit them, predators and prey coevolve with each other via evolutionary feedback akin to an arms race (Van Valen, 1973). This feedback can create complex evolutionary dynamics with cascading effects on the taxa involved.

In our lineage, stretching back to the earliest primates and beyond, both predator avoidance and prey capture are ancient adaptive problems. The earliest primates were insectivorous. Predation on insects, as well as frugivory and an arboreal lifestyle, may have shaped some basic features of our clade, including vision and motor skills (Cartmill, 1992). However, the kinds of predation that humans engage in—hunting of large prey such as mammals and birds (in addition to insects)—is of more recent origin, probably originating within the ape clade and intensifying within our own genus, *Homo*. Increased reliance on hunting by humans is likely to have shaped us in profound ways, favoring increased reliance on cooperation, social learning, long lifespans, big brains, and cognitive mechanisms related to hunting and foraging (Kaplan, Hill, Lancaster, & Hurtado, 2000). In addition, we may owe our evolutionarily unique abilities as long-distance runners to hunting (Bramble & Lieberman, 2004; Carrier, 1984).

Predators, in turn, have had a profound influence on the biology and behavior of primates, including us. Primatologists have long thought that predation risk is one of the primary factors (though not the only one) favoring sociality (Hart & Sussman, 2005; Isbell, 1994; Kappeler & Van Schaik, 2002; Van Schaik & Van Hooff, 1983). Again, this is likely to be an ancient selection pressure in our lineage, as a high degree of sociality characterizes the primate clade in general (Isbell, 1994). More recently, predators might have had specific effects on evolution within the hominin lineage, especially given the relatively open, predator-dense habitats hominins are likely to have occupied for much of our evolution (Brain, 1981; Hart & Sussman, 2005; Kruuk, 2002).

First, I will review general features of the selection pressures that predation and hunting impose, and how they are likely to shape suites of mechanisms in body and mind. Then I will turn to specific aspects of human psychology that may have been shaped by predator-prey interactions.

SELECTION BY PREDATORS

Dangerous animals have coexisted with our ancestors since long before we were human. The archaeological record has permitted reconstructions of the array of predators in ancestral environments at various points in space and time (Blumenschine, 1987; Rose & Marshall, 1996). This array included fast-moving mammalian predators such as felids (cats) and hyaenids (hyenas), and the diversity of predators in past environments was even higher than today. Human encounters with predators occurred in several contexts, including hunting of humans by predators and competitive interactions between humans and predators over kills (Brain, 1981; Brantingham, 1998; Rose & Marshall, 1996; Stanford & Bunn, 2001). In modern environments, where the ranges of humans and predators such as large cats overlap and human activities such as hunting and foraging bring them into close proximity with predators, attacks occur regularly (Kruuk, 2002; Treves & Naughton-Treves, 1999). Together, these data suggest that cognitive mechanisms involved in predator detection and evasion would have been under selection in our lineage both before and after the origin of *Homo sapiens*.

Predator encounters are likely to have selected for a variety of traits in our lineage, both prior to and after the split with the chimpanzee-human common ancestor. Because predation is thought to be a major factor selecting for sociality in primates, many aspects of social cognition—in particular, mechanisms sustaining relationships with nonkin—may have been initially selectively favored because of predation. Reduction in predation risk could have provided the benefits that outweighed the various costs of social life, such as competition and increased exposure to pathogens. But in order to provide these benefits, other adaptive problems would have to have been surmounted: namely, all the problems involved with tolerating the presence of others. Although problems of cooperation might seem to be a different "domain" than predator avoidance—and indeed, many cooperation mechanisms might not process information about predators *per se*—they could have their origins, at least in part, in predators as a source of selection.

The role of predators in shaping our evolution is likely to have changed in various ways from our earliest primate ancestors to our most recent hominin ones. Predation as a source of mortality is known to be a factor shaping life histories, selecting for fast growth and early reproduction (Reznick & Endler, 1982). It also shapes, for example, decision-making about risk (Coss, 1999; Lima, 1998; Stankowich & Blumstein, 2005). However, increasing sociality in our lineage would have relaxed these selection pressures, allowing for longer lifespans and longer time horizons for decision-making. Still, one would still expect a variety of contingent mechanisms for inference and decision-making in contexts in which predation risk is high. These would include, for example, mechanisms for detection of predators and prediction of predator behavior (Barrett, 1999; Barrett, Todd, Miller, & Blythe, 2005; Coss & Goldthwaite, 1995;

Frankenhuis & Barrett, 2013; Frankenhuis, House, Barrett, & Johnson, 2013; Gao, McCarthy, & Scholl, 2010; New, Cosmides, & Tooby, 2007; Thorpe, Gegenfurtner, le Fabre-Thorpe, & Bulthoff, 2001), specialized learning and memory processes having to do with danger and survival (Barrett & Broesch, 2012; Nairne, Thompson, & Pandeirada, 2007), as well as emotional and motivational mechanisms, including anxiety and fear, that modify behavior in light of predation risk (LoBue, Rakison, & DeLoache, 2010; Öhman & Mineka, 2001; Stankowich & Blumstein, 2005). These will be discussed in more detail later.

Additionally, humans have engaged in warfare and smaller-scale intraspecific conflict for a long time. To some extent, intraspecific conflict may make use of mechanisms originally involved in predator-prey contexts; however, there may be mechanisms evolved for human-on-human aggression, and defense against it (Duntley & Buss, 2005).

Selection by Prey

In addition to the role of prey, humans can adopt the role of predator. Hunting probably predates the origin of the hominin lineage because it is also practiced by our closest evolutionary relatives, chimpanzees. Moreover, the archaeological record suggests that meat has been an important part of hominin diets for millions of years. Increased reliance on meat, a risky, high-variance food source, may have played an important role in the evolution of human sociality and social cognition (Stanford, 1999). The earliest evidence for persistent, as opposed to occasional, carnivory dates back to approximately 2 million years ago (Ferraro et al., 2013). Hunting was and is a dangerous activity, not only because prey animals can themselves be dangerous, but also because of potential competition with other carnivores. There are many sources of archaeological evidence that humans could and did kill game animals, either with tools or by other means, and that they hunted a wide variety of prey, from large, fast ungulates to small rabbits and birds, which would have required diverse strategies and intuitive understanding of prey behavior (Mithen, 1996; Potts, 1989; Stanford & Bunn, 2001).

Hunting is likely to have shaped our lineage in diverse ways. As was the case for predation, the many ways in which a reliance on hunting might have shaped our bodies and minds is not intuitively obvious. According to Kaplan and colleagues, for example, accelerating reliance on hunting in the human lineage had multiple cascading effects on our life histories, social organization, and cognition (Kaplan et al., 2000). They suggest that the shift to meat, as well as other nutritionally dense and hard-to-process food sources, created a cascading, self-reinforcing coevolutionary process. Meat as a food source allows humans to grow large brains, which, in turn, improves our ability to hunt, as well as to cooperate. Increasingly long life histories are selected for because of the benefits of skill acquisition, as well as resource transfers across generations: up to three generations, in humans, which is rare among primates. According to Kaplan et al. (2000), hunting selected for both lengthened childhoods and increased adult lifespans, sociality, reliance on socially transmitted information and skills, and, perhaps, most importantly of all, intelligence. As was the case with predation, hunting may, therefore, be responsible for many aspects of our physiology and cognition that do not appear to be immediately tied to hunting: aspects of intelligence, cooperation, social learning, and paternal investment in offspring, for example.

An examination of the skills involved in hunting in preindustrial societies points to some of the ways that hunting might have shaped our cognition. The knowledge required for successful hunting is incredibly complex and increases into late adulthood. As a skill, hunting is in many ways more akin to mathematics or engineering than, for example, running a marathon (though it is that too; Bramble & Lieberman, 2004). Among the Ache and the Hiwi, for example, Kaplan and colleagues have documented that male hunting returns do not peak until around age 40. If hunting were more about strength and stamina than knowledge, one would expect hunting returns to peak earlier. Instead, hunting is clearly a knowledge-dependent skill at which older individuals can surpass younger ones, and anthropologists have documented elaborate and detailed knowledge related to hunting in adults in traditional societies (Blurton Jones & Konner, 1976; Kruuk, 2002; Liebenberg, 1990).

The cognitive skills involved in hunting span various domains of cognition, and the benefits of hunting may have been a major factor shaping their evolution. For example, virtually all hunting involves tool use, and up until relatively recently in human evolution most human-manufactured tools were probably related to hunting and subsistence in some way. This means that domain-specific skills of tool use in the brain may ultimately have their source in selection for hunting and foraging (Johnson-Frey, 2004). Moreover, mechanisms involved in social learning and teaching, or pedagogy, may have first evolved primarily for transmission of information about tools (Csibra & Gergely, 2009). More generally, foraging is likely to have selected for a variety of mechanisms, including mechanisms of spatial cognition, mechanisms for making decisions about resource distributions in the environment, mechanisms of search, and even the brain's dopamine-modulated risk-reward system (Hills, 2006; Hills, Todd, & Goldstone, 2008; Hutchinson, Wilke, & Todd, 2008; Wilke & Barrett, 2009).

Finally, direct interactions with prey, as well as predators, may have shaped mechanisms for detection of animate agents and predictive inferences about their behavior, including mechanisms of "mindreading," or "theory of mind." For example, from infancy humans, like many other animals, are attuned to interactions of chasing and pursuit, which capture attention and generate strong intuitions about goals and outcomes (Csibra, Bíró, Koós, & Gergely, 2003; Frankenhuis et al., 2013; Rochat, Striano, & Morgan, 2004). Indeed, it is possible that predator-prey interactions were an important, nonsocial source of selection on mechanisms of mindreading (Van Schaik & Van Hooff, 1983). Given the ancient origins of predator-prey interactions, which in vertebrates evolutionarily predate some forms of within-species social interaction such as parental care and cooperation, predation may be one of the oldest sources of selection for mindreading abilities.

Next I turn to the variety of psychological mechanisms in humans that might have been shaped by interactions with predators and prey, including mechanisms of perception, learning, inference, motivation, and decision-making, briefly reviewing the ways in which the designs of these mechanisms might have been shaped by predators and prey.

PERCEPTION

Predators and prey are likely to have shaped a variety of perceptual mechanisms, in diverse ways. Indeed, the origin of visual perception itself may be due, in part, to the benefits of detecting danger and finding food (Parker, 2003). Other senses, such as olfaction and audition, also play a major role in finding food and escaping predators. It is likely that every sense has been shaped in some way by interactions with predators and prey.

Perhaps the most important feature of both predators and prey is that they are *agents:* animate objects, capable of goal-directed motion (Leslie, 1994). In turn, the defining feature of agents is action: They move, in the service of goals (prey capture, escape). Across sensory modalities, but particularly in vision and audition, the detection and interpretation of motion is deeply embedded in the design of perception.

In vision, motion detection and processing is phylogenetically widespread, and makes use of a common set of computational principles that can be found at many levels of organization, from the level of single neurons to entire networks. For example, nervous systems often detect motion based on correlations in neural activity across parts of a network in time (Borst & Egelhaaf, 1989). Given that these design features are present in the nervous systems of distantly related, nonsocial animals, such as insects, they are likely to predate the evolutionary origins of sociality. It is plausible that the proper domain of our ability to detect motion—on which nearly all social perception and cognition depends—is predator-prey interactions, and that social-action processing evolved on top of these ancient mechanisms.

Beyond just detecting motion itself, there is the use of specific motion cues to detect and categorize agents and their goals. From a computational perspective, the problems of discriminating agents from nonagents and discriminating between different kinds of agents are enormously difficult. Consider how difficult it would be to write a computer program that could reliably pick out and identify animals from the churning confusion of information that reaches our eyes and ears and that could do so across the range of environments and conditions that humans encounter. Add to this a premium on speed and the possibility of extremely impoverished information (a brief movement in peripheral vision, ripples in the grass, something glimpsed through a gap in the leaves), and you have a task that is both extremely difficult and of utmost importance to survival. Yet there is evidence that selection has built just these kinds of things.

Motion can be used both to identify things that behave (agents) and to discriminate types of agent on the basis of how they behave. There is a substantial literature on the use of motion cues both to detect agents and to make inferences about behavior (Johnson, 2000; Rakison & Poulin-Dubois, 2001; Scholl & Tremoulet, 2000). Cues such as autonomous motion and change in trajectory are important cues to agency, and even very simple cues such as the direction of motion of a bilaterally symmetric object can be used to categorize it as an agent, with a front end (Hernik, Fearon, & Csibra, 2014, Tremoulet & Feldman, 2000). Beyond simple self-propulsion, there are a variety of cues that can be used to detect motion that is goal-directed, such as pursuit. Gergely, Csibra, and colleagues have demonstrated that motion that appears to be goal directed—for example, one object chasing another—triggers the intentional stance and specific expectations about how the objects will behave in infants as young as 9 months (Csibra, Gergely, Bíró, Koós, & Brockbank, 1999; Csibra et al., 2003; Gergely, Nádasdy, Csibra, & Bíró, 1995; Rochat et al., 2004). The motion signature of pursuit and evasion cannot only trigger the agency system but also be used to discriminate predation from other kinds of behavioral interaction and to activate inference systems and procedures specific to predators and prey. Several studies have shown that people are good at discriminating pursuit and evasion from other types of motion (Abell, Happé, & Frith, 2000; Barrett et al., 2005; Castelli, Happé, Frith, & Frith, 2000). This is true not just of dyadic interactions but interactions among multiple agents. For example, Gao et al. (2010) have demonstrated a "wolfpack effect" in perception, in which the simultaneous orientation of multiple agents toward oneself is immediately noticeable and compels escape responses.

Because of the cost–benefit asymmetries entailed by detection of predators and prey, error management logic applies (Haselton & Buss, 2000). Detection thresholds may be biased in favor of false positives, because failures to detect predators and prey may be more costly than false alarms—tempered, on the other hand, by the costs of excessive vigilance. One such bias appears to occur in responses to rapidly approaching objects. In the phenomenon known as visual looming, a rapidly expanding circular shadow (but not a rapidly shrinking shadow) was found to trigger defensive behaviors in rhesus monkeys, from ducking and flinching to alarm calling (Schiff, Caviness & Gibson, 1962). These reactions have been found in a variety of species, from fishes and frogs to human infants, and specialized neural circuits have been found that compute estimated time to contact for looming visual objects (Sun & Frost, 1998). In hearing there is a similar phenomenon of auditory looming, in which approaching sounds are perceived as starting and stopping closer than receding sounds the same distance away, possibly acting as an early-warning bias (Neuhoff, 2001).

In addition to whole body motion, the visual system is sensitive to the ways that body parts of animals move and can use such cues to discriminate types of animal, types of behavior, and other qualities such as size and formidability. A variety of studies have shown that people can distinguish animals from nonanimals and can even discriminate between kinds of animals (human, dog, horse, etc.) from point light displays in which illuminated points are placed on limbs or joints and the rest of the body is blacked out; this effect disappears when the displays are inverted (Johansson, 1973; Mather & West, 1993). Such "biological motion" perception is present from early infancy, and babies prefer right-side-up point-light displays (Simion, Regolin, & Bulf, 2008). Interestingly, the perception of biological motion is also present in chickens, suggesting that it may predate the origins of primate sociality (Vallortigara, Regolin, & Marconato, 2005).

In addition to motion cues, it is sometimes possible to detect predators through the use of static cues. Classic examples are the sinusoidal shape of snakes and the characteristic appearance of eyes. A variety of studies, for example, have shown that snakes "pop out" of perceptual arrays. Öhman, Flykt, and Esteves (2001) found that subjects could rapidly pick out pictures of snakes and spiders from arrays of fear-irrelevant objects (flowers and mushrooms) much faster than they could do the opposite task, suggesting that snake detection is a parallel process using a specialized detector, different from serial search for flowers. Similarly, the perceptual importance of eyes as cues to being seen is phylogenetically widespread, as evidenced by the commonness of eyespots and behavioral reactions to eyes.

Broken wing displays in plovers—a clear anti-predator response—are triggered by eyes (Ristau, 1991). Eye stimuli exacerbate the tonic immobility response, a last-ditch emergency response to capture by a predator, in restrained chickens (Gallup, 1998). Humans are known to be exquisitely sensitive to gaze direction (Baron-Cohen, 1995), and, although gaze as a triggering stimulus for antipredator mechanisms has not been specifically examined in humans, it is known to cause arousal in humans and perhaps the activation of antipredator responses (Coss & Goldthwaite, 1995).

Finally, perceptual detection experiments suggest that there may be additional cues that the visual system uses to detect and track predators, prey, and other animals.

Thorpe et al. (2001) found that subjects can detect animals better than other classes of stimuli in far peripheral vision, where visual acuity is generally poor. This suggests another early-warning system for animals in the periphery. Using a change blindness paradigm, New, Cosmides, and Tooby (2007) found that subjects' abilities to detect changes in a scene that involved animals were significantly greater than their abilities to detect changes that involved nonliving objects, even when the object was much larger than an animal, such as a building. This provides evidence for an animate monitoring hypothesis: Mechanisms exist that are dedicated to tracking and updating locations of animates, but not inanimates, in visual scenes, because only animates are likely to move in the real world.

FORAGING

Just as the evolutionary roots of predator avoidance are ancient, so are the evolutionary roots of foraging. Not all foraging is for animate prey, but, in primates, at least some of it is. Although hunting as humans know it—hunting for comparatively large game with human-made tools—is likely to be relatively recent in origin, prey search and capture is ancient, dating back at least to the earliest insectivorous primates, and beyond.

In keeping with this, some of the effects of foraging on the design of our nervous systems are likely to be ancient. The "reward" system of our brain, the dopaminergic system, bears evidence of being designed for what is sometimes called area-restricted search, or search based on the clumpiness or patchiness of resources in the environment—causing us to perseverate when something good has been detected, and to become distracted when the rate of reward drops (Hills, 2006). Indeed, some pathologies, such as excessive perseveration on goals, may result from disruptions to this system.

Prey animals and other foraged resources are usually not evenly dispersed in the environment; they come in clumps. Our psychology of search and reward appears to be deeply organized around an expectation of patchiness (Hills, 2006; Hills et al., 2008; Hutchinson et al., 2008; Scheibehenne, Wilke, & Todd, 2011; Wilke & Barrett, 2009). This expectation extends across diverse domains, from foraging for food, to foraging for information on the Internet, to internal search in memory (Hills et al., 2008). Wilke and Barrett (2009) have suggested that the phenomenon known as "hot hand," in which subjects overperceive clumps in distributions that are in fact random, reflects an adaptation to the clumpiness of ancestral resources. In a recent study, they found evidence that habitual gamblers are more likely to fall prey to the hot-hand illusion, suggesting that the evolved design of our foraging system may have significant real-world consequences (Wilke, Scheibehenne, Gaissmaier, McCanney, & Barrett, 2014).

The importance of the dopaminergic system in foraging reveals the deep and inseparable evolutionary link between cognition and motivation. Although these are sometimes treated as distinct in the psychological literature, the function of cognition is (ultimately) action, and action does not occur in the absence of motivation (Tooby, Cosmides, & Barrett, 2005). Motivation plays a role in all stages of cognition, shaping what we attend to, how we respond to it, and what we learn from it. In the case of foraging, motivations such as hunger and the satisfaction of getting a "hit" in prey search play a large role, and these subjective sensations shape our learning and future behavior in terms of where, how, and when we decide to look for things. In the case of predator avoidance, fear, anxiety, and risk assessment play a similarly large role.

FEAR

Although fear and anxiety do not have to do exclusively with predation—there are, for example, social fears and anxieties—it may be, as was the case for perception, that predation is the most phylogenetically ancient selection pressure shaping the fear system (Cosmides & Tooby, 2000; LeDoux, 1996; Öhman & Mineka, 2001). Fear not only organizes escape and avoidance responses to dangers but also deactivates certain cognitive processes (e.g., mate search) and activates others (e.g., predator-prey routines) and may alter sensitivity thresholds of many systems. As an adaptive problem, predator avoidance shares some features with other danger-avoidance problems such as avoiding cliffs or sharp objects but also has some unique characteristics such as the fact that predators are mobile agents that seek to cause harm, unlike other sources of harm such as rotting food, which engenders its own danger-avoidance emotion, disgust.

The psychological literature on fear and fear learning is enormous, and there is not room to review it all here (for reviews, see LoBue, Rakison, et al., 2010; Öhman & Mineka, 2001). In this literature, there are debates about how "specific" fear learning is—that is, how tuned it is toward particular targets, such as snakes, predators, dangerous conspecifics, and artifacts—and about the nature of the learning mechanisms that lead to fear acquisition. Much research has examined the role of fear in conditioning, showing that fears of some types of objects and situations are easier to develop than others, and harder to extinguish. There are many demonstrations of such "content effects" or "biases" in fear learning.

For example, a variety of studies have compared conditioning stimuli such as snakes and spiders with fear-irrelevant controls such as houses, flowers, and mushrooms to demonstrate that conditioned associations between picture items and aversive conditioning stimuli, such as shocks, occur much more readily, and disappear more slowly, for dangerous than for nondangerous items, with fear generally being acquired more readily for ancestrally dangerous stimuli such as snakes (Hugdahl & Öhman, 1977; Mineka, Davidson, Cook, & Keir, 1984; Öhman & Mineka, 2001). In addition, studies with young children have provided evidence for a bias in attending to dangerous animals, such as snakes and spiders, and a tendency to associate these stimuli with fear (DeLoache & LoBue, 2009; LoBue & DeLoache, 2008, 2010; Rakison, 2009; Rakison & Derringer, 2008). Interestingly, Rakison (2009) found a sex difference in the association of snakes and spiders with fearful faces, with this association being found in 11-month-old girls, but not boys. And, a variety of studies have shown that preferential attention to, and learning about, danger stimuli need not be restricted to dangerous animals—they can include, for example, angry faces—nor to ancestral stimuli, as they can include stimuli such as syringes and guns (Blanchette, 2006; LoBue, 2010). This suggests a role for experience of current dangers in calibrating the fear learning system.

There are a variety of theories regarding the mechanisms underlying fear learning, varying in the type and degree of specificity they attribute to these mechanisms, and where they act in the flow of information processing in the brain. Öhman and Mineka (2001) offer a modular account of the fear learning system, proposing that the system possesses four distinguishing characteristics: stimulus-specificity; preferential activation by evolutionarily prepared danger stimuli, such as snakes, spiders, and falling objects; automatic triggering; impenetrability to conscious control; and dedicated neural circuitry, particularly in the amygdala. They suggest that in the most evolutionarily ancient fear systems, perceptual threat detectors were directly connected to motor reflexes designed to move the organism away from danger and that intervening control systems, though, in humans, higher-level processes can also mediate predator evasion strategies.

LoBue, Rakison, and DeLoache (2010) suggest a more minimal design that is rooted in perceptual biases to attend to dangerous stimuli, such as snakes, spiders, and human threats. On this view, the content effects seen in learning emerge from perceptual biases interacting with more general-purpose learning mechanisms, such as mechanisms of association and statistical learning.

LEARNING

For some kinds of dangerous animals, such as snakes, there appear to exist evolved perceptual templates or "prepared" cues, such as sinusoidal shapes or rapid looming, that allow response to the threat in the absence of learning. However, learning is clearly important in shaping responses to predators and prey, and one should expect it to be so, because learning is a useful adaptive tool.

There is some reason to expect that the most general-purpose forms of learning, such as classical conditioning, might not be ideally suited to learning about predators. For one, an equipotential learning system that had no evolved priors about the informativeness of predator-related cues might not learn as efficiently as a "prepared" learning system (Öhman & Mineka, 2001; Seligman, 1971). There is an even larger problem in learning about danger exclusively from one's own experience; some of the most informative learning opportunities can lead to injury or death.

For this reason, Barrett and Broesch (2012; Barrett, 2005) proposed that humans might possess a prepared social-learning system for learning about dangerous animals. Mineka and colleagues (1984) showed that juvenile rhesus macaques, reared in the lab with no prior experience with snakes, could acquire snake fear in a single trial if shown the face of an adult conspecific exhibiting fear toward a snake. The logic of prepared social learning makes sense here, because the costs of individual learning (e.g., a snake bite) might greatly outweigh the costs of learning from a knowledgeable conspecific (e.g., a possible false positive), and the benefits of social learning could be large. Thus, Barrett and Broesch proposed that humans might possess a similar mechanism, perhaps homologous to that of macaques, but potentially modified in the human case to admit not just facial expressions of fear but verbal statements of danger. They hypothesized a danger learning system with several features: a domain-specific preference for learning about danger as opposed to other types of information about animals; single-trial learning without feedback; retention of danger information in long-term memory; and similar memory effects across cultures. In an experimental memory task with American and Shuar children, they found evidence for all of these hypotheses (Barrett & Broesch, 2012). Follow-up work has found similar learning biases across the life course in Fiji (Broesch, Henrich, & Barrett, 2014).

Nairne and colleagues have demonstrated an additional facet of adaptive memory related in part to interactions with predators and prey: "survival processing" (Nairne et al., 2007; Nairne, Pandeirada, Gregory, & Van Arsdall, 2009). The survival-processing hypothesis posits that it is not just information "content" that determines whether and how it is stored, but also how the information is processed, that is, whether subjects process the survival value of the information as it is being encoded. They showed that merely asking subjects to rate the survival relevance of items (e.g., for securing food or water or avoiding predators) increases recall and recognition of these items in later surprise tests, compared to conditions in which the items are rated along some other dimension (e.g., pleasantness).

In addition, there are likely to be many other learning phenomena related to predator-prey interactions, such as disgust learning, triggered strongly by animal products as sources of disease transmission (Fessler, 2002), and learning about tool use, which may be rooted most anciently in learning to make and use tools for hunting (Csibra & Gergely, 2009).

INFERENCE

Perhaps the most important way in which predators and prey differ from other obstacles or problems in the environment is that predators and prey are intentional agents: They are animate, sentient beings that process information and behave in the service of specific goals that they are well-adapted to achieve and that are in direct opposition to those of humans, either as prey or as hunters. This means that predators and prey are not passive, static components of the environment that simply need to be avoided or found. The biggest problem with predators is that, unlike other dangers such as cliffs or toxins, predators come to find you and are well designed to do so. The biggest problem with prey is that, unlike tubers or berries, they move, have the goal of avoiding capture, and possess adaptations such as camouflage and finely tuned sensory systems that help them achieve that goal.

These considerations suggest that predator avoidance and prey capture are likely to make use of mechanisms involved in understanding agency, from mechanisms for detecting the presence of agents in the environment to theory of mind mechanisms for reasoning about mental states (Baron-Cohen, 1995; Leslie, 1994). Because humans are intentional agents, too, many of the mechanisms that are brought to bear in social interaction—gaze direction detection mechanisms, for example—will also be brought to bear in predator-prey encounters. However, there are important elements of predator-prey interactions that have no analogy in human social interactions, because the goals of predators and prey are distinctly asocial. Barrett (1999, 2005) proposed that humans may possess a reliably developing "predator-prey schema," a set of rules for predicting predator and prey behavior, embedded within (interacting with) the mindreading system (Barrett, 1999, 2005). One might think of this as an "island of competence" within the larger domain of mindreading (Frankenhuis & Barrett, 2013). What might appear to be a single, flat, undifferentiated domain such as mindreading might actually contain internal structure: Some types of interactions might be more easily conceptualized than others, and possibly earlier-developing, because they map onto ancestral forms of interaction whose understanding might yield survival benefits early in life. Predator-prey interactions—in addition to several others, such as kinship and dominance interactions—might be some of the most ancient, recurring, and fitness-relevant forms of interaction, and thereby might represent particularly important islands of competence within the domain of mindreading.

Consistent with this idea, there is evidence that young infants are particularly attentive to, and able to make predictive inferences about, interactions of pursuit and evasion, or chasing. Attention to and inferences about chasing develop similarly across cultures (Barrett et al., 2005), and early in infancy (Csibra et al., 2003; Frankenhuis et al., 2013; Rochat, Morgan, & Carpenter, 1997). Csibra et al. (2003) used a dishabituation paradigm to test 12-month-old infants' expectations regarding pursuit-evasion scenarios, presented using moving objects on a computer screen. These studies showed that infants not only encode the goals of a chaser and chasee (capture and escape, respectively), they form expectations about how each agent will most effectively pursue its goal: For example, a prey animal might attempt to escape through a hole that a predator is too large to fit through, and the predator might anticipate this escape route by going around an obstacle with a small hole in it to catch the prey on the other side. This work suggests that at least part of a predator-prey inference system is present by 12 months of age.

Several other studies support the idea of an evolved predator-prey schema. For example, Rochat et al. (1997) showed that 3- to 6-month-old infants, as well as adults, preferred to look at displays of contingent chasing, rather than displays of non-contingent motion with similar properties displayed side by side. Frankenhuis et al. (2013) later replicated this, and additionally decomposed the displays into their distinct cue components, showing that acceleration particularly drew infants' attention. In a follow-up to their original study, Rochat et al. (2004) showed that 8- to 10-month-old infants assigned distinct roles to chaser and chasee, as evidenced by surprise when these roles were reversed—suggesting distinct conceptual placeholders for the different roles within an early-developing predator-prey schema. At older ages (3–5 years), Barrett (1999) showed that both Shuar and German children are capable of producing realistic predictions about what happens in encounters between predators and prey, suggesting a schema organized around pursuit and killing that is not contaminated with information from friendly cartoon depictions of lions and other predators. A cross-cultural study with German and Shuar adults by Barrett et al. (2005) demonstrated that the chasing schema, as well as schemas for courtship, play, and several others, manifest reliably across cultures, leading to similar levels of discrimination on a perceptual categorization task.

Interestingly, it appears that these basic interaction schemas may involve attribution of distinct goals—as suggested by the role-reversal findings of Rochat and colleagues—but do not require attribution of beliefs. Castelli, Frith, Happé, and Frith (2002) found that autistic subjects were able to identify goal-directed sequences including pursuit and evasion but not sequences that required attribution of belief. Thus, the predator-prey or chasing schema may be an early-developing island of competence that involves goal attribution, but does not require attribution of knowledge and belief states, an ability that seems to be impaired, along with some other abilities, in autism (Baron-Cohen, 1995). However, this does not mean that calculation of beliefs and knowledge is never relevant for predator-prey interactions. It just means, minimally, that some action predictions can be done without the belief attribution system. In a series of studies, Keenan, Ellis, and colleagues (Ellis et al., 2014; Keenan & Ellis, 2003) have shown that predator-prey scenarios can influence children's judgments in a modified false belief task: When the correct answer to the task involves sending a prey animal to its death at the hands of a hidden predator, they are more likely to provide the incorrect answer.

One important consequence of predator-prey interactions is death. As prey, we face possible death from predators. As predators, we kill prey animals. Although the conventional wisdom in the developmental literature has been that children's understanding of death is poor, Barrett and Behne (2005) proposed that children might possess another early-developing island of competence within the larger domain of death understanding: in particular, understanding death as the cessation of agency. Children face an inferential problem when an animal dies: Unless they specifically remove the agency tag from the object—a now-dead piece of meat—they will continue to generate inferences such, as, for example, that the animal will react if touched. Barrett and Behne conjectured that the costs of this mistake might select for a mechanism that removes the agency tag from agents given certain cues of death, allowing them to cease monitoring it for change, and to be unafraid to approach or eat it. In a cross-cultural study with 3- to 5-year-old children, they found that by age 4 children were well above chance in disattributing agency properties to dead animals, compared to sleeping animals.

CONCLUSIONS

Given the importance of predators and prey in human evolution, it is likely that we have only begun to uncover the full array of predator-prey adaptations that the mind contains. Indeed, if one expands one's view to include phylogenetically ancient and widespread ways in which predator-prey interactions shape biology, there may be few aspects of our bodies and minds that have not been influenced in some way by the need to avoid predators and obtain food. This presents a challenge for a view of human nature as restricted to only those derived features that have evolved uniquely in us since our divergence from the other great apes. It also challenges a view of "domains" as cleanly separable, at least as sources of selection, because—for reasons outlined earlier—many aspects of our social cognition may initially have been selected for due to the benefits of cooperation for hunting and predator avoidance. This does not contradict the view that the mind is composed of many functionally specialized mechanisms; instead, it is consistent with a hierarchical specialization view, in which the mind's domains and mechanisms overlap on some levels of organization and design, and diverge on others (Barrett, 2012).

Until very recently, attack by predators was a real and constant possibility in everyday life. Selection to be aware of these creatures, of their thoughts, plans, and intentions, as well as a strategic intelligence to take advantage of this awareness, would have been strong. Here, we need to think in science-fiction terms. Imagine the human mind as an exquisitely designed computer, armed with state-of-the-art sensors, trackers, detectors, and inference engines all engineered for the purpose of predator defense and evasion. What would these look like? Without doubt, the best equipment designed by military science does not even come close. Yet, across psychology and neuroscience in general, relatively little attention has been paid to predator detection and evasion as adaptive problems that could shed light on the design of our minds.

On the other side of the coin, humans are predators by nature. We have been hunters of other animals for millions of years. Far from diminishing with time, selection for the skills necessary to stalk and kill animals has accelerated over the course of human evolution, as hunting has played an ever-increasing role in human subsistence. For those who have never hunted, the difficulty of the task is easy to underestimate. Dawkins (1976) coined the term the "life/dinner principle" to refer to the asymmetry in fitness payoffs to predators and prey for the two possible outcomes of a predation event: If the predation event is a success, the predator wins dinner, but the prey loses his life; vice versa, if it fails. There is another asymmetry, which might be called the "anywhere but here" principle: For a predator to succeed, the predator must manage to be in exactly the same place as the prey at exactly the same time; for the prey to succeed, it need only be anywhere else. Obviously, it is much easier to satisfy the latter condition than the former. This means that whereas prey can use a variety of "dumb" tactics to avoid predation, including hiding, crypsis, and living in holes or trees, predators must be designed to bring about a very unlikely and nonrandom physical state of the world, which prey are expressly designed to avoid. For tool-using predators, there is an added complication: We must either cause our own position to converge with that of the prey or cause the position of a projectile or trap to do so. This poses other adaptive problems such as the perceptual and motor problems involved in successfully aiming a projectile. Predation, then, may select for particular kinds of intelligence, and our evolutionary legacy as hunters is likely to have played an important role in the evolution of the human mind. Some aspects of our intelligence that we do not attribute to our history as hunters—from mindreading, to tool use, to strategic coordination—may nevertheless exist at least partly because of it. Additionally, our minds are likely to be full of many detection, tracking, and behavior anticipation mechanisms of which we might not be fully aware.

It is possible that investigating evolutionarily relevant problem domains such as predation, which are rarely considered by most contemporary cognitive and developmental psychologists, could lead to drastic reconsideration of how the domains of thought are organized. Rather than thinking of broad domains such as social cognition and theory of mind, we might realize that the mind is not organized around a few large problems but around many small ones such as agency detection, tracking objects, and inferring intention from motion, which do not map neatly onto the intuitive categories of contemporary psychology.

This "micro-modularity" view of mechanisms organized around rather specific adaptive tasks is, in many ways, more consistent with recent findings in cognitive neuroscience than with a view of domains as analogous to university departments, e.g., psychology, mathematics, and physics (see Boyer & Barrett, Chapter 5, this volume). Indeed, brain mapping studies are increasingly supporting a view of cognition that is both heavily "distributed" across many brain systems, and that involves the large-scale coordination of many smaller subsystems (Bullmore & Sporns, 2009). This is also consistent with a hierarchical modularity view, namely, that large-scale abilities such as "theory of mind" or "social cognition" involve the operation of mechanisms nested within larger assemblies, potentially in a flexible mix-and-match way (Barrett, 2012). Although evolutionary psychologists have argued for some time that the true domain map of the human mind is not likely to correspond to the way domains are carved in psychology textbooks, much work remains to be done in finding the mind's true joints. Adaptations to predators and prey provide a useful case study in how this might be done. There is probably not a cleanly delineated domain of predators and prey in the mind, but rather, a constellation of systems each shaped in unique ways by predators and prey—some exclusively so, and some not. For other potential domains of cognition, then—contagion, cooperation, sex—we might consider a broader set of possible models of how the underlying mechanisms are organized, including hierarchical, distributed models that involve the interaction of diverse mechanisms, some exclusive to the domain and some not.

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CHAPTER 10

Adaptations to Dangers From Humans

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ALTHOUGH THERE ARE more victims of aggression than perpetrators, violent humans have received the majority of interest from researchers and the public. This chapter explores the evolutionary logic and evidence of adaptations that defend against dangers from humans.

DANGEROUS AT DIFFERENT LEVELS

What constitutes a danger from other humans depends on the unit of analysis. Intuitively, people tend to focus on the individual person as the unit of analysis when considering survival dangers. It is the individual who can be punched, stabbed, raped, or killed. From this view, dangers from other humans are limited to behaviors that threaten a person's survival and physical health.

Using the gene as the unit of analysis requires the consideration of a greater range of dangers from humans. The survival of genes is not limited to a single lifespan or a single individual. Genes can simultaneously exist in multiple, different individuals and continue to exist across thousands of generations. For genes, contributions to genetic fitness are the relevant indicators of success. Any behaviors from other humans that put genes at a replicative disadvantage can be considered a danger. A physical attack on one's child, being cheated on by a spouse, or being humiliated by a rival are all behaviors that endanger the replicative success of genes. But none are dangers to the focal individual's survival or physical health. That human psychology reacts to these and other dangers to genetic fitness as something akin to life-and-death threats to personal well-being provide a clue that our psychology was shaped, ultimately, to ensure the replicative success of our genes. Genetic cuckoldry, reputational damage, and the loss of reproductive value of a child *are* life-and-death situations for genes. Although the survival of the individual is not sufficient to ensure genetic fitness, it is necessary. This chapter focuses on dangers to this necessary element of genetic fitness: dangers to the survival and physical health of the individual that other humans can pose.

HOW DANGEROUS?

There is no question that humans are dangerous. Among animals, humans are second only to mosquitoes in the number of people they kill each year (GatesNotes, 2014). Of the 5.8 million deaths from injuries that occur globally each year, about 1 in 7 result from homicide or warfare (World Health Organization [WHO], 2008). Among 15- to 29-year-olds, who experience among the highest levels of competition for reproductively relevant resources (Buss, 2003), homicide is the fourth leading cause of death, after traffic injuries, HIV/AIDS, and tuberculosis (WHO, 2008). Warfare is the ninth leading cause of death for this group. Across all ages, almost twice as many men than women die from injuries and violence.

DANGEROUS ADAPTATIONS

For some ancestral contexts, such as big-game hunting, cooperation would have produced the greatest inclusive fitness benefit for individual hunters, given that their individual contributions to the hunt were proportional to the benefits they received. For other ancestral contexts, however, a behavior that increased the inclusive fitness of one individual would have simultaneously decreased the fitness of another, creating conflict between the parties involved (Buss, 1989). Given adequate fitness benefits to power the engine of selection, any trait can be favored, including those that make humans dangerous to one another.

Many of the human activities that make humans the most dangerous have been proposed to be the result of psychological adaptations. Evidence suggests psychological adaptations have a role in producing spousal violence (Buss & Shackelford, 1997a), aggression (Buss & Shackelford, 1997b; Campbell, 1993; Daly & Wilson, 1988; Wilson, Daly, & Pound, 2002), rape (Thornhill & Palmer, 2000), homicide (Buss, 2005; Duntley & Buss, 2011), and warfare (Tooby & Cosmides, 2010; 1988) (see Pinker, 2011, more broadly, for a comprehensive review of the historical trajectory of these and other dangers). At the core of the selection pressures that shaped these adaptations is conflict and competition for limited resources and social relationships.

Violence can offer a potential solution to a wider variety of adaptive problems than other behaviors can. For example, consider the use of two strategies to obtain resources: violence and clandestine theft. While theft can be effective at getting resources, violence can be used as a strategy to simultaneously aid in theft, demonstrate physical prowess to potential mates, and intimidate rivals.

Although perpetrators of cost-inflicting strategies can gain much through their behavior, victims can incur costs ranging from strategic interference with evolved goals to death. On average, death is the most costly outcome that victims face. It is implausible that selection would not have acted to prevent or stanch the costs of victimization.

COEVOLUTION OF COST INFLICTION AND DEFENSES

Antagonistic coevolutionary arms races are part of the evolutionary history of most species, if not all of them. They can occur *between* species, as with predators and their prey, or between competitors *within* species. They can create massive selection pressures, capable of producing rapid evolutionary change (see Phillips, Brown, & Shine, 2004). Any recurrent context of conflict between conspecifics has the potential to be a hotbed for the coevolution of competing strategies to best a competitor and defend against being bested.

The evolution of adaptations to inflict costs creates selection pressures for the coevolution of counteradaptations to defend against them. The amount of selection pressure is a function of the magnitude and frequency of the costs over evolutionary time. The evolution of adaptations to defend against incurring costs creates new selection pressure for refinements of adaptations designed to inflict costs or new adaptations for that purpose. These refined adaptations for cost-infliction, in turn, create new selection pressure for refinements in adaptations to defend against costs. New combinations of shifting adaptations and counteradaptations can lead to antagonistic coevolutionary arms races between adaptations to inflict costs and adaptations to defend against them that go on perpetually, unless the source of the conflict and competition is resolved or otherwise eliminated.

The existence of adaptations that are designed to counter the cost-inflicting strategies of competitors is a source of evidence that the competitor's strategy is the product of adaptations. Counteradaptations to a given competitor's strategy can evolve only when the strategy has been sufficiently recurrent in predictable contexts over evolutionary time. Adaptations are more likely than by-products of adaptations or noise to produce evolutionarily recurrent, contextually predictable behaviors. Moreover, defensive counteradaptations may function by making a competitor's cost-inflicting behavior too costly to perform (e.g., killing a sexual aggressor), which would create selection pressure against the cost-inflicting strategy. A cost-inflicting strategy that continues to persist over evolutionary time despite the costs suggests that it may, on average, be functional in producing a net benefit in a particular context. Evidence of such functionality is necessary evidence of adaptation, but is not sufficient. Additional evidence could be sought in the complexity and specificity of the design features of evolved defenses and their match to design features of the hypothesized adaptation. A complex set of highly functional design features in mechanisms that produce cost-infliction and correspondingly complex and specific defenses against them would strengthen the case that both are adaptations.

THREE TEMPORAL CONTEXTS OF VICTIM DEFENSES

There are important differences between the form and function of victim defenses that depend on the timing of their activation. Victims can defend themselves against the costs inflicted by dangerous humans: (1) before the victimization occurs, (2) while the cost-inflicting event is occurring, or (3) after being victimized. The strength of selection pressures operating to shape adaptations to address each temporal context varies as a function of the nature of the costs inflicted. For example, there would be selection pressures on victim adaptations against rape in all three temporal contexts. Women should have adaptations to avoid victimization, to minimize costs during victimization, and to take steps to prevent future victimization in the aftermath of rape.

However, there would not be selection pressures on all three of the temporal contexts of adaptations of people who are murdered. The primary victims of homicide are incapable of directly influencing events after their deaths.

Previctimization Adaptations

The best defense against being victimized is to not become a victim. To the extent that strategies of cost infliction were perpetrated by predictable conspecifics in predictable contexts there would have been selection pressure for the evolution of defensive adaptations to avoid them. Individuals with psychological mechanisms that led them to recognize situations and competitors associated with a higher likelihood of incurring the costs and avoid them would have had a large fitness advantage over those who lacked such mechanisms. Fear while walking through dark alleys at night, of people who seem "shifty," and stranger anxiety in infants are examples of the hypothesized outcomes of adaptations to prevent falling victim to the cost-inflicting strategies of others.

Concurrent Victimization Adaptations

Selection also shaped adaptations to minimize the costs of victimization while it is occurring. Defensive postures, verbal attempts at manipulation, and seeking or creating opportunities to flee an attacker are defensive strategies hypothesized to have been selected because they decreased the costs of victimization. Curling into a fetal position may help to deflect the blows from an attacker away from a victim's head and internal organs. The use of language to activate sympathy or empathy in an attacker, or to frighten an attacker away, may be effective in decreasing the duration or severity of the cost infliction. Creating or waiting for an event that distracts an attacker, or temporarily incapacitating an attacker, might give victims an opportunity to escape or to hide and seek protection. Selection would have favored any adaptation that decreased the magnitude of costs that victims might otherwise have incurred.

Postvictimization Adaptations

Victim adaptations activated after the occurrence of the cost-inflicting event that function to minimize the impact of the victimization or to prevent future victimization also would have been favored by selection. For example, acting as though the injuries sustained during a fight are not as debilitating as they actually are, or verbal assaults on an attacker that impugn the effectiveness of the person's attack, such as "you punch like a 3-year-old," may decrease the status loss associated with being beaten in a physical fight.

There are numerous avenues for the prevention of future occurrences of victimization. One is learning cues to danger. By recognizing and subsequently avoiding dangerous contexts and individuals, victims will be less likely to incur costs from them in the future. A person victimized in a certain part of a city, for example, subsequently may be motivated to avoid that part of the city. A victim may avoid future interactions with an attacker. Victims also may be proactive in avoiding conflicts by fortifying defenses against future attacks by conspecifics. For example, carrying a weapon for self-defense may decrease the likelihood of incurring serious costs in future confrontations.

Another avenue for the prevention of future victimization is to retaliate against an attacker. Demonstrating an effective ability to retaliate may decrease the likelihood of future victimization by sending a message to the perpetrator and others that attacks or exploitation will be avenged. Revenge has been suggested to be built into our psychology by natural selection (Buss & Duntley, 2006). fMRI research has demonstrated that pleasure centers of men's brains become activated upon exacting revenge against someone they believe perpetrated a wrong against them (Singer et al., 2006). The research suggests that the motivation for men to seek revenge may have evolutionary underpinnings and supports the contention that maintaining status in social competition was important for the inclusive fitness of ancestral men.

Selection pressures for each temporal category of victim adaptations were unlikely to be equal. Because entirely avoiding being a victim was ancestrally associated with the lowest victimization costs, there probably was more selection pressure for the evolution of previctimization adaptations than for victim adaptations that function during or after victims have incurred costs. As a result, previctimization adaptations are hypothesized to be larger in number than the other temporal categories of victim defense adaptations.

Although it can be useful to conceptualize three distinct temporal categories of victim defenses for the purpose of exploring their design features, it is also possible that some defensive strategies bridge more than one temporal category, such as storing information about victimization in memory and using it to prevent becoming a victim in the future.

In sum, it is useful to consider three temporal categories of victim adaptations: those aimed at avoiding victimization, those that minimize the costs of victimization while it is occurring, and those that function after victimization to minimize its costs and to prevent its recurrence. The nature of the victimization will determine the degree of selection pressure for adaptations in each of these contexts.

THE COEVOLUTION OF DANGERS FROM HUMANS AND DEFENSES AGAINST THEM

A range of strategies may be employed to inflict costs on others, too many to adequately address in this chapter. Behaviors that inflict the greatest costs create the strongest selection pressure for defenses against them. To get the clearest picture of the coevolution of strategies of cost infliction and defenses against them, the next section focuses on three contexts associated with the greatest costs for its victims: Violence, rape, and homicide.

VIOLENCE

Physically injuring rivals clearly inflicts physiological costs on them. The use of violence can also be an effective competitive tactic. Healthy individuals can compete more effectively than the rivals they injure. Rivals may be more likely to avoid or drop out of competition with individuals who injured them in the past. Individuals who inflict greater injuries than they sustain in a conflict may gain a reputation of being difficult to exploit (Buss, 2011). This reputation may protect individuals against violent confrontations and grant them easier access to resources with less resistance from rivals.

An effective strategy for preventing violence is to avoid the violent confrontation altogether. Because it is easier to attack an individual than a group, human adaptations to form alliances may provide one form of deterrence against violent rivals (Tooby & Cosmides, 2010). Adaptations that lead to the avoidance of contexts likely to make an individual the target of violence may provide another kind of protection against being injured by a conspecific. Humans also may possess adaptations designed to attempt to reason with an attacker, arguing that the costs of the attacker's violent behavior outweigh the benefits, offering some other possible resolution to the conflict, or threatening to use violence to defend themselves. If an attack cannot be avoided, individuals may resort to aggression or even murder to defend against becoming a victim of violence (Daly & Wilson, 1988).

An analysis of the structure of the bones of men's faces suggests that they evolved for fighting, specifically to minimize injury caused by being punched by another man (Carrier & Morgan, 2014). The boney structures argued to provide protection from the blows of a rival provide a good example of physiological adaptations against violence.

Rape

Rape is a cost-inflicting strategy with a direct link to reproduction. Rapists may benefit by fathering offspring that they may not have otherwise produced. Rape inflicts not only emotional costs (Block, 1990; Burgess & Holmstrom, 1974; Jerin & Moriarty, 2010) and physical costs (Geist, 1988) on women, but also fitness costs by bypassing female choice in mates and the timing of reproduction (Buss, 2011; see also Perilloux, Duntley, & Buss, 2012 for a discussion of the range of costs). Although scholars have concluded that there is not enough evidence to determine whether men have adaptations to rape (Buss, 2003, 2011, 2014; Symons, 1979), ethnographies and historical records suggest that rape occurs cross-culturally and was recurrent over human evolutionary history (Buss, 2003, 2011; McKibbin & Shackelford, 2011).

Numerous researchers have proposed the existence of anti-rape adaptations. The formation of alliances with men and other women for protection has been argued to represent evolved counterstrategies to rapists' tactics (Smuts, 1992). The "bodyguard hypothesis" proposes that women's preference for mates who are physically formidable and high in social dominance is, in part, an adaptation to prevent rape (Wilson & Mesnick, 1997). As noted, Carrier & Morgan (2014) argue that the bony structures in men's faces are particularly well adapted for fistfights with other men. These bony structures, which include a larger and broader jawbone, thicker cheekbones, and more pronounced bones around the nose and eyes, are present only in men. Women lack any facial bones that approach the thickness and strength of those possessed by men. Research has demonstrated, however, that women exhibit a mate preference for men with more masculine faces, particularly when they are ovulating (Gildersleeve, Haselton, & Fales, 2014). Women's preference for masculinized male faces, particularly at the time that women are most fertile, could function to help women choose to associate with men best able to protect them from rapists. Women's evolved mate preference for masculinized facial features can be thought of as creating, through sexual selection, adaptations in male physiology that enable the men with whom they prefer to associate to better defend their female partners from attacks by other men.

Specialized fears that motivate women to avoid situations ancestrally predictive of an increased likelihood of being raped have been proposed to help preemptively defend against rape. To prevent conception resulting from rape, women may avoid risky activities during ovulation (Bröder & Hohmann, 2003; Chavanne & Gallup, 1998). The psychological pain of rape motivates women to be more vigilant in the future (Thornhill & Palmer, 2000). Women blame themselves for being victimized more than others blame them (Perilloux, Duntley, & Buss, 2014), perhaps creating a sense of personal control to alter behavioral patterns to better avoid future victimization. In addition, women may possess adaptations to minimize the costs of rape after it has occurred. To avoid the reputational damage that can be associated with rape or to avoid losing their romantic partner, women may feel motivated to keep their ordeal a secret. Women may feel a strong urge to bathe themselves after being sexually coerced, washing physical evidence of the forced encounter away so it cannot be detected, especially by their romantic partner. Women may seek revenge against their attacker by marshalling male relatives and allies to attack him, especially if the rapist represents a persistent threat to the women or their female relatives. Spontaneous abortion, premature delivery, and infanticide may also represent female defenses to avoid investing in a rapist's child (for a detailed review, see McKibbin & Shackelford, 2011).

ADAPTATIONS THAT PRODUCE HOMICIDE

Homicide is a strategy capable of solving or contributing to the solution of conflict with other individuals (Buss & Duntley, 1998, 1999, 2003, 2004, in progress; Duntley & Buss, 1998, 1999, 2000, 2001, 2002, 2011). According to homicide adaptation theory, homicide is unique from nonlethal solutions to conflict because it represents an absolute end to the competition between individuals. Living and dying are drastically different outcomes of behavior, large enough to have created selection pressure for the evolution of cognitive algorithms capable of guiding behavior toward either nonlethal or lethal outcomes. Addressing conflict with competitors with strategies that leave them alive allows them to create the same problems in the future that they did in the past. Once dead, a person can no longer damage reputations, steal resources, prevent others from attracting romantic partners, or poach others' mates. It would be astonishing if selection did not operate differently on cognitive algorithms that produce lethal and nonlethal outcomes.

The fundamental and profound difference in the outcomes of nonlethal and lethal behaviors leads to the hypothesis that homicide is the designed output of evolved psychological mechanisms. Inflicting a lethal injury on a rival is the evolved function of homicide adaptations. Killing conspecifics could have helped to solve a variety of ancestral problems (Duntley & Buss, 2008, 2011), including: (a) preventing the exploitation, injury, rape, or killing of self, kin, mates, and coalitional allies by conspecifics in the present and future; (b) reputation management against being perceived as easily exploited, injured, raped, or killed by conspecifics; (c) protecting resources, territory, shelter, and food from competitors; (d) eliminating resource-absorbing or costly individuals who are not genetically related (e.g., stepchildren); and (e) eliminating genetic relatives who interfere with investment in other vehicles better able to translate resource investment into genetic fitness (e.g., deformed infants, the chronically ill or infirm).

The infliction of an unrecoverable injury that slowly kills a victim through infection or other gradual decline in health can be just as effective as causing the victim's instant death, but is more subtle and may motivate less vengeance in the victim's kin and social allies. With the help of time, age, starvation, pathogens, parasites, and poor wound healing, killers could achieve the evolved goal of eliminating a rival while maintaining some plausible deniability about their intentions to kill.

FITNESS COSTS OF BEING KILLED

Conspecific killing was a recurrent feature of human evolutionary history (Chagnon, 1988; Keeley, 1996; Trinkaus & Shipman, 1993). A victim's death has a much larger impact on his or her inclusive fitness than just the loss of the genes housed in the person's body. The inclusive fitness costs of dying at the hands of another human can cascade to the victim's children, spouse, and kin. The specific costs include:

> *Loss of future reproduction.* A victim of homicide cannot reproduce in the future with a current mate or with other possible mates, a cost greater for younger individuals.
>
> *Damage to existing children.* Children of a murdered parent receive fewer resources, are more susceptible to being exploited, and may have more difficulty ascending status hierarchies or negotiating mating relationships. Children of a murdered parent may see their surviving parent's investment diverted to a new mating relationship and the children born from it. Single parents, whose investment is less than what two parents can provide, might abandon their children in favor of better mating prospects in the future. And the children of a murdered parent risk becoming stepchildren, bringing with it physical abuse and homicide rates 40 to 100 times greater than those found for children who reside with two genetic parents (Daly & Wilson, 1988).
>
> *Damage to extended kin group.* Homicide victims cannot protect or invest in kin. A family member's murder can lead their entire kin network to gain the reputation of being vulnerable to exploitation. A homicide victim cannot influence the status trajectories or mating relationships of family members. And the open position left by the victim in a coalition's status hierarchy could create a struggle for power among the surviving family members.

A homicide victim's fitness losses can become rivals' fitness gains. Killers can benefit from the residual reproductive value and parenting value of the surviving mate of their victim, sometimes at the expense of the victim's children with that mate. A killer can ascend into the vacancy in a status hierarchy left by his victim. The children of killers would thrive relative to the children of homicide victims, who would be deprived of the investment, protection, and influence of a genetic parent. Many family members who would have survived if the person was not killed will die before they can reproduce. Many children who would have been born in the family will never be born.

The magnitude of rivals' fitness gains will be heavily dependent on group size and the presence of formidable rivals. In smaller groups and with fewer rivals present, a slight local increase in resources or mates, following a murder, can bring a substantial benefit to the murderer. In larger groups and when more rivals are present, however, the fitness benefits could be diluted because the newly available resources could be harder to control.

AVOIDING CONTEXTS IN WHICH HOMICIDE IS LIKELY

One hypothesized design feature of homicide avoidance mechanisms is sensitivity to high-risk contexts. Cues to the presence of such contexts include:

Who controls the territory. Who controls the territory an individual is occupying is an important cue that was reliably correlated with the ancestral likelihood of being killed by hostile conspecifics. Individuals are more vulnerable to attack when away from their home territory. Being in a rival's territory or even a neutral territory would be a cue to an increased risk of attack. Chagnon (1996) reports that the Yanomamö sometimes lure members of a rival group to their territory to share a large meal, only to ambush them when their guards are down. Individuals should experience more fear of being killed in the presence of cues indicative of being in territory controlled by others.

Characteristics of the surroundings. It is easier for a competitor to hide in the shadows than in the light. Individuals are more likely to be ambushed where there are visual obstacles than in areas that afford unobstructed visual scanning. An individual is more vulnerable to attack when his back is to an open room than against a wall. Individuals should experience more fear of homicidal attack and ideation that their life may be in danger in the presence of such cues to their vulnerability. Kaplan (1992) made similar arguments when he suggested that the process of evaluating the attractiveness of landscapes involves considering places for surveillance, places for hiding, refuges from predators, and possible routes of escape.

Characteristics of the rival. Certain personality and life history characteristics of rivals have been recurrently correlated over our evolutionary history with the likelihood that a rival will kill: high levels of narcissism, an anti-social personality, high impulsivity, low conscientiousness, high levels of hostility, and a history of committing acts of violence or homicide against others. A history of violent behavior is one of the strongest predictors of future violence (Douglas & Webster, 1999). The importance of the reputations of rivals in identifying conspecifics who pose an increased threat of killing cannot be underestimated. Recent research suggests that distinct brain regions process information about the personality traits of others. That information is subsequently combined to create personality models that are used to predict the behavior of others (Hassabis et al., 2014). Evidence from ethnographies provide converging evidence, showing that some men develop reputations as killers or thugs. The people who live in the same communities as these men give them a wide berth, trying to avoid doing anything that might antagonize them (Chagnon, 1983, 1996; Ghiglieri, 1999).

Characteristics of the situation. Specific adaptations have evolved to be sensitive to circumstances ancestrally indicative of an increased probability of being killed. These situations correspond to adaptive problem contexts ancestrally solvable by homicide, which include being a person responsible for injuring, raping, killing, or inflicting other serious costs on a rival, his kin, his mates, or his coalitional allies; damaging a rival's reputation, leading others to perceive him or his genetic relatives as easily exploited, injured, raped, or killed; poaching the resources, mates, territory, shelter, or food that belongs to a rival; absorbing the resources of a nongenetic relative (e.g., stepchildren); and interfering with parents' or kin's investment in viable fitness vehicles (e.g., deformed infants, the chronically ill or infirm).

Perhaps the most effective defense against being killed is to completely avoid situations associated with an increased risk of being a victim of homicide. The experience of fear may be one adaptive mechanism that helps us to avoid such situations. In his book *The Gift of Fear* (1997), Gavin De Becker argues that fear can function as a signal that exists to aid in our survival, protecting us from violent situations. It is adaptive to experience fear, he argues, when the fear is enabling—allowing an individual to effectively address the danger he or she faces. Real fear, according to De Becker, "occurs in the presence of danger and will always easily link to pain or death" (p. 285).

Marks (1987) argued that fear and anxiety can be protective in four primary ways. First, it can lead a person to become immobile, which could conceal an individual from a predator or hostile conspecific, allow for assessment of the situation, and perhaps avoid being attacked. This is a valuable strategy when there is uncertainty about whether one has been spotted or cannot determine the exact location of the threat. Second, fear can motivate an individual to escape or to avoid danger in the environment. Third, a person may adopt a strategy of aggression in self-defense. Finally, an individual can adopt of strategy of submission to appease the source of the hostility, a common tactic among social mammals, including humans (Buss, 2014).

Because homicide has unique fitness consequences, the fear of being killed may be a distinct emotional state accompanied by specific decision rules that function to help individuals defend themselves. Rather than consisting of a single, consistent emotional experience, fear of being killed is proposed to be expressed in a range of discreet states. As a victim defense, a variety of fears may be experienced, which include, for example: mild anxiety about groups of unknown strangers in the distance; terror that motivates curling into a fetal position if an attacker has knocked one down and is kicking one in the head; battle-numbness that allows one to ignore moderate injuries if there is still imminent danger from an attacking horde; and a specific aversion to sharp incoming projectile weapons that likely would cause hemorrhaging or infections.

It is interesting that people in modern environments so willingly expose themselves to experiences that they evolved to fear. More than half of the programs at the top of Nielsen Ratings in a typical week (when the NFL playoffs are not occurring) are homicide dramas or documentaries. Murder mystery novels, monster movies, TV crime series, haunted houses, and Halloween masks all activate victim psychology. Why people, especially teenagers and young adults, voluntarily subject themselves to seemingly aversive stimuli may involve the calibration and practice of victim defenses.

DEFENDING AGAINST A WOULD-BE KILLER

Another protection against homicide is defending against the attacks of others. These strategies can take three primary forms:

1. ***Fleeing the potentially homicidal confrontation with the person.*** An individual who is successful in fleeing from someone who tried to kill him may then attempt to change the situation in ways that will decrease the likelihood of being killed. One such strategy may be to leave the area he shares with the intended killer. A proposed explanation for human migration out of Africa, across Europe and Asia, and into the Americas was to avoid hostile confrontations with conspecifics (Diamond, 1997; Richerson & Boyd, 1998). Fleeing homicidal rivals can be an

effective strategy if the intended victims can move out of their reach, but may be only a temporary solution. If nothing about the context of conflict between the would-be killer and intended victim changes, it is likely that a homicidal person will attempt to kill their intended victim again.

2. ***Manipulating the situation to make killing less beneficial and more costly.*** A person who believes he might be killed may be able to alter aspects of the situation to increase the costs or decrease the benefits of a homicidal strategy, making homicide less attractive. Examples include forging alliances with powerful conspecifics; staying in the vicinity of coalitional allies who may serve as bodyguards; turning members of a group against the person who may intend to kill you; resolving the conflict with the conspecific, such as by some form of payment; helping the rival to salvage or restore his reputation; bargaining or begging for one's life; threatening retaliation by one's kin and coalitional allies; and performing preemptive, perhaps homicidal, attacks against the would-be killer, his kin, or his coalitional allies.

   Some of these strategies may be implemented up to the moment that a homicidal behavior is enacted upon a victim. The implementation of these defensive strategies may not always be enough to derail a homicidal strategy in favor of a nonlethal alternative. If not, the person targeted by a killer would have no recourse but to violently defend against attempts at lethal aggression.
3. ***Defending against homicidal attacks.*** At the point a rival is engaging in behaviors capable of killing, it may be too late to flee or derail the homicidal strategy. In such a face-to-face confrontation with a killer, the options are to mount an effective defense or to die. There are two strategies of self-defense: call for help or physically incapacitate the would-be killer to create an opportunity to escape. Screams for help may be uniquely identifiable from other calls for assistance. Selection could have shaped victims' screams for rescue to be uniquely identifiable, honest signals of acute, life-or-death distress, strongly compelling others to provide assistance when fitness gains flowed to rescuers, such as the victim's kin or coalitional allies who might benefit from reciprocal exchange with the intended victim or the victim's kin. Being exposed to the frequent screaming of their children at play may help parents and other adult kin to recognize when the source of cries for help in the distance represents an inclusive fitness threat that demands immediate action. "Death screams" or screams in terror (Buss, personal communication) may represent alarms that function as a call for help or to warn kin and mates to the presence of a dangerous killer as the victim dies. The screams may solicit aid and protection from friends and family, or else warn them away. The screams may also cause the would-be killer to flee before the kill is successful. Death screams may be construed as costly, hard-to-fake, credible calls for help. References to "blood-curdling screams" and "screaming bloody murder" may refer to such uniquely identifiable screams for help by people battling off a rival's attempts to kill them.

Physically incapacitating a killer is another strategy a victim can use in self-defense. Victims can fight back themselves or enlist canine allies. Some research suggests that one of the functions of our ancestors' domestication of dogs was to act as watchdogs and bodyguards against hostile conspecifics (Clutton-Brock, 1999; Shipman, 2010). Invariably, an incapacitation strategy involves physically attacking the would-be killer. At a minimum, the intended victim must incapacitate the attacker enough to flee or buy enough time for help to arrive. Sometimes, the most practical strategy may be to kill the killer in self-defense. Killing in self-defense is likely to be influenced by contextual features such as: a lack of kin or allies in close proximity to help; the failure of nonlethal strategies to incapacitate the attacker or otherwise derail the progression of his lethal behavior; and a lack of other options.

One of the key differences between a would-be killer and victim in hostile confrontations is that the killer is more often prepared to carry out a homicidal strategy than the victim is to defend against being killed. The killer can select the time and place when it is best to kill. Selection would have favored adaptive design that led killers to catch victims alone and by surprise, reducing the possible costs of killing (e.g., being injured or killed by a victim or the victim's kin). Because the genetic relatives of a homicide victim suffer fitness costs, adaptations to defend against being killed should be also found in victims' kin.

STANCHING THE COSTS OF THE HOMICIDE OF GENETIC RELATIVES

At least two forces may have selected for adaptations in kin that function to stanch the negative consequences of a family member being killed. First, damage to a homicide victim's family reputation may be repaired by inflicting reciprocal costs on the killer. A family that is capable of striking back against the killer may be able to demonstrate that it is no longer exploitable. Second, the killer may be a persistent threat if he were to continue to live. Avenging the death of a family member by killing the killer may eliminate a source of recurrent fitness costs.

Homicide defense adaptations are costly for killers. The evolution of adaptations to defend against being killed would have created selection pressures for the evolution of refined adaptations for homicide that were capable of circumventing the evolved defenses. The presence of refined homicide adaptations, in turn, would have selected for further refinements to homicide defenses, and so on, setting up an antagonistic coevolutionary arms race between adaptations to kill and adaptations to defend against being killed.

EVIDENCE OF ADAPTATIONS FOR HOMICIDE AND HOMICIDE DEFENSES

Several sources of evidence suggest that mechanisms dedicated to conspecific killing could have evolved. The first source of evidence is comparative. In some insect and arachnid species, where mate-killing and cannibalism is known to increase the number or viability of offspring (including mantids, black widow spiders, and scorpions), males cautiously approach females to mate and then retreat quickly. During copulation, males of sexually cannibalistic species use diverse strategies to decrease their chances of being cannibalized (Elgar & Crespi, 1992): Male scorpions sometimes sting the female after deposition of the spermatophore (Polis & Farley, 1979); male black widows (Gould, 1984) and crab spiders (Bristowe, 1958) often restrain females in silk prior to copulation. Conspecific killing, as well as mechanisms to prevent getting killed, appear to be common among insects and arachnids.

Among the roughly 5,400 species of mammals, many also have well-documented patterns of conspecific killing. Male tigers, lions, wolves, hyenas, cougars, and cheetahs have been observed to kill the infants of rival males (Ghiglieri, 1999), hastening the estrus of the mothers, which often mate with the killers. Among primate species, conspecific killings have been well documented among langur monkeys (Hrdy, 1977), chacma baboons (Busse & Hamilton, 1981), red howler monkeys (Crockett & Sekulic, 1984), savanna baboons (Collins, Busse, & Goodall, 1984), mountain gorillas (Fossey, 1984), chimpanzees (Bygott, 1972; Suzuki, 1971), blue monkeys (Butynski, 1982), and others (Hausfater & Hrdy, 1984). The killing of conspecific rival males has also been well-documented among chimpanzees (Wilson et al., 2014) and mountain gorillas (Fossey, 1984). If conspecific killing was favored by selection in other animals, it could have been favored in humans as well.

Homicide has the potential to occur wherever there are humans interacting with other humans. This is as true of mother and child as it is of enemy nations. It is even true of the relationship between a pregnant mother and her developing fetus. For a woman, the fetus she carries may not represent her last opportunity to reproduce. Women were selected to invest more in those offspring who will yield the greater reproductive benefit, even in utero. If a fetus is not viable, it would make more sense, in terms of fitness, for a pregnant woman to forgo her investment in its development in favor of investing in a subsequent pregnancy. Most fertilized eggs do not result in a full-term pregnancy. Up to 78% fail to implant or are spontaneously aborted (Nesse & Williams, 1994). Most often, these outcomes occur because the mother detects chromosomal or other developmental abnormalities in the fetus. The mother's ability to detect such abnormalities is the result of adaptations that function to prevent the mother from investing in offspring that will likely die young. Most miscarriages occur within the first 12 weeks after conception (Haig, 1993), at a point when the mother has not yet invested heavily in a costly pregnancy and a spontaneously aborted fetus is less likely to lead to infection (Saraiya et al., 1999). The fetus, however, is not passive in its mother's evolved reproductive strategy. The fetus has only one chance to live. The production and release of human chorionic gonadotropin (hCG) by the fetus into the mother's bloodstream, which is normally an honest signal of fetal viability, may be a fetal adaptation against being spontaneously aborted. This hormone prevents the mother from menstruating, allowing the fetus to remain implanted. Maternal physiology reacts to the production of hCG as a sign that the developing fetus is viable (Haig, 1993). After a child is born, other humans do not cease to be dangerous. Ample evidence can be found by examining child-killing by parents and parent-substitutes.

A newborn infant has few options for defending itself from homicidal attacks perpetrated by adults. To defend against maternal infanticide, a newborn's best strategy may be to display cues that it is a vehicle worthy of investment. Immediately after birth, an infant should display cues to its health and vigor, cues capable of satisfying maternal adaptations that evolved to judge the probability of fitness payoffs for investing in the infant (Soltis, 2004). Newborns who nurse in the first hour after birth stimulate a surge in maternal oxytocin levels, strengthening the bond between mother and newborn. Nursing mothers' priorities become shifted. They become less motivated to self-groom for the purposes of attracting a mate and more motivated to groom their infants (Insel, 1992). By contrast, new mothers who do not nurse are more likely to suffer from postpartum depression (Papinczak & Turner, 2000; Taveras et al., 2003), a condition associated with higher rates of maternal infanticide (Hagen, 1999; Knopps, 1993; Spinelli, 2004) and maternal thoughts of harming their babies (Jennings, Ross, Popper, & Elmore, 1999; Kendall-Tackett, 1994). More active newborns are less likely to die (Chong & Karlberg, 2004; Morales & Vazquez, 1994), and would be a wiser object of maternal investment than newborns that are less active. Selection may have favored early nursing, the production of loud cries, and robust movements in newborns as defenses against maternal infanticide.

As they develop, infants are increasingly able to move about on their own. As a result, they are increasingly likely to encounter dangers while outside the range of their caregivers' protection. Infants who possess some ability to recognize potential dangers in the environment would have a significant advantage over infants with no such ability. Selection would have favored fears of specific dangers, to steer infants away from threats to their survival. The developmental timing of the emergence of fears provides evidence that selection played a part in shaping them. For example, the fear of heights emerges when children begin to crawl, which corresponds with infants' greater risk of falling. Fear of strangers emerges at about the same time (Scarr & Salapatek, 1970), corresponding with a greater risk of encountering hostile conspecifics. Stranger anxiety prevents children from approaching those they do not know well and motivates them to seek parental protection. It has been documented in countries and cultures from Guatemala and Zambia, to the !Kung and the Hopi Indians (Smith, 1979). Infant deaths at the hands of unrelated conspecifics have been documented among nonhuman primates (Ghiglieri, 1999, Hrdy, 1977; Wrangham & Peterson, 1996) and in humans (Daly & Wilson, 1988; Hrdy, 1999). Human children are more fearful of men than of women strangers, which corresponds to the greater threat posed by unrelated males over evolutionary history (Heerwagen & Orians, 2002). If a fear of strangers prevented even a tiny fraction of children from being killed in the evolutionary past, stranger anxiety would have been favored by selection.

Strangers are not the only threat to the lives of children. With a stepparent in the home, children are between 40 and 100 times more likely to be killed than children raised by two genetic parents (Daly & Wilson, 1988). Stepfamilies were likely a recurrent feature of ancestral environments. Without modern medical treatments, disease killed many adults. Fathers sometimes died in battles or on hunts. Mothers sometimes died during childbirth. After their partner's death, it probably was common for a surviving parent to find a new mate. New long-term relationships bring benefits to single parents, but also carry the potential for great costs to their children. The increased risk of their existing children being killed may affect single parents' mate preferences or the decision of whether to seek a new mate at all. Single parents' preferences for new partners could reflect, in part, evolved defenses against the homicide of their existing children (Buss, 2005).

Stepchildren also may possess adaptations to help defend against potentially homicidal stepparents, including the ability to predict a stepparent's likelihood of being homicidal and inflicting other costs. Children's evolved intuitions about potential stepparents may lead them to influence their custodial parent's mate choice, decreasing the children's risk of being killed. Genetic parents may have done well to pay attention to their children's preferences: Bringing a preexisting child into a new long-term relationship is a predictor of intimate partner homicide as well (Campbell, Glass, Sharps, Laughon, & Bloom, 2007).

Selection also may have favored adaptations that lead stepchildren to minimize their costliness to their stepparent by keeping a low profile and demanding few resources. Stepchildren also should recognize opportunities to make themselves valuable to their stepparent, such as contributing to the care of half siblings that result from the relationship between their genetic parent and stepparent. A possible strategy for stepchildren who feel their life is in danger may be to sabotage their genetic parent's long-term relationship by inflicting costs on the stepparent or inflicting costs on themselves, which could drive the stepparent away or redirect their genetic parent's investment away from a new mateship to ensure the offspring's survival. Engaging in delinquent behaviors, self-mutilation, disordered eating, drug use, and suicide attempts may be strategies children use to redirect their genetic parent's investment. Living in a stepfamily compared to living with two genetic parents more than doubles a child's risk of engaging in juvenile delinquent behavior (Coughlin & Vuchinich, 1996; Zill, 1994).

The presence of a stepparent is a good example of a recurrent context of increased risk of homicide that may have selected for antihomicide defenses in stepchildren and their kin. These adaptations become activated in stepchildren, but remain dormant in children who reside with genetic parents. Specialized adaptations to defend against homicide are proposed to exist for all contextual domains where there was a recurrent risk of being killed. Many situations, however, do not provide complete information about the probability that a person may fall victim to homicide. Because being killed is so costly, selection may have fashioned adaptively patterned biases that lead people to systematically overestimate the likelihood that they will be killed in conditions of uncertainty.

MANAGING ERRORS TO AVOID HOMICIDE

Because many inferences about whether one will be targeted by a killer are clouded by uncertainty, contexts of homicide can be considered compatible with the logic of error management theory (Haselton, 2003; Haselton & Buss, 2000). In situations involving uncertainty, making an erroneous inference about the intentions of others can carry high fitness costs. In contexts ancestrally predictive of homicide, it would be better, on average, to infer that rivals might want to kill you when they really do not, than to infer that rivals do not want to kill you when they actually do. In this way, people would avoid making the more costly of the two errors. A hypothesized design feature of the psychology of homicide avoidance is a cognitive bias that leads people to overestimate homicidal intent in the presence of cues to adaptive problems historically solvable by homicide.

The amount of uncertainty surrounding a potentially high-cost situation is also likely to have an effect. In conditions of uncertainty about the identity of another person, in unclear social situations, and in the absence of information to the contrary, the safer error would be to overestimate a conspecific's hostile intentions. In fact, the safest error may be to assume that the other person intended to kill you. Selection would have favored decision rules that are quickly sensitive to potentially costly meetings with conspecifics. When facing uncertainty from environmental cues, selection should mold psychological design to assume that the worst possible fitness event is going to occur, so its heavy costs can be more effectively avoided. The strategies people employ to defend against homicide (e.g., avoiding the context, fleeing, or killing one's attacker) would simultaneously defend against a number of nonlethal, cost-inflicting strategies. As a result, strategies capable of defending against homicide also can help to protect an individual from a range of other dangerous situations.

In summary, uncertainty about the nature of situations, including uncertainty about the identity or history of an individual, provided selection pressures that influenced the design of human error management psychology. Adaptations to minimize costly errors evolved in the form of cognitive biases that overestimate the likelihood that another individual intends to inflict costs proportional to the uncertainty surrounding the individual and the context. The bias toward inferring that another individual intends to inflict costs should increase as uncertainty about the individual and the context increases. This is not to say that such an error management bias will be applied equally to different individuals. The bias should be proportional to the ancestral threat that different individuals posed. It should be especially strong for those who posed the greatest threat, such as young adult males, and less strong or absent for others (e.g., infants, young children, the elderly).

There is evidence that people's perceptions are biased in the direction predicted by error management theory (Haselton & Buss, 2001). Experiments using schematic facial stimuli demonstrate that different facial expressions are not processed the same way (Öhman, Lundqvist, & Esteves, 2001). Participants identified threatening faces more quickly than happy faces from among distracters. Additionally, faces with V-shaped eyebrows of a schematic angry facial display were identified more quickly and accurately than were faces with inverted V-shaped eyebrows (friendly faces), among distracters. These results are consistent with a perceptual bias predicted by error management theory that leads individuals to be especially sensitive to the presence of potentially hostile conspecifics. Natural selection would have favored a greater sensitivity to angry faces than to friendly faces, as those with hostile intentions would have posed an adaptive problem often requiring immediate action to avoid incurring potentially heavy costs, particularly from out-group members (Ackermann et al., 2006).

Despite sensitivity to dangerous humans, many people still enter into situations that could get them killed. People have extramarital affairs, derogate competitors, and poach the material resources and mates of others. What makes them think that they can get away with their lives?

SECRECY AS A DEFENSE AGAINST HOMICIDE

The answer may lie in the use of secrecy as a defense against being killed. People only become homicidal if they are aware that they are being wronged. Their ignorance can provide those who sneak behind their backs some measure of protection from being killed. A sexual relationship behind the back of one's partner, for example, could benefit men in the form of additional offspring and benefit women in the form of access to superior or different genes, and to additional resources from an affair partner (Greiling & Buss, 2000). Selection should have favored the use of secrecy to defend against the costs of an infidelity being discovered, which includes being killed by a jealous mate or rival. In the case of sexual infidelity, there is a clear pattern in the risks of being killed. Men are more likely than women to kill their partner for a sexual infidelity (Serran & Firestone, 2004; Wilson & Daly, 1992). As a result, selection pressures may have been stronger on women than on men to adopt clandestine tactics to conduct their affairs. This may help to explain why men indicate a greater amount of uncertainty about whether their romantic partner is having an affair than women do (Buss, 2000): Men encounter fewer cues to their partner's infidelity. Clandestine strategies, however, are not always successful. Sometimes men discover their partner's infidelity. As homicide statistics demonstrate (Buss, 2005; Daly & Wilson, 1988;

Ghiglieri, 1999), perhaps the most dangerous human a woman will encounter in her lifetime is her romantic partner.

KILLING IN SELF-DEFENSE: PREEMPTIVE HOMICIDE TO PREVENT BEING KILLED

In a review of 223 appellate opinions of the cases of battered women who killed their male partners in Pennsylvania, 75% of the homicides occurred while the woman was being assaulted by her romantic partner (Maguigan, 1991). In a study of mate homicides in North Carolina between 1991 and 1993, violence perpetrated by men preceded 75% of cases in which women killed their romantic partners. In contrast, there is no evidence that violence perpetrated by women preceded any of the homicides committed by men (Smith, Moracco, & Butts, 1998). It can be argued that the majority of women who kill their romantic partners do so in self-defense or to protect their children or other kin (Serran & Firestone, 2004). Female-perpetrated mate homicide may be an example of the ultimate anti-homicide defense: killing an attacker before the attacker kills you.

The ancestral costs of being murdered were substantial enough to select for adaptations designed to eliminate the threat of homicidal conspecifics by killing them. Killing someone to prevent them from killing you would have had distinct evolutionary advantages over strategies of nonlethal violence. By killing a homicidal conspecific, you eliminate any future threat the person may pose. Whereas an injured rival can recuperate and attempt to kill you again, a dead rival cannot. By killing the person who would kill you, one also demonstrates a willingness and ability to end a life, sending a powerful signal to others that attempts on your life will be met with the ultimate cost.

Most legal systems do not treat homicides committed in self-defense the same as other homicides. The law considers killing in self-defense to be a form of justifiable homicide if the killer "reasonably believes that killing is a necessary response to a physical attack that is likely to cause serious injury or death" (Costanzo, 2004, p. 83). In the evolutionary history of adaptations to produce preemptive homicides, however, the management of errors in conditions of uncertainty would have played a pivotal role in determining what a person reasonably believes. Individuals in the past who erred on the side of preemptively killing those perceived to be a credible threat to their lives or the lives of their kin would have had an advantage over others who erred in the opposite direction. The consequence of this overestimation is the preemptive killing of some individuals who would not have become killers. In the calculus of selection, however, it is better to be safe and alive than dead.

HOMICIDE AS A BY-PRODUCT OF OTHER EVOLVED MECHANISMS

Adaptations for homicide need not be involved in the production of all homicidal behavior. When not agnostic about whether some adaptations function to produce homicide, Daly and Wilson (1988, 1990; see also Daly, Chapter 26, this *Handbook*, Volume 2) have argued that homicides may be the by-products of psychological mechanisms favored by selection for their nonlethal outcomes. For example, adaptations that produce nonlethal spousal violence to prevent the defection of a mate could overreact and mistakenly generate levels of violent behavior that result in a spousal homicide. Following this logic, the death of a child from neglect could be the accidental by-product of a failure in the activation or engagement of adaptations responsible for the production of parental solicitude.

Homicide adaptation theory does not preclude the possibility that some homicides are by-products of the activation of other mechanisms or simply mistakes (Duntley & Buss, 2011). However, there is disagreement about whether evidence supports the theory that the majority of homicides are the designed output of psychological adaptations (Buss, 2005; Duntley & Buss, 2008). One source of evidence is the conscious thoughts that people report having about killing others (e.g., Kenrick & Sheets, 1993). Daly (Chapter 26, this *Handbook*, Volume 2) dismisses evidence from studies of homicidal fantasies, homicidal intent, and willingness to kill because people experience fantasies of video game playing more often than fantasies of killing and formulate plans to do many things that were not targets of selection, such as watching TV.

First, homicide adaptation theory does not purport to be a general explanation for all conscious thoughts or intentions; it is *not* intended to provide an explanation for the frequency of fantasies about videogame playing or about people's intentions to do things that were not targets of selection. (Although, it is interesting that first person shooter video games were the top seller in 7 of the 10 past years (TheCHIVE, 2014), and that 6 of the 10 most popular TV shows involve murder mysteries (TV Guide, 2014).) Instead, Duntley and Buss (2011) propose that some design features of the psychology that produces lethal violence can be explored through examining people's thoughts of killing, a strategy no different than using sexual fantasies to better understand psychological adaptations that influence sexual behavior (Ellis & Symons, 1990). Second, the relative frequency or duration of thoughts about any topic would not seem to provide conclusive evidence about whether those thoughts are the functional outputs of adaptations. People think about sex less frequently than food, sleep, personal hygiene, social contact, time off, coffee, watching TV, checking email, and using other social media (Hofmann, Vohs, & Baumeister, 2012). But it would be difficult to argue that thoughts of sex are not products of adaptations because they occur less frequently than thoughts about other topics, some of which do not have obvious adaptive significance.

There is also disagreement about what source of evidence of the fitness impact of being a killer should be used to evaluate homicide adaptation theory. Daly (Chapter 26, this *Handbook*, Volume 2) argues that homicide does not promote individual fitness in the human groups that he has observed. However, it is difficult to draw conclusions about the fitness outcomes of homicide based on observations of a limited number of individuals for a few generations. Selection operates on genetic variability in populations over thousands and thousands of generations. Over deep time, a trait providing as little as a 1% average fitness advantage can be favored by selection (Nilsson & Pelger, 1994). Rather than relying on a single source of evidence to evaluate the fitness outcomes of killing conspecifics, additional sources should be considered (Duntley & Buss, 2008, 2011).

For example, evidence that tracks the historical transmission of Y-chromosome variants suggests that homicide was fitness promoting. One study found that as many as 0.5% of the world's total population could be descendants of Genghis Khan. Roughly 16 million men living in the former Mongol empire are argued to carry Khan's Y-chromosome (Zerjal et al., 2003). Khan's reproductive dominance was the result of his crushing military might, which resulted in the killings of thousands of his same-sex rivals, putting the reproductive value of the women of those he vanquished under his control.

Although there likely is no single source of evidence that clearly favors Homicide Adaptation Theory over the by-product hypothesis of homicide, the total weight of growing evidence supports the view that the function of some of our psychological adaptations is to produce behavior that is lethal to conspecifics (Duntley & Buss, 2008, 2011). Whether homicides are the functional output of adaptations or not, lethal aggression was a powerful selective force over human evolutionary history.

CONCLUSIONS

The evolution of adaptations to inflict costs created selection pressures for the coevolution of adaptations in victims to help them avoid or prevent incurring the costs. These coevolved victim adaptations, in turn, created selection pressures for the evolution of refined and new adaptations for cost-infliction, setting up antagonistic, coevolutionary arms races between strategies to inflict costs and strategies to defend against them. Coevolutionary arms races can be extremely powerful. They can exert selection pressures on numerous physiological and psychological systems simultaneously, leading to rapid evolutionary change and great complexity of adaptive design. Adaptations for homicide and adaptations to defend against homicide are argued to be results of just such an antagonistic coevolutionary arms race. The costs of being killed are among the greatest an individual can incur at the hands of a conspecific. These tremendous costs created unique and powerful selection pressures for the evolution of adaptations to defend against being killed.

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PART III

MATING

Challenges of Mating

DAVID M. BUSS

THE STUDY OF human mating strategies must surely count as one of the first empirical success stories in evolutionary psychology. The conceptual foundations of human mating can be traced to Darwin's monumentally important theory of sexual selection, which identified intrasexual competition and preferential mate choice as key processes in the evolution of mating adaptations (Darwin, 1871). Although largely ignored by biologists for many decades, sexual selection theory was given new life by Robert Trivers a century later with his seminal 1972 paper, "Parental Investment and Sexual Selection," in which he identified relative parental investment as a driving force behind the two components of the process of sexual selection.

The next critical watershed in the study of human mating strategies was the publication in 1979 of Donald Symons's trenchant classic, *The Evolution of Human Sexuality*. Many of the foundations of human mating strategies described in this section owe a great debt to Donald Symons. He was the first to articulate the theoretical foundations of a fully adaptationist view of male and female mating minds, arguing that they should be no less dimorphic than male and female bodies. Symons was the first social scientist to take the writings of George C. Williams (1966) to heart, applying rigorous standards for invoking the onerous concept adaptation. Indeed, although evolutionary psychologists are often accused of being "hyperadaptationist," Symons argued forcefully that certain aspects of human sexuality failed to meet the criteria needed to invoke adaptation, and were therefore likely to be by-products. Symons's 1979 book is regarded, by some, as the first major treatise on evolutionary psychology proper, highlighting the centrality of psychological mechanisms as adaptations, and using human sexuality as a detailed vehicle for this more general argument. Hence, it is a great intellectual treat to have an original essay by Symons on adaptationism and human mating psychology, with an illustration using the fascinating phenomenon of "mating anxiety."

David Schmitt (Chapter 11) furnishes a broad and insightful overview of the foundations of human mating strategies. He considers the large menu of evolved human mating strategies, and outlines the evolutionary processes of sexual selection by which they evolved. He then proceeds to review the ways in which human mating strategies are highly sex differentiated and exquisitely sensitive to context, in particular the temporal dimension of short-term and long-term mating, as proposed by Sexual Strategies Theory (Buss & Schmitt, 1993). He then discusses individual differences in mating strategies within sex. Finally, based on his own massive cross-cultural project and the prior work of others, he discusses the ways in which culture and ecology predictably affect the activation of human mating strategies from the universal menu.

Lawrence Sugiyama (Chapter 12) provides a comprehensive, up-to-date, and penetrating update of his original chapter on the evolutionary psychology of attractiveness. Conceptually, he locates the study of attractiveness within a broader framework of relationship value, including mate value, coalition value, and kin value. He provides the most compelling arguments to date for why attractiveness is important in all social relationships, not merely mating relationships. Some elements, such as cues to health, are important components of social value across relationship types. Others are specific to mate value, and some of these differ for males and females. Sugiyama summarizes the voluminous empirical evidence on specific attributes that contribute to our standards of attractiveness, including skin condition, hair, symmetry, waist-to-hip ratio, and many others.

David Puts (Chapter 13) provides an entirely new chapter on a key topic that fills an important gap in the first *Handbook*: contest competition. In logical fashion, Puts reviews the empirical evidence for *special design* in humans for contest competition. This includes the design of the human body (e.g., size, strength, nature of muscle fibers, and visual and acoustic signals) and the human mind (e.g., behavioral and psychological) that all point to a deep evolutionary history of human contest competition, both dyadic and coalitional. This chapter fills a critical gap in sexual selection theory applied to humans, which has historically focused primarily on the preferential mate choice component. Both components of sexual selection are clearly important.

Steven Gangestad, Randy Thornhill, and Christine Garver-Apgar (Chapter 14) provide a chapter on adaptations to ovulation—a long ignored, but now burgeoning, area of theoretical and empirical analysis. They place the study of adaptations to ovulation within the broader theoretical context of sexually antagonistic coevolution. Gangestad and his coauthors then discuss the theories and empirical evidence for the evolution of relatively concealed ovulation and extended female sexual receptivity across the menstrual cycle. This establishes the groundwork for conflicts of interest, the evolution of female infidelity, and cyclic changes in female mate preferences and sexual interests. This chapter, highlighting the long ignored importance of the female ovulation cycle, heralds a sea of change in the way scientists think about the evolution of human mating strategies. Simultaneously, it offers an example *par excellence* of the heuristic value of evolutionary hypotheses, guiding researchers to discover phenomena that otherwise would have remained entirely unexamined without an evolutionary psychological framework. Finally, it offers a serious challenge to mainstream nonevolutionary psychologists, whose theories currently cannot explain, even in principle, why males and females both would show such well-designed adaptations to ovulation.

Todd Shackelford, Aaron Goetz, Craig LaMunyan, Michael Pham, and Nicholas Pound (Chapter 15), discuss the evolutionary psychology of sperm competition, a form of postcopulatory sexual selection. Starting with a brief review of the nonhuman literature on sperm competition, they assemble compelling evidence that sperm competition has been a recurrent phenomenon for humans. They discuss physiological, anatomical, and psychological evidence for sperm competition adaptations in men. Then they turn to hypothesized sperm competition adaptations in women, including precopulatory female choice and the timing of the female orgasm. They conclude by suggesting that sperm competition has been an important, and relatively neglected, arena for sexually selected adaptations in humans. This excellent chapter highlights the heuristic value of evolutionary thinking in discovering phenomena entirely missed by psychological theories that ignore evolutionary processes.

A new, exciting chapter by Debra Lieberman (Chapter 16) focuses on a retrospectively obvious, but strangely neglected domain—that of adaptations for inbreeding avoidance. She highlights two key selective forces leading to these adaptations—avoiding disease-causing organisms and preventing defects through making deleterious recessive genes homozygous. She reviews arguments and evidence that inbreeding avoidance adaptations are not invariant, but rather are sensitive to fertility status, mate value, and opportunity costs. Lieberman provides novel insights into the information processing architecture of inbreeding avoidance adaptations and explores the fascinating issue of why third parties should object to inbreeding among others.

Mark Huppin and Neil Malamuth (Chapter 17) provide an excellent chapter on another region of conflict between the sexes: sexual coercion by men. They furnish a judicious analysis of competing hypotheses about rape—whether it is caused by adaptations specifically designed for forced sex, or instead is a by-product of more general adaptations to use force to achieve a variety of ends (e.g., stealing resources). They then focus on one potential candidate design feature of a rape adaptation—men's sexual arousal to forcing women into unwanted sex. In particular, they discuss individual differences among men in sexual arousal to force, and attempt to identify the variables that lead some men, and not others, to adopt force in the context of sex. Strong conclusions about the conceptual status of rape are not possible at this point, but these authors provide a nuanced description of the possible psychological mechanisms involved and an up-to-date description of the relevant empirical evidence.

Lorne Campbell and Tim Loving (Chapter 18) conclude the mating section with a stimulating chapter on love, commitment, and mate retention. They highlight the different adaptive benefits men and women would accrue from forming long-term pair bonds, and delve into the underlying motivational and emotional mechanisms underlying such relationships. They nicely interweave theory and research emanating from mainstream (not explicitly evolutionary) researchers with more functional analyses of long-term mating. Whereas they propose that an underlying psychological system captured by "love" motivates relationship formation, they suggest that anger and upset are motivational mechanisms designed to monitor signals of "strategic interference" with the relationship. The Campbell and Loving chapter nicely illuminates the complexity of the evolutionary psychology of long-term mating, relationships formed and maintained by emotions ranging from love to rage.

Although these chapters take stock of the current status of the science of mating, it is worthwhile to step back and see how far the field has come. In the mid-1980s, the field of mating was barely visible on the scientific map. Social psychologists had discovered a few things about attraction, but theories of mating were woefully simplistic. Most invoked single variables responsible for the selection of mates, such as similarity, proximity, or equity. Most theorists implicitly assumed that all mating was exclusively for the long term. Short-term mating was largely ignored. Little was known about the processes of mate selection or mate attraction. Concepts such as mate value, mate retention, sexual conflict, adaptations to ovulation, sexually antagonistic coevolution, contest competition, mate poaching, and many others were entirely absent.

Beginning in the mid- to late 1980s, the first raft of empirical studies on human mating appeared. In the 1990s, work on the evolutionary psychology of human mating mushroomed to become the most studied domain of evolutionary psychology. Although much scientific evidence has now cumulated supporting many hypothesized human mating adaptations, the area continues to yield new discoveries. Because mating is so close to the reproductive engine of evolution, it follows that selection has fashioned a rich array of psychological adaptations to deal with the complex and recurrent adaptive problems that mating poses. The chapters in this section take stock of what we now know about human mating and point to fertile fields of mating adaptations yet to be discovered.

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Adaptationism and Human Mating Psychology

DONALD SYMONS

An orchid, *Trichoceros antennifer*, that I tend on my back porch is gravid with lessons for students of human mating psychology. When a naïve house guest first encounters a *T. antennifer*, usually there is a brief moment of confusion followed by a burst of delighted laughter, as the guest realizes what he or she is seeing. While most orchids attract pollinators by offering them a food reward, *T. antennifer* is pollinated by the males of a certain type of Ecuadorian fly as they attempt to copulate with the orchid's flower. The males do this because the *T. antennifer* is an astonishingly realistic mimic of a female fly. (And if the flower is realistic to the *human* eye, how much more realistic is it likely to be to the eye of the male fly that it was designed by natural selection to bamboozle?)

The first lesson that I draw from this orchid's sex life is that we really should *not* be astonished by the complexity and precision of its flower's mimicry; or, rather, we should not be *more* astonished than we are by the complexity and precision of biological adaptations in general. What makes *T. antennifer*'s mimicry seem so uncannily superb is that it is one of the rare cases in which we have immediately available in our mind's eye an image of optimal design (in this case a fly), and thus we can instantly and intuitively compare the actual adaptation (the orchid's flower) to this standard. For the vast majority of biological adaptations, however, we do *not* have an image of optimal design in our mind's eye and thus cannot quickly or intuitively assess how closely most adaptations approximate optimality.

Human psychological mating adaptations, though buried deep between our ears rather than worn on our sleeves, were designed by the same evolutionary processes as was *T. antennifer*'s flower, and there is no reason to expect these human adaptations to be less exquisitely adapted for their purposes than *T. antennifer*'s flower is for its purpose. This adaptationist view of life informs the scientific imagination of Darwinian students of human mating psychology. The result—as represented in the following chapters—is a body of research that very likely would never have been conceived or conducted absent an explicit, conscious Darwinism. Researchers innocent of Darwinism can palaver about learning, culture, gene-environment interaction, levels of analysis, and how complicated everything is until the cows come home, but they're unlikely to ask such a simple research question as the following: Do our brains contain species typical devices whose functions are to (unconsciously) detect deviations from bilateral symmetry in the faces we observe and to cause us to prefer individuals with more symmetrical faces as mates (all else equal)? The 20th-century histories of psychology and the social sciences do not encourage the belief that such a question ever would have been asked had evolutionary psychology not come along.

A nutshell summary of modern Darwinism is this: An organism is an integrated collection of problem solving devices—that is, adaptations—that were shaped by natural selection over evolutionary time to promote, in some specific way, the survival of the genes that directed their construction. The specific way that an adaptation was designed to promote gene survival is that adaptation's *function* (or goal, or purpose). The function of the heart is to pump blood, the function of pancreatic beta cells is to secrete insulin, and so forth. Unlike nonliving matter, living matter is not just complexly organized, it is *functionally* organized. The specific aspects of the environment to which an adaptation is adapted, and upon which its normal functioning and development depend, are sometimes called its "environment of evolutionary adaptedness," or EEA.

The second lesson that I draw from *T. antennifer*'s sex life is that it is logically impossible to describe an adaptation without (at least implicitly) describing the adaptation's EEA. Without the EEA there is no science of adaptation. Any scientifically useful description of *T. antennifer*'s flower will necessarily include a description of the morphology of certain female flies and the mating psychology of male flies found in *T. antennifer*'s natural habitat, the high-altitude cloud forests of Ecuador. Moreover, my brief description of *T. antennifer*'s flower would be intelligible only to those readers who possessed a basic understanding of the nature of flowers and their evolved relationships with environmental vectors, such as insects.

The EEAs of the vast majority of human adaptations still exist today and usually are too obvious to merit explicit mention. For example, a neurophysiologist describing the function of a certain component of the human visual system probably will simply assume that her colleagues know (a) a great deal about the nature of electromagnetic radiation, and (b) that the (natural) light falling on human retinas today is essentially identical to the light that fell on our ancestors' retinas during the evolution of our visual system. But human environments, especially those of modern industrialized societies, have changed in many ways in the brief period since the origin of agriculture 10,000 years ago, and some of these changes potentially affect the functioning of human mating adaptations. Darwinian students of human mating psychology thus have another advantage over other researchers: The Darwinian is alert to potentially significant differences between current and ancient environments, and this *EEA mindedness* can inform hypothesis formation. In some cases, it can even lead the Darwinian to posit the existence of adaptation where others perceive pathology or folly.

Here is an example of the sort of thing I have in mind. A striking feature of human courtship—in its broadest sense—is the powerful effect that fear of rejection seems to have on behavior. Sexual/romantic rejection hurts; the memory of being rejected hurts; the thought of being rejected hurts; hence, it is not surprising that the possibility of being rejected affects most people's mating behavior. Yet on the face of it, fear of rejection seems to be astonishingly dysfunctional. The potential benefits of propositioning an attractive member of the other sex, which include everything from a sexual fling to a lifetime mateship, would appear to vastly outweigh the potential costs, which seem to consist mainly of a small amount of wasted time.

The potent effect that fear of rejection has on human courtship should inspire students of human mating psychology to consider whether this fear might have been adaptive during the vast majority of human evolution, even if it is not adaptive in many current environments. In other words, sexual/romantic rejection might have entailed real and significant costs in the human evolutionary past that it does not usually entail today. I propose the following hypothesis. During most of human evolutionary history our ancestors lived in relatively small face-to-face groups wherein sexual/romantic rejections were very likely to become common knowledge. When Ann the gatherer rejected Andy the hunter's proposition, everyone in their community probably found out about it before long (assuming that our ancestors were no less interested in other people's sex lives, and no less prone to gossip, than we are). The information that Ann had rejected Andy could diminish his perceived mate value in the eyes of others, including other potential mates (Ann may have rejected Andy because she had acquired mate-value-relevant information about him that others were not privy to). On a modern university campus, with thousands of students and enormous scope for anonymity, Bob's anxiety at the prospect of hitting on Bobbi is, perhaps, irrational in the sense that he has little to fear but fear itself; but the underlying motivational system may have been shaped by selection to function in an environment in which rejection had real and substantial costs.

Even if the historical, ethnographic, and archeological records did not unanimously indicate that humans evolved in, and are adapted to, life in much smaller groups than most of us encounter today, many aspects of our psychology, including fear of rejection, might allow us to infer the existence of such an ancestral world—just as Darwin correctly inferred that the orchid *Angraecum sesquipedale*, whose nectar producing organ lies 30 cm inside it, must be pollinated by a then unknown insect with a proboscis at least 30 cm long.

In conclusion, although Darwinism does not confer on its practitioners some sort of magical pipeline into human mating psychology, a conscious, explicit adaptationism does give the Darwinian at least two advantages in generating scientifically productive hypotheses. First, Darwinians expect the human brain to contain many complex, exquisitely engineered devices that were shaped by selection to solve the specific mating problems that our ancestors reliably encountered during the course of human evolutionary history. Second, Darwinians are ever mindful that these devices, whatever they may be, are adapted to a world that, in some respects, no longer exists. These are no mean advantages.

CHAPTER 11

Fundamentals of Human Mating Strategies

DAVID P. SCHMITT

> Primates are a diverse lot . . . some are monogamous, some polygynous, and some promiscuous . . . at least one—the human primate—is all of these.
>
> —Mealey, 2000, p. 262

EVOLUTIONARY PSYCHOLOGISTS CONTINUE to debate the most fundamental mating strategy of humans. Some maintain that humans are solely designed for lifelong monogamy (Hazan & Zeifman, 1999; Lovejoy, 1981). Others argue that humans are designed for mating with more than one person during their lifetime, either through polygynous, polyandrous, or promiscuous mating (Baker & Bellis, 1995; Ryan & Jethá, 2011). Still others posit that humans possess a "pluralistic" mating repertoire (Barash & Lipton, 2001; Gangestad & Simpson, 2000), and that men and women have evolved facultative, context sensitive strategies of reproduction (Buss & Schmitt, 1993; Kenrick, Sadalla, Groth, & Trost, 1990). Cross-species and cross-cultural comparisons by anthropologists, biologists, and behavioral ecologists have produced conflicting accounts of human mating adaptations (Dixson, 2009; Mealey, 2000). As a result, a definitive characterization of humanity's fundamental mating strategy remains elusive.

In this chapter, evidence is reviewed regarding the reproductive strategies—and specialized mating psychologies—fundamental to humans. Cross-species comparisons and ethnological patterns observed across foraging cultures—cultures that practice the hunting and gathering lifestyle prevalent for 99% of human history—help to clarify our most basic human mating adaptations (Brown, 1991; Marlowe, 2003). Overall, extant evidence suggests there is no single mating strategy in humans. Humans evolved a pluralistic mating repertoire that is facultatively responsive to sex, temporal contexts, personal characteristics such as mate value and ovulatory status, and evocative features of culture and local ecology (Buss, 1994).

SEX AND TEMPORAL CONTEXT DIFFERENCES IN HUMAN MATING STRATEGIES

Humans appear to have a menu of mating strategies at their disposal, or a *pluralistic* mating repertoire (Gangestad & Simpson, 2000). According to this line of reasoning, humans come equipped with specialized mating adaptations for both long-term and short-term mating (Buss & Schmitt, 1993). Not all people pursue both mating strategies at all times. Instead, design features for long-term and short-term mating are differentially triggered depending on the mating strategy being actively pursued (see Schmitt, 2014).

Polygynous mating strategies, for instance, could be explained as arising from both long-term and short-term mating adaptations in men. In polygynous unions, men engage both the long-term adaptations of pair-bonding that are inherent in their monogamous mating psychology (Fisher, 1998) while also satisfying the desires for sexual variety so central to men's short-term mating psychology (Symons, 1979). Polyandrous mating strategies, on the other hand, activate the long-term pair-bonding adaptations of women, and in some cases may satisfy their short-term desires for genetic quality and diversity (see Thornhill & Gangestad, 2008), especially in the case of nonadelphic polyandry. Patterns of extra-pair copulation, or infidelity, may follow from the sex-specific short-term mating adaptations of both sexes (Schmitt, 2005a). Premarital sexuality could psychologically function as preparatory to long-term mating (e.g., evaluating the quality of a potential monogamous partner over a long temporal span) or as means of precocious reproduction in the context of a lifelong life history strategy of short-term promiscuity (Lancaster, 1994).

Most pluralistic theories of human mating evolution argue that a flexible, facultative mating design—comprised of both long-term monogamous adaptations and short-term promiscuous adaptations—would have provided reproductive benefits to humans in our ancestral past, allowing individuals to functionally respond to a wide range of familial, cultural, and ecological contexts (Del Giudice, 2009; Pedersen, 1991; Schmitt, 2005b). Pluralistic theories further acknowledge humans can benefit from shifting between long-term and short-term mating strategies during their lifespan and when in different stages of romantic relationships (Schmitt et al., 2002; Schwarz & Hassebrauck, 2012). Humans also facultatively shift mating strategies depending on hormonal status, ovulatory status, and relative mate value (Bale & Archer, 2013; Camargo, Geher, Fisher, & Arrabaca, 2013; Frederick & Haselton, 2007). In short, humans have evolved a mix of different strategies calibrated to adaptively respond to local reproductive contingencies.

Most pluralistic approaches also postulate that men and women possess sex-specific design features that reliably generate sex differences in human mating (Buss & Schmitt, 1993; Gangestad & Simpson, 2000). For example, men appear motivated by evolved desires for sexual variety—desires that lead men to functionally pursue numerous mating partners and to consent to sex relatively quickly within certain cost-benefit contexts (Buss & Schmitt, 2011; R. D. Clark & Hatfield, 1989; Schmitt, Alcalay, Allik, et al., 2003). In contrast, women's short-term mating motivations appear not to be rooted in the desire for numerous sexual partners *per se*, and seem focused, instead, on other factors such as obtaining men of high status, who impart immediate resources, who display social dominance, intelligence, or otherwise show genetic quality (Greengross & Miller, 2011; Jonason, Tost, & Koenig, 2012; Schmitt, 2014). As a consequence, pluralistic approaches predict men's and women's intersexual mate choices and intrasexual competition tactics will differ in important ways. Most evolutionary theories of human mating strategies are based on this assumption, which can be traced partly to the seminal logic of Parental Investment Theory.

PARENTAL INVESTMENT THEORY

According to Parental Investment Theory (Trivers, 1972), the relative proportion of parental investment—the time and energy devoted to the care of individual offspring (at the expense of other offspring)—varies across males and females. In some species, males provide more parental investment (e.g., the Mormon cricket). In other species, females possess the heavy-investing parental burdens (e.g., most mammals). Importantly, sex differences in parental investment burdens are systematically linked to the intrasexual and intersexual processes of sexual selection (Darwin, 1871). The sex that invests less in offspring is intrasexually more competitive, especially over gaining reproductive access to the opposite sex. The lesser-investing sex is willing to mate more quickly, at lower cost, and with more partners than is the heavier-investing sex. The lesser-investing sex also is reliably more aggressive, dies earlier, matures later, and generally competes for mates with more vigor (see Alcock, 2001).

Much evidence in favor of Parental Investment Theory comes from species where males are the lesser-investing sex. Males of these species display much more competitiveness with each other over sexual access to heavier-investing females, and to exhibit more intrasexual competition through greater aggressiveness, riskier life history strategies, and earlier death (Archer & Lloyd, 2002; Trivers, 1985). Lesser-investing males also discriminate less in mate choice, often seeking multiple partners and requiring less time before consenting to sex (see Alcock, 2001).

Perhaps the most compelling support for Parental Investment Theory has come from "sex-role reversed" species. In species where males are the heavy-investing parent (e.g., the red-necked phalarope), females are expected to vie more ferociously for sexual access to heavy-investing males and to require little from males before consenting to sex. This form of sexual differentiation exists among many sex-role reversed species including the red-necked phalarope, the Mormon cricket, katydids, dance flies, water bugs, seahorses, and a variety of fish species (Alcock, 2001). Parental Investment Theory, therefore, is not a theory about males always having more interest in low-cost, indiscriminate sex than females. Instead, it is a theory about sex differences in parental investment tendencies systematically relating to sex differences in mating strategies.

Among humans, many males invest heavily as parents (Lovejoy, 1981). Nevertheless, men incur lower levels of obligatory or minimum parental investment in offspring than women do (Symons, 1979). Women are obligated to incur the costs of internal fertilization, placentation, and gestation in order to reproduce. The minimum physiological obligations of men are considerably less—requiring only the contribution of sperm. Furthermore, all female mammals, including ancestral women, carry the obligations of lactation. Lactation can last several years in human foraging environments, years during which it is harder for women to reproduce and invest in additional offspring than it is for men (Blurton Jones, 1986). Finally, across all known cultures men *typically* invest less in active parenting effort than women (Low, 2000).

This human asymmetry in parental investment should result in the lesser investing sex (i.e., men) displaying greater intrasexual competitiveness and lower intersexual *choosiness* in mate preferences. Numerous studies have shown that men exhibit greater physical size and competitive aggression (Puts, Chapter 13, this volume), riskier life history strategies (Daly & Wilson, 1988), relatively delayed maturation (Geary, 1998), and earlier death than women do across cultures (Kruger, 2009). In addition, men's mate preferences are, as predicted, almost always less *choosy* or discriminating than women's, primarily in the context of short-term mating (Buss & Schmitt, 1993).

Because men are the lesser investing sex of our species, they also should be more inclined toward low cost, short-term mating than women. Human sex differences in the desire for short-term sex have been observed in studies of sociosexual attitudes and behaviors (Lippa, 2009), motivations for and prevalence of extramarital mating (Wiederman, 1997), quality and quantity of sexual fantasies (B. J. Ellis & Symons, 1990), quality and quantity of pornography consumption (Ogas & Gaddam, 2011), motivations for and use of prostitution (McGuire & Gruter, 2003), willingness to have sex with strangers (R. D. Clark & Hatfield, 1989), affective reactions to short-term mating (Galperin et al., 2013), and in fundamental differences between the mating experiences of gay males and lesbians (Lippa, 2007). Sex differences in parental investment obligations appear to have profoundly influenced the evolution of men and women's fundamental mating strategies.

Sexual Strategies Theory

Buss and Schmitt (1993) extended Trivers' (1972) theory by proposing Sexual Strategies Theory. According to Sexual Strategies Theory, men and women have evolved a complex repertoire of mating strategies. One strategy within this repertoire is "long-term" mating. Long-term mating is typically marked by extended courtship, heavy investment, pair bonding, the emotion of love, and the dedication of resources over a long temporal span to the mating relationship and any offspring that ensue. Another strategy within this repertoire is "short-term" mating, defined as a fleeting sexual encounter such as a hook-up or one-night stand. Between the ends of this temporal continuum are brief affairs, prolonged romances, and other intermediate-term relationships. Which sexual strategy or mix of strategies an individual pursues is predicted to be contingent on factors such as opportunity, personal mate value, sex ratio in the relevant mating pool, parental influences, regnant cultural norms, and other features of social and personal context (see also Buss, 1994).

Sex Differences in Long-Term Mating Although Sexual Strategies Theory views both sexes as having long-term and short-term mating strategies, men and women are predicted to psychologically differ in what they desire and how they tactically pursue these strategies. In long-term mating, for example, the sexes are predicted to differ in their psychological adaptations of mate choice. Men are hypothesized to place a greater mate choice premium on signals of fertility and reproductive value, such as a woman's youth and physical appearance (Buss, 1989; Cloud & Perilloux, 2014; Grillot, Simmons, Lukaszewski, & Roney, 2014). Women, in contrast, are hypothesized to place a greater premium on a man's status, resources, ambition, and maturity—cues relevant to his ability for long-term provisioning—as well as his kindness, generosity, and emotional openness—cues to his willingness to provision women and their children (B. J. Ellis, 1992; Feingold, 1992).

Numerous studies have replicated or confirmed Sexual Strategies Theory related findings using nationally representative, cross-cultural, or multicultural samples (see Schmitt, 2014). Lippa (2007), for example, conducted an Internet survey of samples from 53 nations and confirmed across 100% of cultures that women demonstrate heightened long-term mate preferences for good financial prospects, social status, ambition, and older age, whereas men demonstrate heightened long-term mate preferences for good looks. In a recent review of sex differences in long-term mate preferences, Eastwick, Luchies, Finkel, and Hunt (2014) concluded, "It is currently uncontroversial that these sex differences describe the average stated preferences of men and women in complex modern societies" (p. 4). Other investigators have used nonsurvey techniques to study courtship effectiveness, marital choice, marital conflict, and divorce—including experimental, behavioral, and naturalistic methodologies—and have validated key Sexual Strategies Theory hypotheses concerning sex differences in long-term mate preferences (Cantú et al., 2014; Li et al., 2013; Maestripieri, Klimczuk, Traficonte, & Wilson, 2014a; Yong & Li, 2012). Men who display cues to long-term provisioning, and women who display cues to youth and fertility, tend to be the ones that are most effective at attracting monogamous long-term mating partners (Guéguen & Lamy, 2012; Schmitt, 2002). Most importantly, the ultimate functionality of Sexual Strategies Theory predicted mate preferences has been documented in studies showing marriages of older, higher-status men and marriages of younger and more physically attractive women tend to produce increased numbers and survival of offspring (Bereczkei & Csanaky, 1996; Fieder & Huber, 2007; Nettle & Pollet, 2008; von Rueden, Gurven, & Kaplan, 2011).

Sex Differences in Short-Term Mating According to Sexual Strategies Theory, both sexes are hypothesized to pursue short-term mateships in certain contexts, but for different reproductive reasons that reflect sex-specific adaptive problems of short-term mating (Buss & Schmitt, 1993). For women, the asymmetry in obligatory parental investment leaves them little to gain in reproductive output by engaging in indiscriminate, short-term sex with numerous partners. However, for men, the potential reproductive benefits from promiscuous mating can be profound (Symons, 1979). A man can produce as many as 100 offspring by mating with 100 fertile women over the course of a year, whereas a man who is monogamous will tend to have only one child with his partner during that time. In evolutionary currencies, this represents a strong selective pressure—and a potent adaptive problem—for men's short-term mating strategy to favor a desire for sexual variety. Of course, 100 instances of only one-time mating between a man and 100 women would rarely, if ever, produce precisely 100 offspring. However, this selective pressure remains potent because a man mating with 100 women over the course of a year—particularly repeated matings when the women are nearing ovulation and are especially interested in short-term mating (Thornhill & Gangestad, 2008)—would likely have *significantly more* offspring than a man mating with only one woman over the course of a year.

Whether a woman mates with 100 men or is monogamously bonded with only one man, she will still tend to produce only one child in a given year. The potential reproductive benefits from indiscriminate mating with numerous partners, therefore, are much higher for men than women (Symons, 1979). It is important to note that women can reap evolutionary benefits from short-term mating as well (Greiling &

Buss, 2000). A key caveat, though, is that women's psychology of short-term mating appears to center more on obtaining men of high quality rather than numerous men in high-volume quantity (Thornhill & Gangestad, 2008).

A key premise of Sexual Strategies Theory, therefore, is that both sexes can reap reproductive rewards from engaging in short-term mating under certain circumstances. Even though both sexes may adaptively pursue brief mateships, however, men and women are hypothesized by Sexual Strategies Theory to differ in the evolved psychological design of their short-term mating strategies. According to Sexual Strategies Theory, three of the more distinctive design features of men's short-term mating psychology are: (1) Men possess a greater desire than women do for a variety of sexual partners, (2) men require less time to elapse than women do before consenting to sexual intercourse, and (3) men tend to more actively seek short-term mateships than women do (Buss & Schmitt, 1993, p. 210). In each case, these hypothesized desires function to help solve men's adaptive problem of obtaining large numbers of short-term partners.

This suite of hypothesized sex differences has been well supported among studies of college student and community samples (Fenigstein & Preston, 2007; Kennair, Schmitt, Fjeldavli, & Harlem, 2009; McBurney, Zapp, & Streeter, 2005). Schmitt and his colleagues (Schmitt, Alcalay, Allik, et al., 2003) replicated these fundamental sex differences across 10 major regions of the world. When people from North America were asked "Ideally, how many different sexual partners would you like to have in the next month?" over 23% of men, but only 3% of women, indicated that they would like *more than one* sexual partner in the next month. This finding confirmed that many men desire sexual variety in the form of multiple sexual partners over brief time intervals, whereas very few women express such desires. Similar degrees of sexual differentiation were found all around the world. Moreover, when men and women actively pursuing short-term mates were asked whether they wanted more than one partner in the next month, over 50% of men, but less than 20% of women, expressed desires for multiple sexual partners. This finding supports the key Sexual Strategies Theory hypothesis that men's short-term mating strategy is very different from women's and is based, in part, on obtaining large numbers of sexual partners.

Schmitt and his colleagues (Schmitt, Alcalay, Allik, et al., 2003) also documented that men universally agree to have sex after less time has elapsed than women do, and that men from all world regions expend more effort on seeking brief sexual relationships than women do. For example, across all cultures nearly 25% of married men, but only 10% of married women, reported that they are actively seeking short-term, extramarital relationships. These culturally universal findings support the view that men evolved to seek large numbers of sex partners when they pursue a short-term mating strategy. It is critical to note that many men and women focus solely on long-term mating (Stewart-Williams & Thomas, 2013), and some women also pursue short-term sexual relationships as a key mating strategy (Lancaster, 1994). However, when women seek short-term mates they are more selective and tend to seek out men who are physically attractive, symmetrical, masculine, and/or possess other hypothesized markers of good quality genes (Thornhill & Gangestad, 2008).

As noted earlier, the special design of men's short-term mating psychology—desire for partner variety, quick to consent to sex, and actively seeking short-term mates—has been confirmed in studies of sex differences in sociosexuality (Lippa, 2009; Simpson & Gangestad, 1991). Schmitt (2005b) assessed the sociosexuality of men and women across 48 nations and found men were more unrestricted than women in every culture (average $d = .74$). Lippa (2009) replicated Schmitt's results across a larger sample of 53 nations, including exactly replicating the overall sex difference of $d = .74$. Men's specialized design of short-term mating has been revealed in studies of extra-pair mating, sexual fantasies, pornography consumption, prostitution consumption, affective reactions to short-term mating, and in fundamental differences between mating psychologies of gay males and lesbians (see Buss & Schmitt, 2011).

Perhaps most compelling are real world behavioral tests of hypothesized sex differences in short-term mating. In the 1970s, R. D. Clark and Hatfield (1989) had experimental confederates approach college students on American campuses and ask if they would like to have sex. Around 75% of men agreed to have sex with a complete stranger, whereas no women (0%) agreed to sex with a stranger. R. D. Clark (1990) found nearly identical results in a replication attempt in the 1980s. More than 20 years later, Hald and Høgh-Olesen (2010) largely replicated these findings in Denmark, with 59% of single men and 0% of single women agreeing to the proposition, "Would you go to bed with me?"

Schützwohl, Fuchs, McKibbin, and Shackelford (2009) asked participants to estimate what men and women would do in a similar situation, but they also manipulated the physical attractiveness of the confederate. Men were thought to agree to sex with a stranger if she was highly attractive 54% of the time, whereas women were thought to agree to sex with a stranger if he was highly attractive 8% of the time. Guéguen (2011) had confederates of various levels of physical attractiveness *actually* approach real-life strangers and ask if they would have sex, finding 83% of men agreed to have sex with a highly attractive woman and 60% of men agreed to sex with a woman of average attractiveness. For women, 3% agreed to have sex with a highly attractive man, but no women (0%) agreed to sex with a man of average attractiveness. It appears men of high physical attractiveness are most able to successfully pursue a short-term sexual strategy, given women's specially designed psychology of short-term mating. For the average-looking man, short-term mating may not represent a viable reproductive option (see also Greitemeyer, 2005).

INDIVIDUAL DIFFERENCES IN HUMAN MATING STRATEGIES

The previous section addressed the evolutionary psychology of *how* men and women pursue short-term and long-term mating strategies. Another important question is *why* an individual man or woman would opt to pursue a long-term monogamous strategy versus a short-term promiscuous strategy. Several theories have suggested personal circumstances—including stage of life, personal characteristics, and physical attributes—play an adaptive role in shaping or evoking people's strategic mating choices (Buss & Schmitt, 1993; Gangestad & Simpson, 2000). Among the more important sex-specific features affecting mating strategies are mate value, age, and, among women, their ovulatory status.

SEXUAL STRATEGY PLURALISM

According to Sexual Strategies Theory (Buss & Schmitt, 1993), whether a man pursues a short-term or long-term mating strategy depends, in part, on his status and prestige. In foraging cultures, men with higher status and prestige tend to marry multiple women and reap fitness benefits from doing so (Betzig, 2012; Gurven & Hill, 2009). In modern cultures, men with high status are usually unable to legally marry more than one woman. Some evidence suggests modern men with high status—whether due to hunting ability, physical strength, or other locally-relevant attributes—still manifest a greater potential for fertility by copulating more often (Kanazawa, 2003), having sex with more partners (Gallup, White, & Gallup, 2007), engaging in more extra-pair copulations or affairs (Schmitt et al., 2004), and practicing legalized *de facto* polygyny (or "effective polygyny") via divorcing and remarrying a series of highly fertile women over time (i.e., serial monogamy; Nettle & Pollet, 2008). Of course, given an equal sex ratio of men and women in a given culture, this results in other men—namely those with low status and prestige—being limited to monogamy. In addition, some low-status men are left with no wives at all, and may be forced to resort to coercive, promiscuous mating strategies (McKibbin, Shackelford, Goetz, & Starratt, 2008; Thornhill & Palmer, 2000). Consequently, one important source of individual variation in mating strategy is male status.

Mating Differences Within Men Men's expressed mate preferences and pursued sexual strategies depend on other factors as well, including their overall value in the mating marketplace (Bailey, Durante, & Geary, 2011; Lukaszewski, Larson, Gildersleeve, Roney, & Haselton, 2014; Saad & Gill, 2014). A man's "mate value" is determined, in part, by his status and prestige. It is also affected by his current resource holdings, long-term ambition, intelligence, interpersonal dominance, social popularity, sense of humor, reputation for kindness, maturity, height, strength, and athleticism (B. J. Ellis, 1992).

Most studies of men in modern cultures find that, when they are able to do so as a result of high mate value, men opt for short-term mating strategies (Penke & Denissen, 2008; Surbey & Brice, 2007). For example, Lalumière and his colleagues (Lalumière, Seto, & Quinsey, 1995) designed a scale to measure overall mating opportunities. This scale, similar to overall mate value, included items such as "relative to my peer group, I can get dates with ease." They found among North American men that those with higher mate value tended to have sex at an earlier age, to have a larger number of sexual partners, and to follow a more promiscuous mating strategy overall (see also von Rueden et al., 2011).

Another indicator of overall mate value is the social barometer of self-esteem (Kirkpatrick, Waugh, Valencia, & Webster, 2002). Similar to the results with mating opportunities, North American men who score higher on self-esteem scales tend to engage in more short-term mating strategies (Camargo et al., 2013). In a cross-cultural study involving over 50 nations, Schmitt (2005b) revealed this trend was evident around the world. The same relationship was usually not evident, and was often reversed, among women in modern nations (see also Mikach & Bailey, 1999). Women with high self-esteem were more likely to pursue monogamous, long-term mating strategies. These findings would seem to support Parental Investment Theory (Trivers, 1972), in that when mate value is high and people are given greater choices, men prefer frequent short-term mating whereas women strategically opt for more monogamous mateships.

According to Strategic Pluralism Theory (Gangestad & Simpson, 2000), men should also be more likely to engage in short-term mating strategies when they exhibit the physical characteristics most preferred by women, especially traits indicative of low genetic mutation load (Lukaszewski et al., 2014; Thornhill & Gangestad, 2008). Evidence that physically attractive men adaptively respond to women's desires and become more promiscuous comes from several sources. Rhodes, Simmons, and Peters (2005) found, for example, that attractive men have more short-term, but not long-term, partners; whereas attractive women have more long-term, but not short-term, partners. Men who possess broad and muscular shoulders, a physical attribute preferred by short-term oriented women (Frederick & Haselton, 2007), tend toward short-term mating as reflected in an earlier age of first intercourse, more sexual partners, and more extra-pair copulations (Hughes & Gallup, 2003). In numerous studies of North American college students, Gangestad and his colleagues have shown that women who seek short-term mates place special importance on the physical attractiveness of their partners, and that physically attractive men are more likely to pursue short-term mating strategies (Gangestad & Cousins, 2001; Simpson, Gangestad, Christensen, & Leck, 1999). In a cross-cultural study of several dozen nations, Schmitt et al. (2004) replicated these results and found that men who consider themselves attractive in nearly all cultures are more likely than other men to engage in short-term mating strategies. Among women, physical attractiveness was generally associated with more monogamous mating desires (Buss & Shackelford, 2008), though this trend was not evident in Eastern Europe and Southern Europe (Schmitt, 2005a). In sum, several findings suggest that when men have the opportunity to pursue a short-term mating strategy, due in part to their physical attractiveness, they tend to do so.

Some research suggests that genetic and hormonal predispositions may affect men's mating strategies (Garcia et al., 2010; Hönekopp, Voracek, & Manning, 2006). Much of this research focuses on the moderating effects of testosterone (Dabbs & Dabbs, 2000; Welling et al., 2008). For example, married men, compared to their same-age single peers, tend to have lower levels of testosterone (Burnham et al., 2003), and men who are expectant fathers and hope to parent children only with their current partner have lower testosterone yet (Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002; Hirschenhauser, Frigerio, Grammer, & Magnusson, 2002; van Anders & Watson, 2006). Married men who maintain interest in additional mating and those who exert no effort at parenting, however, do not experience testosterone declines (Edelstein, Chopik, & Kean, 2011; McIntyre et al., 2006). Men who are especially high in testosterone and possess high testosterone-related traits (e.g., enhanced muscularity, prominent browridge, wide jaw, deep voice) tend to have more sexual partners (Hill et al., 2013; Maestripieri, Klimczuk, Traficonte, & Wilson, 2014b), to start having sex earlier (Udry & Campbell, 1994), to exert more effort at mating (Gray et al., 2004), to be more likely to have affairs in adulthood (Booth & Dabbs, 1993), to divorce more frequently (Mazur & Booth, 1998), to have more wives in polygynous cultures (Alvergne, Jokela, Faurie, & Lumma, 2010), to have higher sperm counts (Manning, 2002), and to have more children (Apicella, Feinberg, & Marlowe, 2007; Jasienska, Jasienski, & Ellison, 2012).

Related findings involving testosterone and variability in men's mating strategies may lie in prenatal testosterone exposure and its organizational effects on the human brain. Exposure to heightened levels of testosterone in utero around the second month of gestation typically causes increased masculinization of the human male brain (L. Ellis, 2011; Manning, 2002). If men's brains are designed to produce a mating psychology that, when short-term mating is pursued, is rooted in relatively indiscriminate mating (Symons, 1979), this would lead to the hypothesis that those human males who are exposed to higher testosterone in utero would be more likely to develop indiscriminate short-term mating strategies in adulthood.

One clue to testosterone exposure can be found in the relative length of human fingers (Manning, 2002). Essentially, if one's ring fingers (fourth digits or "4D") are longer than one's pointer fingers (second digits or "2D"), high levels of in utero testosterone exposure and high circulating levels of testosterone in adulthood are implicated. Men with especially long ring fingers (i.e., those with a low 2D:4D ratio) have been found to follow faster life history pathways and more short-term oriented mating strategies (Schwarz, Mustafić, Hassebrauck, & Jörg, 2011). Men with low 2D:4D ratios are also likely to have more children overall, to have more sperm motility, to be more competitive and assertive, and to be perceived as more attractive than other men (Manning, 2002; Stenstrom, Saad, Nepomuceno, & Mendenhall, 2011). These findings further implicate testosterone as an activating factor in men's short-term strategies. Importantly, most of these relationships are not typically found among women (though masculine women have been found to engage in more short-term mating; A. P. Clark, 2004; Mikach & Bailey, 1999). In women, other factors appear much more relevant to the adaptive evocation of evoke mating strategy choice.

Mating Differences Within Women Women's desires for sex tend to peak during the late follicular phase, just before ovulation when the odds of conceptive sex are maximized (Regan, 1996). It was once thought this shift in sexual desire evolved because it increased the probability of having conceptive intercourse in our monogamous female ancestors. However, several studies have documented that many design features of women's mating strategies change over the cycle, with short-term desires for men with high quality genes peaking in the highly fertile days just before ovulation (Cantú et al., 2014; Durante, Griskevicius, Simpson, Cantú, & Li, 2012; Durante, Li, & Haselton, 2008; Gildersleeve, Haselton, & Fales, 2014).

Women who are interested in short-term mating, for example, tend to prefer men who are high in dominance and masculinity (Buss & Schmitt, 1993), as indicated by testosterone-related attributes such as prominent brows, large chins, and other features of facial, bodily, and behavioral masculinity (Mueller & Mazur, 1998; O'Connor et al., 2012; Perrett et al., 1998). Short-term oriented women may prefer these attributes as "sexy son" markers of testosterone that are honest indicators of immunocompetence quality in men (Thornhill & Gangestad, 2008). During the late follicular phase, women's preferences for men with masculine traits reliably increase (Gildersleeve et al., 2014), precisely as though women are shifting their mating psychology to follow a more short-term oriented strategy (see Cantú et al., 2014; Durante et al., 2012).

Overall, there is compelling evidence that women's mating strategies—both their desires and behaviors—strategically shift, from a long-term mating psychology to a more short-term oriented mating psychology, precisely when they are most fertile (Grammer, Renninger, & Fischer, 2004). It is possible these shifts function, for some women, as a mechanism to obtain high-quality genes from extra-pair copulations while maintaining a long-term relationship with a heavily investing partner (Thornhill & Gangestad, 2008).

In addition to ovulatory shifts, there is evidence that women's mating strategies change across their lifespan. For example, an early-30s peak in sexual desire may have been functional for our female ancestors. The percentage of fertile ovulatory cycles—cycles that include an ovulation that could lead to pregnancy—varies tremendously over a woman's lifespan, peaking at 70% in women during their early 30s (see Baker & Bellis, 1995). In a study of 1,400 women from the United States and Canada, Schmitt and his colleagues (2002) found that women in their early 30s experience a peak in sexual desire, as measured by subjective feelings of lust and behavioral manifestations of seductiveness and increased sexual activity. Along with evidence from orgasmic output, the cognitive emotional focus of sex, and social perceptions of sexual peak (see Barr, Bryan, & Kenrick, 2002), it appears that women's sexual desire peaks in their early 30s and may have the specific evolutionary function of either increasing reproduction with one's primary long-term mating partner, or leading women in their early 30s to engage in more extramarital affairs or more promiscuous sex, perhaps in an effort to increase the genetic quality or diversity of their offspring.

Several other individual differences and personal situations seem linked to adaptive variability in women's mating strategies. For example, short-term mating strategies are more likely to occur during adolescence, when one's partner is of low mate value, when one desires to get rid of a mate, and after divorce—all situations where short-term mating may serve specially-designed adaptive functions (Greiling & Buss, 2000). In some cases, short-term mating seems to emerge as an adaptive reaction to early developmental experiences within the family (Belsky, Steinberg, & Draper, 1991). For example, short-term mating strategies are more likely to occur among women growing up in father absent homes (Webster, Graber, Gesselman, Crosier, & Schember, 2014) especially in homes where a stepfather is present (B. J. Ellis, 2004). In these cases, the absence of a father, and presence of a stepfather, may indicate to young women that mating age men are unreliable. In such environments, short-term mating may serve as the more viable mating strategy in adulthood (Belsky, 1999; Lancaster, 1994; Sheppard, Garcia, & Sear, 2014; also see Comings, Muhleman, Johnson, & MacMurray, 2002).

Finally, some have argued that frequency-dependent or other forms of selection have resulted in different heritable tendencies toward long-term versus short-term mating (Gangestad & Simpson, 2000). There is behavioral genetic evidence that age at first intercourse, lifetime number of sex partners, mate preferences, and sociosexuality—a general trait that varies from restricted long-term mating to unrestricted short-term mating—are somewhat heritable (Lyons et al., 2004; Verweij, Burri, & Zietsch, 2012) and hormone dependent (Grant & France, 2001; Law Smith et al., 2012).

CULTURAL DIFFERENCES IN HUMAN MATING STRATEGIES

In addition to sex and individual differences, evolutionary psychologists expect human mating strategies to vary in adaptive ways across cultures (Gangestad, Haselton, & Buss, 2006; Gaulin, 1997). Indeed, evolutionary psychologists, anthropologists, and behavioral ecologists have long demonstrated that many aspects of culture—particularly ecological harshness, warfare, kinship, residence, and inheritance patterns—are systematically related to mating strategies, as well as to rules governing premarital sex (Barber, 2000), jealousy and adultery (Korotayev & Kazankov, 2003), love (Schmitt et al., 2009), marital dynamics (Weisfeld & Weisfeld, 2002), mate preferences (Marcinkowska et al., 2014; Moore et al., 2013), and sexual issues such as postpartum sex taboo and incest avoidance (Hartung, 1985; Pasternak, Ember, & Ember, 1997). Evolutionary psychologists clearly expect culture to play an important role in activating and evoking human mating adaptations (see Pirlott & Schmitt, 2014). Even so, some critics persist in ignoring this feature of evolutionary psychology, asserting that, "By relying on outmoded theories that emphasize biology to the exclusion of culture, evolutionary psychologists may be missing some of the most important, characteristically human, evolutionary processes" (Wood, Kressel, Joshi, & Louie, 2014, p. 17). Such statements reveal an astounding lack of knowledge regarding the foundation of evolutionary psychology and its emphasis on culture (Tooby & Cosmides, 1992).

Among the earliest and most well documented links between culture and human mating are those involving adaptive variation in polygynous versus monogamous marriage systems (Ember, Ember, & Low, 2007; Henrich, Boyd, & Richerson, 2012; Marlowe, 2003). For example, Low (1990) documented that tribal cultures with high pathogen stress are more likely to have polygynous marriage systems. Monogamous systems, in contrast, are relatively absent in high-pathogen environments (Dow & Eff, 2013). This pattern of mating pluralism can be explained, in part, by high pathogen ecologies causing men to prefer genetic diversity in their offspring (diversity that would protect against pathogens and could be achieved through polygyny) while women prefer particularly healthy men who can support multiple wives, of which there are few in high pathogen areas of the world—a pattern also related to the polygyny threshold model (Low, 2000). Mating adaptations designed to respond to pathogen levels may also give rise to different forms of polygyny. For example, in high pathogen environments, polygynous men tend to marry exogamously, outside their local tribe, which further increases their offspring diversity. Sororal polygyny, when men marry women who are sisters, would provide less genetic diversity and rarely occurs in high pathogen environments (Low, 2000).

Operational Sex Ratios and Mating Dynamics

Another well-researched aspect of culture that appears to differentially evoke human mating adaptations is operational sex ratio (Guttentag & Secord, 1983; Pedersen, 1991). Operational sex ratio can be defined as the relative balance of marriage-age men versus marriage-age women in the local mating pool, though other formulations have been proposed (Hardy, 2002). When computing operational sex ratios, marriage age is usually treated as between 15 and 49 years (Guttentag & Secord, 1983). Sex ratios are considered "high" when the number of men significantly outsizes the number of women in a local culture. Conversely, sex ratios are considered "low" when there are relatively more women than men in the mating market. In most cultures women tend to slightly outnumber men, largely because of men's polygynous tendency to have a higher mortality rate (Daly & Wilson, 1988). Nevertheless, significant variation often exists in sex ratios across cultures, across ages, and within cultures when viewed over historical time (Kruger, 2009; Marlowe & Berbesque, 2012; Pollet & Nettle, 2008).

Pedersen (1991) argued that a combination of Sexual Selection Theory (Darwin, 1871) and Parental Investment Theory (Trivers, 1972) leads to a series of predictions concerning the effects of sex ratios on human mating strategies. According to sexual selection theory, when males desire a particular attribute in potential mating partners, females of that species tend to respond by competing in the expression and provision of that desired attribute. Among humans, when sex ratios are especially low and there are many more women than men, men should become an especially scarce resource that women compete for with even more intensity than normal (see also Griskevicius et al., 2012; Stone, Shackelford, & Buss, 2007).

When combined with the parental investment notion described earlier in which men tend to desire indiscriminate short-term mating (Buss & Schmitt, 1993), this leads to the hypothesis that humans in cultures with lower sex ratios (i.e., more women than men; traditionally ratios below 100) should pursue more short-term oriented mating strategies. The logic of Pedersen's (1991) theory is that in cultures with many more women than men, men are scarce and can afford to demand from interested women that men's greater desires for short-term sex be fulfilled. As a result of these mating market forces, the culture as a whole should become more oriented toward short-term mating.

Conversely, when sex ratios are high and men greatly outnumber women, men must enter into more intense intrasexual competition for the limited number of potential female partners (see also Hudson & Den Boer, 2004; cf. Schacht, Rauch, & Borgerhoff Mulder, 2014). Women's preferences for long-term monogamous relationships become the key desires that must be responded to if men are to remain competitive in the courtship marketplace. In this case, Pedersen's (1991) logic suggests that humans in cultures with higher sex ratios (i.e., more men than women; ratios above 100) should possess more monogamous mating proclivities.

Using data from sex ratio fluctuations over time within the United States, Pedersen (1991) marshaled a compelling case for causal links between sex ratios, sexual selection processes, and human mating strategies. For example, high sex ratio fluctuations have been historically associated with increases in monogamy, as evidenced by lower divorce rates and men's greater willingness to invest in their children. Low sex ratios have been historically associated with indexes of short-term mating, such as an increase in divorce rates and a reduction in what he termed female "sexual coyness." In a cross-cultural study of over 40 nations, Schmitt (2005a) examined whether national sex ratios were correlated with direct measures of basic human mating strategies in an attempt to test Pedersen's (1991) theory. As expected, cultures with more men than women tended toward long-term mating, whereas cultures with more women than men tended toward short-term mating (see also Barber, 2000; Schmitt & Rohde, 2013). As shown in Figure 11.1, women's sociosexuality tends to increase (i.e., become more unrestricted or short-term oriented) as the operational sex ratio decreases (i.e., more women than men in the mating pool; scores below 100), $r(46) = -0.50$, $p < .001$. Overall, it appears that human mating strategies are facultatively responsive to the balance of men versus women in the local mating pool, supporting the fundamental postulate of strategic pluralism in human mating (see also Barber, 2008; Chipman & Morrison, 2013).

PSYCHOSOCIAL ACCELERATION THEORY

Combining aspects of life history theory (Low, 1998), attachment theory (Bowlby, 1982), and concepts such as reaction norms, phenotypic plasticity, gene-environment interactions, and prepared learning (Figueredo et al., 2008; West-Eberhard, 2003)—several researchers have suggested experiences during childhood play a pivotal role in the facultative development of human mating strategies. Perhaps most prominent among these is a lifespan model developed by Belsky et al. (1991). According to this model, early social experiences adaptively channel children down one of two reproductive pathways. Children who are socially exposed to high levels of stress—especially insensitive/inconsistent parenting, harsh physical environments, and

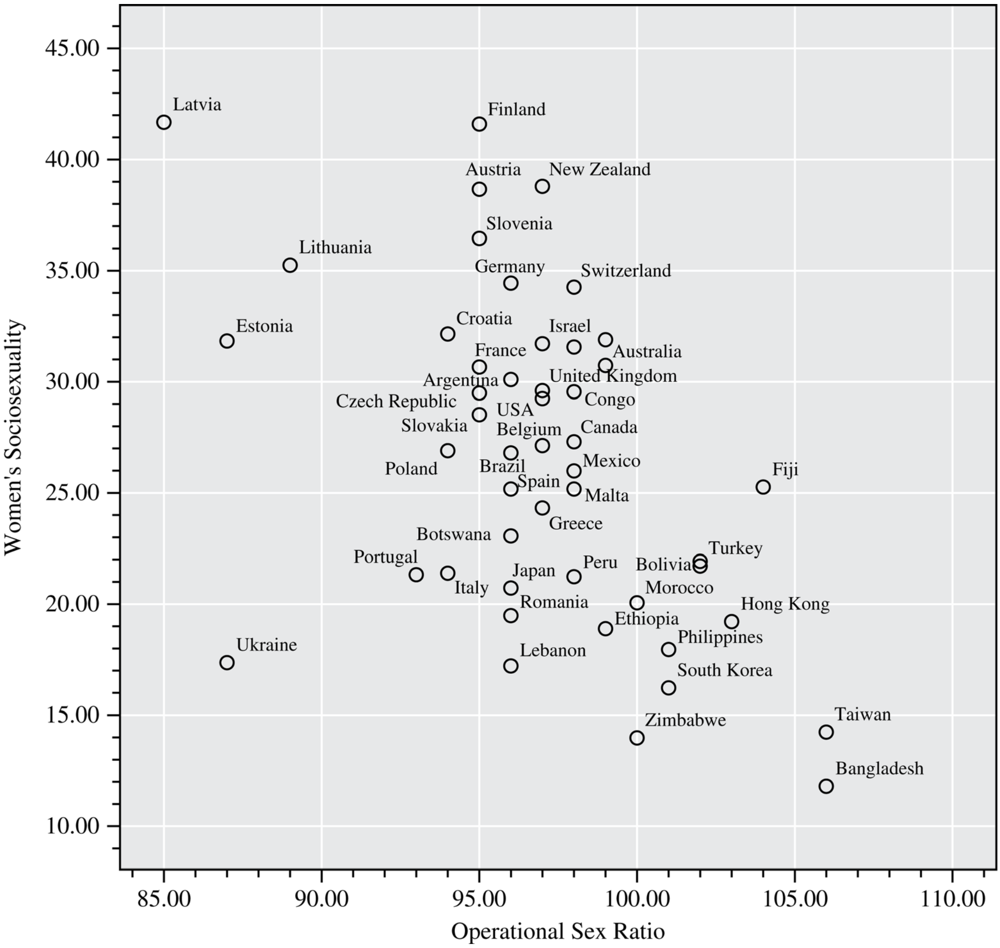

Figure 11.1 National Levels of Women's Sociosexuality Related to Operational Sex Ratios Across 48 Nations of the International Sexuality Description Project. *Source:* Schmitt, 2005b.

economic hardship—tend to develop insecure attachment styles. These children also tend to physically mature earlier than those children who are exposed to less stress. According to Belsky and his colleagues, attachment insecurity and early physical maturity subsequently lead to the evolutionary adaptive development of what is called an *opportunistic* reproductive strategy in adulthood (i.e., short-term mating). In cultures with unpredictable social environments, it is therefore argued, children adaptively respond to stressful cues via phenotypic plasticity by developing the more viable strategy of short-term mating (see also Del Giudice, 2009).

Conversely, those children exposed to lower levels of stress and less environmental hardship tend to be more emotionally secure and to physically mature later. These children are thought to develop a more "investing" reproductive strategy in adulthood (i.e., long-term mating) that pays evolutionary dividends in low stress environments. Although the causal mechanisms that influence strategic mating are most prominently located within the family, this model also suggests that certain aspects of culture may be related to mating strategy variation.

A closely related theory has been proposed by Chisholm (1996). Chisholm argues that local mortality rates—presumably related to high stress and inadequate resources—act as cues that facultatively shift human mating strategies in evolutionary adaptive ways (see also Griskevicius, Delton, Robertson, & Tybur, 2011). In cultures with high mortality rates and unpredictable resources, the optimal mating strategy is to reproduce early and often, a strategy related to insecure attachment, short-term temporal orientations, and promiscuous mating strategies. In cultures that are physically safe and have abundant resources, mortality rates are lower and the optimal strategy is to invest heavily in fewer numbers of offspring. In safer environments, therefore, one should pursue a long-term strategy associated with more monogamous mating. Collectively, the Belsky et al. (1991) and Chisholm (1996) theories can be referred to as a "psychosocial acceleration theory" of human mating strategies.

Numerous studies have provided support for psychosocial acceleration theory (Cohen & Belsky, 2008; Figueredo et al., 2008). In an attempt to test psychosocial acceleration theory, Schmitt and his colleagues (Schmitt, Alcalay, Allensworth, et al., 2003) measured the romantic attachment styles of over 17,000 people from 56 nations. They related insecure attachment styles to various indexes of familial stress, economic resources, mortality, and fertility. They found overwhelming support for psychosocial acceleration theory. For example, nations with higher fertility rates, higher mortality rates, higher levels of stress (e.g., poor health and education), and lower levels of resources tended to have higher levels of insecure romantic attachment. Schmitt (2005b) also found that short-term mating was related to insecure attachment across cultures. As expected, the dismissing form of insecure attachment was linked to short-term mating in men and fearful/preoccupied forms of insecure attachment were linked to short-term mating in women. These findings support the view that stressful environments cause increases in insecure romantic attachment—increases presumably linked to short-term mating strategies (Figueredo et al., 2006).

CONCLUSIONS: EVOLUTION AND HUMAN MATING STRATEGIES

Humans possess a pluralistic mating repertoire, organized in terms of basic long-term/high-investment and short-term/low-investment mating psychologies. The activation and pursuit of these mating psychologies differs in adaptive ways across sex, personal circumstance, and cultural context. Men's short-term mating strategy, for example, is based on opportunistic mating, including the relatively indiscriminate acquisition of numerous partners. Women's short-term strategy, in contrast, is more heavily rooted in obtaining men of high genetic quality (including men who possess masculine and symmetrical facial features), securing additional resources, using short-term mating to secure a long-term mate, or "mate switching" to a different partner. High mate value men tend to pursue short-term mating strategies more than other men, and, when possible, strive for polygynous or serial marriages. Women nearing ovulation express desires indicative of their short-term mating psychology, including being more sensitive to the symmetry and masculinity of men. Men who fulfill these desires are successful as short-term sexual strategists. In cultures with high stress and fertility, insecure attachment and short-term mating adaptively emerge, and female-biased sex ratios appear to adaptively generate short-term mating strategies as well.

An important area for future research will be to more precisely gauge the adaptive ways in which different cultures constrain or permit the expression of one or more strategies within the human repertoire, and to find ways of applying these results to solving social problems and informing public policies. For example, based on the cross-cultural relationship between sex ratio and women's sociosexuality (see Figure 11.1), once women outnumber men at a sex ratio of about 95, women's sociosexuality conspicuously increases. In many American urban environments, women significantly outnumber men as a result of gang-related homicides and high rates of male imprisonment. Public policies that exacerbate excesses of women (e.g., drug laws that place large numbers of local men in prison) may well serve to increase the short-term mating of local populations. Such a shift could have unintended secondary effects on single-parenting (Lancaster, 1994) and sexual aggression (Thornhill & Palmer, 2000). Utilizing new knowledge about the facultative nature of mating strategy deployment and its adaptive calibration to local ecologies should prove useful for evolutionary-minded policy makers (Crawford & Salmon, 2004; Roberts, 2011).

In the future, evolutionary perspectives on human mating strategies need to be better integrated with other perspectives, including religious, historical, and feminist scholarship (see Buss & Schmitt, 2011; Vandermassen, 2005). Religious teachings frequently address sexual and reproductive behavior, often in evolutionary-relevant ways (Kirkpatrick, 2005; Weeden, Cohen, & Kenrick, 2008). The same may be true for other aspects of life that, at first glance, seem disconnected from human evolution. Political ideology, sexual orientation, gender identity, gender equality, education, climate, geography, ethnicity, and linguistic heritage may all impact human mating strategies (Barber, 2002; Pirlott & Schmitt, 2014), yet none of these topics were adequately addressed in this chapter. The adaptationist perspective emphasized here represents a starting point for future theorizing and research on the fundamental nature of human mating strategies. With a strong foundation in evolutionary psychology, future efforts at improving human sexual science will be faster in coming and more effective in execution.

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CHAPTER 12

Physical Attractiveness: An Adaptationist Perspective

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If all humans of the same developmental stage and sex share the same attractiveness-assessment psychology, why don't they all find the same individuals attractive? How and why do our minds work to produce these effects? This chapter frames these questions in terms of a set of basic principles for understanding physical attractiveness: the Evolutionary Rules of Attraction. Research using evolutionary theory to understand human attractiveness is vast and growing, so not all can be covered herein. This chapter, therefore, (a) reviews alternative evolutionary explanations for an attraction; (b) highlights the general components of attraction systems; (c) identifies causes of variation in attractiveness assessment; (d) identifies domains of social value for which attractiveness assessment is relevant; (e) reviews evidence for some attractiveness-assessment adaptations in those domains; and (f) highlights research avenues calling for increased attention. In so doing, it updates my earlier argument (Sugiyama, 2005) that human physical attractiveness assessment is generated by adaptations functioning to evaluate evolutionarily relevant cues to human social value across multiple domains of interaction. It also extends my argument that evolutionary human life history theory and data from small-scale foraging societies are instrumental in generating predictions about these domains of social value, the cues or signals associated with them, adaptations selected to regulate attraction to them, and trade-offs predicted among them.

THE EVOLUTIONARY BASES OF ATTRACTION AND ATTRACTIVENESS

Objects are not intrinsically disgusting or attractive: These feelings are generated by cognitive adaptations. Humans are strongly attracted to some stimuli and repulsed by others, while remaining emotionally neutral to most. Attraction and disgust were relevant to many adaptive problems faced by our ancestors, such as what to eat, where to camp, whom to ally with, whom to mate with, and which juveniles to provision.

Because the cues associated with, and behavior resulting in the fitness-promoting aspects of ancestral environments varied from task to task, different preference suites evolved for different tasks. No general attractiveness adaptation applies to all stimuli. A simple thought experiment illustrates why: If we assessed potential mates using the same attraction mechanisms with which we assessed food, we would find meat and fruits as sexually arousing as healthy, sexually mature members of our own species.

Attractions do not operate like an on-off switch: They are regulated in response to local evolutionarily relevant parameters. The physiological bases of an attraction include a network of complex biochemical and cellular information-processing systems designed to receive sensory information that identifies cues to the relevant attractiveness contexts. These systems activate the assessment processes, and direct attention to environmental cues to take as input. For each cue occurring above threshold, input must be encoded and its value computed. That information must be sent to mechanisms that integrate it with values of other cues relevant to the assessment, produce an emotional response scaled to the value of that cue integration, and then motivate specific behavior of a given intensity. These systems encompass receptors, neural organization and firing, neurotransmitters, and hormonal pathways and processing. Receptors, signal transmission, assessment processing, and emotional outputs are all components of attraction systems, and the same signal must produce different levels of attraction in different circumstances to function adaptively.

Although progress is being made (e.g., Roney, Simmons, & Lukaszewski, 2010), the genetic and neurophysiological bases of human interpersonal attraction adaptations remain largely to be explored, but taste mechanisms illustrate that attraction is based on coordinated gene action on cascades of biochemical and cellular processes. Humans are attracted to taste cues of "umami" or *savory taste*. Umami attraction begins with two closely related proteins, TAS1R1 (taste receptor type 1+1) and TAS1R3 (taste receptor type 1+3) that when chemically bound function to detect L-amino acids, particularly L-glutamate, an amino acid in meat and other foods such as mushrooms. TAS1R1 is encoded by the *TAS1R1* gene, and TAS1R3 by the *TAS1R3* gene. TAS1R1+3 receptors are located on the tip of complex biological structures—taste buds (which require other genes for other aspects of their production and function). When L-amino acid concentrations in the mouth reach a threshold, about 0.0007 M, signaling molecules trigger calcium release, activating melastatin 5 (TrpM5), which leads to membrane depolarization and release of the neurotransmitter ATP. Umami receptors don't have synapses. The ATP activates serotonin release from neighboring taste receptors that do, and these signals are transmitted via gustatory chorda tympani (and facial, glossopharyngeal, and vagus nerves) to multiple processing centers of the brain via additional structurally and functionally specific and physiologically complex biochemical and neurobiological processes. Resultant analyses of umami are then integrated with results of other taste system analysis (e.g., sweet, bitter) to generate different aspects of taste, including quality, intensity, pleasantness (or unpleasantness), location, and persistence. These, in turn, are integrated with visual, olfactory, and hunger regulatory mechanisms. The final output regulates attraction and motivates behavior.

A functional analysis provides an ultimate explanation for these adaptations. Amino acids are critical to many life functions (e.g., building muscle tissue, antibodies, enzymes; transportation of molecules such as hemoglobin). Umami taste signals the presence of amino acid L-glutamate, and attraction to such foods is rewarded by pleasurable taste, motivating their pursuit and consumption. This attraction evolved because it increased the probability of our ancestors consuming L-glutamate rich foods, increasing frequency of alleles generating the structures producing the preference (e.g., TASIR1+3 receptor arising with jawed vertebrates), and it was retained, built upon and fine-tuned by selection over time (Roper, 2007; Zhang et al., 2003). Conversely, revulsions discourage us from interacting with agents and substances in ways that were detrimental to fitness. For example, ingestion of moldy fruits can lead to intestinal distress from mycotoxins, and many plants have evolved biochemical defenses to keep predators from eating them (Jensen et al., 2013). Ingestion of these toxins can have high fitness costs, including death. Bitterness receptors respond to some of these chemotoxins and, as predicted for this threat-detection system, have a much lower activation threshold than sweet or umami receptors. The ultimate causal explanation expressed in cognitive terms (savory, taste, attraction, revulsion) is necessary for understanding these mechanisms, provides a useful explanation in its own right, and is consonant with the proximate genetic, biochemical, physiological level, and the functional explanation makes sense of the biochemical processes.

One possible explanation for an attraction then, is that it is the function of an adaptation. The most compelling case for adaptation is when one can show: (a) the species' ancestors recurrently faced a particular adaptive problem; (b) the structure has a complex functional design so improbably well-suited to solving the adaptive problem that pure chance must be rejected as an alternative hypothesis; and (c) the organism shares that design (or a facultative developmental program that builds that design) with all normally developing conspecifics.

However, we may also be attracted to objects exhibiting cues that were associated with a fitness-enhancing entity in ancestral environments but lack the fitness-enhancing properties themselves (Symons, 1987; Tooby & Cosmides, 1990, 1992). Consider soft drinks. Sweetness receptors initially evolved because carbohydrates in solution and sugar content provided were a statistically reliable cue of nutritious, energy-packed foods. The receptors were retained in humans because they generated attraction to foods such as fruit and honey. In modern environments, soft drinks exhibit similar cues, but do not provide the same fitness benefits (Eaton, Shostak, & Konner, 1988; Nesse & Williams, 1994). Sweet receptors and attraction respond (in some individuals) to aspartame and saccharine, even though attraction to these substances was not under selection. Similarly, pornography exhibits cues of willing, available, and fertile mates, but time spent viewing one's computer screen lacks the fitness-enhancing consequences for which attraction to these cues evolved.

Another possibility is that an evolved preference may bias responses to similar cues in other domains. Burley and colleagues accidentally discovered that finches have species-typical mate preferences with respect to the bands put on their legs by researchers. Female zebra finches prefer males with red rather than blue leg bands, whereas double-bar finches prefer light blue rather than red bands (Burley, 1986; Burley, Krantzberg, & Radman, 1982). Each species prefers colors similar to its own species' plumage, suggesting that these preferences are a by-product of species-recognition mechanisms. Similarly, some guppy species exhibit preferences for orange-colored foods, which may explain over 90% of the variation in female preferences for orange spots on males (Rodd, Hughes, Grether, & Baril, 2002). Humans may exhibit similar nonfunctional preferences, and complete understanding of human attractiveness will need to distinguish these.

Once a sensory bias evolves in a given domain, it may be subject to further selection in others. When subjected to selection for a different function, the result is an adaptation. In the natural world of mating, when sensory drive is present, it is likely to exert selection pressure on the target sex, so that preference and target trait become linked, and selection favors both trait and preference (e.g., Kokko, Brooks, Jennions, & Morley, 2003; Payne & Pagel, 2001). Distinguishing between an attraction due to sensory bias and sensory bias that has been under further selection requires fine-grained analysis. For instance, instead of a mate preference for facial symmetry being an adapation for attraction to high genetic or phenotypic quality, an alternate hypothesis is that symmetry preference is the result of sensory bias (Enquist & Johnstone, 1997). However, more symmetric faces are more attractive than less symmetric faces when right side up but not upside down, (Little & Jones, 2003, 2006). Greater symmetry preference is also associated with greater preference for sexually dimorphic facial features in the opposite sex, so sensory bias alone cannot account for facial symmetry preference (Little et al. 2008). Because there is no principled way to predict nonfunctional preferences, it is more useful to focus on adaptive problems for which attractions are expected to have evolved, and test by-product, sensory bias, pathology, or evolutionary mismatches as alternative explanations.

Finally, locally variable contingencies between cues we have evolved to assess and other associated cues may explain attractions that otherwise seem variable or idiosyncratic. This is because these associated cues may enhance local signal quality, or become emotionally attached to it. For instance, Damasio (1994) shows how an emotional response may link an adaptation's functional operation with stimuli recurrently associated with the stimuli for which an attraction evolved. If so, locally variable attractions may be the joint effect of attraction adaptations, association adaptations, and recurrent linkage between them. This is probably the basis for how many particular local cultural products become associated with stimulation of attraction responses, when such attractions per se could not be the direct products of selection. Of course, humans also employ artifacts to enhance those cues for which we have assessment adaptations (e.g., high heels, makeup, symmetrical face paint).

Naive cultural determinism does not offer an alternative scientific means of explaining attraction. The belief that "learning" or our "capacity for culture" accounts for attractions overlooks or grossly simplifies the psychological architecture requisite to generating preferences and other cultural phenomena (Tooby & Cosmides, 1992). On the cultural determinist view, who and what are found attractive varies arbitrarily across cultures: Individuals assess the physical attractiveness of both sexes based on local cultural dictates, and tend to prefer the sex that society tells them to. If this view were correct, standards of attractiveness would vary *randomly* across the cultural and geographic landscapes of human experience, but they do not (e.g., Sugiyama, 2005). Moreover, we would not expect to see behavior and attractions that are nonnormative within a culture, except perhaps as pathology. In 1950s American society, for example, we should find no straight parents with gay offspring, because the heteronormative determinants of straight culture should produce only straight individuals: This was not the case.

In sum, we have five basic options when formulating hypotheses regarding an attraction. It is either: (1) an adaptation; (2) a necessary by-product of an adaptation; (3) a nonfunctional effect of an adaptation that was not under selection to produce that effect per se; (4) the result of chance, pathology, or an idiosyncratic stochastic event; or (5) the product of an adaptation and statistical cue association, where the recurrent association of a local stimuli with an evolved preference cue binds the attraction to the local stimuli.

SOURCES OF VARIATION IN ATTRACTIVENESS ASSESSMENT

Adaptations for attraction and disgust are expected to be facultative within reaction norms. We expect them to be sensitive to the cost–benefit structure of their bearer's current circumstances and phenotypic condition, and also to the local conditions under which they develop. For social relationships, we expect these mechanisms to be sensitive to the kind of relationship (e.g., mating, trading, alloparental) for which an individual is being assessed. Evolutionary life history theory (LHT) points to age- and context-related trade-offs that were likely at play in the evolution of attractiveness-assessment mechanisms. Thus, with insights derived from the study of small-scale societies, LHT provides a framework for generating predictions about why and how the operation of attractiveness-assessment mechanisms varies under different circumstances.

Because success in the human ecological niche depends on multiple social relationships, the first prediction suggested by LHT is that attractiveness assessment will vary depending on the social value being assessed. A second source of variation in attractiveness assessments is the phenotypic state of the assessor, including the individual's sex, developmental stage, and reproductive state. For example, female assessments of male sexual attractiveness vary across the ovulatory cycle, and assessments of others' sexual attractiveness are affected by the assessor's relative sexual attractiveness as a short- or long-term mate. Individuals also vary in their socio-sexual orientation, or the degree to which they desire, approve of, and engage in committed versus uncommitted sexual relations, and this too can affect the relative attractiveness of different traits (Penke & Asendorpf, 2008; Simpson & Gangestad, 1992). Disentangling the effects of genetic variation on phenotypic state is critical here, as some kinds of variation are more relevant than others to explaining why different assessors find different individuals attractive. For example, the major histocompatibility complex (MHC), a gene complex involved in immune function may affect sexual "chemistry" between individuals.

Variation in reproductive and sexual strategies provides a third basis for variation in assessments of sexual attractiveness, and this same principle should apply to other strategies and social values. Consider cooperation: When there are physical cues associated with differences in cooperative strategies, individuals exhibiting different cues should be more or less attractive depending on the cooperative strategy of the assessor. For instance, an individual deploying a hawk strategy should find individuals exhibiting cues associated with a dove strategy more attractive as potential prey than individuals exhibiting cues associated with a hawk strategy.

Another source of variation in attractiveness assessments is local differences in the range of available variation in the cues being assessed (Sugiyama, 2005). This principle should hold regardless of the social value(s) being assessed, because attractiveness for any social value is relative to the available alternatives within a particular context. Research suggests that some of the available range of variation is based not only on local variation in the cues being assessed but on the phenotypic condition of the assessor.

In mating, another source of assessment variation is the range of competitors and the relative competitiveness of the assessor. The costs and benefits of different strategies are contingent on the assessor's phenotypic condition relative to competitors and the assessor's access to resources relative to competitors. Consequently, the mate value of a given individual will vary, in part, depending on the mate value of the individual making the assessment.

LIFE HISTORY TRADE-OFFS AND IMPLICATIONS FOR ATTRACTIVENESS RESEARCH

Human survival and reproduction are dependent on solving adaptive problems associated with multiple, partially overlapping spheres of social interaction, such as mates, offspring, kin, and allies. Individuals who were attracted to conspecifics exhibiting cues of high social value would have been more successful than those who were less discriminating. Our evolved attractiveness-assessment psychology is, therefore, expected to index social value across these domains. Human evolutionary life history provides the key to understanding these domains of human social value and the physical cues correlated with them.

Life history theory examines how and why natural selection produces age-related allocation of resources to different life functions both across and within species. Because resources are finite, there are trade-offs in the allocation of energy to different life functions (e.g., Charnov, 1993; Del Giudice, Gangestad, & Kaplan, Chapter 2, this volume; Stearns, 1992; Williams, 1966). Within a species' typical life history pattern, then, selection is predicted to produce adaptations that generated adaptively "strategic" trade-offs in energy allocation in response to evolutionarily relevant variables (e.g., Hill & Hurtado, 1996; Stearns, 1992; Trivers, 1972). These variables include extrinsic and intrinsic factors. Extrinsic factors include mortality and morbidity risk, the relative value of available resources, their spatial distribution, and costs of acquisition. Intrinsic factors include ego's sex, developmental and life-history stage, phenotypic condition, fertility, health, constraints, and options. Determining how individuals use local environmental cues to adjust their allocation of life resources is a main goal of understanding variation within a species' general life-history parameters (e.g., Hill & Hurtado, 1996).

Human life history includes a unique constellation of traits including: altricial birth; a long period of postweaning dependence; delayed reproduction; short interbirth intervals resulting in multiple dependent offspring; menopause; long postreproductive lifespan; allo-maternal investment; intra- and intergenerational resource transfers; facultative care of the sick and injured; and high levels of skill and knowledge acquisition, and social knowledge transmission (e.g., Flinn, Geary, & Ward, 2005; Hill, Barton, & Hurtado, 2009; Kaplan, Hill, Lancaster, & Hurtado, 2000; Leigh, 2001). Humans devote more of their energy to brain function, and have higher diet quality to support it (based on data from extant foragers), than expected of a primate our size. Conversely, we expend relatively less energy on muscle tissue, and more on fat reserves during infancy and early development, and to support fetal cognitive growth (Lassek & Gaulin, 2008; Leonard, Robertson, Snodgrass & Kuzawa, 2003). Food transfers, health care, and allo-maternal care help offset these costs.

At a general level, age-related trade-offs are expected between somatic (growth and maintenance) and reproductive (mating and parental) investment. However, adaptations regulating these investments are expected to be fine grained. For example, trade-offs documented among Shuar forager-horticulturalists include: quantity and quality of offspring (Blackwell, 2009); growth, body fat, and immune function (e.g., Blackwell, Pryor, Pozo, Tiwia, & Sugiyama, 2009; Blackwell, Snodgrass, Madimenos, & Sugiyama, 2010; Urlacher et al., 2014); branches of immune function (Blackwell et al., 2010), pregnancy, lactation, bone maintenance, and reformation (Madimenos, Snodgrass, Liebert, Cepon, & Sugiyama, 2012); pregnancy and lactation and mate's activity levels (Madimenos, Snodgrass, Blackwell, Liebert, & Sugiyama, 2011); helminth (intestinal worm) infection and disgust sensitivity, mediated by local costs of avoidance of fecal contamination (Cepon-Robins et al., 2013; Cepon-Robins et al., 2014); growth and childhood stress (Liebert et al., 2014). Trade-offs between Shuar childrens' growth and immune function are apparent during the week of illness and for a month thereafter, and are mediated by the child's body fat reserves (Urlacher et al., 2014). Tradeoffs between quantity and quality of offspring differ by sex and region, apparently due to differences in growth costs and age-related value of juvenile male and female labor across Shuar territory (Blackwell, 2009; Blackwell, Tiwia, et al., 2010). Further, different dimensions of growth are prioritized over others: Shuar have high prevalence of stunting (short height for age) but almost no wasting (low weight for height). These and studies in a variety of other populations point to complex temporal and socioecological regulation of life history trade-offs, and long-term dynamic and cumulative effects on phenotypic quality, reproduction, and health-related outcomes associated with fitness (e.g., Bribiescas, Ellison, & Gray, 2012; Ellison, 2003; Hill & Hurtado, 1996; Jasienska, 2009; Kramer, Greaves, & Ellison, 2009).

In short, adaptations regulate a vast number of trade-offs that ultimately affect how we look, smell, and sound, and these trade-offs vary based on a plethora of local and individual conditions. Phenotypic and behavioral results of these trade-offs are complex and varied, both across and within socioecological contexts. Documentation of trade-offs requires large sample sizes, repeat measures, and data on multiple variables, and presents a host of other methodological and theoretical challenges. Phenotypic correlation—where interindividual variation in physical condition or access to resources leads to positive or no correlation, instead of negative correlation, among traits that trade off (Stearns 1989)—is also an issue in interpreting study results. The fact that many aspects of attractiveness covary within individuals is at least in part a function of phenotypic correlation.

The past decade has seen a small but welcome increase in cross-cultural studies of attractiveness among nonwestern, nonindustrialized, nonstudent populations. However, cross-cultural testing has required a rethinking of hypotheses and methods and tempering of conclusions in light of variation in the socioecological context in which these adaptations play out (e.g., Schmitt, 2014; Scott, Clark, Boothroyd, & Penton-Voak, 2012; Scott et al., 2014). A life history approach predicts that, depending on the functional design of adaptations for attraction, local conditions will often produce variation in attraction to different levels of a trait and in the prioritization of traits used to make assessments. This is because different trade-offs are expected within and across cultures and mating strategies deployed. Thus, we expect variation in behavioral outputs (e.g., assessments of relative attractiveness) as functional products of evolved attractiveness-assessment mechanisms.

DOMAINS OF HUMAN SOCIAL VALUE IN LIFE HISTORY PERSPECTIVE

Conspecifics are of value to us in a range of social contexts that affect fitness. Individuals differ in their ability and willingness to provide benefits to us—and also in their ability to inflict costs on us—in each of these domains. For each domain of social value, then, some individuals are more valuable than others to the assessor. Accordingly, we would expect selection to have produced mechanisms that assess conspecifics in terms of the degree and kinds of social value they hold for us (e.g., Sugiyama, 2005).

For example, women face the problem of assessing a potential long-term partner's ability and willingness to invest in themselves and their offspring, which they must then weigh against the candidate's ability and willingness to invest in other women. Males face a similar assessment for long-term mating. Lukaszewski and Roney (2010), therefore, predicted that mate preferences for personality traits would depend on the target of the partner's behavior. Subjects rated kindness and trustworthiness toward the subject or his/her family much higher than the same behaviors directed toward others. Conversely, subjects preferred partners who were dominant to members of the partner's sex over partners who directed their dominance toward the subject.

Methodologically, studies of attractiveness must be precise in stipulating the social value being assessed and trade-offs between different aspects of social value. Some cues of social value will be recurrent across domains, whereas others will be domain specific. For example, across all domains of social value, cues of health are predicted to influence attractiveness because health is a valuable asset for all positive interaction partners (Sugiyama, 2005). Another factor to consider is the temporal scope and informational integration of the assessment process: The perception of a person's relative attractiveness in a given domain may change with long-term observation or behavioral interaction. For example, an otherwise physically beautiful person who too highly overvalues him/herself relative to the assessor's evaluation will be found less attractive as a cooperative partner (Sell, Tooby, & Cosmides, 2009; Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008). A methodological concern is the terminology used to elicit preferences and assessments from subjects: *attractive, cute, sexy*, and *handsome* do not mean the same thing, and each term appears to reflect a different constellation of social value traits (Sugiyama, 2005). The question of how different attractiveness adaptations relate to each other and to different aspects of social value requires much additional work, but headway is being made.

MATE VALUE

Finding, attracting, and maintaining a relationship with another individual long enough to reproduce is complicated, fraught with potential missteps, and conflicts of interest. Raising offspring entails additional problems. Only a very limited subset of attractions and behaviors lead to successful reproduction under a given set of circumstances. Mate selection and mating strategies have therefore been under intense selection.

Human mating is flexible, exhibiting both long- and short-term mating strategies, serial monogamy, some degree of polygyny and lesser degrees of polyandry (e.g., Buss & Schmitt 1993; Daly & Wilson, 1983). Both sexes may engage in extra-pair copulations (e.g., Greiling & Buss, 2000; Thornhill & Gangestad, 2008). Mating effort includes the identification and assessment of potential mates, and the allocation of time and energy to courtship. People differ in mate value, defined as the degree to which an individual would promote the reproductive success of another individual by mating with him/her. Mate value includes residual reproductive value—the probable number of future offspring a person of a certain age and sex will produce (Symons, 1979). Human reproductive value is usually discussed in species-typical perspective, but because reproductive value may vary across local and individual conditions, we must frame our predictions accordingly. Over time, selection favors alleles that organize developmental properties that identify, assess, and integrate cues of high mate value, and motivate individuals to be attracted to conspecifics exhibiting these cues, because these preferences likely led to more successful reproduction than alternative designs. The sum of these assessments contributes to our perception of a potential mate's "physical attractiveness."

Components of human mate value include species, sex, age, degree of relatedness, health, status, kindness, intelligence, and willingness and ability to mate with ego and invest in ego's offspring. Our mate-selection psychology must assess a potential mate for cues associated with each of these components, weigh their relative importance under current and probable future conditions, integrate these inputs to arrive at a comprehensive estimation of mate value, and regulate a graded emotional and behavioral response. Some features associated with high male-mate value differ from those associated with high female-mate value; criteria of male and female attractiveness are expected to differ when this is the case (e.g., Buss, 1989; Symons, 1979).

Some individuals have higher mate value than others. The result is competition for access to mates, especially high-quality ones. Darwin referred to the selective force created by this competition as *sexual selection*. Intrasexual selection refers to the selection of traits (e.g., tusks, body size, and musculature) that enhance their bearer's chances of gaining sexual access to the opposite sex relative to same-sex competitors. Intersexual selection is the process whereby individuals with a given trait are preferred by the opposite sex as mating partners, with the result that said trait is spread, elaborated, or maintained in the population even if it has no survival value (Darwin, 1871). If members of the choosing sex are sexually attracted to a feature of the chosen sex (e.g., a longer-than-average tail), and if offspring inherit these traits and preferences, then the preferred trait can become highly exaggerated (e.g., the peacock's tail), a phenomenon referred to as *runaway sexual selection*. Alternatively, good-genes sexual selection hypothesizes that attractive individuals who have higher mating success may also have other high-fitness attributes associated with heritable genetic variation, such as lower mortality or greater parasite resistance (Hamilton & Zuk, 1982). Mate choice for these attributes (or their correlates) would thereby increase the genetic quality of the offspring. Besides good genes selection, a number of species appear to exhibit mate choice for material provisioning and protection of mate and offspring.

Biologists differentiate cues from signals: Signals are traits selected for because they carried specific meanings that changed the behavior of recipients in ways that benefited the receiver, whereas cues were not modified by selection to carry meaning per se (e.g., Bradbury & Vehrencamp, 1998; Smith & David, 2003). In practice, it is sometimes difficult to distinguish signals from cues, because what are initially cues can be shaped by sexual selection to carry specific meanings that change the behavior of perceivers. Costly signaling theory posits that traits associated with good genes or provisioning of material benefits can evolve into elaborate displays, which function as "honest" signals about underlying phenotypic and genotypic qualities of their bearers (Grafen, 1990; Zahavi & Zahavi, 1997). When a trait signals information about its bearer that is useful for the bearer to transmit and for the recipient to receive, then false signals might also be selected for, undermining the signal value of the trait for both sender and receiver. However, if the cost of producing the signal is such that only some individuals can afford to fully develop it, and that cost is linked to the underlying phenotypic or genotypic quality being signaled, then recipients can be assured of the signal's "honesty." Elaborate anatomical features, such as the peacock's tail, can evolve this way: Only high-quality males can produce the finest displays, so peahens can reliably use male display in their mate choices, and the fitness costs of the display to the peacock are offset by his increased mating opportunities. Costly signals are not restricted to mating: They can evolve whenever the conditions outlined previously are met (Grafen, 1990; Zahavi & Zahavi, 1997; c.f. Donaldson-Matasci, Bergstrom, & Lachmann, 2013). Without clear evidence that a trait used in attractiveness assessment has evolved as a signal, we should first consider hypotheses that it is used as a cue.

Because mating competition is costly, selection produces adaptations that assess one's mate value relative to potential rivals. This saves time, energy and physical costs by averting competition with rivals the individual is unlikely to outcompete. Conversely, our ancestors could also increase their mating access by driving off, dominating, outshining, or undermining (e.g., poaching mates from) rivals against whom they had a reasonable chance of success. This evaluation entails same-sex attractiveness assessment—not for the purpose of mating, but for determining one's relative mate value and intrasexual competitiveness (e.g., Pawlowski & Dunbar, 1999; Puts, 2010).

For example, men have traits indicating strong selection for intrasexual competition. They can accurately assess the relative strength of other males using body, vocal, or facial features, and these correspond to assessments of fighting ability and intrasexual competitiveness (Puts, 2010; Sell et al., 2009). These physical traits develop under regulation from an increase in androgens, particularly from puberty (e.g., Bribiescas, 2006). Females, in turn, exhibit mate choice for these features of size and musculature associated with strength (Sugiyama, 2005). Dijkstra and Buunk (2001) show that males experience more jealousy in response to a potential rival with higher shoulder-to-hip ratio (i.e., a V-shaped torso). Taller and more dominant men are less sensitive to these cues than shorter and less dominant men, and are also less jealous, indicating regulation of these perceptions in relation to self-other relative competitiveness (e.g., Buunk, Park, Zurriaga, Klavina, & Massar, 2008; Watkins, Fraccaro, et al., 2010; Watkins, Jones, & DeBruine, 2010). Men find these traits unappealing in mating competitors but may find them attractive in allies or cooperative partners, whereas women prefer cues of strength and intrasexual dominance in mates. We may thus expect some concurrence in male and female assessments of an individual's sexual attractiveness to members of the opposite sex. But we should also expect systematic variation in these assessments, partly affected by context (including relative intrasexual rivalry between assessor and assessee) and the social value of these cues in other domains.

For women, male-mate value includes traits associated with genetic quality, health, and physical formidability, as well as traits associated with ability and willingness to invest in a woman and her offspring (Symons, 1979). Assessments based on these two criteria may diverge. In long-term relationships, women often have to trade off physical attractiveness for willingness to invest, because they often have to trade off genetic and phenotypic quality for investment (Gangestad, Thornhill, & Garver-Apgar, Chapter 14, this volume). However, these trade-offs are context dependent: Women place more importance on physical characteristics in short-term and extra-pair sex partners, and during the fertile phase of their ovulatory cycles. A woman's own attractiveness, mating status, and preference for short-term mateships affect the degree of this ovulatory cycle effect, because they affect the relative trade-off she faces between a mate's genetic or phenotypic quality. For instance, in western and some nonwestern contexts, women show greater preference for "masculine" faces, voices, and bodies in short-term mates than in long-term mates. Recent research also shows cross-cultural variation in women's preference for degree of facial masculinity (Scott et al., 2014). In assessing rivals, women focus on physical cues and behaviors related to female mate value (e.g., nubility, youth, fertility, fecundity, health). Women's intrasexual competition enhances these for self and downplays them in rivals, mediated by their own physical attractiveness. Conversely, women downplay their own promiscuity and denigrate it in others, especially in long-term mating competition (e.g., Bleske & Shackelford, 2001; Buss & Dedden, 1990).

It follows that cue/signal detection, assessment, integration, and motivational adaptations are integrated-but-separable components of attractiveness psychology, just as receptors, cue-assessment integration, and pleasure responses are separate components of umami attraction. In assessments of male sexual attractiveness, for example, women might experience feelings of desire (if the male were judged attractive), repugnance (if the male were judged unattractive or identified as close kin), or indifference. In contrast, men might experience feelings such as submissiveness (if the male were judged attractive or dominant) or self-confidence and dominance (if the male were judged unattractive or less dominant). Men and women have different adaptive objectives when evaluating the sexual attractiveness of a given male or female. Men must decide whether they should provoke, avoid a confrontation with, or cooperate with another male, and have, therefore, been under selection to evaluate the prowess of other males *vis-à-vis* their own. Women must decide whether they should copulate with, ally with, or avoid a given male, and have, therefore, been under selection to evaluate males in terms of the fitness costs and benefits they present as mates and fathers. In evaluations of female attractiveness, men must decide whether they should copulate with, cooperate with, or avoid a given female, and have, therefore, been under selection to evaluate females in terms of their fertility and sexual accessibility. Women must decide whether they should provoke, avoid a confrontation with, or befriend another female, and have, therefore, been under selection to evaluate the attractiveness and dominance of other females *vis-à-vis* their own.

Note that costs and benefits associated with these outcomes may vary by sex, individual, and circumstance. This gives rise to interindividual variation in attentiveness to different cues/signals, cue/signal assessment and integration, perceptions of attractiveness, and behavior. In long-term contexts, some factors are important for both sexes (e.g., kindness, social status, physical attractiveness) but differ in relative importance to men and women. For example, Shackelford, Schmitt, and Buss (2005) used factor analysis to examine trade-offs among four dimensions of mate preference: dependable/stable versus good looks/health; love versus status/resources; education/intelligence versus desire for home/children; and sociability versus similar religion. Physical cues are hypothesized to be involved in assessment of all these dimensions of mate value, except preference for similar religion. Further, well-documented sex differences indicate that overall, men place more value on good looks in a long-term mate than do women, whereas women place more value on mate's status and resources (e.g., Buss, 1989).

Determination of mate value entails a number of adaptive problems, the solution to each of which will affect perceptions of attractiveness on the part of the assessor. The first step in this process is identification of viable mates. Obviously, copulation with inanimate objects, other species, or sexually immature humans is ineffectual for reproduction. Copulation with members of the same sex is similarly ineffectual for reproduction per se, although it may be of indirect benefit as a means of recruiting allomothers. Copulation with carriers of contagious disease entails fitness costs, and copulation with individuals bearing genetic anomalies can result in pregnancies that produce non- or less-viable offspring, as can copulation between close genetic relatives. Forced copulation with fertile human members of the opposite sex entails opportunity, reputational, and possibly retributive costs. In assessing rivals, men may, therefore, focus more on physical cues associated with potential rivals' formidability and dominance in assessing themselves *vis-à-vis* competitors because these attributes could spell death or loss of a mate at the hands of a rival or rival coalition. Data from psychological studies, homicide patterns, and intratribal conflict support the view that various aspects of mating competition are often causes of violence, and size and strength are assets in this competition (e.g., Buss, 2006; Chagnon, 1988; Daly & Wilson, 1988; Macfarlan, Walker, Flinn, & Chagnon, 2014; Puts, 2010; Scalise Sugiyama, 2014).

Male Mate Value Women's attractiveness-assessment psychology is predicted to include mechanisms for evaluating cues associated with male genotypic quality. One cue to genotypic quality is phenotypic condition, part of which is heritable. Male mate value also includes material provisioning of mates, offspring, and other adults: Among foragers, men provide about 85% of the protein and 65% of the calories to the diet (Cordain et al., 2000; Kaplan et al., 2000; Marlowe, 2001), with positive effects on female fecundity and offspring immune function, health, and survival (Gurven & Hill, 2009). Across societies, women appear to assess prospective long-term mates using cues of willingness and ability to invest in a mate and her offspring, such as kindness, intelligence, industriousness, and ability to acquire resources (e.g., Buss, 1989). Male ability and willingness to invest is important for females because of the high costs of pregnancy, lactation, the long period of juvenile dependence, and short interbirth intervals resulting in multiple dependent offspring (e.g., Kaplan et al., 2000). Ache juveniles with father living suffer a third lower mortality than those whose father has died (Hill & Hurtado, 1996), and hunter-gatherer males contribute significantly to subistence (e.g., Gurven & Hill, 2009), although effects of fathers on correlates of offspring fitness vary across social and ecological contexts (e.g., Bribiescas et al., 2012; Hewlett & Macfarlan, 2010; Marlowe, 1999a, 1999b, 2001, 2005; Sear & Mace, 2008).

Human males grow for a longer period, mature more slowly, and reproduce later than females (e.g., Bogin, 1999). They also exhibit higher interindividual variance in reproductive success than females (e.g., Betzig, 2012). Because paternity is less certain than maternity, men's age at first reproduction is harder to track directly, but males in foraging societies appear to begin reproducing in their early 20s—several years later than females. Age-related changes in male fertility among the Ache, !Kung, and Yanomamö indicate a rise in fertility beginning in the late teens and peaking in the mid-30s to early 40s. Mean age at last birth for 23 Ache men who lived to at least age 60 was 48 years: Although half of the men ceased reproducing as early as women did, the other half reproduced for longer periods, including six who continued past their mid-50s. Further, male foraging success peaks relatively late in life, ranging from the 30s to almost age 50 (Kaplan et al. 2000; Walker, Hill, Kaplan, & McMillan, 2002). Apicella (2014) found that strength predicts reproductive success and reputation for hunting ability among Hadza foragers of Tanzania; however, strength peaks much earlier than hunting return rates, indicating the important role of knowledge in hunting (e.g., Gurven, Kaplan, & Gutierrez, 2006). Because male mate value is not so closely linked to youth, female preference mechanisms are expected to target cues of genotypic and phenotypic quality and productive ability rather than youth per se (Buss, 1989). Selection is expected to have favored female assessment for phenotypic cues of male fertility. However, since one fertile male can potentially inseminate multiple females, preference for cues to fertility per se is less intense in women than in men (Symons, 1979).

Women can benefit from pursuing a mix of long- and short-term mating strategies, to reduce trade-offs inherent in each (e.g., Buss & Schmitt, 1993; Gangestad & Simpson, 2000). It is now clear that studies should incorporate methods that disentangle these considerations. From a female perspective, poor health and genetic quality are liabilities in any prospective mating partner. However, women are expected to find physical traits linked to underlying genetic qualities relatively more important in short-term than in long-term mates. Long-term mateships entail childrearing; thus, prospective long-term partners must be evaluated for their parenting abilities and good-partner qualities as well as their physical attributes. Thus, size, strength, pugnacity, and physical dominance may be traded for ability and willingness to invest in the woman and her offspring, although attractive women don't face these trade-offs so they desire high levels of both (Buss & Shackelford, 2008). For women, parenting skills are less important in a short-term mate, for obvious reasons. Because men relax their standards for short-term mates, short-term mateships can offer some women access to higher genetic quality sires for their offspring than they could acquire in a long-term partner, and many of the traits associated with aggressive formidability—for example, size, strength, and facial masculinity—are proximate cues of genetic quality (e.g., Buss & Schmitt, 1993; Gangestad, Merriman, & Thompson, 2010; Thornhill & Gangestad, 2003).

Males face investment trade-offs between mate quantity and mate quality. Local paternal effects on offspring fitness affect the costs and benefits associated with each and the relative costs and opportunities of obtaining multiple mates. The latter will be affected by a given male's mate value, local degree of effective polygyny or operational sex ratio, and relative values of long-term and short-term mating for women. Some physical traits are associated with differences in male-mate value that may influence the male's propensity to pursue short- or long-term mating strategies. Females may use these traits as cues to probable male-mating behavior. Women may be expected to use these same criteria in their assessments of the relative social value of their fathers, brothers, and other male kin to others, but to weight the criteria differently.

Female Mate Value Access to women's reproductive capacity constitutes a primary constraint on men's relative reproductive success. Human female mate value is, therefore, closely linked to age-related reproductive life stage, health, fertility, and parity (see Sugiyama, 2005). Women have delayed maturity compared to that expected for a primate of our size, and cease reproduction some 20 years prior to death, resulting in a compression of the reproductive life span. Age at first birth for female chimps is around 12 years, whereas for female foragers in natural fertility conditions it is about 17 years (Hill & Hurtado, 1996; Kaplan et al., 2000; Thompson et al., 2007). A woman's reproductive value is highest just before she begins fertile ovulatory cycles, because the number of reproductive years ahead of her is highest and the probability that she will die prior to reproduction is lowest. Fertility varies across the reproductive lifespan. Peak age-specific female fertility in industrialized nations is around 22 years and may show significant declines by 27. Data from foraging populations indicate peak age-specific fertility varying from about 22 to 25 years among the !Kung of Botswana and the Yanomamö of Venezuela to about 28 to 35 years among the Ache of Paraguay. Diet, work effort, pathogen and social stress, and other social variables affect hormonal indices of female fertility and fecundity, suggesting that female reproduction varies with socioecological variables affecting energetic availability (e.g., Ellison, 2001, 2003; Jasienska, 2009; Valeggia & Ellison, 2009).

Women's minimum necessary maternal investment is high. It includes accumulation of bodily reserves and maintenance of a positive energy balance, placentation, gestation, and the mortality risk associated with bearing a large-headed offspring through a relatively narrow pelvic opening (e.g., Ellison 2001, 2008; Rosenberg & Trevathan, 2002). Fecundity depends on hormonally regulated ovarian function, which tracks energetic availability and demands. For women of normal BMI, pregnancy increases energetic requirements by roughly 90, 300, and 466 calories a day during the first, second, and third trimesters, respectively. Breastfeeding increases energy requirements by about 450 to 500 calories per day in healthy western women who are not particularly active (Butte, Wong, Treuth, Ellis & Smith, 2004). Lactation suppresses reproductive function in relation to a woman's energy budget (e.g., Ellison, 2003). Humans have shorter interbirth intervals than expected given these costs. The mean weaning ages for 30 hunter-gatherer groups reported in R. L. Kelly (1995) averages 30.9 months (Sugiyama, 2005). The interbirth interval for women in a group of 11 foraging societies is 3.47 years, and the average total fertility rate is between five and six children. The costs of pregnancy, lactation, short interbirth intervals, and multiple dependent children appear to be offset by slow child growth and allomaternal work effort and food provisioning (e.g., Gurven & Walker, 2006; Hrdy, 1999).

Women experience reproductive decline earlier than senescence of other bodily functions (e.g., Hill & Hurtado, 1996; Thompson et al., 2007). Female foragers may thus live well past their reproductive years, although maternal and grand-maternal investment of resources and social support in offspring may continue into offsprings' adulthood. Among Ache women, the average age of last birth is 42. By age 46 the yearly probability of birth is 0 (Hill & Hurtado, 1996). R. L. Kelly (1995) lists data on mean age at last birth for women in 10 foraging societies; the average mean is 34.9 years (Sugiyama, 2005).

The human female reproductive environment of evolutionary adaptiveness (EEA) was such that for most of the time between menarche and menopause a woman was not fecund. Symons (1995) calculated that a Yanomamö woman can possibly conceive on just 78 of 8,030 days during her average reproductive lifespan. My calculations (Sugiyama, 2005) based on R. L. Kelly's (1995) data on foragers yielded a broadly similar conclusion. With an average age at first birth of 17 and average age at last birth of 42 (for Ache), an average female forager's potential fertile lifespan is about 25 years, during which she is likely to have five children. On average, she would have been pregnant or lactating for 5,985 days—almost two-thirds of her reproductive lifetime. With 3 fertile days per month she might be fecund on only 314 days in her 9,125-day fertile lifetime, assuming she suffered no ill health, food deficiencies or other stressors that limited fecundity.

Since female reproductive value declines with age after menarche, cues associated with advancing age are expected to be negatively correlated with female sexual attractiveness (Symons, 1979). With each birth, the average forager woman loses another sixth of her reproductive value. Thus, cues associated with parity are expected to be negatively correlated with female sexual attractiveness. Because some cues to fecundity are observable, we may also expect adaptations that use statistically reliable cues to fecundity-related hormonal status in assessments of female mate attractiveness. Symons (1979, 1995) predicted that this would result in males being attracted to cues of nubility, or highest reproductive value (i.e., female has begun ovulatory cycling but not yet given birth). Since women do not advertise estrus (or do not do so widely), attraction to cues of nubility would dramatically increase a male's chances of reproducing. A man who maintained exclusive mating access to a woman over her reproductive lifetime could, on average, sire five or six children with her. Preference for cues of peak fertility would increase probability of conception, particularly for short-term mates (e.g., Symons, 1979).

Women with positive energy balance and good health are likely to be more fertile than those with negative energy balance and poor health. Thus, men are expected to have evolved preference mechanisms that find cues of good health and nutrition attractive, and women are expected to use the same cues in assessments of their reproductive rivals. Even though selection may have produced attraction to cues of nubility, attraction to these cues alone might compromise long-term mateships, and would have the effect of concentrating male reproductive effort on fathering only the first of a woman's average six offspring. Other cues that a woman is resuming ovulatory cycling postpartum, such as lightening of the skin (Symons, 1995) or having a child approaching weaning age, should predict some of the variance in real-world female sexual attractiveness. Although self-report measures and other studies have failed to find male preference for peak residual reproductive value, experimental tests including the relevant range of stimuli do (Blackwell & Sugiyama, 2008). Across cultures, physical attractiveness ranks high among the criteria that men look for in mates (e.g., Buss, 1989). Even where self-report findings suggest that attractiveness is not so highly valued, more detailed methods reveal strong preference for physical attractiveness (Pillsworth, 2008). Women appear to be sensitive to this preference, as indicated by the highly lucrative cosmetics and associated beauty industries.

KIN VALUE

Anthropologists have long recognized that, in prestate societies, social relationships are organized by kinship and kinship-like institutions. All known human cultures include three basic kinds of social relationships based on relatedness: marriage, descent, and kinship classification systems. Classificatory kinship systems are based on three conceptual primitives: sex, descent, and generation. These systems fall into several basic types, which vary in terms of how kinship is parsed along these basic dimensions. Who is and is not an appropriate marriage partner is often based on both classificatory kinship and descent (e.g., Chagnon, 1997). These common features of social organization reflect the value placed on kinship cross-culturally (e.g., Brown, 1991; D. Jones, 2003).

Kin selection and parental investment theories help explain these values, even though classificatory kinship and biological kinship do not completely overlap.

Individuals can increase the alleles they bear not only via their own reproduction, but also via aid to those with whom they share those alleles by virtue of recent common descent. Hamilton (1964) thus showed how one evolutionary pathway by means of which altruism can arise: when the cost to the altruist is less than the benefit to the recipient devalued by the probable degree to which they are related. From ego's perspective, then, others vary in kin value both as potential investors and as foci of investment.

Trivers (1972) predicted the adaptive problems parental investment mechanisms need to solve, and the logic of his argument can be extended to kinship more generally and to other domains of human social value. People vary in (a) their probable degree of relatedness to ego, (b) their ability to translate investment by ego into fitness or inclusive fitness, (c) the opportunity costs to ego imposed by that investment, and (d) their willingness and ability to invest resources in ego, ego's offspring, and ego's other kin. The probability that kin can translate investment into successful reproduction is affected by their phenotypic and genotypic quality, including the related variables of health, age, fertility, fecundity, and sex, all of which are associated with physically observable cues. To the degree that potential kin exhibit reliable cues to these values, they are expected to be more attractive than others as sources or targets of investment. Conversely, because inbreeding with close genetic relatives increases the probability that offspring will be homozygous for deleterious alleles, close kinship should negatively affect attractiveness as a sex partner (or *sexual value*; Tooby et al., 2008).

Data from nonwestern, natural fertility populations show that kin effects on fitness-related traits are significant and vary locally by context. For instance, Hagen, Barrett, and Price (2006) found older brothers had positive effects, and older sisters negative effects, on younger sibling growth among Shuar (see also Hagen & Barrett, 2009). In a larger regional sample of Shuar villages, Blackwell (2009) found quantity/quality trade-offs between number of household siblings and growth. However, they also found a U-shaped relationship between distance to road and boys' effects on siblings' growth, and an inverse U-shaped relationship between distance to road and girls' effects on younger siblings' growth. These results are hypothesized to reflect local sexual division of labor, resulting in sexual variation in productive abilities depending on where villages are located.

The regulation of behavior based on kinship requires cues statistically associated with relative degree of relatedness and adaptations that assess these cues to estimate kinship. Estimated kinship, in turn, regulates emotional outputs and discriminative behavior in relation to the social value at issue (e.g., Lieberman, Tooby, & Cosmides, 2007). Tooby et al. (2008) refer to this kinship regulatory variable as the *kinship index*. The kinship index can be based on contextual cues, prior association during development, or phenotype matching (Axelrod, Hammond, & Grafen, 2004; Mateo, 2015). In humans, we see evidence of all three, and their effects on attractiveness.

Mother-offspring mutual recognition occurs quickly, based on olfactory, visual, tactile, auditory, and behavioral interactions. One cue of sibship is one's mother caring for an infant (*maternal perinatal association*, or MPA). For older siblings, one's mother nursing an infant is a statistically reliable cue of sibship or half-sibship. For younger siblings, these cues are not available, and duration of childhood coresidence is used instead (e.g., Lieberman et al., 2007). Kinship index influences at least two different aspects of attractiveness, but in opposite ways. For those indexed as siblings, it increases attractiveness as a target of altruism, but decreases attractiveness as a sexual partner (Lieberman et al., 2007). The same logic holds for parent-offspring altruism and sexual aversion. Kinship index should also regulate assessments of altruistic, reciprocal, and coalitionary value. Other evolutionarily relevant cues of an individual's relatedness to ego are: observing a close female relative give birth to or nurse said individual; observing kin exhibiting altruistic behavior or sexual avoidance toward said individual; and perhaps the use of kinship labels by kin in reference to said individual (e.g., Lieberman et al., 2007).

Evidence suggests that phenotype matching based on visual and olfactory cues is also used in kin estimation and attraction. Facial self-similarity increases trust and cooperation, but decreases sexual attraction (e.g., DeBruine et al., 2011, Lieberman et al., 2007). Phenotype matching based on olfactory cues is also apparent, based in part on underlying genetic influences (e.g., Porter, Balogh, Cernoch, & Franchi, 1986; Roberts et al., 2005). Moreover, father-daughter and brother-sister pairs show odor-based mutual sexual aversion (Weisfeld, Czilli, Phillips, Gall, & Lichtman, 2003). The interest of kin in the mating behavior of others is mediated by degree of perceived physical similarity (Faulkner & Schaller, 2007). Tellingly, independent raters can discriminate relatedness of others based on photographs (e.g., Alvergne, Faurie, & Raymond, 2010; DeBruine et al., 2009; Kaminski, Dridi, Graff, & Gentz, 2009).

People differ in their probable value to kin of ascending generations in terms of their social value as reproductively successful descendants and as contributors to other kin. Parental investment (PI) theory focuses on resource allocation trade-offs among existing offspring, current and future offspring, and the quantity and quality of offspring (e.g., Trivers, 1972). Trivers predicted that parental investment should be allocated in response to three assessments: the probability that the juvenile is (1) one's own progeny, (2) is able to translate investment into future reproductive success, and (3) is a better investment of those resources than alternate potential uses. Some cues to (1) and (2) are observable, and selection has produced adaptations that use these cues to assess a juvenile's attractiveness as a target of investment.

In both women and men, offspring recognition is effected in part via adaptations that enable rapid learning of olfactory, visual, auditory, and tactile cues associated with the infant (e.g., Porter, 1991). These cues regulate attention and attraction by means of hormonal and neurological mechanisms that motivate bonding and caretaking behavior (e.g., Swain et al., 2014; Winberg, 2005). For example, the odor of newborns stimulates greater activation of the dopaminergic system in new mothers than in nulliparous women (Lundström, Boyle, Zatorre, & Jones-Gotman, 2009; Lundstrom et al., 2013). Oxytocin levels are affected by pregnancy, birth, and lactation, and are positively associated with a mother's attraction to her infant, including infant-directed gaze, monitoring of infant, and use of "motherese," affect, and touching. Women also exhibit attentional biases that appear to help regulate childcare. Mothers pay more attention to infant faces than do nulliparous women. This enhanced attention is not a general response to all faces. Mothers pay more attention to infant than child, adolescent, or adult faces, and more attention to infant and child faces when they exhibit distress. Fathers' oxytocin levels parallel those of mothers, but generate slightly different behavior, including more stimulatory contact with the infant, exploratory encouragement, and infant-directed attention to objects (Feldman, Weller, Zagoory-Sharon, & Levine, 2007; Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010). Individual differences in mothers' oxytocin levels are regulated by epigenetic processes linked to early childhood environment, and to mechanisms that take in more immediate contextual variables to compute available resources and probable and actual allomaternal aid (Hrdy, 2009; Swain et al., 2014).

Conversely, research indicates that stepparents invest less in their stepchildren than their biological offspring, and that stepchildren are less attractive or even aversive as investment targets. A number of studies show that stepfathers invest less than biological fathers (e.g., Anderson, Kaplan, Lam, & Lancaster, 1999; Anderson, Kaplan, & Lancaster, 1999; Flinn, 1988). For example, Hadza men living with stepchildren bring in less food than those living with biological children only (Marlowe, 1999a). Stepparents also invest less time and energy in supervision, making stepchildren more vulnerable to fatal accidents (Tooley, Karakis, Stokes, & Ozanne-Smith, 2006). Children living with stepparents are also at elevated risk of abuse and homicide (Daly & Wilson, 1985, 1988). Stepparental investment by males does occur but, tellingly, research suggests that it is used as a means of forming a mateship with the mother (Anderson, 2000). Stepfathers are reported by women as perpetrators of sexual abuse much more often than are biological fathers (Russell, 1984), as expected if sexual attraction is down-regulated by kinship index.

Depending on how and why data were gathered, an estimated 1.7%–30% of children are estimated to be sired by men who are not the putative father (Anderson, 2006). Ability to recognize their own versus others offspring via phenotype matching would provide beneficial input into the kinship index, regulating paternal investment in putative offspring.

Resemblance to self affects attractiveness for investment in hypothetical and real life contexts. When presented with different facial morphs, created using each subjects' image and those of children, males were more likely to choose their own child/face morphs over others as recipients of aid in hypothetical investment scenarios (Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek et al., 2003; Platek et al., 2004). Volk and Quinsey (2007) found facial resemblance more important to men than women in hypothetical adoption scenarios, but other studies found that both men and women used facial self-similarity in investment decisions (Bressan & Zucchi, 2009; DeBruine, 2004). Functional magnetic resonance imaging also showed men's and women's neural activation patterns differed when viewing self but not nonself-morphs, suggesting sex differences in neural processing of facial self-resemblance cues, and Alvergne, Perreau, Mazur, Mueller, and Raymond (2014) found specific facial features used as paternity cues, and that these features are those that change less with development. Apicella and Marlowe (2004) found that men reported greater investment in their children when they thought their children had greater psychological and physical resemblance to themselves. Burch and Gallup (2000) found that among men in a domestic-abuse facility, resemblance was positively associated with men's self-reports of relationship quality with their children and negatively with severity of spousal abuse. Alvergne et al. (2010) found that although mothers' assessments of facial resemblance to children corresponded with fathers' perceptions, fathers' but not mothers' self-reported emotional closeness to children was predicted by actual facial self-resemblance. Mothers also exhibit interest in the resemblance between offspring and putative fathers, as it provides a cue to probable paternal behavior (Daly & Wilson, 1982; Regalski & Gaulin, 1993).

Porter, Cernoch, and Balogh (1985) found that third parties could correctly match mother-offspring odors but not husband-wife pairs, suggesting an underlying genetic mediation of olfactory kin recognition. Among Senegalese coastal populations, Alvergne, Faurie, and Raymond (2009) presented subjects with a child's face or odor, and asked them to pick the true father from amongst either three (facial) or two (odor) choices. Subjects correctly identified the father more often than expected by chance using both visual and olfactory cues. Facial and olfactory resemblance was also positively associated with paternal investment as rated independently by the child's mother, and paternal investment was positively related to the child's BMI and upper arm circumference. Olfactory phenotype matching can be based at least in part on a resemblance to self, because our ancestors could obviously experience the chemosensory cues to their own as well as others' odors. This is particularly useful in generating estimations of close relatedness. Kinship estimate can also be based on chemosensory exposure to individuals exhibiting other cues of close kin, useful in determining "family" resemblance for slightly more distantly related kin.

Understanding the socioecological context in which phenotype-matching systems evolved is critical to hypothesis formulation and testing. For example, facial morph studies primarily use self-based resemblance, but it is unlikely that human environments of evolutionary adaptedness (EEA) provided sufficient opportunities for self-observation to support the evolution of solely self-referential facial phenotype matching. It seems more likely that visual phenotype matching is generated using a kin template constructed by observing close kin (e.g., DeBruine, Jones, Little, & Perrett, 2008). To test this, Bressan and Zucchi (2009) took facial photos of 17 monozygotic and 18 dizygotic Italian twin pairs and morphed each of these with a model's face to produce images composed of 65% of the model's face and 35% of the subject's face. Two months later, subjects were presented with the morphs of their own and their twin's faces and asked to choose (a) which they would help in case of danger and (b) which they would encourage an opposite-sex sibling to marry. Subjects could not recognize the faces as self and twin morphs. For both questions, though, the self-morph was chosen significantly more often than the twin morph, with no difference by twin type or sex.

Bressan and Zucchi conclude that this shows self- rather than twin-referential phenotype matching, arguing that because subjects saw their own twins more often than their own faces, a kin-based phenotype matching template system would generate a sibling rather than self-referential bias. However, all subjects in the study had access to mirrors, so their own facial features may have been input disproportionately into the kin phenotype template (e.g., DeBruine et al., 2008). A functional facial phenotype-matching template generator could not be indifferent to the kinship index of individuals used in generating the template, for the simple reason that our ancestors lived in a densely kin-populated environment. Clearly, more research is needed to illuminate these processes. One obvious test would be to determine whether people with little access to mirrored surfaces also use self-referential similarity over kin-referential templates. Or, less optimally, where there is variation in mirror access, one could determine whether greater access is associated with greater use of self-referenced cues. The number of populations in which such a study is possible is rapidly approaching zero, so it will need to be done soon.

The probability that a juvenile will translate a given amount of investment into successful reproduction is related to that individual's sex, age, genotypic and phenotypic condition, and to socioecological context (e.g., Trivers, 1972; Trivers & Willard, 1973). Physical cues that were evolutionarily correlated with good health and high genetic quality provide observable correlates of a juvenile's probable ability to translate investment into reproduction, and are expected to be found attractive in offspring. Physical cues of low genotypic or phenotypic quality are associated with reduction in parental care, suggesting that these traits are unattractive to parents. For instance, physical deformity is a recurrent proximate cause for infanticide cross-culturally (Daly & Wilson, 1988), and vocal qualities associated with premature birth are aversive to adults (Furlow, Armijo-Pruett, Gangestad, & Thornhill, 1997; Mann, 1992). Poor physical tone, lethargy, or lack of pedomorphic characteristics in infants increase risk of abuse and maternal neglect when resources are scarce (e.g., Daly & Wilson, 1981; Hrdy, 1999; McCabe, 1984). Conversely, physical cues associated with infancy such as large eyes, small noses, and a rounded head are attractive to parents and others (Alley, 1983; Zebrowitz, 1997). Parents of attractive infants are more attentive and affectionate toward them (Langlois, Ritter, Casey, & Sawin, 1995), as are those in allomaternal roles (e.g., teachers) and nonrelated others (Glocker et al., 2009). Meta-analysis shows that less attractive children receive less caregiving (Langlois et al., 2000), and parents rate less attractive infants as older and developmentally more mature (Ritter, Casey, & Langlois, 1991), even though this is objectively not the case.

Resources are finite, and parents must decide whether, and how much, to invest in existing offspring, future offspring, own somatic resources, and mating effort. Trade-offs between investment in quantity and quality of offspring are documented in some cases (e.g., Blackwell, 2009; Gillespie, Russell, & Lummaa, 2008; Hagen, Hames, Craig, Lauer, & Price, 2001; Hagen et al., 2006; Sellen, 1999; Strassman & Gillespie, 2002). The outputs of mechanisms that make these assessments, in conjunction with outputs of the kin index and phenotypic quality evaluators, are thus expected to up- or down-regulate the attractiveness of offspring. Of course offspring are not passive recipients of whatever care others might deign provide. They are predicted to have adaptations that evaluate their own condition, that of their potential caregivers, and other options for acquiring resources, which in turn generate behavior to enhance their own ability to survive and reproduce (e.g., Hewlett & Lamb, 2005; Konnor, 2010; Sugiyama & Chacon, 2005). Possible responses include attempting to increase investment in themselves by others, reducing risks of losing investment, or acquiring more resources on their own. Crying is used by infants to gain attention and investment, and foragers children can and do contribute to their diet by acquiring resources on their own, although this varies across ecological conditions (e.g., Bliege Bird & Bird, 2002; Blurton Jones, Hawkes, & Draper, 1994; Sugiyama & Chacon, 2005). Parents and alloparents, in turn, are expected to be sensitive to juveniles' ability to contribute to their own welfare, and to adjust their reproductive and investment strategies accordingly (e.g., Blurton Jones, Hawkes, & O'Connell, 1997; Daly & Wilson, 1988; Trivers, 1972).

COOPERATIVE VALUE

The human ecological niche is characterized by a high degree of cooperation. Studies of modern and prehistoric foraging societies indicate that ancestral cooperative activities included mate acquisition (Apostolou, 2007), child rearing (Hill & Hurtado, 2009; Hrdy, 2007), foraging (e.g., Alvard, 2003, 2005; Hill, 2002), information transmission (e.g., Scalise Sugiyama, 2011), warfare (e.g., Chagnon, 1997; Ember & Ember, 1997; Keeley, 1996), and aid during health crises (Sugiyama, 2004a). Although people probably lived among relatively more kin than we do in the United States, not all those allies would have been close kin (Apicella, Marlowe, Fowler, & Christakis, 2012; Chagnon, 1979; Hill et al., 2011). Even individuals with whom ego does not directly cooperate can have social value when they yield positive externalities such as increasing ego's food supply, attracting potential mates to ego's proximity, deterring attacks, providing information, or helping ego's allies (e.g., Tooby & Cosmides, 1996). Conversely, individuals may have unintended negative effects upon us. For example, unhealthy individuals may increase disease exposure, and impulsively aggressive individuals may incite conflict. Health, physical abilities, generosity, cooperativeness, and intelligence provide at least some cues to a person's value with regard to these recurrent problems of human life.

Although he overstated the case, Levi-Strauss saw marriage in what he called "primitive" society as an exchange between men (i.e., the consanguinial male relatives of the bride and groom). Certainly, who mates with whom is of interest not only to the principals. With its concomitant social, economic, and reproductive rights and obligations, the universal institution of marriage reflects the fundamental interests of individuals in the mateships of their offspring, siblings, and other close relatives. Mateships build alliances and serve as vehicles for a descent groups' reproductive future, and sons- and daughters-in-law play integral social and economic roles. Accordingly, family members regularly assess potential daughters- and sons-in-law regarding their coalitional, productive, and reproductive assets, and the ethnographic literature reveals that many marriages are arranged (Apostolou, 2007). Parents' and offspring's assessments may overlap with regard to long-term mate value (except for assessments contingent on individual's phenotypic condition), but in other respects they may differ. For example, parents might place more importance than offspring on a prospective mate's cooperative qualities and coalitional ties.

Another critical sphere of cooperation is child rearing. Human life history is characterized by a high degree of investment in juveniles provided by individuals other than the biological mother, including biological and social fathers, aunts, uncles, and grandparents. Evidence suggests humans are cooperative breeders, with multiple females and males cooperating in the raising of offspring (e.g, Hill & Hurtado, 2009; Hrdy, 2007; Kramer, 2010; Mace & Sear, 2005). People may thus cultivate relationships with others based on their suitability as alloparents. Relevant cues in making this choice may overlap with cues of long-term mate value, but will diverge in some areas. Obviously, sex of alloparent is less important than sex of mate. Fertility and fecundity might oppositely affect mate and alloparent value: A postmenopausal woman has low reproductive value, but could provide valuable benefits as an alloparent, and would not face a trade-off between investment in allochildren and her own current reproduction. Similarly, prereproductive age females often provide alloparental support for younger siblings. But the opportunity costs of doing so increase as they have children of their own, thus decreasing their alloparental value to their parents.

Cooperation is also critical in the context of coalitional violence, where estimated male mortality from violence in tribal societies ranges from 10% to 30% or more (e.g., Beckerman et al., 2009; Chagnon, 1997; Patton, 2000; Pinker, 2011; Walker & Bailey, 2013), and the evolution of neuroendocrine regulation of coalitionary behavior (Flinn, Ponzi, & Muehlenbein, 2012). In a world without police, standing armies, or hereditary leadership, a reputation for being willing and able to strategically use violence is a deterrent to attack, and a necessary component of becoming a "headman" (e.g., Chagnon, 1997; Patton, 2000). And in a world of close-range, nonmechanized weaponry, individual strength, size, speed, and agility are highly advantageous. *Headman* often translates as "big" or "big man," and tribal leaders are often bigger than average (Brown, 1991). Leadership, organizational abilities, and strategic acumen are also valued in coalitional politics, and the value of a coalitional partner is also based in part on his/her reliability, loyalty, intelligence, and willingness and ability to back up coalitional interests with force (e.g., Chagnon, 1997).

Some of these abilities may be assessed through physical and behavioral cues. For example, reliability and ability to defend coalitional interests will be affected by health: Individuals in frail health will be less reliable and less able defenders, and immune-compromised individuals may increase disease transmission among coalition members. Because they further success in foraging, fighting, and deterrence of violence, physical prowess and aggressive formidability are linked to male survival, social status and, consequently, their social value to other males. Thus, cues of physical prowess and aggressive formidability are likely to be important in assessments of male attractiveness by males. Men are expected to display these qualities to other males, and be adept at predicting the outcomes of physical conflicts based on assessment of traits correlated with these qualities (e.g., dominance, tenacity, pugnacity, pain tolerance, agility, strength, endurance). All else equal, men should find males who exhibit these cues attractive as coalition partners. Because successful coalition building, maintenance, and deployment also require certain social and intellectual skills, traits associated with these qualities should also be found attractive in potential coalition partners. Male coalitional assessment psychology must, therefore, be able to weigh the degree to which a given male possesses these abilities, and their relative importance to the coalition in question. A coalition of brawny, athletic warriors lacking planning ability could benefit from adding to its ranks a man who is physically deficient but strategically brilliant.

ASSESSMENT OF CUES TO SOCIAL VALUE: HEALTH, PHENOTYPIC, AND GENOTYPIC QUALITY

Phenotypic condition refers to an individual's ability to efficiently acquire resources and convert them into fitness. It can include components such as metabolic efficiency, robustness, foraging efficiency, and toxin clearance. One aspect of phenotypic condition is health, defined as relative presence or absence of injury and/or infectious, chronic, or genetic disease (e.g., Tybur & Gangestad, 2011). Direct benefits of good health for social value include lower infectious- disease-transmission risk, and greater ability to provide the fitness benefits of the value at issue (e.g., Sugiyama, 2005). Healthy associates also reduce costs associated with health-care provisioning and loss of productive contributions (e.g., Sugiyama, 2004a; Sugiyama & Chacon, 2000). Indirect benefits of healthy associates include reduced replacement and buffering costs (e.g., search, pursuit, and opportunity costs of replacing a mate, offspring, or alliance partner; Sugiyama & Chacon, 2000). To the extent that phenotypic condition and health are heritable, mating with healthy individuals also confers those benefits to offspring (Tybur & Gangsestad, 2011). Factors affecting health are complex. Current conditions (e.g., energy stores, diet, exposure to pathogens) affect health, but environmental variables during fetal and childhood development also affect adult health, via their effects on life-history trade-offs. For example maternal nutrition and endocrine status can have epigenetic effects on glucocorticoid receptors affecting stress sensitivity or resilience, offspring metabolism, fat deposition, and muscle development (e.g., Gluckman, Hanson, & Mitchell, 2010; Kuzawa, 2012; Nepomnaschy & Flinn, 2009), each of these are hypothesized to be used in assessments of attraction. However, health consequences of these early life factors are often not apparent until adulthood, and their impact may not be directly evident via just one cue. For example, the concept of allostatic load—the long-term effects of stress on degrading biological function—is now used to generate health measures of the effects of stress, because single measures do not adequately capture or measure these effects (e.g., McEwen, Nasveld, Palmer, & Anderson, 2012). Similarly, if adaptations exist to assess health, single phenotypic health cues may show very little relationship with health outcomes, whereas multiple cue integration may show larger effects.

When testing links between health and attractiveness in postepidemiological transition societies, we must bear in mind that the causes of mortality and morbidity are quite different for most of us than for our foraging ancestors (Harper & Armelagos, 2010; Nesse & Williams, 1994). Foragers and forager-horticulturalists exhibit different mortality profiles than modern industrial populations. Illness was the leading cause of death in 12 out of 13 forager and forager-horticulturalist groups with available data, causing 71% of all deaths overall ($n > 3{,}000$; Gurven & Kaplan, 2007). Some deaths may have been due to introduced diseases, but many were not: respiratory illness accounted for 23.7%, gastrointestinal illness for 13.8%, fever for 7.3%, and other diseases for 16.6%. Accidents accounted for about 8% of deaths overall. Mortality rates among these groups were higher across the lifespan than in the United States—30, 100, and 10 times higher for infants, children, and adolescents, respectively. Although male and female mortality rates differed somewhat, in general, age-specific mortality was high during infancy, dropped steeply until the mid-teens, and then remained fairly level until it hit an adult modal around age 72. Conversely, deaths due to chronic disease were few, although they are often harder to identify.

Illness and injury entail fitness costs besides death. Either can significantly reduce productivity, thereby jeopardizing ability to provision self, offspring, and allies. Among Shiwiar forager-horticulturalists, injuries causing disability over a month in duration are common across the lifespan (Sugiyama, 2004a). Among Yora forager-horticulturalists, topical bacterial infection accounted for the majority of days on which individuals were disabled and could not forage or garden, with significant effects on production (Sugiyama & Chacon, 2000). Infected wounds sometimes lead to loss of limbs (Chagnon, 1997; Sugiyama, 1996), with obvious negative effects on productivity.

The immune system is energetically costly to develop, maintain, and deploy. For example, mounting a fever increases total adult resting energy use by 7%–13% per degree Celsius rise in temperature (Hotamisligil & Erbay, 2008). Even in the absence of fever, immune response to mild respiratory infection increased resting metabolic rate of otherwise healthy men 8%–14%, and was associated with a decrease in serum testosterone of 10%–30% (Muehlenbein, Hirschtick, Bonner, & Swartz, 2010). These costs reduce fecundity, and are complicated by pregnancy and lactation, when energetic needs are high (e.g., Ellison, 2003; McDade et al., 2012). For comparison, humans allocate about 20%–25% of our resting metabolic rate to brain function (Leonard & Robertson, 1994).

C-reactive protein (CRP) is a critical component of innate immunity linked with acute inflammatory response. In a 4-week repeated-measures study, 34% of Shuar adults ($n = 54$) had elevated CRP, indicating new infection at one of the four weekly measures (McDade et al., 2012). In a separate sample of over 300 Shuar, over 50% of participants showed presence of at least one type of helminth, and many had co-infections, with infection prevalence and intensity varying across Shuar territory (Cepon-Robins et al., 2014). Bites or infestation from ectoparasitic insects (e.g., mosquitoes, ticks, chiggers) are common. Besides small but recurrent blood loss and immune activation, many of these result in a secondary infection from being scratched and infected, particularly among children (Sugiyama, 2004a; Chagnon, 1997). Ectoparasitic insects are major disease vectors causing high morbidity and mortality, and people vary in susceptibility to bites and infection (e.g., D. W. Kelly, 2001; Lindsay, Adiamah, Miller, Pleass, & Armstrong, 1993). In some areas of the world, selection pressure from *Malaria falciperum* is so intense it maintains sickle cell trait, even though, in the homozygous condition, sickle cell anemia is fatal (e.g., Nesse & Williams, 1994). Parasite resistance is a critical feature in the evolution of mate choice, and sexual reproduction itself may have evolved in an arms race against rapidly coevolving pathogens (e.g., Hamilton & Zuk, 1982; Tooby, 1982).

Illness and injury also negatively impact growth. Among Shuar children, elevated CRP is associated with lower growth rates across 1- to 3-week periods. These trade-offs with growth are mediated by body fat reserves mobilized for energy during illness (Urlacher et al., 2014). Immunoglobulin E (IgE) provides a biomarker of past intensity of helminth infection and current infection, and children with higher IgE are shorter. Catchup growth, particularly at the growth spurt, doesn't appear to fully offset these diversions of energy from growth to immune function among the Shuar, but may to some degree in other groups, depending upon age at peak infection (Blackwell et al., 2011).

Individuals vary in susceptibility to illness and accidents due to differences in: (a) developmental and current energetic availability; (b) immune development and function, (c) chemical and behavioral factors affecting exposure to insects that are disease vectors, (d) individual factors associated with disgust sensitivity, risk taking, and coordination (e.g., Cepon-Robins et al., 2013; Mukabana, Takken, Coe, & Knols, 2002). At least some of this variance is heritable. Cues associated with health, phenotypic, and genotypic quality are therefore expected to be attractive across all social value domains. However, optimal level of health and phenotypic quality for any domain will be different. Accordingly, relative preferences for these cues are expected to vary systematically across domains, and also by age, sex, and individual and socioecological conditions that structure the costs and benefits of health for social value. For instance, in large cross-cultural samples, relative strength of mate preferences for good health, physical attractiveness, and youth (amongst females) increased with evolutionarily relevant health risk/pathogen prevalence (e.g., Gangestad & Buss, 1993; Gangestad, Haselton, & Buss, 2006).

This idea has been extended to particular traits hypothesized to be related to health. For example, trade-offs exist between investment in immunity and testosterone, and testosterone appears to have immunosuppressant effects. The immunocompetence handicap hypothesis proposes that traits developing under the influence of testosterone, such as facial masculinity or musculature, are costly signals of underlying genetic quality and immunocompetence. Because the relative value of immunocompetence is greater in high pathogen environments, female preference for facial masculinity was predicted to be positively correlated with pathogen prevalence. Various studies find positive association between degree of female preferences for masculinity in mens faces, voices, and bodies and pathogen prevalence, and between masculinity preference and degree of pathogen but not other kinds of disgust (e.g., DeBruine, Jones, Crawford, Welling, & Little, 2010; DeBruine, Jones, Tybur, Lieberman, & Griskevicius, 2010; B. C. Jones et al., 2013). However, recent data and analysis suggest the testosterone-immunocompetence hypothesis may require reevaluation (e.g., Boothroyd, Scott, Gray, Coombes, & Pound, 2013; Puts, 2010; Scott et al., 2012; Scott et al., 2014) or more nuanced assessment of relative trade-offs (e.g., Schmitt 2014). There may be more direct intrasexual and coalitional competitive benefits to men with masculine features—e.g., musculature, dominance, authority—as well as relative costs and benefits to women of mating with them under various circumstances (e.g., relative cost-benefit structure of men's contributions to subsistence, risks of violence by the male and by other males, desertion, women's reproductive status, and so forth). Other cues may provide more direct indicators of health status, such as skin, hair, oral, movement patterns, or olfactory qualities (e.g., Grammer, Keki, Striebel, Atzmüller, & Fink, 2003; Sugiyama, 2005).

SKIN QUALITY

Skin functions in protection, regulation, and sensation. Smooth, unblemished skin indicates less exposure to or damage by parasites and/or disease. Skin condition also provides a window on strength of immune function, indicated by ability to heal without infection (Singh & Bronstad, 1997; Sugiyama, 2004a). Skin damage accumulates with age, such that smooth skin and even skin tone are associated with youth (e.g., Jablonski, 2013). Skin quality also reflects current and chronic nutritional state (e.g., Piccardi & Manissier, 2009). Dandruff can indicate vitamin insufficiency or scalp microbiome imbalance, and psoriasis is a T-cell mediated inflammatory disease linked to immune dysregulation, oxidative stress, and genes of the MHC (e.g., Feng et al., 2009; Nestle, De Meglio, Qin, & Nickoloff, 2009; Tsoi et al., 2012).

Intrapopulation variance in skin color is associated with nutrition, disease, and fertility. For example, hepatitis and anemia can produce a pallid skin cast. In contrast, betacartonoids increase yellowish hue, while cardiovascular efficiency, sexual excitement, anger, and other emotional states are related to greater red coloration. Women tend to have lighter skin than men, probably to increase vitamin D absorption for calcium needs during pregnancy and lactation (Jablonski & Chaplin, 2000). Skin darkens with age, such that comparatively light skin is predicted to be attractive in females, as a cue of youth (Symons, 1979). Women's skin has many estrogen and progesterone receptors, which change skin characteristics over the ovulatory cycle, such as lightening of the skin during the fertile phase, and with age. In addition, lipid secretion, skin thickness, fat deposition, elasticity, hydration, and skin microbiota change over the cycle (Farage, Miller, Berardesca, & Maibach, 2009). Fine lines and wrinkles increase with age, as does unevenness in skin tone.

A growing body of research is testing the longstanding prediction that smoother and relatively lighter skin are related to female sexual attractiveness (e.g., Darwin, 1871; Symons, 1979; van den Berghe & Frost, 1986). Fink, Grammer, and Thornhill (2001) presented subjects with standardized face shapes varying in texture, and found that skin texture significantly influenced attractiveness ratings. Attractiveness ratings of small skin patches are positively correlated with those of the whole face, as well as perceived health and ratings of male facial attractiveness (B. C. Jones, Little, Burt, & Perrett, 2004). Effects of skin color homogeneity and texture independently affect attractiveness. Fink, Grammer, and Matts (2006) had male subjects rate three-dimensional computer models of female faces standardized for shape and skin texture, varying only in skin color homogeneity. Male subjects rated more homogeneous skin color more attractive, healthy, and younger looking.

Multiple variables affect skin color distribution, including melanin, carotenoids, hemoglobin concentration and oxygenated blood, and tanning (Coetzee et al., 2012; Stephen, Coetzee, Smith, & Perrett, 2009; Whitehead, Coetzee, Ozakinci, & Perrett, 2012), and these affect both male and female attractiveness (e.g., Fink, Bunse, Matts, & D'Emiliano, 2012). Matts, Fink, Grammer, and Burquest (2007) used images of skin from cheeks from photos of 170 girls and women from 11 to 76 years of age, and had 353 subjects rate them for attractiveness, healthiness, and youthfulness. Skin homogeneity was positively correlated with perceived attractiveness and youthfulness, and negatively associated with perceived age. Image maps of both hemoglobin and melanin distribution each showed the same results, indicating multiple components of skin homogeneity contribute to this effect. Fink and Matts (2008) used a subsample of images of the women over 40 to examine the relative effects of skin texture and color on attractiveness. From these, they created four sets of images: original, skin texture removed, skin color smoothed (homogenized), and skin texture removed and color smoothed, which subjects rated for age and health. Results indicated that color-smoothed images were rated most healthy, indicating that evenness of skin color is a cue to health. Significant age differences were found among all image sets, with the largest differences found between the original set and the set with texture removed and color smoothed. The latter set was rated youngest, with greatest effect due to texture cues.

Carotenoids, important for protection of tissues and DNA from oxidative stress damage, also play roles in immune activity, increasing cell surface expression of MHC molecules. Because carotenoids accumulate in the skin, yellowness of skin may provide a cue to health and, for this reason, be found attractive. Similarly, redness of the skin is associated with vascularization and oxygenation of blood, and women's estrogen levels. In some nonhuman primates, it is associated with reproductive status, diet, lack of parasites, and immunity, and is also used in sexual signaling. Stephen et al. (2009) suggest that this may explain why redness in human skin is associated with health and found attractive. Using the CIELab color system, they allowed male and female subjects to digitally shift facial image skin color along one or two of three dimensions (light-dark, red-green, and yellow-blue) associated with lightness and the effects of melanin and carotenoids, respectively. As predicted, subjects increased both yellow and red hues of faces to optimize perception of health. Coloration was not increased to extremes, suggesting the existence of optimal levels of these color components. Subjects also enhanced sexual dimorphism in skin color, by lightening women's faces more than men's and increasing redness and yellowness in men's faces more than women's. Similar results hold for South African and Asian subjects (Whitehead, Coetzee, et al., 2012), suggesting that these components of skin color are attractive across populations. Even small changes in frequency of fruit and vegetable intake had measurable effects on carotenoid-related skin color; these changes are detectable and sufficient to affect perceived health and attractiveness (Whitehead, Re, Xiao, Ozakinci, & Perrett, 2012). Studies also suggest that coloration related to carotenoids is relatively more important than melanin in perception of health and attraction (e.g., Stephen, Coetzee, & Perrett, 2011).

Differences in the cue value of these skin features are likely stronger under the dietary, pathogen/parasite, and fertility conditions characteristic of the human EEA. Ideally, future research should be aimed at systematically documenting the relative strength of their cue values to health, age, sex, and reproductive status across conditions more representative of ancestral environments. Examining the relationship between skin tone and biomarkers of health and immune function under these conditions would be particularly instructive: Proposed attraction to healthy skin tone may increase under conditions of dietary and immunological challenge. However, doing so will be challenging, due to lack of uniform lighting at most relevant field sites and the costs of measuring hypothesized correlates such as pathogen prevalence and control variables.

Hair Quality

Hair grows at the rate of about one half inch per month, until it falls out upon reaching 2 to 3 feet in length. Energy constraints or illness affect growth rate or hair loss. Hair also gets thinner and dryer with age, as cebum (scalp oil) production is reduced. Graying hair is also associated with reduction in melanocytes and aging-related oxidative stress, and is closely tied to underlying genetics (Commo, Gaillard, & Bernard, 2004). As a result, greying occurs at different times in different populations (Trüeb, 2009). Given the visible effects of aging on hair condition, we would expect male choice for reproductive value and/or peak fertility to be negatively related to gray hair in women. Conversely, female choice for status and productive ability in males, and the later age at which these occur, may be related to female preference for some level of gray hair in males, although association with actual age will vary across populations.

Hair also reflects nutritional and health status. Starvation, nutritional deficiencies, and stress increase hair loss, damage, and fragility, and malnourishment causes observable changes in hair color (Rushton, 2002). Dry, brittle, and/or dull hair is associated with lower dietary keratin, fatty acids, protein, vitamins A, B, folic acid, and minerals such as iron, zinc, calcium, magnesium, and copper (Haneke & Baran, 2011). Iron deficiency, for example, is related to reduction in hair growth and hair loss a few months later (Karadag, Ertugrul, Tutal, & Akin, 2011). Iron is critical to cellular function, and iron withholding may be used as a part of the body's innate immune system. Anemia affects about 2 billion people worldwide, and is associated with fatigue, headaches, low blood pressure, shortness of breath, reduced infection resistance and, over the long term, poorer growth, development, cognitive function and reproductive outcomes (WHO/UNICEF/UNU, 1998). Anemia is of particular concern for women and children in developing countries because pregnancy and rapid growth increase iron requirements. Micronutrient deficiencies are also related to disruption of enzyme function and metabolism regulation (Park, Choi, & Nam, 2009). Zinc deficiencies, for example, are associated with impairments of neurological function (e.g., in autism, depression, and other psychiatric conditions) and impaired immune response and healing (Grønli, Kvamme, Friborg, & Wynn, 2013; Prasad, 2013; Priya & Geetha, 2011; Stechmiller, 2010). Zinc in hair is also negatively correlated with age and with below-normal testosterone levels. Vitamin D deficiency is associated with rickets, and suboptimal levels with a variety of health problems, mood disturbances and poor hair health (e.g., Amor, Rashid, & Mirmirani, 2010; Holick, 2007).

Hair, therefore, provides an observable continuous record of an individual's health, stress and nutrition over a 2- to-3-year period. It also reflects heritable genotypic quality (Etcoff, 1999) and age. Shiny, strong hair provides a cue to recent good health, developmental condition, phenotypic, and genotypic quality. The longer the hair, the longer the record of health. Tellingly, long hair is often preferred across cultures, and long, lustrous hair is often associated with beauty (Etcoff, 1999). Grammar, Fink, Thornhill, Juette, and Runzal (2002) found that hair length was significantly correlated with female attractiveness. In a sample of over 200 women aged 13–73, Hinsz, Matz, and Patience (2001) found that younger, higher-reproductive-value women tended to have longer hair than older women, as predicted if higher-reproductive-value women use their hair as an advertisement of that fact. Interestingly, hair grows fastest among women around the ages of peak fertility (Etcoff, 1999), with the result that evidence of environmental damage has less time to accumulate before new hair grows in, and evidence of health or dietary problems would reflect a shorter period of time.

Body hair and beards are male secondary sex characteristics associated with age and androgen profiles, but have a heritable component and vary across populations (e.g. Dixson & Vasey, 2012; Puts, 2010). Body hair has been hypothesized to be costly to produce and a signal of ability to afford testosterone, as it may entail trade-offs with immune function. Research to date shows women's sexual preference for body hair varies across populations. Dixson, Halliwell, East, Wignarajah, and Anderson (2003) found that male body line drawings with trunk hair were rated as older and more attractive than those without by both British and Sri Lankan women. Women from Cameroon rating shaded photos of male figures found those with body hair sexually attractive, but less so than British women, while women in the United States, China, and New Zealand found male figures without trunk hair most attractive (Dixson, Dixon, Bishop & Parish, 2010; Dixson, Dixson, Morgan, & Anderson, 2007). In Finland, postmenopausal but not premenopausal women found male images with chest hair attractive (Rantala, Pölkki, & Rantala, 2010). Although cross-cultural data is especially welcome and needed, these studies again point to an intrinsic problem in understanding cross-cultural variation: They do not take into account assessment of local trade-offs and sources of interpopulation variance in relative value of qualities associated with higher androgen profiles. Local information such as the relative value to women of male investment, cost of mate desertion or extra-pair copulation, costs and benefits of mate's use of aggression; pathogen prevalence; local range of observable distribution of torso hair; rater's menstrual cycle phase, number of offspring, and sociosexual orientation are needed to make sense of this variation.

Male facial hair also grows in association with androgen surges beginning at male puberty, and continues to cover more area and become thicker with age into adulthood. Beard and eyebrow growth make male lower faces and brows look larger, emphasizing testosterone-related traits (Guthrie, 1970), and may thus signal reproductive maturity, dominance, status or aggressive formidability associated with testosterone levels. Long beards (and long head hair) also provide handles with which to control and harm one's opponent in fights, leading Zahavi and Zahavi (1997) to hypothesize that they provide costly signals of intrasexual competitive ability. A number of studies make it clear that bearded faces are perceived as older, more dominant, and/or more aggressive (e.g., Dixson & Brooks, 2013; Dixson & Vasey, 2012; Neave & Shields, 2008), supporting the claim that facial hair is the product of intrasexual selection. Studies on effect of beards on women's assessments of attractiveness are inconsistent, perhaps due in part to variation in the range of stimuli presented. These inconsistencies may also reflect trade-offs between mating for good genes and ability/willingness to invest, which in turn vary depending on whether the woman is pursuing a short- or long-term mating strategy. Neave and Shields (2008) therefore made three sets of five computer-generated young adult male faces (age 18–25), ranging from clean-shaven to full beard for each. Results from 60 female undergraduate raters showed the predicted positive linear relationships between amount of facial hair and masculinity, dominance, aggression, social maturity, and age. Attractiveness ratings showed a curvilinear relationship with amount of facial hair, with light stubble rated most attractive and full beard rated least attractive. In long-term contexts, light stubble was also the most favored but clean-shaven faces were less favored. For the age range of participants tested, the ability to display signs of dominance in the future (light stubble) trumped actual possession of the signal, probably due to subjects' relatively young age. Obvious next steps are to replicate the study with a wider rater age range.

Fluctuating Asymmetry

Developmental instability (DI) results from an individual's inability to buffer development against environmental stressors, and is thought to be negatively related to fitness. Many features of animals' bodies are designed to be bilaterally symmetrical, and although developmental disturbances are expected to affect development on both sides of the body equally, mutational load or homozygosity may increase small random variations from symmetry during development, known as *fluctuating asymmetry* or FA (e.g., Watson & Thornhill, 1994). FA is therefore hypothesized to be a measure of DI and a proxy for fitness (e.g., Dongen, 2006; Polak, 2003). If so, it provides a potentially assessable cue of phenotypic and genotypic quality (via ability to buffer developmental stress and/or less exposure to developmental disturbances), and an explanation for why symmetrical individuals are found more attractive than less symmetrical individuals. Epigenetic effects of early life stress on hypothalamic–pituitary–adrenal axis (HPAA) regulation may also be related to individual differences in FA, although results are complex and more research is needed (e.g., Flinn, Duncan, et al., 2012). Because maintaining symmetrical development in the face of developmental disturbances is costly, FA has also been hypothesized to be an "honest" (costly) signal of genotypic and phenotypic quality related to a number of fitness-related outcomes. For example, because testosterone exhibits trade-offs with immune function, male display of physical features associated with higher testosterone was thought to amplify signal quality of FA (e.g., Thornhill & Gangestad, 1993), and a similar case has been made for estrogens (Little et al., 2008). Even if low FA provides a measure of an individual's ability to withstand developmental disturbances, low FA preference need not be based on costly signaling *per se*. FA is a partially heritable trait (Dongen, 2000), since homozygosity and mutational load increase susceptibility to environmental developmental stressors, and since condition-dependent traits will necessarily include some heritable variation (Gangestad & Thornhill, 1999; Rowe & Houle, 1996).

Nonhuman animal research suggests that FA is negatively correlated with a wide range of fitness-related measures of growth, survival, fecundity, intra-sexual competitiveness, and mating success, but results are mixed (Dongen, 2006). In human research, studies report FA associated with health measures, fetal outcomes, psychological outcomes, hormones or morphological correlates of sex hormones (masculine/feminine features), number of sex partners, and attractiveness, but results are also mixed depending on methods, study population, and the hypothesized correlates of fitness measured (Møller, 2006; Thornhill & Gangestad, 2006).

For instance, Thornhill and Gangestad (2006) found facial and body FA positively associated with 3-year retrospective self-reported respiratory infections but not intestinal sickness in a sample of 406 men and women (see also Shackelford & Larsen 1997, 1999). In a sample of over 900 26-year-old men and women, Milne et al. (2003) found FA significantly related to the likelihood of women, but not men, self-reporting two or more medical conditions. Waynforth (1995) found FA associated with higher morbidity among Mayan men in Belize, and Gangestad, Merriman, and Thompson (2010) found oxidative stress positively associated with FA. However, Rhodes et al. (2001) found that facial symmetry did not predict illness in medical records of 294 U.S. 17-year-olds born between 1920 and 1929. In a large study of 4,732 English children, Pound et al. (2014) found no association with FA and longitudinal health measures, but found a very small negative relationship between FA and IQ (see also Banks, Batchelor, & McDaniel, 2010). Other studies also found positive association between FA and psychiatric dissorders (e.g., Arboleda-Florez, Ramcharan, Hreczko, & Fick, 1998, Markow & Wandler, 1986; Mellor, 1992).

FA and cues of phenotypic quality are also reportedly linked with sexually dimorphic traits under developmental regulation by androgens and estrogens. For example, more symmetrical men are reported to have greater musculature (Gangestad & Thornill, 1997), body size (Manning, 1995), grip strength (Fink, Weege, Manning, & Trivers, 2014), testosterone-related facial cues of dominance and reproductive health (Gangestad & Thornhill, 2003), and lower resting metabolic rate (Manning, Koukourakis, & Brodie, 1997) than less symmetrical males. Men with low FA report earlier age of first intercourse, higher numbers of sex partners, higher number of extra-pair copulation partners, and shorter time elapsed until sex with a new partner (Gangestad & Thornhill, 1997; Thornhill & Gangestad, 1994). More symmetrical men also are reported to have more sperm per ejaculate, as well as higher motility (Manning, Scutt, & Lewis-Jones, 1998; Soler et al., 2003). Among Mayan men, FA was associated with lower fecundity, and marginally associated with higher age at first reproduction and fewer lifetime sex partners (Waynforth 1995). Gangestad, Thornhill, and Garver-Apgar (2010) found oxidative stress positively associated with FA and negatively associated with attractiveness and ratings of health and masculinity. Development of these traits is predicted to be condition-dependent: Higher-quality males may be best able to develop and maintain large size, musculature, and high testosterone, and to buffer oxidative stress (Gangestad et al., 2010; Gangestad & Thornhill, 1997, 2003). These masculine traits evolved for intrasexual competition, and may also be the target of female mate choice. A number of studies show that women find masculine traits particularly desirable in short-term mates and extra-pair sex partners (Schmitt, Chapter 11, this volume), and are more attracted to and more likely to have sex with men exhibiting these "masculine" traits during the fertile phase of their ovulatory cycle.

This pattern appears to be the product of facultative mating strategies conditional on a male's relative attractiveness and hormone-mediated sociosexual strategies that covary with FA (Gangestad & Simpson, 2000). This may exacerbate the trade-off women face between good genes and investment. Evidence suggests that female attraction to low-FA males increases with a woman's current fecundity and in short-term (or extra-pair) mating contexts, as does preference for male physical attractiveness and its correlates generally (e.g., Gangestad, Thornhill, & Garver-Apgar, Chapter 14, this volume). Degree of male symmetry predicts a significant amount of their partners' copulatory orgasms (Thornhill, Gangestad, & Comer, 1995), which may bias paternity toward symmetrical males, and women experience more frequent orgasm with extra-pair mates (Thornhill & Gangestad, 2003). Women showed greater preference for symmetrical male faces as a function of probability of conception based on phase of ovulatory cycle (Little, Jones, Burt, & Perrett, 2007; cf. Peters, Simmons, & Rhodes, 2009). Similarly, when presented with T-shirts worn by different men, non-hormonally contracepting women preferred the body scent of more symmetrical men, but only during the fertile times in their cycle; hormonally contracepting women showed no shift (Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999). Score on the sociosexual orientation inventory (SOI) is also associated with female preferences. When 99 women chose between pairs of original and symmetrically manipulated versions of 10 male and 10 female faces, women with higher SOI showed greater preference for more symmetrical faces (Quist et al., 2012).

Studies also report negative correlation between FA and female health and fitness-related variables. Manning (1995) shows an association between body weight and FA in women. Milne et al. (2003) found that female FA was associated with body mass index (BMI) and overall reported number of medical conditions, but not with blood pressure, cholesterol, or cardiorespiratory fitness. This may be due to relatively low levels of environmental stressors in Westernized societies, leading to more homogeneity in FA. For example, among Hadza foragers, FA is higher than in U.S. college students, suggesting that the Hadza experience more developmental stress (Gray & Marlowe, 2002), and more strongly prefer symmetry than a UK sample, and when pregnant or nursing (Little, Apicella, & Marlowe, 2007). More symmetrical women were also found to have earlier age at first birth and more offspring (Manning, Scutt, Whitehouse, & Leinster, 1997; Møller, Soler, & Thornhill, 1995). This may be because attractive women have greater mating opportunities and thus marry earlier, have higher-socioeconomic status mates, and more lifetime offspring. Jasienska, Lipson, Ellison, Thune, and Ziomkiewicz (2006) found more symmetrical Polish women had significantly higher mid-menstrual cycle estradiol levels, indicating significantly greater conception probability, than less symmetrical women, even when controlling for height and BMI. Because estradiol levels in reproductive-age women are related to their size at birth, and FA is hypothesized to be linked with developmental stress, Jasienska et al. (2006) suggest this may form a link between FA and later estradiol levels. This link may provide a direct benefit of preferring symmetrical women as mates. Further, they point out that estrogen levels are linked with many aspects of female health, and that estrogen in premenopausal women actually has an immunostimulant effect, providing potential links between lower FA and female health.

FA is negatively correlated with facial attractiveness ratings of both males and females (e.g., Rhodes, 2006; Rhodes, Louw, & Evangelista, 2009). Most studies on natural variation in facial symmetry show a positive relationship between symmetry and attractiveness (e.g., Sugiyama, 2005). Rhodes et al. (2007) found that most of this association was due to perceived health. They had subjects rate Western and Japanese faces, and found symmetry associated with perceived health, and most effects of symmetry eliminated when perceived health was statistically controlled. B. C. Jones et al. (2001) also found that the relationship between attractiveness and facial symmetry is mediated by the association of symmetry and apparent health, although the direct effect of facial symmetry on attractiveness was small (see also, e.g., Fink, Neave, Manning, & Grammer, 2006). These effects remain even in genetically identical twins (Mealey, Bridgestock, & Townsend, 1999).

If low FA is associated with the ability to withstand developmental disturbance, such that symmetry is correlated with other cues of phenotypic condition, then low FA individuals may be found attractive because of those other cues, in addition to symmetry per se. If so, the link between symmetry and attractiveness would not be direct. Scheib, Gangestad, and Thornhill (1999) found that, when presented with male half-faces (split along the vertical midline), women's attractiveness ratings of half-face images were associated with symmetry of the full face, just as strongly as the women's ratings of the full faces. More symmetrical men had longer lower jaws and more prominent cheekbones, features that appear to reflect developmental influence of testosterone. B. C. Jones et al. (2001) also found that the relationship between attractiveness and facial symmetry is mediated by the association of symmetry and apparent health, while the direct effect of facial symmetry on attractiveness was small.

Body symmetry is also associated with facial symmetry and ratings of attractiveness, health, and fitness, supporting the idea that FA is related to underlying features of phenotypic condition. Thornhill and Gangestad (1994) measured seven nonfacial body traits of 122 undergraduates and found a positive correlation between age at first copulation and degree of asymmetry. They also found negative correlation between FA and self-reported number of lifetime sex partners, even when age, height, ethnicity, marital status, physical attractiveness, and physical anomalies were controlled. FA was important in evaluations of both male and female attractiveness. Gangestad and a naïve research associate measured FA of men from a small village on Dominica using nine different body traits. Both male and female college students rated facial photographs of the more symmetrical men more attractive (Thornhill & Gangestad, 2003). Hume and Montgomerie (2001) studied the relationship between facial attractiveness ratings, FA (based on 22 traits), BMI, health, and age, among male and female subjects, whose attractiveness was then rated by a large number of other men and women. For both males and females, there was a negative association between attractiveness and FA. BMI and past health problems were the best predictors of female attractiveness; for males, it was the socioeconomic status of the environment in which they were raised. However, Hönekopp, Bartholomé, and Jansen (2004) found women's facial attractiveness associated with physical fitness, but that symmetry did not mediate this association, and Tovée, Tasker, and Benson (2000) found no association between FA and bodily attractiveness. Brown et al. (2008) used 3-D body scans of 40 male and 37 females to create 360-degree videos of the body shapes, and had 87 subjects rate them for physical attractiveness. Among male bodies, FA was negatively related to height, shoulder breadth, and torso volume, and positively related to WHR and torso-to-leg length. Among female bodies, FA was positively associated with height and torso volume, but negatively related to WHR and leg length. Principle components analysis (PCA) revealed a single component associated with masculine body shape accounting for 60% of variance in attractiveness, with shoulder breath, torso volume, WHR, and height variables loading positively on this component, and breast size and longer slender legs loading negatively. Lower body FA was less than upper body FA, which the authors suggest may be in part because symmetry is important for locomotor efficiency.

In a recent meta-analysis, Dongen and Gangestad (2011) found 94 studies testing 293 hypothesized relationships between FA and health and disease, reproductive and fetal outcomes, psychological problems, sexually dimorphic hormones or their correlates, and attractiveness. After accounting for publication bias and sample size, they estimate a small but statistically robust association between FA and outcome. Further, they show variation in strength of associations across outcome variables. Considering attractiveness and mate choice, facial but not body FA predicted facial attractiveness, probably because the effect of facial symmetry on attractiveness is direct, whether or not it is the result of DI per se (e.g., Dongen, Cornille, & Lens, 2009; Haufe, 2008). Effects of FA on scent, body, movement, and vocal attractiveness were also apparent, as were associations with health. Associations between FA and correlates of reproductive success (particularly males' number of sexual partners) were also clear, as were effects on maternal risk factors and fetal anomalies. Effect sizes for health-related outcomes were smaller but apparent. Importantly, variation in results across studies could be due to low sample sizes: Obtaining 80% power to detect the effect if present requires a sample size of 350 subjects, well over that included in most studies. A separate meta-analysis found no relationship between FA and morphological correlates of investment in sex hormones related traits (facial masculinity/femininity, digit ratios). However, confidence intervals were wide, so no firm conclusion could be reached either way. Importantly, the largest effect sizes were for those studies that measured hormone profiles directly (Dongen, 2012).

These studies highlight a number of issues relevant to many studies of attractiveness. For instance, many studies use college student subjects and/or western populations, and associations between FA and health outcomes might be greater in evolutionarily relevant populations under higher disease, pathogen, and dietary stress. Most health measures are via self-report, and are limited in scope. Several studies do not measure hormonal profiles, stress, or immune activation directly or longitudinally, when effects of DI on FA are expected to be most salient. These methodological considerations matter because FA is a weak measure of individual differences in developmental instability for multiple reasons (Dongen & Gangestad, 2011). Individuals do not experience the same levels of developmental stress, nor do they experience them at the same times during development (e.g., Blackwell et al., 2011; Urlacher et al., 2014). Traits may vary in how well they are buffered from developmental stability: Those under recent directional selection or sexual selection may be less buffered than functionally critical traits, such as pelvic or leg length symmetry (Clarke, 2003). Associations between FA and fitness-related traits may be apparent only under relatively high stress where lower-quality individuals are significantly challenged, such as we would expect under evolutionarily relevant conditions. However, resource allocation to health trades off against reproduction, and the optimal allocation will be dependent on individual condition. To the degree that, at some point, investment in sexually dimorphic traits associated with reproduction has relatively greater effects on fitness than additional investments in health, individuals in better condition may benefit more from greater investment in reproductive effort than those in poorer condition. This may result in positive correlation between sexually dimorphic traits and fitness, but little to no relationship between sexually dimorphic traits and general health. Under conditions of intense sexual selection, high quality individuals may benefit from investing so much in reproduction that health or survival suffers (Getty, 2002; Kokko et al., 2003; Puts, 2010). Further, different forms of stress may affect DI in unpredictable ways and not in a linear or additive fashion.

Evidence suggests that human female reproductive state, across both the reproductive lifespan and the ovulatory cycle, affects trade-offs in female mate choice which may obscure links between FA and mating preferences if not well controlled for (e.g., Gangestad, Thornhill, & Garver-Apgar, 2005; Sugiyama, 2005). Research on female mate preferences must distinguish between short- and long-term female mating context, subjects' SOI, preferences during fertile and nonfertile phases of the ovulatory cycle, reproductive lifestage, and subjects' own attractiveness. Because hormonal regulation of ovarian function is highly context-sensitive, studies in human biology ideally seek to measure hormonal variation across the cycle to determine individual baseline and variation; future research will need to take this into account. Finally, greater variance in male reproductive success suggests that optimal trade-offs between investment in health and intrasexually selected traits may be lower for men, while trade-offs between health and intersexually selected traits may be higher for women. Finally, similar to the case of the testosterone as costly signaling hypothesis, we must reconsider the claim that FA is primarily a costly signal, rather than a cue to phenotypic and underlying genotypic quality the correlates of which have been under intersexual selection.

THE MAJOR HISTOCOMPATIBILITY COMPLEX (MHC)

Pathogen prevalence and intensity of infection affect allocations to different branches of immunity during development, with consequences in adulthood that vary depending on the timing of health insults (e.g., Blackwell et al., 2011). The number of pathogen antigenic molecules is vast, and changes via pathogen coevolution to immune defenses. The immune system thus includes mechanisms functioning to increase the number of antigens that can be recognized. The major histocompatibility complex (MHC; also called human lymphocyte antigen [HLA] in humans) generates cell surface molecules that bind to specific foreign proteins and present them to Killer T-cells that attack the pathogen directly, or Helper T-cells that signal other systems to coordinate attack. The MHC shows evidence of intense selection for diversity in binding surfaces. It is highly polygenic, highly polymorphic, and codominant. Finally, there is somatic mutation in the genes, which generates additional antigen receptors (Janeway, Travers, Walport, & Schlomchik, 2004).

Selection has produced mechanisms to increase MHC diversity, but a given individual has only a small subset of these alleles. If cues to MHC diversity are assessable, these could be used in mate choice, as well as kin and offspring recognition. Hypothesized mechanisms primarily involve olfactory detection of biochemical cues to MHC, either directly or via its effects on variation in the microbiome of different individuals. Potential benefits of MHC-biased mate choice include inbreeding avoidance, increased offspring heterozygosity, recruitment of rare alleles to counter coevolving pathogens, and increased variability between offspring under conditions of uncertain and changing pathogen pressure (e.g., Brown, 1997; Havlíček & Roberts, 2009; Oliver, Telfer, & Piertney, 2009; Penn & Potts, 1999; Tybur & Gangestad, 2011). However, local selection may favor MHC alleles that bind to antigens of locally prevalent pathogens; hence, there may be selection favoring particular MHC alleles within local populations (Neff & Pitcher, 2005). This strong localized selection may promote mate attraction for MHC similarity, at least at relevant loci. For example, Coetze et al. (2007) found no relationship between HLA heterozygosity and self-reported illness in women, but women with more common alleles reported fewer illnesses and better health than did women with rare alleles. MHC dissimilarity between mother and fetus may also cause problems in pregnancy. Conversely, Lie, Simmons, and Rhodes (2009) found a small but significant relationship between both MHC and non-MHC allelic diversity and self-reported health over a 4-month period. However, some alleles are under stronger selection for diversity than others (Huchard, Baniel, Schliehe-Dieck, & Kappeler, 2013).

In nonhuman organisms, results are complicated, sometimes indicating mate choice for MHC similarity, dissimilarity, or a balance between good genes and heterozygosity (e.g., Bernatchez & Landry, 2003; Piertney & Oliver, 2006). Research indicates that MHC-based choice in humans is similarly complex, although it generally shows a role of MHC in attraction (Havlíček & Roberts, 2009). Sorting out the variation will require good cross-cultural data from evolutionarily valid populations. Wedekind, Seebeck, Bettens, and Paepke (1995) had male subjects wear T-shirts for two nights, and had female subjects rate the shirts for odor intensity, sexiness, and pleasantness. Orally contracepting women preferred MHC-similar men, while noncontracepting women preferred the odor of MHC-dissimilar men. The smell of MHC-dissimilar men also reminded women of their current or previous mates. A follow-up study showed male odor preference for MHC dissimilarity regardless of the sex of the T-shirt wearer (Wedekind & Füri, 1997). Using a similar design, Thornhill et al. (2003) found male preference for both MHC dissimilarity and common alleles. Women's facial attractiveness was positively associated with their scent attractiveness. Men also preferred the scent of women during the fertile phase of the menstrual cycle, based on other scent cues. During the anovulatory phase of their menstrual cycle women preferred the odor of MHC heterozygous men, but during the ovulatory phase they exhibited no MHC preference. There was no relationship between facial attractiveness and MHC heterozygosity. Roberts, Gosling, Carter, and Petrie (2008) also found no odor-based MHC preference during the fertile phase of women's ovulatory cycles. However, single women preferred the odor of MHC-similar men, while women in long-term mateships preferred MHC-dissimilar men. In three studies, women using oral contraceptives preferred the scent of individuals with MHC-similar genotypes (Roberts et al., 2008; Wedekind et al., 1995; Wedekind & Füri, 1997). Using EEG, Pause et al. (2006) found more rapid and intense preattentional brain activity in response to odors of MHC-similar than to MHC-dissimilar individuals. Subjects also rated MHC-similar individuals less attractive as potential partners, suggesting MHC-based incest avoidance. Brain activity patterns for male (frontal lobe) and female (parietal lobe) raters differed when exposed to MHC-similar people of the same sex, suggesting sex differences in MHC odor processing. Jacob, McClintock, Zelano, and Ober (2002) had 49 nulliparous single women choose which of six T-shirts they would "prefer to smell all the time." Women preferred the smell of males with greater MHC similarity. Women could discriminate odor based on differences in one MHC allele, but only for paternally inherited alleles, leading the authors to suggest that paternal MHC-related odors may be used in offspring-father recognition. This study is often taken as evidence of mate preference for MHC similarity, but subjects were not asked to choose based on mate preference. Ferstl, Eggert, Westphal, Zavazava, and Müller-Ruchholtz (1992) also found evidence for MHC similarity bias among friends, perhaps the result of kin recognition biases expressed in evolutionarily novel circumstances.

A number of studies have examined MHC-biased facial attraction. Roberts, Little, et al. (2005) showed that women preferred faces of MHC-heterozygous men, perhaps assessable via skin quality. Counter to the MHC dissimilarity bias hypothesis, women rated MHC-similar male faces more attractive than MHC-dissimilar faces. Among the Tswana, Coetzee et al. (2007) found no relationship between male ratings of female facial attractiveness or health, and women's heterozygosity or allele frequency (although women with more common alleles reported better health). Coetzee et al. (2012) point out that Tswana practice consanguineal first cousin marriage, which may remove deleterious alleles and decrease heterozygote advantage.

Lie, Simmons, and Rhodes (2010a) had male and female subjects rate opposite-sex facial attractiveness of 80 females and 79 males, respectively. Men rated faces of MHC-dissimilar women more attractive for both short- and long-term mates. In contrast, female raters showed no effect of MHC or non-MHC dissimilarity on ratings of male facial attractiveness. Men found non-MHC genetic diversity attractive in female faces, while women found MHC genetic diversity attractive in male faces for both long- and short-term mating. This provides some evidence for both the genetic dissimilar mating and good genes heterozygosity hypotheses.

Studies of mated couples show mixed results. Among 411 Hutterite couples, Ober et al. (1997) found fewer MHC haplotype matches between spouses than expected based on population genotype frequencies. Ober, Hyslop, Elias, Weitkamp, and Hauck (1998) showed significantly greater fetal loss for MHC-similar couples on individual MHC loci, and even greater loss when couples matched on all 16 loci studied (Ober, 1999). Markow et al. (1993) also show evidence of balancing selection in MHC-biased mating among the Havasupai. However, Hedrick and Black (1997) examined 10 MHC alleles in 194 couples from 11 Indigenous South American groups and found no bias toward MHC-dissimilar mating. Ihara, Aoki, Tokunaga, Takahashi, and Juji (2000) similarly found no evidence of MHC-dissimilar mate preference in Japanese married couples. Chaix, Cao, and Donnelly (2008) found more mate dissimilarity in MHC than in the rest of the genome in 30 Euro-American couples from Utah, but no evidence for MHC-dissimilar mate choice among 30 Yoruba couples from Nigeria. In a study of 145 Australian university students, Lie, Rhodes, and Simmons (2010) found women but not men with higher genetic diversity, both generally and at MHC loci, had greater number of sexual partners.

This pattern of mixed results points to a number of problems with study design. Large samples like the Hutterite are needed to find small but significant effects. However, Markow et al. (1993) did show evidence of MHC-biased mating among the Havasupai, and point out that populations like this are more likely to show evidence of MHC mating bias than large, nonevolutionarily relevant ones. In most studies, only a few alleles were tested, with no a priori predictions about local selection for diversity or "good genes" (e.g., Huchard & Pechouskova, 2014). Only a very large effect size could have been detected in the Indigenous South American sample because only a few alleles were studied across several populations, each with a small sample size, without controlling for degree of inbreeding (Beauchamp & Yamazaki, 1997; Penn & Potts, 1999). The Yoruba have a long precolonial history of monarchy and gerontocracy, and the sample size for the study was only 30. Finally, most studies used marriage as a proxy for sexual preference rather than actual mating behavior.

Garver-Apgar, Gangestad, Thornhill, Miller, and Olp (2006) looked for more subtle evidence of MHC-biased mating preference among 48 romantic couples. They found a negative association between number of MHC alleles a couple shared and women's sexual responsiveness and satisfaction with how much their partner aroused them. Further, MHC similarity was positively correlated with women's number of extrapair partners while with her current partner, but not previous ones. Conversely, MHC similarity was not associated with nonsexual aspects of relationship satisfaction. Men showed no relationship between MHC similarity to partner and sexual responsivity or arousal to her, or to extra-pair partners.

Evidence suggests that MHC-related odors and faces affect preferences, but methodologies are diverse and wording of preference questions is often equivocal (Havlíček & Roberts, 2009). Consequently, results are mixed. Genererally, MHC similarity appears to down regulate sexual attraction but may upregulate nonsexual attraction, while dissimilarity is associated with sexual attraction. Future studies will require larger sample sizes and a greater number of targets. Questions regarding sexual attraction and/or behavior must be more explicit, and must determine whether MHC similarity is related to kin selection. Both MHC and non-MHC alleles should be tested, and analyzed to determine whether they are under selection for diversity or commonality. Tests should examine choice for dissimilarity and diversity. Sociosexual orientation and, for female subjects, phase of menstrual cycle and oral contraceptive use should be included as variables. Systematic inclusion of these variables will go a long way toward determining how MHC affects mate choice, kin recognition, and kin selection.

Sexually Dimorphic Cues to Health and Phenotypic and Genotypic Quality

Sexually dimorphic traits provide cues to the relative social value of both men and women, although the cues associated with each sex are expected to differ in certain predictable ways. Different morphological traits may be associated with higher or lower social value in a given domain, and be more or less important depending on local context. Our attractiveness-assessment psychology is thus expected to generate different assessments of these traits based on local environmental features. For both men and women, the trade-off between additional growth and reproduction can have significant effects on lifetime fitness. The optimal trade-off point can be formally modeled and tested, and is expected to be affected by variables such as diet, workload, stress, birth spacing, and age-specific extrinsic mortality risk (Hill & Hurtado, 1996). Because individuals and their condition vary, some may invest less, more, or the optimal amount in growth prior to reproduction. This opens the door for the evolution of attractiveness-assessment mechanisms that use environmental and social cues to arrive at local preferences for various sexually dimorphic traits, for example height, body size, and muscle development and fat distribution.

Strength Because mammalian males have higher variance in reproductive success than females, intrasexual competition is typically higher among males, and males correspondingly larger or possessing of armaments. If females preferentially mate with more formidable males, selection for these traits is enhanced. Human sexual dimorphism in muscle and fat composition is much greater than overall dimorphism in body size suggests. Men have 75% more arm muscle mass, 50% more leg muscle mass, and 61% more total muscle mass than women, as well as 90% greater upper body strength and 60% greater lower body strength (Lassek & Gaulin, 2009), indicating strong intrasexual selection for musculature (Puts, 2010; Sell, Hone, & Pound, 2012). Conversely, women have substantially higher fat stores than do men, much of it around the gluteofemoral region and breasts. This offsets much of the dimorphism in overall body mass, and may be one reason that Marlowe (2012) found the human operational sex ratio high compared to that expected by overall body mass.

The importance of these traits is reflected in adaptations for assessing men's relative strength and fighting ability. In both U.S. undergraduates and Tsimane forager horticulturalists, perceived strength based on body, face and vocal characteristics are all highly correlated with actual strength, controlling for height and weight (Sell, Cosmides, et al., 2009; Sell et al., 2010). Strength cues in men include upper body musculature, v-shaped torso, facial width to height (fWHR) associated with width of the bizygomatic structure (e.g., Windhager, Schaefer, & Fink, 2011; Zilioli et al., 2014), and low fundamental frequency and other characteristics of the voice (e.g., Hodges-Simeon, Gaulin, & Puts, 2011; Hodges-Simeon, Gurven, Puts, & Gaulin, 2014; Puts, Apicella, & Cárdenas, 2011). Controlling for age, marital status, and body mass index (BMI), fat-free mass (FFM) and limb muscle volume (LMV) also predict men's number of self-reported sex partners, and lower age at first intercourse among men in the NHANES sample (Lassek & Gaulin 2009; see also Gallup, White, & Gallup, 2007). Strength is associated with fighting ability, and better fighters more readily anger, use aggression, and feel entitled to getting better treatment from others (Archer & Thanzami, 2007; Hess, Helfrecht, Hagen, Sell, & Hewlett, 2010; Petersen, Sznycer, Sell, Cosmides, & Tooby, 2013; Sell et al., 2010; Sell et al., 2012; Sell, Tooby, et al., 2009).

Although among male foragers, strength peaks earlier in the lifespan than hunting return rates, body size and strength appear to play a role in productive ability. For example, among the Ache, Hadza, and Tsimane, body size was related to bow and arrow shooting accuracy (Blurton Jones & Marlowe, 2002; Gurven et al., 2006; Walker et al., 2002). Among the Hadza, upper body strength is the most consistent predictor of hunting ability, and men with stronger bodies had highest reproductive success (Apicella, 2014; see also Gurven & von Rueden, 2006).

Because caloric needs increase significantly with muscle mass (Lassek & Gaulin, 2009), too much musculature can be overly costly. As predicted there is an inverted U shaped relationship between musculature and sexual attractiveness among a U.S. sample of women (e.g., Fredrick & Haselton, 2007). In humans, higher testosterone levels scaffolding development and maintenance of greater muscle mass appear to trade off against immunity; however, men in better phenotypic condition may be better able to afford both, so this phenotypic correlation may mask the trade-off. For example, Rentala et al. (2012) found higher testosterone associated with greater facial attractiveness and greater response to hepatitis B vaccination (mediated by cortisol levels). In the NHANES III, more muscular men had lower CRP levels and white blood cell counts, suggesting a trade-off of greater testosterone (Lassek & Gaulin, 2009). This can be interpreted as support for the testosterone-as-immunological-handicap hypothesis (Hamilton & Zuk, 1982). However, CRP is an acute phase reactant that, in the absence of infection, should be near zero in the blood; thus, because no chronic elevation in CRP is found under evolutionarily relevant high-pathogen conditions (Blackwell et al., 2010; McDade et al., 2012), it is possible that males with greater Fat FM and VFM in the NHANES sample were either less prone to be infected at the time of measurement, or less likely to have chronic inflammation, reflecting better health. Similarly, white blood count increases in response to infection. Because patterns of pathogen immune development and activation and energy availability differ in foraging populations, more direct research is needed to disentangle relationships between investment in muscle mass and immunity.

In primates with multi-male/multi-female groups, males may form coalitions to prevent solitary males or other coalitions from gaining sexual access to group females. For humans, having larger, stronger, more aggressively formidable allies is likely beneficial in coalitional aggression and cooperative work. However, coalition and cooperative partners are also potential rivals in the contest to mate with female group members: The more formidable one's allies, the more formidable one's potential intrasexual competitors. More muscular men are not only more likely to have extra-pair mates, and more of them, but also are more likely to be the extra-pair mates of women, and to be found sexually attractive (e.g., Fredrick & Haselton, 2007). And, stronger males are more likely to have deployed physical force and to approve of its use in the service of their interests (Sell et al., 2009). In response to this problem, men appear to have evolved adaptations regulating competition between close allies. Men's testosterone rises in response to competitive wins against outside coalitions, but not in response to wins against friends. Further, men's testosterone usually increases in the presence of fertile women, but declines when the woman is one's friend's mate (Flinn et al., 2012).

Females face the risk that males will use their size and strength advantage coercively. For men, the costs of short-term mating can sometimes be reduced by choosing mates who exhibit cues of exploitability (Buss & Duntly, 2008; Goetz, Easton, Lewis, & Buss, 2012). This may help explain male attraction to cues of helplessness or low power in females. One solution to this problem is for females to obtain physical protection from other males (e.g., Buss & Schmitt, 1993; Scalise Sugiyama, 2014). Women who preferred larger, stronger, more dominant men as sires for their offspring would gain both indirect and direct benefits of alliance with those men, including sons and daughters (Cashdan, 2008) who inherited these qualities. On the other hand, females who preferred males exhibiting ability and willingness to invest in their offspring would tend to rear more offspring to maturity. The costs entailed by each of these preferences are affected by local resource constraints, intensity of intra- versus intergroup conflict, and operational sex ratio, and are mediated by the risks of domestic violence and desertion. In humans, adaptations reducing mating conflict within male coalitions could reduce the intensity of intragroup mating conflict, particularly when intergroup conflict is high (Flinn et al., 2012). Formal modeling of these trade-offs is necessary to predict evolutionarily stable mixes of strategies within specific constraints, including relative importance of testosterone-mediated traits in intrasexual competition vs. female mate choice (e.g., Puts et al., 2011). Increasingly, evidence suggests the nuanced distinctions among the constellation and degree of male androgen-linked traits found dominant and aggressive and those found sexually attractive may differ somewhat (e.g., Blackwell & Sugiyama, 2008; Hodges-Simeon et al., 2011; Windhager et al., 2011), and may differ in degree to which they are preferred across cultures (Scott et al., 2014).

Height Throughout the juvenile period, individuals face a number of trade-offs, including among basal metabolism, activity, immune function, and growth. Adult height is partially heritable, but nutrition, pathogen exposure, and immune function affect how much energy is allocated for growth. In subsistence societies larger males are those who had better nutrition, fewer parasites and illness, less psychosocial stress, and/or more efficient metabolism than smaller males. As noted though, weight (primarily muscle in males and fat in females) is prioritized over height (e.g., Blackwell et al., 2009; Urlacher et al., 2014).

Further, for females, human growth is determinate: Longitudinal growth ends when reproduction begins because the energetic costs of doing both simultaneously are too high (e.g., Walker et al., 2006). For women, the fitness benefit of additional growth prior to reproduction includes accumulation of somatic resources for later reproductive effort (Jousilahti, Tuomilehto, Vartiainen, Eriksson, & Puska, 2000), lower offspring mortality (Allal, Sear, Prentice, & Mace, 2004), and lower maternal and infant mortality. Women with more gluteofemoral fat have higher fertility, and taller women tend to have wider pelvises, easier births, and higher infant birth weights (Kirchengast, Hartmann, Schweppe, & Husslein, 1998; Martorell, Delgado, Valverde, & Klein, 1981;

Rosenberg, 1992; Rosenberg & Trevathan, 2002). The potential benefits of earlier reproduction include lower prereproductive mortality risk and a potentially longer timespan in which to reproduce, so females in high mortality, resource-constrained populations show rapid growth for adult body size (Hill & Hurtado, 1996; Walker et al., 2006).

Adult height is affected by heritable factors and life history trade-offs associated with level and timing of developmental resource access, metabolic efficiency, mortality risk and pathogen exposure (e.g., Blackwell et al., 2010; Urlacher et al., 2014, Walker et al., 2006). Greater height offers various biomechanical advantages (Samaras, 2007). In sports, for example, taller elite athletes have an advantage in middle-distance running, swimming, and jumping. Disadvantages of greater height are apparent in the total energy required by taller people, aerobic activity in which maximal performance occurs for 30 seconds or more, and heat regulation and dehydration under heavy work load. Depending on local ecology, greater height can also make travel much more difficult: For example, tall individuals face more obstacles (e.g., low vines, branches) than shorter individuals in tropical rainforest foraging (e.g., Hill & Hurtado, 1996).

Although male strength has a larger effect, height also increases perceived fighting ability, which may underlie ability to get one's way (Sell et al., 2009). Height is positively associated with strength and reach, and may be correlated with actual fighting ability, although results are mixed (e.g., Carrier, 2011; von Rueden et al., 2008; Sell et al., 2012). Taller males report engaging in more frequent aggressive acts (Archer & Thanzami, 2007). Taller individuals self-report higher self-esteem, engage in and are perceived to engage in more dominant behavior, are less sensitive to dominance cues in other men, are perceived as being more intelligent, and were more influential in a negotiation experiment (e.g., Gawley, Perks, & Curtis, 2009; Judge & Cable, 2004; Watkins et al., 2010). Taller men also report less jealousy in response to dominant rivals than do shorter men (Buunk et al., 2008). However, because strength is a more powerful predictor of perceived fighting ability, entitlement, positive attitude toward and actual use of force, and deployment of anger (Sell et al., 2012), associations between these outcomes and height must ultimately be revisited to control for effects of strength.

In mates, both men and women generally prefer that the man be taller than the woman, and men tend to have partners who are shorter than themselves (e.g., Courtiol, Raymond, Godelle, & Ferdy, 2010; Salska et al., 2008). Height is associated with rated attractiveness of men, and women more strongly prefer relatively taller men to themselves during the fertile (follicular) phase of their menstrual cycle (e.g., Pawlowski & Jasienska, 2005). Taller-than-average men are preferred to men of short or average stature as dates and mating partners in questionnaire studies (e.g., Buss & Schmitt, 1993; Fink, Neave, Brewer, & Pawlowski, 2007), have more attractive mates (Feingold, 1982), and are more likely to be married (Pawlowski et al., 2000). In analyses of personal ads, 80% of women who stated height preferences wanted men 6 feet tall or taller (Salska et al., 2008). Ads placed by taller men receive more responses (Pawlowski & Koziel, 2002), and taller men were rated more desirable in the context of speed-dating (Kurzban & Weeden, 2005). Women even seem to take height into consideration in sperm donors (Scheib, 1997; Scheib, Kristiansen, & Wara, 1997). Sear and Marlowe (2009), however, report no male height bias in marriage partners among Hadza foragers. However, both extreme shortness and tallness may be associated with health problems in both sexes (Mueller & Mazur, 2001; Nettle, 2002a).

Associations between male height and reproductive success are mixed. A review by Stulp, Pollet, Verhulst, and Buunk (2012) found studies that reported no effect, positive effects, and negative effects of height on RS; however, the authors note that many of those studies were not based on men's entire reproductive career and did not test for curvilinear effects of height on RS. Curvilinear effects have been found in several studies of male height and RS. Stulp et al. (2012) found that average-height men married earlier, which likely accounted for their greater reproductive success. However, they note that studies (including their own) do not account for reproduction in the context of extra-pair or nonmarital relationships. This may account for additional reproductive success of taller men in particular. Relatively taller men also have numerical advantages in number of potentially accepting mates in the mating market (Pawlowski et al., 2000; Pawlowski & Koziel, 2002).

Height preferences are not limited to the sphere of mate selection. Coalitionary leadership and height appear to be associated in both small-scale (Brown, 1991) and state societies (Stulp, Buunk, Verhulst, & Pollet, 2013), although some of this effect is likely a product of strength. For example, in addition to other factors such as generosity, von Rueden et al. (2014) found strength but not height associated with leadership in two Tsimane communities. In U.S. presidential elections, the taller candidate is more likely to win, with the margin of victory positively correlated with height (McCann, 2001; Stulp et al., 2013). Senators and CEOs appear to be taller than the average American man (Etcoff, 1999; Keyes, 1980). Further, there appears to be a positive association between height and socioeconomic and social success in modern societies (e.g., Bielicki & Szklarska, 1999; Deaton & Arora, 2009). Interestingly, Mueller and Mazur (2001) found no relationship between height and either status (final military rank) or socioeconomic success among a sample of the West Point graduating class of 1950, even though they did find a significant indirect effect of stature on lifetime RS. However, the West Point cohort is more homogeneous, both in height and in determinants of success that may covary with height, than the general population.

The use of industrialized populations to study height preferences is problematic on several counts. For example, mate selection accounts for higher reproductive success among taller men in the West Point sample, who had higher probability of having a second family with a younger, fecund, wife. The authors conclude that directional mate selection for height appears to be unconstrained in this sample. However, military officers are extremely unlikely to have experienced the level of dietary and health constraints predicted to trade off against height that almost certainly affected our foraging ancestors. Another study found that taller-than-average British men had higher numbers of live-in partners, and lower chance of either being childless or having had no significant mating relationship (Nettle, 2002a), but no significant association between total number of offspring and height. However, the men had not yet completed fertility, and had ready access to contraceptives. In modern societies with ready access to birth control, number of sexual partners may be a better indicator of the links between preferences and reproductive success under ancestral conditions, than reproductive success per se.

If male size is positively associated with aggressive formidability yet involves costs, we may expect selection for a context-sensitive assessment mechanism functioning such that intensity of male height and strength preferences increase with increasing levels of intrasexual competition. Intensity of preference for taller males is also expected to vary with resource stress: although taller males are those who could better afford the costs of growing larger and relative height provides a signal of developmental phenotypic quality. However, at some level of resource constraints the energetic and mortality costs of maintaining large size may outweigh the benefits of signaling phenotypic quality. This accords with findings of an inverted U-shaped function between height and attractiveness. Since hominid evolution no doubt included periods of extreme resource scarcity, height assessment adaptations might well reflect this trade-off.

Findings on men's preferences for partner height run the gamut from below-average to above-average height (e.g., Grammer et al., 2002; Hensley, 1994; Swami et al., 2008). Again, this may be because there is an inverted U-shaped relationship between male preference and female height, with males preferring slightly taller than average females who are nevertheless shorter than the male assessor (Courtiol, Picq, Godelle, Raymond, & Ferdy, 2010; Courtiol, Raymond, et al., 2010). Male preference for partner height varies as a function of the assessor's own height (e.g., Fink et al., 2007; Salska et al., 2008; Swami et al., 2008). For example, in a large Polish sample, preferred difference between ego's height and partner height was affected in part by the rater's own height, with taller men and shorter women preferring greater height differential in their partners, thus increasing effective mating pool size (Pawlowski, 2003). However, in the fertile phase of their menstrual cycle, and for short-term mateships, women exhibited greater preference for taller men, independent of the rater's own height (Pawlowski & Jasienska, 2005). Below-average or average height women are reported to have greater RS than tall women generally (e.g., Mueller, 1979; Nettle, 2002b), although there is variation across populations (e.g., Stulp et al., 2012).

In a natural fertility population of Gambian women, Sear (2010) found the expected trade-off between growth and age of sexual maturity: Taller women had later age at first birth, but their offspring exhibited lower mortality. The study found no evidence of a relationship between female height and marriage patterns, divorce, or spouse's height. Higher mortality was observed at both ends of the female adult height continuum, but not enough to negate the positive relationship between height and reproductive success. Nor was there evidence of positive associative mating for height, which suggests that female height was not a significant factor in men's marriage arrangements in this population. However, the authors note that men's preferences per se were not tested, and the relative benefit of choosing taller women as wives may be offset by desire for quantity of mates in this polygynous society.

Using data from Britain's National Child Development Study, Nettle (2002b) found a weak but highly significant inverted U-shaped relationship between relative female height at age 23 and reproductive success at age 42, controlling for own or husband's socioeconomic status. Highest reproductive success was for women between .7 and 1.7 standard deviations below the mean. Women of mean height had the highest number of marriages or long-term mates, and were least likely never to have had a long-term mating relationship. Nettle also found the expected trade-off between growth and age of sexual maturity, with taller women beginning to reproduce later. However, the sample population had ready access to hormonal contraceptives, and mean fertility was low for all heights observed, so later first reproduction of taller women cannot account for their lower reproductive success. As predicted, preferred female height appears to change with (mild) socioecological risk. Pettijohn and Jungeberg (2004) found a significant positive correlation between yearly indicators of economic stress (predicted to covary with perceived ecological risk) and the height of Playboy Playmates of the Year.

Body Shape: Waist-to-Hip Ratio Singh (1993a, 1993b) noted that the ratio of waist to hip circumference (waist-to-hip ratio or WHR) provides a potential cue to female mate value. Estrogen during puberty stimulates fat deposition on the thighs, hips, and buttocks, and is associated with the widening of the female pelvis. Androgen profiles lead to male fat deposition in the abdominal region. The result is postpubertal sex differences in WHR, with a normal WHR for Western women of ~.7 and a normal male WHR of ~.9 (Singh, 1993a). Western women with normal WHR (.67–.80) are at reduced risk for primary infertility and certain health problems (e.g., cardiovascular disease, stroke, diabetes, female carcinoma), independent of overall level of body fat (Singh, 1993). However, except for primary infertility, most health risks associated with higher female WHR are probably evolutionarily novel (Lassek & Gaulin, 2008; Sugiyama, 1996, 2005). In clinical studies, women with low WHR have significantly higher fecundity but as Lassek and Gaulin (2008) point out, clinical studies are largely based on older women trying to conceive. In a well-nourished sample of Polish farmers, Jasienska, Ziomkiewicz, Ellison, Lipson, and Thune (2004) found that women with low WHR and large breasts were the most fecund quartile in their sample and had estradiol levels suggesting a conception probability 3 times that of the rest of the sample.

Singh (1993a, 1993b) proposed that selection shaped men's mating psychology to prefer female WHR of ~.7, and women's mating psychology to prefer male WHR of .9 regardless of preferences for overall body fat. In females, WHR provides potential cues to sex, lifestage, parity, and pregnancy. Significant evidence for WHR-associated assessment and preference psychology is found in studies using line drawings, standardized body photos, eye direction detection, and archival materials, across both time and cultures.

Only three studies report no effect of WHR on attractiveness. Yu and Shepard (1998) and Wetsman and Marlowe (1999) used a subset of Singh's (1993) 12 line drawings of female figures varying in three levels of body weight (high, medium, and low), and four levels of WHR (.7, .8, .9, 1.0). This subset presented WHRs of .7 and .9 only. A follow-up Hadza study (Marlowe & Wetsman, 2001) used a wider range of WHRs from .4 to 1.0. In all cases men preferred heavier-weight figures, with no apparent effect of WHR. However, males in these societies showed clear preference for higher-body-weight figures, and potential stimulus confounds between WHR and body weight mean that effects of preference for higher body weight could have swamped WHR preferences. Further, in the Matsiguinga case, the highest WHR presented was average for the population. Marlowe, Apicella, and Reed (2005) later showed preference for lower WHR when figures were presented in side view, with buttocks extension visible. Sugiyama (1996, 2004b) also found that Shiwiar forager-horticulturalists preferred heavier-weight figures, but that a preference for lower WHR was apparent when weight was better controlled and high and low WHR were classified in relation to the female population average (see Sugiyama, 2005, for discussion).

Some researchers contend that WHR accounted for very little of the variance in bodily attractiveness, and was primarily a by-product of preferences for body mass index (BMI: weight kg/height meters^2; e.g., Cornelissen, Tovée, & Bateson, 2009; Tovée, Maisey, Emery, & Cornelissen, 1999). However, the by-product view lacks surface validity and has not stood up to scrutiny. At 6′3″ and 185 pounds, Prince William has essentially the same BMI as UFC women's bantamweight champion and *Sports Illustrated* swimsuit model Ronda Rousey at 5′6″, 134 pounds (fighting weight): Look at their bodies and see if they are equally sexually attractive to you. For the vast majority of readers, I'll bet not. Studies using photos of actual people presented only a small section of the evolutionarily valid range of WHR relevant to mate value. Primarily, they presented figures of one sex, with primary and/or secondary sexual characteristics visible: For instance, females shown were primarily nulliparous or low-parity women with mean age around peak fertility. This greatly limits the WHR variation presented to subjects (Sugiyama, 2005). I predicted that because WHR varies across populations, instead of uniform cross-cultural preference for a specific WHR, lower WHR relative to the normal female range to which a man is exposed should be preferred (Sugiyama, 1996, 2004b). Further, men exposed to a higher range of healthy nubile female WHR should find higher WHR more acceptable than men exposed to a lower range of female WHR, and lowering the natural range of WHR to which men are exposed should predictably lower their expressed WHR preference, at least within the limits of the reaction norm for these adaptations (Sugiyama, 1996, 2004b, 2005).

Additional research now supports this general prediction, originally proposed by Symons (1979), that attractiveness assessment is calibrated by local range of variation in the cue in relation to local optima as one moves across different ecologies, groups, or subgroups (e.g., Kościński, 2008, 2012; Tovée, Swami, Furnham, & Mangalparsad, 2006). Although earlier studies showed that Playboy models and film actresses tended to have WHRs of ~.68), there is variation in the absolute WHR preferred. For example, Voracek and Fisher (2002) show decrease in WHR of *Playboy* models through time, and women in Reubens paintings have average WHRs of .78 (Swami, Gray, & Furnham, 2007). For example, Pettijohn and Jungeberg (2004), show change in body shape correlated with times of socioeconomic hardship, when playmates of the year were heavier and had larger waists and WHR.

Preference is also regulated in relation to options. This same principle is illustrated in the "closing time effect" (whereby standards of attractiveness decrease but perceived attractiveness increases as bar closing time approaches, regardless of alcohol intake), and by the negative effects of viewing highly attractive females on male relationship satisfaction and on female body image, respectively (e.g., Kenrick, 2011). Nevertheless, preference for relatively lower female WHR is apparent even without past visual exposure: Both men born blind and those who developed blindness later in life preferred the shape of mannequins with lower WHR (Karremans et al., 2010).

I (2005) argued that because multiple anatomical features are associated with waist and hip circumference, the precise shape receptor, assessment, and preference mechanisms might not consist of a waist-to-hip circumference assessor per se. Rather, they are likely based on more complex shape-assessment mechanisms, such as curve detectors, angle detectors, or the ratio itself. WHR is composed of numerous shape dimensions, including factors associated with skeletal functional morphology and body fat deposition. I therefore predicted that WHR-associated attractiveness assessment should take as input the observable range of female WHR and body fat, based on adaptations that incorporate assessment of critical WHR subcomponents associated with sex differences in functional anatomy, including: (a) pelvic width, shape, and angle, (b) hip width and circumference, (c) hip shape, (d) buttocks extension, (e) buttocks shape, (f) waist width and circumference, (g) waist shape, (h) stomach shape, and (i) stomach extension in relation to (j) other aspects of skeletal structure—for example, shoulder and/or ribcage width, distance from pelvis to shoulder, and length of long bones (which provide reference points for assessing pelvic width and fat deposition)—in relation to overall growth, developmental health, and biomechanical efficiency (Sugiyama, 1996, 2004, 2005). This section updates this information, and discusses new findings in relation to predictions or issues I raised previously.

One major development comes from Lassek and Gaulin (2008), who note that gluteofemoral fat (GFF) deposition is prioritized in women, with most fat composed of GFF, a pattern not seen in other primates. GFF is richer in long-chain polyunsaturated fatty acids (LCPUFAs) than abdominal and visceral fat, and the primary source of LCPUFAs necessary for fetal and infant brain development. GFF is protected from use until peak infant brain growth late in pregnancy and during lactation, even when women are under conditions of food restriction. Conversely, abdominal fat is prioritized for mobilization for short-term energy use and may decrease availability of LCPUFAs. The primary LCPUFAs in our brains are arachidonic acid (ARA) and omega-3 docosahexaenoic acid (DHA), with about 20% of brain weight comprised of DHA. Studies of mothers' milk, and of DHA supplementation and dietary intake, show improved cognitive performance in humans and nonhuman animals (Cohen, Bellinger, Connor, & Shaywitz, 2005; Koletzko et al., 2008; Lassek & Gaulin, 2014; McCann & Ames 2005). Further, gluteofemoral fat stored early in life is not replenished, so declines with parity, as does blood-circulating DHA, and some studies show that cognitive performance of offspring declines with birth order. Conversely WHR increases with parity. Lassek and Gaulin (2008) therefore predicted that women's WHR would therefore be negatively associated with own and offsprings' cognitive abilities. They further predicted that, because women who reproduce while they are still developing face competing demands from their own brain development, gluteofemoral fat storage, and their fetus' brain development, teen mothers and their offspring would have impaired cognitive development, but that this would be buffered in women with low WHR (i.e., high LCPUFA stores). Analysis of data from the U.S. Centers for Disease Control and Prevention National Health and Nutrition Examination Survey (NHANES) supported each of these predictions. Their working hypothesis is that, as selection acted to increase brain size in humans, female adaptations to support the increasing costs of providing resources for neurodevelopment included the acquisition, storage, and allocation of LCPUFAS to offspring. Those resources came to be stored in the gluteofemoral region, and thus came to be the targets of male mate choice. WHR may be a cue to the LCPUFAS resources a woman has available for fetal and infant brain development. Interestingly, DHA is reported to be particularly concentrated in the prefrontal cortex, an area of the brain hypothesized to have been the area most enlarged in later hominin brain expansion (e.g., Crawford et al., 1999; Van Essen & Dierker, 2007) and important for short-term working memory and association.

A related development is research showing that, under dietary energy constraints more characteristic of our evolutionary past, women face more noticeable trade-offs between gluteofemoral fat deposition for reproduction and abdominal fat deposition for energy mobilization to buffer food shortages and other environmental stressors. Trade-offs are in part regulated by steroid hormones, including cortisol, estrogens, and androgens. Stress activates the HPA axis and cortisol production, which mobilizes energy stores to deal with sources of stress. It also shifts allocation to storage in central adiposity in preparation for future stressors, and is therefore associated with higher WHR (Cashdan, 2008; Flinn & Ward, Chapter 24, this volume).

A possible evolutionary scenario is that as increasingly dimorphic fat deposition arose with later hominin increases in brain size, it provided cues to multiple components of female mate value, leading to evolution of WHR assessment and preference mechanisms that generated or enhanced it as a target of male mate choice. Deposition of fat on the gluteofemoral region may have initially been driven by preexisting male primate sexual attention to and assessment of this region in response to proceptive female primate sexual displays, and/or the energetic and structural efficiency of storing fat in this region, particularly during pregnancy. Moreover, as selection for gluteofemoral fat deposition increased to support brain development, and trade-offs between somatic and reproductive investment directed the timing of this deposition toward puberty, WHR provided an important cue to sex, onset of female reproductive lifestage, and parity, which intensified selection pressure on WHR-assessment mechanisms.

As GFF deposition evolved, WHR increasingly provided a cue to developmental markers of reproductive value. In a sample of 329 Shuar and Shiwiar forager-horticulturalists, female WHR decreases linearly from a high of almost 1.05 at 2 years of age, to an average low of 8.5 by around 12 years of age (Sugiyama & Blackwell, 2008). Change over this period reflects early prioritization of body fat deposition in childhood to buffer energetic fluctuation and trade-offs between basal metabolic needs, growth, immune function, and activity, transitioning to a major increase in reproductive investment of gynoidal fat distribution in girls near and at puberty (e.g., Ellison, 2001; Lassek & Gaulin, 2008). Despite earlier studies suggesting that critical levels of body fat stimulated onset of menarche (e.g., Frisch & McArthur, 1974), human biologists now widely accept that menarche is related to skeletal maturation and not total body fat (Ellison, 2001). However, using NHANES data, Lassek and Gaulin (2007, 2008) found that odds of menarche increase with gluteofemoral fat more than with height or biiliac breadth, and decrease with larger waist circumference. Among Shuar, the intersection of low female WHR with increasing body fat converges on age of peak female reproductive value (Sugiyama & Blackwell, 2008). Further, among well-nourished Polish farmers, women with low WHR and large breasts had estradiol levels associated with a conception probability 3 times greater than that of other women (Jasienska et al., 2004).

WHR also provides a reliable indicator of sex post-pubertally. Even though the range of Shuar female WHR is significantly higher than that of western industrialized populations, Shuar show significant differences in WHR by sex (Sugiyama & Blackwell, 2008). Experimental studies in Western/industrialized populations using standardized photos of 18- to 42-year-old western women showed that BMI (and WHR co-vary, with BMI accounting for over 80% of the variance in attractiveness ratings, while WHR accounted for less than 2%). Tovée et al. (1999), concluded that WHR preference was a by-product of BMI preference (see, e.g., Tovée & Cornelissen, 2001; Tovée, Hancock, Mahmoodi, Singleton, & Cornelissen, 2002). However, Shuar BMI does not differ by sex, and shows similar age-related change for both sexes. Typical of humans, adolescent and post-adolescent females are shorter and have more body fat, while males are taller and have more muscle. This contributes to very different body *shapes* even though age-related BMI does not differ: Male and female preferences based *only* on BMI would find male and female body shapes equally sexually attractive. This is not the case. Further, Shuar WHR and BMI are not correlated for either sex, so WHR preferences cannot be a by-product of preferences for BMI, unless the Shuar (a natural fertility, subsistence population) rather than Westerners are an evolutionary anomaly. Cashdan (2008) shows that across 33 non-Western populations (including the Shuar), WHR is above 0.8 in almost all populations, with high variability across them. Further, in populations without obesity, there is no correlation between BMI and WHR. After reviewing a large (n = 32,000) international (19 countries) sample from the WHO MONICA study, Cashdan notes that BMI could possibly account for only 18% of variance in female WHR, and that only ~30% of variance in female WHR could be explained even after taking into account height, age, BMI, and population. Most of the association between BMI and WHR was due to the contribution of evolutionarily invalid obese populations (about half the sample). While preference for body fat levels is an important contributor to attractiveness, varies cross culturally, and is functionally regulated by the probability of resource hardship, it cannot account for preferences in WHR. Moreover, even when one cue is a more important component in attractiveness assessment than another, this is not relevant to the argument that we have assessment adaptations for the latter cue.

In earlier experimental studies using line drawings, WHR was potentially confounded with body mass, because lower WHR was manipulated by reducing waist size. This did not affect interpretation of results in most studies, but among Matsiguenga and Hadza, where men preferred the highest weight figures, it was impossible to determine if there was no preference for low WHR, or whether preference for high body weight swamped preference for lower female WHR (Sugiyama, 2004a, 2005). When presented with figures that bracketed high and low WHR in the local population but represented only one weight category, Shiwiar exhibited preference for locally lower female WHR (Sugiyama, 2004b; see also Marlowe et al., 2005). Singh, Dixson, Jessop, Morgan, and Dixon (2010) had subjects rate photos of pre- and postoperative plastic surgery patients in which fat was removed from the abdomen and placed in the buttocks: Pre- and postoperative photos thus had identical body fat and BMI, but postoperative photos had lower WHR. Cross-culturally (including among subjects in Cameroon, Indonesia, and Samoa), the postoperative photos were judged more attractive. Additionally, fMRI scans showed distinct activation of neural reward centers when men viewed the postoperative photos (Platek & Singh, 2010).

Under natural conditions, WHR-associated preference mechanisms operate in a social context that includes people of all ages, both sexes, and different parity. Morphometric measures of WHR and its relation to mate value tend to encompass this evolutionarily relevant range, but experimental studies rarely do: Female stimuli usually represent nulliparous or low-parity women around the age of peak fertility. If low female WHR is attractive in part because it signals sex and reproductive value, then the limited range presented in most experimental stimuli may artificially reduce the relative effect size of WHR on attractiveness (Sugiyama, 2005). To address the lack of studies bracketing the critical range of variation associated with women's peak reproductive value, Blackwell and I examined effects of sex and reproductive value across a previously unexplored range of WHR variation associated with the transition from childhood to reproductive maturity. We had heterosexual male and female subjects rate images from Tanner and Whitehouse's (1982) *Atlas of Children's Growth*. The *Atlas* includes front and back naked images in standard pose, anthropometric measures, and developmental markers, taken at 1- or 2-year intervals from age 4–6 to 20. Male short- and long-term attractiveness ratings did not differ. As predicted, across this critical range of variation WHR accounted for much more of the variance in attractiveness than BMI or body fat, and body fat accounted for more variance than did BMI. Using nonlinear quadratic or cubic terms in the models eliminated significant effects of both BMI and body fat, while effects of WHR remained significant. Because previous studies only used images of reproductive-age females, we then repeated analysis for reproductive-aged females only. As predicted, this removed much of the relevant variation in WHR: Although effects of WHR on attractiveness remained significant, effects of body fat or BMI had relatively greater effects on attractiveness than when male body images and prereproductive female body images were included (although not nearly as much as in other reported studies) (Blackwell & Sugiyama, 2008).

Lower WHR was also strongly associated with figures being perceived as female, and less strongly but positively associated with perceived age. Conversely, body fat was strongly associated with perceived age, but less strongly associated with the figure being perceived as female. WHR was a strong predictor of perceived sex, while body fat was a stronger predictor of age, and both perceived sex and perceived age had stronger direct effects on attractiveness than either WHR or body fat (although the latter two also had significant direct effects in the model). Using all data from female subjects included in Tanner and Whitehouse (1982) showed that female WHR reaches its lowest point before body fat reaches adult levels, just before Tanner developmental stage 5 (breast and pubic hair development). This occurs at around 15 years of age, the age closest to peak reproductive value in our stimulus set, and the age of figures (early adolescence) ranked highest in sexual attractiveness by our male raters. For male raters, there was significantly and strikingly greater attractiveness for the early adolescence female photos, associated with WHR. This contrasted with ratings by female subjects, for whom there was greater inter- than intraindividual stimuli effects on attractiveness.

In short, when a greater range of evolutionarily relevant stimuli are presented, as predicted the effects of WHR on attractiveness are much greater than previously reported. Further, preference for peak residual reproductive value was apparent. Previous studies used questionnaires to ask preferred age of a mate, and subjects may have been reluctant to consider women deemed inappropriate as mates by their respective cultures. Our study found a strong effect of actual stimulus figure age even though subjects' age estimates for the figures were not accurate. Of course, there is no reason to believe selection could produce adaptations to assess actual chronological age per se (Symons, 1979), and our subjects assumed that all figures were over the age of consent. Self-reported age preferences do not necessarily coincide with behavior. Consider the preferred age range advertised by male OkCupid members. The median 31-year-old male advertises a 22-year-old minimum and a 35-year-old maximum mate preference; however, the average 30-year-old man sends as many messages to 18-year-old women as he does to women his own age (http://blog.okcupid.com/index.php/the-case-for-an-older-woman/). Thus, stated age preferences are relatively poor indicators of actual strength of male preferences for youth. This may explain why, to date, questionnaire data have generally not found preferences for age of female peak reproductive value.

To examine how perceptions besides perceived sex and age contribute to perceived attractiveness, and to identify additional relevant variations in shape, a new set of subjects rated the Tanner and Whitehouse photo set for masculinity/femininity, physical dominance, health, and social status, as well as sexual attractiveness and perceived age. Principal Components Analysis showed complex shape dimensions involved in attractiveness assessments that are not easily described by simple anthropometrics such as WHR, BMI, and shoulder-to-stature ratio, even though they are sometimes related. For example, one factor accounting for 34% of the variance in shape preferences included high WHR with broad stance, and was associated positively with sitting height and shoulder to stature ratio, but negatively related to BMI. This factor was strongly positively associated with perceived masculinity, and with dominance and age, but only moderately attractive to female raters. It was also negatively related to perceived health and social status. Males found it sexually unattractive. Another factor included high WHR and square shoulder shape, but was unrelated to other dimensions previously hypothesized to affect attractiveness, such as BMI or shoulder to stature ratio. It was moderately sexually attractive to females, unattractive to males, and moderately associated with perceived masculinity and dominance (Blackwell & Sugiyama, 2008). Other studies using more sophisticated stimuli also show preferences for complex aspects of body shape (e.g., Brooks, Shelly, Fan, Zhai, & Chau, 2010).

Women's WHR also provides a cue of pregnancy: Pregnant women have higher WHR and, in the later stages of pregnancy, a distinctive body shape. Women's WHR is also related to parity and lactation. For example, from its lowest point around the age of peak residual reproductive value, Shuar female WHR increases with age and parity. NHANES data also shows that gluteofemoral fat stores are diminished by pregnancy and lactation, even among American women not facing major constraints in energy availability (Lassek & Gaulin, 2006). One avenue of inquiry that remains to be explored is the effect of pregnancy on attractiveness in long-term and short-term mating contexts. In the latter, we would expect pregnancy to reduce bodily attractiveness. In the former, the body shape of pregnancy may not enhance sexual attractiveness per se, but may increase attractiveness associated with bonding and investment in the woman by her long-term mate.

Trade-offs between maternal maintenance, pregnancy, immunity, basal metabolism and activity, maternal energy, and nutrient balance can have intergenerational fitness effects: Maternal nutrition and stress have significant epigenetic effects on offspring life history trajectories and health (Worthman & Kuzara, 2005). These trade-offs may explain, in part, why women in non-Western societies have higher average WHR (Cashdan, 2008). Relative energy allocation to gluteofemoral fat deposition early in the female reproductive lifespan reflects a life history bet on the future probable value of that fat for reproduction, regulated by trade-offs among uses of that energy for current reproduction, growth, maintenance, activity, and immunity. This trade-off has fitness effects. For example, the cross-sectional Shuar data suggests that women with higher WHR have slightly higher reproduction early in the lifespan than women with low WHR, but that women with low WHR have greater lifetime reproduction. Longitudinal data are needed to see if this observation holds up. If a male is following a shorter-term mating strategy, then favoring women with faster reproductive life history may yield preference for (slightly) higher WHR. Long-term mating strategy should favor lower WHR in this context.

Evidence of trade-offs and maternal depletion can also be seen in the cross-sectional Shuar data. Even though body fat is positively related to both waist and hip circumference, lower WHR is positively related to live births, whereas overall body fat is negatively associated with total live births (Sugiyama & Blackwell, 2008). Nenko and Jasienska (2009), however, found no evidence for maternal depletion among a sample of 296 well-nourished Polish women, perhaps because they had high dietary intake of LCPUFAs. Further, Jasienska et al. (2004) show optimal sex hormone profiles associated with low WHR, but only in women with large breasts. Cashdan (2008) notes another trade-off that may influence body shape and variance in male attraction. Women's ability to influence others, gain status, and get others to favor their interests is linked to hormonal regulation of behavioral correlates of assertiveness, such that women may face trade-offs in balancing androgen and estrogen profiles. Thus, in contexts where female status is relatively more important for mate value, males may show preference for slightly higher WHR.

FUTURE RESEARCH DIRECTIONS

Mates and kin are often cooperative and coalitional allies; thus, some cues of mate, offspring, kin, and coalitional value may overlap. However, others may not—for example, one may desire kindness in a mate but ruthlessness in a war ally. We must therefore understand how adaptations generating our perceptions of attractiveness are organized, and why we see cross-cultural and individual variability in assessments of attractiveness.

Complex information-processing adaptations are often expected to embody context-sensitive rules. These rules generate different psychological and behavioral outputs in response to different conditions within the range of those to which the adaptation is designed to respond (a.k.a. *reaction norms*). Hypotheses regarding such adaptations must ask how the mind processes local environmental cues to produce a given effect (e.g., Buss, 2000; Tooby & Cosmides, 1992). This means that hypotheses regarding the design/function of human attractiveness-assessment mechanisms must delineate specific psychological properties (or their by-products) that process local environmental cues to generate the intra- and intercultural similarities and differences found in attractiveness standards (Sugiyama, 2005). Simply documenting the variation is not enough.

A critical variable in the deployment of many adaptations is the phenotypic state of the assessor. For mating, parenting, and alliance formation, this includes developmental stage and sex, as well as health, nutritional, reproductive, and mating status. Other variables these adaptations must assess include: (a) number of assessor's co-resident kin; (b) number of people who value the assessor, how much they value him/her, and for what; (c) whether the assessor's father and/or mother are still living (e.g., Hill & Hurtado, 1996; Sugiyama, in press); (d) how aggressively formidable the assessor is compared to others; (e) how attractive the assessor is to others as a mate (e.g., Buss, 2000); and (f) how attractive the assessor is as a friend or ally. Even though the underlying functional design of attractiveness-assessment adaptations is expected to be universal, we should expect to see strategic variation in their psychological output and behavioral expression at the population, group, and individual levels.

Certain cues are expected to be weighted differently in arriving at an assessment of overall physical attractiveness. Variance in these weightings will be based on: (a) which features are statistically more likely to be associated with a particular aspect of the social value in question; (b) local environmental features (e.g., famine, health risk) that reliably change the relative value of attractiveness cues; (c) ecologically variable cues most highly cross-correlated with each other in the local environment; and (d) the phenotypic condition of the assessor. Overall judgment may reflect trade-offs among the outputs of each of these components. Additionally, outputs of different assessment components may conflict with or enhance others in the production of a final perception of attractiveness.

Each assessment mechanism can vastly reduce the computational complexity of its task by processing only a minute set of the information available in its environment. Nevertheless, each mechanism must be deployed under the evolutionarily relevant conditions, and doing this requires information intake and analysis. This implies a hierarchically organized but parallel processing system of feedback loops that inform the system based on cues received and instantiated. For instance, a cue may be related to sex and/or relative age (or stage of lifespan), and the outcome of those analyses fed into emotional adaptations that affect attractiveness, rather than affecting attractiveness directly. This view of attractiveness-assessment cognition markedly differs from the view that attractiveness-assessment mechanisms will produce cross-culturally uniform standards, with some criteria always weighted more than others. Anomalous findings and individual and cross-cultural differences in attractiveness assessments may well resolve under this approach.

Research over the last decade has been catching up with theory that psychological hypotheses and testing must take into account that psychological adaptations are expected to be context sensitive, and involve trade-offs dependent on socioecological contexts and individual phenotypic state. Here, I have focused on just a few hypothesized cues to social value to illustrate some of these complexities of attractiveness assessment psychology. Similar research is examining context sensitive regulation and trade-offs in facial, olfactory, movement and vocal cues used in attractiveness assessment, but the literature is vast so trade-offs between depth and breadth of coverage had to be made. In 2005 I called for greater collaboration between psychologists and anthropologists, particularly behavioral ecologists with established fieldsites in non-Western, nonindustrialized contexts, and this is increasing. Oddly, integration with other branches of physical anthropology, particularly human biologists who should be natural allies in the endeavor to discover the functional biology of the mind has, with a few notable exceptions, been limited. The welcome increase in cross-cultural study of attractiveness assessment, and psychology generally, make clear the need to measure, test, and control for relevant contextual variables, and that generalization from undergraduates is no longer sufficient as the basis for conclusions. However, the time, energy and monetary costs of systematic cross-cultural field collection and processing of relevant comparative data are larger than that for university lab based studies, so the coming decade will require a shift in funding priority toward cross-cultural research integrating psychological, socio-ecological, and human biological data.

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CHAPTER 13

Contest Competition in Men

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INTRODUCTION

In this chapter, we explore how men's phenotypes, including their psychologies, have been shaped by an evolutionary history of contest competition. Sometimes called intrasexual selection, contest competition is one of several mechanisms of sexual selection and involves the use of force or threat of force to exclude same-sex competitors from mating opportunities (Andersson, 1994). Other mechanisms of sexual selection include mate choice (favoring ornaments and displays for attracting mates), sperm competition (occurring when multiple males' sperm occupy a female's reproductive tract during one fertile period), and sexual coercion. Multiple mechanisms of sexual selection can operate simultaneously in one species.

We begin by evaluating the intensity of sexual selection in men. For sexual selection to shape a trait, the trait must be partly heritable, it must influence mating success, and mating success must influence reproductive success (Jones, 2009). Thus, we assess the association between mating and reproductive success using such conventional correlates as the operational sex ratio, parental investment, reproductive rate, and reproductive variance. We then examine correlations between male phenotypes and mating and reproductive success. Next, we use a comparative and functional approach to evaluate the extent to which, and in what ways, men's phenotypes were shaped by contest competition. Finally, we explore how contests may have contributed to male mating and reproductive success over human evolution.

THE INTENSITY OF SEXUAL SELECTION

The intensity of sexual selection is frequently estimated using the operational sex ratio (OSR), the average ratio of sexually active males to fertilizable females (Emlen & Oring, 1977). The OSR quantifies the ratio of competitors to contested resources (mates) and describes the potential difficulty in achieving mating opportunities (Kokko, Klug, & Jennions, 2012). At any time, a sizeable proportion of women are removed from the mating pool because they are pregnant, lactating, or postmenopausal, making men the

OSR-majority sex. Marlowe and Berbesque (2012) estimate the OSR among human foragers to be between 11.7 for the physiologically possible OSR and 8.6 for the behavioral OSR (reflecting realized reproductive behavior). This places humans above chimpanzees (OSR = 4.5) and most of the other 17 anthropoid primates evaluated by Mitani, Gros-Louis, and Richards (1996), but well below orangutans and gorillas, which had by far the most male-biased OSRs.

Kokko and colleagues (Kokko & Jennions, 2008; Kokko et al., 2012) demonstrate via mathematical models that the relationship between the OSR and the strength of sexual selection is complex, and conclude that variables that strongly influence the OSR—the lengths of time that individuals spend in and out of the mating pool—rather than the OSR itself, directly influence the extent to which individuals of a given sex will benefit from increased mating opportunities. Less investment in offspring tends to increase maximum potential reproductive rate (number of offspring per unit time), as well as time spent in the mating pool (Clutton-Brock & Vincent, 1991; Trivers, 1972), which should increase the benefits of investing in traits that augment mating success (Kokko et al., 2012). Unlike most mammals and all nonhuman apes, humans exhibit significant paternal investment, which slows male reproductive rates, removing men from the mating pool. However, parental investment is decidedly unequal between the sexes. Women, but not men, invest in offspring via gestation and nursing for up to several years in foraging societies (Eibl-Eibesfeldt, 1989), and women provide more parental care on average than men do in all known societies (Geary, 2000). Combined with menopause, the human sex difference in parental investment leads to a sex difference in potential reproductive rates. Across societies, the ratio of male-to-female maximum achieved reproductive rates varies but always exceeds 1, often by a large margin. The highest recorded male lifetime reproductive output across human societies is over 1000, whereas the female maximum is 69 (Glenday, 2013). Among traditional societies, sex differences in reproductive rates are smaller, but considerable. For the Yanomamö of Venezuela, Chagnon (1992) reports a male lifetime maximum of 43 offspring and a female maximum of 14. Among Xavante Indians from Brazil, the male reproductive maximum was 23, and the female maximum was 8 (Salzano, Neel, & Maybury-Lewis, 1967).

Sex differences in reproductive variance are also often used to assess the strength of sexual selection (Bateman, 1948; Jones, 2009). In traditional societies, men's reproductive variances are approximately 2–4 times those of women (Brown, Laland, & Borgerhoff Mulder, 2009). These reproductive disparities are substantial but are likely far smaller than those among elephant seals and even gorillas, in which more males fail to reproduce, and successful males are able to monopolize more mates. In the average forager society, only 21% of married women are married polygynously (Marlowe & Berbesque, 2012). Still, more men than women remain unmarried, divorce is common (Blurton Jones, Marlowe, Hawkes, & O'Connell, 2000), and men are likelier than women to reproduce with a new mate—all of which effectively increase the level of polygynous mating and reproduction (Daly & Wilson, 1988). Among the Ache of Paraguay, marriages are sequentially monogamous, and men have 4.2 times the reproductive variance of women (Hill & Hurtado, 1996). Moreover, throughout the world, the transition to stratified state-level societies pushed harem sizes and reproductive disparities to extremes far exceeding those found in gorillas and even elephant seals in some cases (Betzig, 1986).

The strength of sexual selection also depends on the degree to which mates can be monopolized (Klug, Heuschele, Jennions, & Kokko, 2010). Temporal clumping of mates due to breeding synchrony tends to hinder the defense of multiple fertile females (Emlen & Oring, 1977). The fact that humans are not seasonal breeders, and that, contrary to early studies, women do not exhibit ovulatory cycle synchrony (Yang & Schank, 2006), should thus increase the potential for polygyny. However, some female characteristics decrease the degree to which estrous females can be monopolized. Although observers can detect phenotypic changes associated with women's ovulatory status in laboratory studies (Havlíček, Dvoráková, Bartos, & Flegr, 2006; Puts et al., 2013), such changes are extremely subtle relative to the dramatic genital swellings of chimpanzees and increased proceptivity of estrous great apes (Graham, 1981). Indeed, there appears to have been selection to conceal ovulation in women (Gangestad & Thornhill, 2008). Permanently enlarged breasts also obscure the cessation of lactational amenorrhea and resumption of ovulation after weaning. A consequence of such cryptic fertility is that men might be expected to compete more intensely to monopolize long-term mates rather than for single copulations, as occurs in chimpanzees and other primates with advertised estrus (Wrangham & Peterson, 1996). The monopolizability of females also depends on how widely females are dispersed in the environment, and hence the costs of locating, courting, or defending multiple females (Emlen & Oring, 1977). If females are social and thus spatially clumped, they may be defensible by a single male, as occurs in gorillas (Harcourt, Stewart, & Fossey, 1981), or by a group of males, as occurs in chimpanzees (Morin, 1993) and humans (see below).

The preceding data suggest a positive and moderately strong relationship between men's mating success and reproductive success. The few datasets that assess this relationship, including data from foragers (Salzano et al., 1967), indeed indicate a positive relationship (Brown et al., 2009). However, sexual selection also requires mating and reproductive success to be associated with phenotypic variation (Jones, 2009; Klug et al., 2010). Several putative sexually selected traits have been associated with elevated mating success in men, including muscularity (Frederick & Haselton, 2007; Lassek & Gaulin, 2009), physical prowess (Faurie, Pontier, & Raymond, 2004; Smith, Bliege Bird, & Bird, 2003), masculine body shape (Hill et al., 2013; Hughes & Gallup, 2003; Rhodes, Simmons, & Peters, 2005), height (Mueller & Mazur, 2001), facial morphology (Johnston, Hagel, Franklin, Fink, & Grammer, 2001), and masculine and attractive voices (Hodges-Simeon, Gaulin, & Puts, 2011; Hughes, Dispenza, & Gallup, 2004; Puts, 2005). In addition to assessing number of copulatory partners, these studies also variously assess number of wives, number of mates with whom a male has reproduced, number of extra-pair copulations, number of affairs with mated women, age at first copulation, age at first reproduction, and the quality of a male's mates. Putative sexually selected traits such as physical formidability (Chagnon, 1988; Smith et al., 2003), height (Pawlowski, Dunbar, & Lipowicz, 2000), facial dominance (Mueller & Mazur, 1997), facial attractiveness (Jokela, 2009), and low voice pitch (Apicella, Feinberg, & Marlowe, 2007) have also been linked to men's reproductive success.

EVIDENCE OF DESIGN FOR CONTESTS

If the competing sex can obtain mates by force, then other mechanisms of sexual selection, such as mate choice and sperm competition, are limited (Puts, 2010). Contest competition tends to evolve when mates, or the resources necessary to win mates, are localized in space or time and are thus economically defensible (Emlen & Oring, 1977). Generally, mate and territory defense appear more feasible in "one-dimensional" mating environments (burrows or tunnels) or "two-dimensional" mating environments (land or floors of bodies of water) than in three-dimensional environments (air, open water, or trees) (Emlen, 2008; Puts, 2010; Stirling, 1975). For example, males engage in more fighting over mates in terrestrially breeding seals (Stirling, 1975) and turtles (Berry & Shine, 1980) relative to aquatically breeding species. The fact that humans are terrestrial rather than arboreal primates should, therefore, facilitate the evolution of male contests.

Grafen (1987) emphasized the difference between selection in progress and adaptation, suggesting that trait-related approaches are most useful in demonstrating past sexual selection. Whereas sexual selection may not always produce sex differences (Hooper & Miller, 2008), the presence of large secondary sex differences suggests an evolutionary history of strong sexual selection. Some of the most conspicuous products of sexual selection are sex differences in life history variables, body size, muscularity, aggression, sexual and threat displays, weaponry and ornamentation (Andersson, 1994)—all of which are present in humans. For example, men mature later and senesce and die sooner, a life history suggesting an effectively polygynous mating system (Daly & Wilson, 1983). The presence of secondary sex differences suggests past sexual selection, but a functional analysis of these traits is required to determine their possible roles in mating competition and the mechanisms of sexual selection that shaped them.

A thorough functional analysis of men's phenotypes indicates an evolutionary history of moderate-to-strong contest competition. Men exhibit all of the hallmarks of contests: same-sex aggression, greater size and strength than females, weapons, and threat displays (Andersson, 1994), as we discuss next.

FIGHTING AND PHYSICAL AGGRESSION

Rates of lethal violence in forager societies are similar to those in chimpanzees (Wrangham, Wilson, & Muller, 2006), and from an early age, human males are more physically aggressive than females. In studies spanning many cultures and time periods, males compared to females have engaged in more rough and tumble play and other types of physical aggression, fantasized more about violence, and more frequently committed violent offences (Ellis et al., 2008). Across societies, the vast majority of murderers and murder victims are men, particularly young men (Archer, 2004, 2009; Daly & Wilson, 1990; Walker & Bailey, 2013). Sex differences in homicide are most extreme for same-sex homicide; men have killed other men far more frequently than women have killed other women in every society and time period for which data are available (Daly & Wilson, 1988). Excluding war killings, about 95% of same-sex homicides are committed by men (Daly & Wilson, 1988). Including war killings, the proportions of same-sex killings perpetrated by men would surely approach 100%. Across all 70 preliterate societies surveyed by Whyte (1978), men were more likely than women to engage in warfare.

Male intrasexual violence is responsible for a significant proportion of deaths, especially in males, in many natural fertility populations (Keeley, 1996). Violent death through homicide or warfare accounts for approximately one in two deaths among the Waorani of Ecuador (Beckerman et al., 2009), one in three deaths among the Dugum

Dani of New Guinea and the Yanomamö of Venezuela and Brazil (Chagnon, 1988), and one in four deaths and one in five deaths, respectively, among the Mae Enga and Huli of New Guinea (Chagnon, 1988). In a study of 10 small-scale Amazonian societies, the percentage of violent deaths ranged from 6% to 56%, with an average of 30% (Walker & Bailey, 2013). Among the !Kung San of Botswana, per capita homicide rates are approximately four times those in a typical year in the United States (Lee, 1984). Archaeological evidence also indicates extensive male-male aggression over human evolutionary history. This evidence includes a lack of female skeletons at gravesites where individuals apparently died in a massacre (Bamforth, 1994), missing bones in male skeletons consistent with warfare-related trophy taking (Andrushko, Latham, Grady, Pastron, & Walker, 2005; Bamforth, 1994), and evidence of traumatic injuries on male skeletons (Milner, Anderson, & Smith, 1991; Walker, 2001).

As well as influencing predispositions toward physical aggression, contest competition may have shaped other aspects of men's psychology and behavior. For example, men's pain tolerance systems are calibrated in ways predicted from a history of male-male fighting. Across studies, males generally have higher pain tolerance than do females (Ellis et al., 2008). Importantly, men's and women's pain systems are influenced by different stimuli. Though both male and female competitive athletes experience analgesic effects after athletic competition, men but not women experience analgesia from competition without exercise, whereas women but not men experience analgesia from exercise without competition (Sternberg, Bokat, Kass, Alboyadjian, & Gracely, 2001). That competition should reduce pain in men but not women is consistent with the hypothesis that men's psychologies are designed to be prepared for potentially injurious competition. Winning (versus losing) a video game simulation of male-male combat increased men's preferences for facial femininity in women, suggesting that ancestral men's ability to obtain and defend high-quality mates was dependent upon their success in male–male competition (Welling, Persola, Wheatley, Cárdenas, & Puts, 2013). Males also take more risks of physical injury than do females, especially when peers are present (Ginsburg & Miller, 1982; Morrongiello & Dawber, 2004) and when these peers are same-sex individuals of similar status (Ermer, Cosmides, & Tooby, 2008).

In addition, the development of group-level competitive activities in boys may subserve male coalitional intrasexual competition in adulthood (Geary, Byrd-Craven, Hoard, Vigil, & Numtee, 2003). Boys spend more time than girls in group activity by age 3, and this difference grows by age 6 (Benenson, Apostoleris, & Parnass, 1997). Boys form denser social networks (Benenson, 1990) and participate in higher levels of competitive and organized play (Rose & Rudolph, 2006). Male dominance behavior is most common when men are first introduced (Savin-Williams, 1987) and decreases thereafter as intergroup competitive behaviors increase. Additionally, men show higher levels than women on several measures of tolerance of same-sex peers (Benenson et al., 2009). Paradoxically, the circumstances under which men act kindly toward each other may be understood partly as consequences of selection for group-level aggression. In a public goods game, men but not women increased cooperativeness after being primed for intergroup competition (van Vugt, De Cremer, & Janssen, 2007). When a defector in an economic game was punished, empathy-related brain responses were reduced, and reward-related brain responses were increased, in men but not women (Singer et al., 2006). Men also show higher testosterone increases following between-group competitive victories than within-group competitive victories (Oxford, Ponzi, & Geary, 2010; Wagner, Flinn, & England, 2002).

SIZE AND STRENGTH

Male contests also tend to favor greater male size and strength. A number of studies have suggested that early hominids such as *Australopithecus afarensis* (3.6–2.9 million years ago [mya]) were characterized by large-size dimorphism approaching or even surpassing that of orangutans and gorillas (Gordon, Green, & Richmond, 2008; Lockwood, Richmond, Jungers, & Kimbel, 1996; McHenry, 1991). However, recent work that has attempted to avoid potential methodological problems of previous studies, such as small samples and size-based sex assignment, have rendered more modest estimates of skeletal sexual dimorphism, comparable to that of modern humans (Reno, McCollum, Meindl, & Lovejoy, 2010; Reno, Meindl, McCollum, & Lovejoy, 2003; Suwa et al., 2009).

Modern human skeletal size dimorphism is intermediate between that of chimpanzees and gorillas, reflecting the moderate difference between male and female maturation rates (Leigh & Shea, 1995). In total body mass, men are approximately 20% heavier than women (Archer, 2009; Marlowe & Berbesque, 2012). This is below the body mass dimorphism of polygynous primates (averaging over 60% greater male size), above that of monogamous primates (averaging less than 10% greater male size), and comparable to that of species with multimale groups (Clutton-Brock & Harvey, 1984). However, humans are more sexually dimorphic than overall body mass alone suggests. This is because, unlike other primates, human females store more body fat than do males (Wells, 2012), perhaps for producing highly encephalized offspring (Lassek & Gaulin, 2008). In estimating the role of male contests in humans, it is thus more appropriate to consider sexual dimorphism in fat-free mass, which is 31%–43% greater in men than in women (Lassek & Gaulin, 2009; Wells, 2012).

Men also put on 61% more lean muscle mass than women, including 50% more lower body muscle mass and 75% more arm muscle mass (Lassek & Gaulin, 2009).

Men possess about 90% greater upper-body strength, so that the average man is stronger than more than 99.9% of women (Abe, Kearns, & Fukunaga, 2003; Lassek & Gaulin, 2009). In addition, men have 65% greater lower body strength (Lassek & Gaulin, 2009), which translates into greater speed and acceleration (Mayhew & Salm, 1990). Even controlling for body mass and proportion of lean body mass, men are stronger, in part because their muscles have shorter fibers and greater angles of pennation (Chow et al., 2000). These sex differences in muscularity are comparable to those of gorillas (Zihlman & MacFarland, 2000).

WEAPONS

Sexual selection often endows the more competitive sex with weapons such as horns, antlers, or canines. Humans lack significant sexual dimorphism in canine size, with both sexes having relatively smaller canines than our closest relatives (Wood, Li, & Willoughby, 1991). The trend toward canine reduction in our lineage can be traced back more than 6 million years to *Sahelanthropus tchadensis* in Central Africa (Brunet et al., 2002) through a largely continuous fossil record including well-represented genera such as *Ardipithecus* (5.8–4.4 mya) and *Australopithecus* (4.2–2.5 mya) to *Homo* after 2.5 mya (Suwa et al., 2009). A number of theories have been proposed to account for this shift in canine morphology including dietary adaptations, selection against threatening displays, or replacement by handheld weapons (Greenfield, 1992). A dietary explanation appears unlikely as there are not other indications of a dramatic dietary shift in *Sahelanthropus* and *Ardipithecus* (Brunet et al., 2002; Suwa et al., 2009). Another hypothesis is that canine reduction indicates reduced intermale contest competition, possibly resulting from selection for cooperative hunting, and/or female choice for less competitive mates more likely to engage in parental care (Halloway, 1967; Lovejoy, 2009). If so, the moderate levels of size dimorphism observed in early hominids may reflect ecological selection and/or female mate choice rather than contest competition (Gordon, 2013; Lovejoy, 1981).

A nonmutually exclusive alternative is that canine weaponry was supplanted by handheld weapons and forelimbs freed by bipedal locomotion (Carrier, 2011; Darwin, 1874; McHenry, 1991). Across societies, the manufacture and use of weapons against same-sex rivals is ubiquitous among men and rare among women (Archer, 2004; Ellis et al., 2008; Smith & Smith, 1995; Warner, Graham, & Adlaf, 2005). Proficiency at weapons use also shows large sex differences. For example, men are more than 1.5 standard deviations more accurate at targeting and intercepting projectiles, and this difference remains large after controlling for experience (Watson & Kimura, 1991). Clubs, spears and hurled stones may have kept enemies at a distance, making biting ineffectual. Similarly, large maxillary canines appear to have been replaced in several deer species with the evolution of antlers, which also keep enemies' mouths at a distance (Barrette, 1977). Male chimpanzees use branches in dominance displays (but not as offensive weapons), suggesting that tools have been used since the last common ancestor of *Pan* and *Homo*. However, the first evidence of stone-tool cut marks on human bones, probably due to postmortem butchering, occurs around 800,000 years ago, and the first evidence of attack with a weapon (a spear thrust through the lower limb and pelvis) does not appear until just over 100,000 years ago (Walker, Hill, Flinn, & Ellsworth, 2011), so the temporal relationship between canine reduction and the use of handheld weapons remains speculative.

Visual and Acoustic Signals

Despite modest differences in overall body mass, men and women differ greatly in appearance. This is due mainly to the sex differences in fat and muscle distribution mentioned above, along with conspicuous sex differences in body hair and especially facial hair. Subjective ratings of trunk, limbs, and head appearance for 124 primate species or subspecies, identified humans as the eighth most "visually sexually dimorphic" primate (tied with gorillas and white-faced sakis), placing humans in the 92nd percentile for visual sexual dimorphism (Dixson, Dixson, & Anderson, 2005). Humans were far more visually dimorphic than their closest relatives, chimpanzees and bonobos.

Beards and deep voices are perhaps the clearest candidates for sexually selected traits in men, and both effectively signal dominance. Bearded male faces are perceived as more dominant than the same faces clean-shaven, but beards have been found to decrease attractiveness to women (Dixson & Vasey, 2012; Neave & Shields, 2008). Facial masculinity also strongly increases the appearance of dominance, but may actually decrease attractiveness relative to unmanipulated or feminized male facial stimuli (Burriss, Marcinkowska, & Lyons, 2013; Puts, Jones, & DeBruine, 2012). Some structural features of men's faces may enhance fighting success more directly. Modern assailants tend to target the face (Carrier & Morgan, 2015; Guthrie, 1970; Shepherd, Gayford, Leslie, & Scully, 1988), and men's greater rates of same-sex violence likely contribute to higher frequencies of facial (Shepherd et al., 1988), and especially mandibular (Puts, 2010), fractures in men than in women. If such conditions prevailed over human evolution, they may have contributed to the greater robusticity of men's faces, despite the overall reduction in robusticity throughout hominid evolution (Carrier & Morgan, 2015; Puts, 2010). Female assault victims suffer a higher proportion of facial fractures than do male assault victims (Shepherd et al., 1988), suggesting that men's skulls are indeed more resilient against violent assault.

Sexual selection often produces sex differences in acoustic signals (Andersson, 1994), and both the acoustic properties of human vocalizations and their underlying anatomy are highly sexually differentiated. Men's voices are approximately five standard deviations lower in fundamental frequency than are women's, a sex difference comparable to that of the highly dimorphic Hamadryas baboon (*Papio hamadryas ursinus*), in which males are twice as massive as females (Puts, Apicella, & Cárdenas, 2012; Rendall, Kollias, Ney, & Lloyd, 2005). This acoustic sex difference is due partly to men having 60% longer membranous portions of the vocal folds (Titze, 2000). Men also have lower and more closely-spaced vocal formant frequencies (corresponding to richer vocal timbre) (Fitch & Giedd, 1999; Puts, Apicella, et al., 2012), due largely to their 15% longer vocal tracts (Fant, 1960). Note that these anatomical sex differences exceed the 7%–8% sex difference in height by two- to more than sevenfold. Experimental masculinization of male voice recordings increases perceptions of dominance among males far more than it increases attractiveness to females (Feinberg, Jones, Little, Burt, & Perrett, 2005; Puts, Gaulin, & Verdolini, 2006). In one study, men who rated themselves as better fighters than their competitor lowered their voice pitch when addressing him, whereas men who believed they were less dominant raised their pitch (Puts et al., 2006).

Thus, contrary to inferences made solely from our modest canine size or height dimorphism, human beings are sexually differentiated along dimensions expected of a species with an evolutionary history of male contest competition. Men mature later, senesce and die sooner, are larger, more muscular, more aggressive, produce and use weapons against each other and exhibit conspicuous sex-specific traits such as beards and deep voices that appear to function as threat displays.

However, male contests and female choice often work in concert across species, with females preferring dominant males (Berglund, Bisazza, & Pilastro, 1996). And, although apparently rare as a cause of sexual dimorphism (Andersson, 1994), niche partitioning may also play a role; some human sexual dimorphisms have been attributed to the sexual division of labor and male hunting (Kaplan, Hill, Lancaster, & Hurtado, 2000). Thus, some secondary sex traits in men were likely shaped by multiple selective pressures. For example, men's greater muscularity is attractive to women (Frederick & Haselton, 2007) and should increase success in both hunting and male combat (Puts, 2010). Likewise, large male advantages in throwing velocity and distance (Thomas & French, 1985), and in targeting accuracy (Ellis et al., 2008), appear equally consonant with male combat (targeting same-sex competitors) and hunting (targeting prey).

Although some of men's traits such as muscularity and targeting abilities simultaneously aid in contests, hunting, and mate attraction, other traits have no clear utility in hunting and have relatively weak or even negative relationships to mate attraction. These traits include beards, deep voices, facial robusticity, high levels of within- and between-group same-sex aggression, willingness to risk physical harm in front of peers, pain tolerance and competition-based analgesia, and various psychological and behavioral traits that promote alliances around intergroup competition. Men appear specially adapted to an evolutionary history of aggressive competition for mating access.

Yet, from our behavioral OSR and the trend among nonhuman primates, Marlowe and Berbesque (2012) estimate that men should exhibit 57% more body mass than women do. Though it is more appropriate to compare fat-free mass than total body mass, even the 31%–43% greater fat-free mass of men seems appreciably lower than the expected 57% difference. One explanation for this discrepancy is that female choice played a relatively large role over human evolution, and females preferred less muscularity than would be favored under contests, as is presently the case (Frederick & Haselton, 2007). Male contest competition may have been concomitantly less important in humans than it was in primates with a comparable OSR. On the one hand, this explanation accords with the pattern of body size dimorphism and reduction in canine size over human evolution. On the other hand, evidence of widespread male fighting and the presence of multiple contest-related traits such as deep voices and beards bring this interpretation into question. It should also be remembered that contest competition can take the form of threats and occasional fights rather than frequent overt aggression. Another possibility is that body size, strength, and canine size underestimate the extent of male contests because of the use of weapons (Marlowe & Berbesque, 2012; Puts, 2010). It is certainly conspicuous that we are the only ape species lacking large canines, and yet even technologically unsophisticated human societies possess weapons capable of dispatching the largest and most powerful animals on the planet. Finally, intergroup aggression may have favored reduced body and muscle mass in men. This is because the benefits of coalitional victories are widely shared, whereas the costs of producing and maintaining muscle mass are borne by the individual.

TRANSLATING DOMINANCE INTO FITNESS

When a male gorilla usurps a harem, or a bull elephant seal becomes a beach master, he wins mating rights. If men have experienced an evolutionary history of contest competition, how has success in male contests—either within or between groups—translated into mating opportunities over human evolution?

Intragroup Aggression

When two men compete over the same unmated female, one may simply kill the other (Daly & Wilson, 1988; Marlowe & Berbesque, 2012). Men also sometimes jealously guard their current mates and use physical aggression to do so (Chagnon, 1992; Daly & Wilson, 1988; Peters, 1987). Men's use of force to win and defend mates is culturally ubiquitous, but it should also be circumscribed within any society. Humans' slow life histories and low mortality due to predation or disease (Muller & Wrangham, 2014) should favor deference to plausible threats and the tendency to await more propitious mating circumstances rather than risk injury over a current mating opportunity. Yet a balance must be met between the risk of injury from competing over a current mating opportunity and the risk of appearing weak, which has ramifying deleterious consequences for future mating. Indeed, male-male violence may as often be about "saving face" by not backing down from challenges as it is about winning any present mating opportunity (Daly & Wilson, 1988).

Men avoid costly fights partly by devising alterative stages on which to advertize their formidability. On the Melanesian island of Mer, men's hunting of 100–150 kg sea turtles is inconsistent with optimal foraging but signals strength and willingness to risk injury and is respected by men (Bliege Bird, Smith, & Bird, 2001; Smith et al., 2003). Turtle hunters have more and higher quality mates, start reproducing sooner, and reproduce at a higher rate, due primarily to their higher numbers of mates (Smith et al., 2003). In general, men's interest in physical competition and displays of physical prowess such as hunting (Hawkes & Bliege Bird, 2002) and sports (Deaner et al., 2012; Deaner & Smith, 2013) appear to be cross-culturally universal. Participation and performance in these activities have also unsurprisingly been associated with higher mating success (Faurie et al., 2004; Smith et al., 2003).

Dominance among men may contribute to mating success partly by making men more attractive to women (Buss, 1988; Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004; Lukaszewski & Roney, 2010). For example, studies of U.S. university students have found that women reported preferring dominant men (Lukaszewski & Roney, 2010) and experiencing more frequent and earlier-timed orgasms when having sexual intercourse with more dominant, masculine men (Puts, Welling, Burriss, & Dawood, 2012). Men also often report displaying strength and physical prowess when attempting to attract women (Buss, 1988). However, in other studies of U.S. university students, men's numbers of sex partners in the past year were positively related to other men's ratings of their dominance and to traits associated with dominance, such as muscularity and deep voices; yet attractiveness to women did not explain significant variance in mating success beyond that explained by dominance (Hill et al., 2013; Puts, Hodges, Cárdenas, & Gaulin, 2007). Additionally, while risky turtle hunting on Mer garners respect among men, it is unassociated with attractiveness to women (Smith et al., 2003). In traditional societies, women's ability to choose their mates is frequently limited not only by male exclusion of competitors by force but also by arranged marriage, which disproportionately limits women's choices (Apostolou, 2007; Walker et al., 2011), and by abduction by males from other villages (Peters, 1987; see also later).

The means by which the threat of aggression translates into mating opportunities are likely manifold. Dominant men may have little hesitation interfering with the mating attempts of less dominant men, whereas the reverse would be less likely. That is, subordinate men may abandon mating attempts in the presence of a dominant interloper, and they may eschew pursuing a mate who is being pursued by a dominant male. Men are also probably less likely to cheat with the mates of formidable men. Bloody and sometimes fatal club fights erupt between Yanomamö men when one suspects the other of trysting with his wife (Chagnon, 1992), and a husband's physical formidability is a powerful deterrent to would-be interlopers (Peters, 1987).

Dominance (coerced deference) can be distinguished from prestige (freely conferred deference; Henrich & Gil-White, 2001), but dominance may also increase prestige, as formidable men may be valued both as allies in inter- and intragroup conflict and as exemplars for men aspiring to achieve dominance. Across traditional and industrial societies, both dominance and prestige have been found to predict men's mating success (Chagnon, 1988; Hill et al., 2013; Pérusse, 1993; Smith et al., 2003; von Rueden, Gurven, & Kaplan, 2011) and reproductive success (Borgerhoff Mulder, 1987; Borgerhoff Mulder, 1989; Chagnon, 1988; Flinn, 1986; Irons, 1979; Smith et al., 2003; Turke & Betzig, 1985; but see Betzig, 1988; von Rueden et al., 2011).

Coalitional Aggression

The tendency of males to form alliances and engage in coalitional violence may have evolved in our common ancestor with *Pan* as a means of cooperative female capture and defense (Wrangham, 1999). The capture of wives during raids on other villages has been documented in traditional societies across all inhabited continents (Ayres, 1974; Barnes, 1999; Chagnon, 1988; Peters, 1987) and occurred in 16 of 30 societies in a cross-cultural sample selected for independence and representativeness (Ayres, 1974). In a study of 10 traditional Amazonian societies, women were captured during 26% of raids occurring within a language family and 54% of raids occurring across language families (Walker & Bailey, 2013). The capture of women is a frequently cited motive for warfare in ethnographies of North American Indians (Keeley, 1996). Archeologically, young women are sometimes underrepresented among massacred villagers, suggesting abduction in samples such as Crow Creek, South Dakota (ca. 1325 AD; Keeley, 1996) and Talheim, Germany (ca. 4900–4800 BC; Bentley, Wahl, Price, & Atkinson, 2008). Yanomamö women may be abducted by larger, more militarily powerful villages from smaller, weaker villages during inter-village feasts. Hosts may prevent visitors' wives and daughters from returning home, or powerful villages may visit weaker villages and return home with their hosts' wives. In militarily strong lowland villages an average 17% of married women have been abducted compared to 11% in weaker upland villages (Chagnon, 2012).

Raids may also function to acquire resources necessary to obtain mates or increase mates' reproductive output. Intergroup aggression among male chimpanzees leads not only to the killing of adult males and offspring from other groups but also to territorial expansion (Mitani, Watts, & Amsler, 2010). Among the Turkana, a nomadic pastoral society in East Africa, men engage in large-scale raids involving hundreds of raiders and in which approximately one percent of raiders are killed (Mathew & Boyd, 2014). These raids allow men to acquire livestock, pasture and watering sites, and men use livestock as brideprice to obtain more wives (Bollig, 1990).

There is likely to be some optimal balance of aggression and deference that varies across individuals and societies. Indeed, Beckerman and colleagues (2009) reported that Venezuelan Waorani warriors who went on the most raids had fewer surviving children than less "zealous" warriors. Coalitional aggression should also tend to reduce within-group aggression, as the well being of fellow group members becomes important to individual fitness. A consequence may be respect for the long-term mating relationships of fellow group members and the emergence of marriage as a "conventional solution to [within-group] contest competition" (Blurton Jones et al., 2000).

CONCLUSIONS

Men's traits suggest an evolutionary history of sexual selection via contest competition. Many of these traits are unattractive to women, so they do not appear to be sexual charms or displays. And where masculine traits are attractive, they are generally more effective at winning dominance. Male traits such as beards, deep voices, and high levels of same-sex aggression are all but inexplicable as adaptations for hunting. Although women have unprecedented economic and political autonomy in many modern societies, their ability to choose their mates was probably more limited ancestrally. In the small, foraging societies in which modern humans spent most of their evolution, a male's ability to obtain and retain mates was almost certainly more dependent on the plausible threat of physical aggression.

An analysis of human sexual dimorphism that confines itself to dentition or overall body size may be misleading. Humans are highly sexually dimorphic in appearance, acoustic signals, muscularity, body fat, physical aggression, and numerous other anatomical and behavioral characteristics. The most parsimonious explanation is that many of men's traits evolved in the context of male contests. Men's greater strength, size, same-sex physical aggression, and use of weapons are typical of species in which males battle one another for mates. A functional analysis indicates that men's beards, deep voices, and relatively robust faces are more effective in establishing dominance than in mate attraction or hunting. Beyond their propensity for same-sex aggression, men possess other psychological traits, such as pain tolerance, risk-taking, and interest in physical competition and coalition formation, that appear to have been shaped by contests. We note that this evidence seems to overturn both the viewpoint that humans lack substantial sexual dimorphism, and the widely held viewpoint (see Puts, 2010) that sexual selection on men's traits primarily took the form of female mate choice.

Nevertheless, the relative strengths of various mechanisms of sexual selection in shaping individual male traits will require additional work to disentangle, and we do not disregard the importance of female choice. Female choice likely mitigated the influence of contest competition in some cases and reinforced it in others. Women choosing mates on genetic quality, protection, or provisioning might obtain information about these qualities by assessing dominance and the traits associated with it (Berglund et al., 1996; Buss, 1988; Trivers, 1972). Across societies, women prefer potential mates with high status (Buss, 1989) and avoid those of low status (Li, Bailey, Kenrick, & Linsenmeier, 2002). In small-scale societies, women's ratings of men's warriorship, status, and hunting ability have been observed to covary with their ratings of men's attractiveness (Escasa, Gray, & Patton, 2010). Women also prefer dominance-related traits such as a muscular build, height, deep voice, and masculine face more strongly during the fertile phase of the ovulatory cycle and for purely sexual (vs. investing) relationships, which suggests that these male traits indicate heritable fitness benefits (Gangestad & Thornhill, 2008).

We also do not discount the importance of human social monogamy and biparental care, derived behaviors that may have a long history in the human lineage (Lovejoy, 1981). Men generally invest in their mates and offspring (Kaplan et al., 2000), and most marriages are monogamous, even though most human societies allow polygyny (Murdock, 1967). Nor does the existence of polygynous marriage imply that all males will attempt polygyny. The typical ancestral male may have maximized his reproduction by mating monogamously, guarding his mate, and investing in their mutual offspring. The "decision" to mate monogamously or attempt polygyny should be conditional upon a male's competitiveness for mates, among other things (Gangestad & Simpson, 2000; Lukaszewski, Larson, Gildersleeve, Roney, & Haselton, 2014).

Nor do we envision an evolutionary past in which our male ancestors were unabatedly at one another's throats. This is not seen in some of the most extreme cases of male contest competition: Male gorillas are largely passive, and bull elephant seals confine their serious fighting to the breeding season. It is necessary only for physical confrontations to have important reproductive consequences. Yet the evidence reviewed above suggests that we have inherited the genes of men who used force against other men to obtain mates. If so, then understanding the form and degree of male contests over our evolutionary history is likely to elucidate such social problems as male-male violence, murder, and war.

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CHAPTER 14

Women's Sexual Interests Across the Ovulatory Cycle

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Normally ovulating women are fertile about 6 days of an ovulatory month (Wilcox, Weinberg, & Baird, 1995), yet copulate throughout the cycle. Why? And are women's sexual interests nonetheless sensitive to their fertility status and the hormones that regulate it? This chapter examines these issues, which are among the most enduring in human evolutionary behavioral science. We first offer an historical overview of the idea that women evolved to lose "estrus," a distinct, discrete period of sexual proceptivity and receptivity typically co-occuring with the fertile period. Second, we discuss evidence that women's sexual interests change across the cycle in terms of intensity and ease of being evoked, as well as the male features that evoke them. Third, we evaluate possible functional explanations for these changes. Fourth, we explore perspectives on the functions of women's infertile sexual interests. Fifth, we ask whether women's fertile-phase sexuality has been importantly modified in the context of pair bonding. Finally, we address whether women's fertility status can be inferred from observable cues and, if so, why.

A HISTORICAL BACKDROP: WOMEN'S PURPORTED LOSS OF ESTRUS

The Concept of Estrus

Estrus refers to "the relatively brief period of proceptivity, receptivity, and attractivity in female mammals that usually, but not invariably, coincides with their brief period of fertility" (Symons, 1979, p. 97). In species possessing classic estrus, as defined here, females are sexually willing and available only during the fertile phase of their cycles (or, at least, minimally outside of that fertile phase). Prototypical examples are dogs and cats, in which *heat* is synonymous with *estrus*.

Nearly a century ago, biologists first discovered a family of reproductive hormones, estrogens (Allen & Doisy, 1923). Named after estrus, these hormones were thought to generate the estrous state. We now know that estrogens play critical roles in organizing many aspects of female reproductive physiology and fertility, including estrus, in virtually all vertebrate species (though other reproductive hormones do too) (e.g., Nelson, 2000).

WOMEN'S "LOSS OF ESTRUS"

Women do not possess a discrete, finite phase of classic estrus but, rather, are sexually proceptive and receptive across the cycle. One study asked roughly 20,000 women from 13 developing countries about their last copulation, and detected no shifts in the frequency with which women copulated with primary partners across the cycle, aside from a drop at menses (Brewis & Meyer, 2005).

Around 1960, evolution-minded anthropologists and human biologists noted women's loss of estrus as an evolutionary significant event, one possibly key to understanding important unique human features. In his classic monograph on human sexuality, Symons (1979) dedicated an entire chapter to women's loss of estrus, and clarified its meaning:

> Beach goes on to say, "Although human females are not continuously 'sexually receptive,' they are continuously 'copulable'; and their sexual arousability does not depend on ovarian hormones. This relaxation of endocrine control contributes to the occurrence of coitus at any stage of the menstrual cycle" (pp. 357–358). I believe that this is the clearest available statement of what the "loss of estrus" means. (p. 106)

In this view, relaxed endocrine control of sexual interests, resulting in a loss of a distinct, discrete fertile-phase sexuality, evolved in women, replaced by continuous sexual interests.

LOSS OF ESTRUS AND CONCEALED OVULATION

Women's loss of estrus begged a question: Why did they lose it? Overwhelmingly, the answer was that it functioned to *conceal ovulation* (or, more precisely, women's fertile window). If women's sexual interests peaked during the fertile phase, their sexual interests could be a cue to their fertility status. Truly continuous sexuality—no changes in sexual interest, aside from menstruation—eliminates these behavioral cues (e.g., Alexander & Noonan, 1979).

But what was the advantage of concealed ovulation to women? A number of answers arose, the most influential of which is the paternal care hypothesis (Alexander & Noonan, 1979; Alexander, 1990): Concealed fertility status changes male cost-benefit calculations, favoring greater care for offspring. If males can perceive fertility status, they may do best by selectively attending to fertile females. If not, they may do best by attending to one or a few females, and care for offspring. The idea was not that concealed ovulation, by itself, gave rise to paternal investment; rather, in the context of emerging benefits of biparental care in humans, concealed ovulation pushed males to exercise greater care.

Strassmann (1981) added an important element to this scenario. Once males mate and successfully reproduce, they can re-enter the mating market and compete for new mates with whom to reproduce or, alternatively, invest energy and time to care for the offspring, thereby increasing its quality (Kokko & Jennions, 2008; mixed effort is also possible). One important factor influencing the relative value of offspring care is the rate of returns from re-entering the mating market, which varies across males: Those most dominant likely have higher rates of return than males who are nondominant. Hence, nondominant males should be most likely to care for offspring. The problem is that, precisely because these males are less competitive, they may only rarely succeed in mating. Indeed, one major reason that male care of offspring is so rare in mammalian species is not that it couldn't pay for males to care, such that they are fated to compete; rather, the males who *would* actually benefit from caring for their offspring simply never become fathers (Kokko & Jennions, 2008).

In moderate to large mixed-sex social groups, dominant males may have a special edge in monopolozing matings when female fertility status can be detected. Dominant males need not attend to and prevent nondominant males from having access to all females, only females in their fertile phases. Unless females synchronize their cycles, the proportion of females that dominant males must guard to sequester all fertile-phase matings is typically a small proportion of the total number of adult, cycling females. By contrast, when female fertility status is concealed from males, dominant males cannot monopolize all fertile-phase matings by attending to only a few females. Hence, concealed fertility status permits nondominant males to pair with females, copulate with them throughout the cycle, and thereby become fathers, while, at the same time, gain enough paternity confidence that renders offspring care worthwhile. Naturally, if fertility status is concealed, nondominant males cannot know which copulations potentially result in conception either—but if they copulate with a female partner throughout an ovulatory cycle, they can "know" that copulation occurred during the fertile phase. Ironically, then, concealed fertility status can bolster the paternity assurance of a male who might be motivated to invest in a resulting offspring, thereby increasing the amount of investment that fathers, on average, provide. (For other perspectives on women's loss of estrus, see Benshoof & Thornhill, 1979; Burley, 1979; Hrdy, 1979; Pawlowski, 1999; Symons, 1979).

VARIATIONS IN WOMEN'S SEXUAL INTERESTS ACROSS THE CYCLE

Variations in Frequency or Intensity of Sexual Desires

The major problem with the idea that truly continuous human sexuality replaced classic estrus is empirical. A large and diverse literature indicates that women's sexual interests do change across the cycle. Hill (1988) reviewed research examining changes in women's level of sexual interests, concluding that, although many individual studies did not detect systematic variations across the cycle, their aggregate revealed robust changes, the strongest upsurge of sexual desires just prior to ovulation (see also Regan, 1996). More recently, multiple lines of research have documented shifts. Notably, Slob and colleagues (Slob, Bax, Hop, Rowland, & tenBosch, 1996; Slob, Ernste, & tenBosch, 1991) found that women exhibit greater genital arousal in response to erotica, and sexually condition to stimuli more readily, during the follicular phase than the luteal phase, with related changes documented by Suschinsky, Bossio, and Chivers (2014), Krug, Pietrowsky, Fehm, and Born (1994) and Krug, Plihal, Fehm, and Born (2000), Van Goozen, Weigant, Endert, Helmond, and VandePoll (1997), and Dawson, Suschinsky, and Lalumière (2012).

A Diary Study of Women's Self-Reported Sexual Desire Roney and Simmons (2013) conducted perhaps the most impressive research examining changes in sexual desire across the cycle to date. Forty-three normally ovulating women reported their level of sexual desire every day for up to two full cycles. Salivary estradiol, testosterone, and progesterone were assayed most days. Women levels of sexual desire were greater during the fertile window, as mediated by two hormones: Estradiol levels (peaking just prior to ovulation) positively related to sexual desire, whereas progesterone levels (rising markedly during the luteal phase) negatively related to sexual desire. Although hormonal influence over women's sexual interests may be relaxed, it is not absent.

VARIATIONS IN THE QUALITIES OF MEN THAT EVOKE SEXUAL INTEREST

Beginning in the late 1990s, researchers began to examine changes across the cycle in sexual interests aside from level of sexual desire—specifically, systematic changes in the male features that evoke sexual interest across the cycle. At this time, over 50 studies have explored this issue.

The Scent of Symmetry Several early studies examined whether fertile women particularly prefer the scent of men who possess symmetrical bodily features (e.g., ear length, wrist width, finger lengths), and thereby evidence "developmental stability"—robust morphological development unperturbed by mutations, toxins, and other purported factors introducing damage to cell lines. With fertility estimated using actuarial data on women based on cycle day and length (e.g., Jochle, 1973; see also Wilcox, Duncan, Weinberg, Trussell, & Baird, 2001), research has found that as women's conception risk increases, their preference for the scent of symmetrical men increases (Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill et al., 2003; Thornhill & Gangestad, 1999). Another study found that fertile women particularly prefer the scent of socially dominant men (Havliček, Roberts, & Flegr, 2005).

The chemical cues in men's scent associated with men's symmetry and particularly preferred by fertile women have yet to be identified. Candidates include androgen metabolites found in sweat, to which fertile women may be responsive (Grammer, 1993; Hummel, Gollisch, Wildt, & Kobal, 1991). Thornhill, Chapman, and Gangestad (2013) found that fertile women particularly prefer the scent of men with high testosterone, though Rantala, Eriksson, Vainikka, and Kortet (2006) did not.

Facial Masculinity Soon after Gangestad and Thornhill's (1998) initial study, researchers began examining shifts in women's preferences for other features, the most studied of which is facial masculinity. Male and female faces differ, on average, from one another, male faces characterized by more massive chins and more prominent brow ridges. One can manipulate facial masculinity in a digitized photograph of a face by morphing the image to be more male-like or, conversely, female-like. Penton-Voak and colleagues found that, when fertile in their cycles, women prefer a degree of facial masculinization greater than that preferred when infertile (e.g., Penton-Voak et al., 1999), a shift only evident when women rated men's attractiveness as short-term sex partners (i.e., men's sexiness), not their attractiveness as stable, long-term partners. Subsequent replications and extensions have yielded mixed results (see Gildersleeve, Haselton, & Fales, 2014a). Relatedly, Roney and Simmons (2008; Roney, Simmons, &

Gray, 2011) report that women's estradiol levels predict preferences for faces of men whose testosterone is relatively high.

Other Masculine Features When fertile in their cycles, women have been found to particularly prefer masculine voices (Puts, 2005) and bodies (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; Little, Jones, & Burriss, 2007). Again, studies have typically found that preferences particularly shift when women rate men's sexiness rather than attractiveness as long-term mates.

Behavioral Dominance Preferences for particular behavioral displays may also be pronounced when women are fertile. Fertile women find men who act in more dominant, confident ways (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004; Gangestad et al., 2007) especially sexually attractive (compared to attractive as long-term mates), and estimated estradiol levels across the cycle predict women's preference for male dominance (Lukaszewski & Roney, 2009).

A Meta-Analysis Recently, Gildersleeve et al. (2014a) conducted a meta-analysis of the preference shift literature. They targeted studies examining changes in preferences across the cycle in seven different domains pertaining to symmetry and masculinity: facial symmetry, scent cues of symmetry, facial masculinity, body masculinity, vocal masculinity, behavioral dominance, facial cues of testosterone. In a broad set of measures (96 effects drawn from 50 studies), they included all studies in these categories as well as studies examining other preference shifts pertaining to masculinity (e.g., preference for chest hair, preference for tallness). In a narrow set of measures (68 effects drawn from 42 studies), they aggregated across only the seven categories just mentioned and, furthermore, restricted their analysis to studies examining "revealed" preferences—measured by having women rate the attractiveness of a number of men varying in the quality examined—rather than "stated" preferences that were assessed by simple self-reports. Because women recalling men attracting them in the past likely affect women's self-reports, stated preferences may not be sensitive to current cycle phase. Finally, Gildersleeve et al. (2014a) examined effects on three kinds of attractiveness: attractiveness in a short-term mating context (i.e., as a sex partner), in a long-term mating context (e.g., as a marriage partner), and with mating context unspecified (though, typically, "physical attractiveness" or "sexiness" is assessed, implying sexual attractiveness).

A number of key findings emerged. First, across both the broad and narrow sets of measures, women's preferences for masculine and symmetrical features in short-term and unspecified contexts were stronger during the fertile phase than infertile phases. Second, no effects of fertility status were found in a long-term mating context; indeed, shifts in sexual attractiveness were significantly more pronounced than shifts in long-term mate attractiveness. Finally, despite robust overall patterns, few preference shifts within specific categories could be detected. Typically, few studies examined a given preference shift, resulting in poor meta-analytic power to detect real effects. Nonetheless, uniformly mean effect sizes with short-term and unspecified mating contexts were in the direction of fertile women exhibiting stronger preference. See Table 14.1.

Average effect sizes were modest: mean Hodge's g .20 and .26 for the unspecified and short-term contexts, respectively, within the narrow set of measures (where g is comparable to Cohen's d). The size of the preference shifts may vary across categories

Table 14.1
Changes in Mate Preferences Across the Ovulatory Cycle:
Mean Effect Sizes (Hodge's *g*) for Narrowly Defined Categories of Cues

	Relationship Context			
Category (# of effects)	Short-Term	Unspecified	Long-Term	ST vs. LT
All cues (68)	.26	.20	.02	***
Facial symmetry (8)	.30	−.02	−.16	+
Scent cues of symmetry (3)	–	.83	–	n.a.
Facial masculinity (23)	−.02	.18	−.01	
Body masculinity (12)	.35	–	.09	*
Vocal masculinity (4)	.40	–	.19	
Behavioral dominance (12)	*.19*	–	−.11	**
Facial cues of testosterone (3)	–	.20	–	n.a.

Source: From Gildersleeve, Haselton, and Fales (2014a).

Notes. Values in bold: $p < .05$. Values in italics: $p < .10$. All values two-tailed.

ST vs. LT: Statistical comparisons between long-term and short-term effect sizes. *** $p < .001$; ** $p < .01$; * $p < .05$; + $p < .10$. All values two-tailed.

and, within categories, the validity of preference measures and conception risk likely varies across studies. Some true effect sizes, then, could be moderate to large.

Wood, Kressel, Joshi, and Louie (2014) also conducted a meta-analysis of preference studies, and claimed to find few systematic shifts. Reanalysis of their data, however, shows that, within short-term and unspecified contexts, preference shifts are robust (Gildersleeve, Haselton, & Fales, 2014b). Moreover, an independent method of assessing effect size, the *p*-curve, reveals preference shifts of effect size in line with Gildersleeve et al.'s meta-analysis (Gildersleeve et al., 2014b).

During the fertile phase, normally ovulating women discriminate men's sexiness on the basis of features that differ, on average, from how they discriminate men's sexiness during infertile phases, though exactly what those features are remains incompletely understood.

WHY DO WOMEN'S SEXUAL INTERESTS VARY ACROSS THE CYCLE?: FUNCTIONAL EXPLANATIONS

Why do women experience greater levels of sexual desire when fertile? And why are their sexual interests evoked by men with particular features during this time?

The Argument That Fertile-Phase Sexuality Functions to Obtain Sperm

One presumed function of fertile-phase sexuality is simple: to obtain sperm (see Nelson, 2000.) Only when female mammals are fertile can they conceive and, hence, only then can females utilize sperm for direct reproductive benefits. If a female were to fail to conceive during a cycle, she pays the cost of delaying reproduction for at least one cycle. Accordingly, fertile-phase sexual interests minimize the likelihood of this fate by ensuring that females are inseminated when fertile. As Roney and Simmons (2013) argue, "Promotion of conception is obvious" (p. 642) as one function of fertile-phase increases in sexual motivation.

Obviousness notwithstanding, the claim that fertile-phase sexuality functions to obtain sperm faces a major theoretical challenge: Females are not typically limited by the number of males willing and able to inseminate them. Males are sexually selected to be motivated to copulate with fertile females. Rarely do females encounter the problem of having to actively solicit sex from males. Rather, females typically face the problem of having far *too many* males, relative to their own optimum, willing and ready to inseminate them (see, e.g., Arnqvist & Rowe, 2005; Holland & Rice, 1999; see also Thornhill & Gangestad, 2008).

FERTILE-PHASE SEXUAL INTERESTS FUNCTION TO OBTAIN GOOD GENES

An alternative explanation for the evolution of women's fertile-phase sexual interests is that they function (at least partly) to bias sire choice toward males who possess features ancestrally associated with genetic benefits. Especially given that females can often choose sires among multiple suitors, females should not be interested in obtaining sperm per se. They should desire sires that offer benefits that promote their fitness. In species in which fathers do not typically care for or otherwise provide direct benefits to offspring, male contributions to female fitness depend on their genetic contributions. Due to the accumulation of random mutations in the genome and possibly other deleterious variants (e.g., arising from host-pathogen coevolution), some males offer genetic benefits to offspring exceeding what other males offer. As well, some males may possess genes that complement a female's better than others.

Empirical data on a variety of species shows that fertile sexual interests are discriminating. In pronghorn antelope (Byers, Moodie, & Hall, 1994), American bison (Wolff, 1998), pygmy loris (Fisher, Swaisgood, & Fitch-Snyder, 2003), for instance, fertile-phase females are particularly attracted to dominant or competitive males. In red deer (Charlton, Reby, & McComb, 2007) and guinea pigs (Hohoff, Franzin, & Sachser, 2003), they prefer large, robust males, and in rhesus macaques (Waitt, Gerald, Little, & Kraiselburd, 2006), testosterone-facilitated traits are preferred. (See Thornhill & Gangestad, 2008, for a fuller discussion.)

Might, then, the masculine features and features associated with developmental robustness be more likely to evoke women's sexual interests when fertile because, ancestrally, they were associated with genetic benefits to offspring? Perhaps preferences for behavioral dominance, robustness, and related features have been characteristic of females in species in deep-time evolutionary history, and have been maintained (with modification) in the hominin lineage, even with the evolution of pair bonding (e.g., Thornhill & Gangestad, 2008). This account has appeal, both in terms of potentially explaining female sexual discriminativeness during the fertile phase and placing humans within a broader phylogenetic context.

That said, no direct evidence shows that the masculine and symmetrical features women find sexually appealing when fertile were associated with genetic benefits to offspring ancestrally. In fact, data on shifting preferences for a feature with a clear genetic foundation—that is, preference for compatible MHC alleles—is mixed:

Garver-Apgar, Gangestad, Thornhill, Miller, and Olp (2006) found that women with partners possessing incompatible major histocompatibility complex (MHC) alleles reported greater attraction to men other than primary partners when fertile. By contrast, Thornhill et al. (2003) detected no shift across the cycle in women's preferences for scents associated with compatible MHC alleles. The argument here, then, is one of "inference to the best explanation" (e.g., Haig, 2014): Lacking any better explanation for this pattern, this one at least offers an account for the observed pattern of preference shifts and generates additional predictions.

FERTILE-PHASE SEXUAL INTERESTS FUNCTION TO OBTAIN NONGENETIC MATERIAL BENEFITS FROM SIRES

Material Benefits Delivered by Dominant Males In humans and some other primates, males may deliver nongenetic benefits to offspring, even absent direct male care. In a group-living species such as chimpanzees, for instance, dominant males may offer protection for offspring against harm brought by other group members, even if only passively given potential costs to harming the offspring of a dominant male. In human foragers, high status males may offer other nongenetic benefits (e.g., Hawkes, 2004). For example, other group members may be more willing to share meat with high status individuals. Possibly, then, heightened female preferences for masculine and dominant male features during the fertile phase were at least partly maintained by the effects of sire choice on benefits offered by these males.

This explanation is not mutually exclusive of the explanation that preferences function, in part, to bias sire choice toward males offering genetic benefits. Ancestrally, dominant males could have offered both genetic and nongenetic benefits.

Nongenetic Benefits Delivered by Long-Term Partners Dixson (2009) has argued, of women's fertile-phase, that most plausibly "such preferences for masculine traits form part of selective mechanisms for primary (i.e., long-term) mate choices" (p. 129). In this view, women's fertile phase preferences not only promote adaptive sire choice; they function to bolster adaptive long-term mate choice as well.

This idea is plausible in principle. In a pair-bonding species, the best sire for a female's offspring is very often the female's long-term social mate. The long-term social mate provides direct care and provisioning and, to the extent that his paternal investment is diminished with compromises in his paternity assurance, benefits a female could derive from a sire other than the primary partner might very well be offset by reductions in paternal investment (e.g., Arnqvist & Kirkpatrick, 2005; Eastwick, 2009). Fertile-phase preferences, then, may simply reflect an accentuation of what women prefer in long-term mates in general.

The primary challenge to the idea is empirical. Gangestad et al. (2007) sought to test the notion that the features fertile women find especially sexually appealing are simply those they prefer in mates generally. Normally ovulating female participants viewed videotapes of men being interviewed as potential lunch dates, and rated their attractiveness as short-term and long-term mates. An independent sample of women rated men's likely attributes based on these interviews: how arrogant, confrontative with a male competitor, socially respected, physically attractive, muscular, kind, intelligent, good father-like, faithful, and capable of financial success they appeared. Fertile women were especially sexually attracted to men who appeared arrogant,

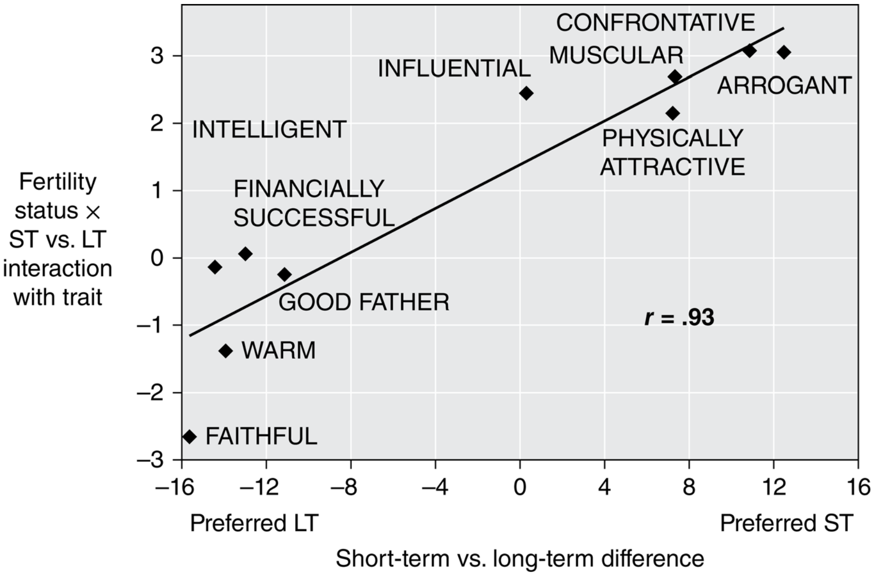

Figure 14.1 *X*-axis: How Much Each Trait Was Preferred in Short-Term Mating Contexts Over Long-Term Mating Contexts. *Y*-axis: How much each trait was especially preferred in short-term mates, relative to long-term mates, when women were fertile. Male behavioral features particularly attractive in sex partners become *especially* attractive in sex partners when women are fertile. Adapted from Gangestad, Garver-Apgar, Simpson, and Cousins (2007).

confrontative, socially respected, physically attractive, and muscular. By contrast, women's preferences for men who appeared kind, intelligent, good fathers, or capable of financial success did not detectably shift. As seen in Figure 14.1, features that women find appealing in sex partners, relative to long-term mates, are also features that women find *especially* sexually attractive when fertile, incompatible with the view that fertile-phase preference shifts simply exaggerate preferences for what women desire in long-term mates. (For other evidence that women particularly prefer some valued traits when infertile, see also DeBruine, Jones, & Perrett, 2005, and Jones, Little, et al., 2005; Jones, Perrett, et al., 2005.)

Later in this chapter, we discuss possible ways that women's choice of sires is biased toward primary partners, despite documented shifts in what women find especially sexually appealing when fertile.

WHY ARE WOMEN SEXUALLY ACTIVE WHEN NONFERTILE?

One major line of work conducted in the past two decades, then, has sought to characterize changes in women's sexual interests across the cycle, with emphasis on understanding fertile-phase interests. Another fundamental issue is why women are sexually active during nonfertile phases in the first place. This issue was, of course, primary to those focused on women's loss of classic estrus. As already noted, the prominent view was that women have sex during nonfertile phases to conceal ovulation. But in the classic view of concealed ovulation (e.g., Alexander & Noonan, 1979), nonfertile phase sexual interests should be indistinguishable from fertile-phase interests, contrary to empirical data. How, then, should one understand the distinct nature of women's *nonfertile* phase sexual interests?

THE GRADED SEXUALITY MODEL

A Diminished Form of the Fertile Phase One view is that women's sexual interests vary in level across the cycle, not in kind. We refer to this perspective as the *graded sexuality model*. In this framework, women's sexual interests during nonfertile phases are evoked less readily or intensely. In effect, nonfertile sexuality is a diminished form of fertile-phase sexuality.

Why should females exhibit a diminished form of fertile-phase sexual interests during nonfertile phases? We can look to other primates for hints (e.g., Dixson, 2012). As Martin (2007) emphasized,

> Copulation at times other than the periovulatory period is not unique to humans, and its occurrence during pregnancy is widespread among mammals. Although the human condition is extreme, extended copulation during the ovarian cycle is the norm among simian primates, in stark contrast to prosimians, in which mating is typically restricted to a few days when the female is in oestrus [p. 59]

Among monkeys and apes, then, sexual abstinence during nonfertile phases is actually rare.

Tolerant Receptivity Females need not reap fitness-enhancing benefits from nonconceptive copulation for nonfertile sexuality to be selected. If males harass females, and the costs of resisting male sexual initiation exceed the costs of accepting it, females may benefit from nonfertile sexual receptivity (e.g., Dixson, 2012).

If nonfertile sexual activity typically arises from tolerant receptivity, then levels of female proceptivity (female-initiated sex) should vary more across the cycle than do levels of receptivity. Dixson (2012) argues that this pattern characterizes many simian primates, including the most intensively studied representatives of New World and Old World monkeys, common marmosets and rhesus macaques. Exceptions do exist. For instance, female Assamese macaques initiate sex at approximately the same rate across both fertile and infertile phases, for up to several breeding months (Fürtbauer, Heistermann, Schülke, & Ostner, 2011).

Loss of Estrus in Women: A Flawed Concept? The prominent view discussed earlier that women lost classic estrus proposed its loss occurred sometime in recent hominin history—< 7 million years ago (mya)—an event purportedly deeply significant to an understanding of distinctly human evolution. Yes simian primates typically lack classic estrus, such that its loss occurred over deep evolutionary time—perhaps 50 mya (Chatterjee, Ho, Barnes, & Groves, 2009). Though loss of estrus may have resulted from interesting features of primate social organization (e.g., a typical group-living arrangement, with females hence often harassed by males), it does not reveal features *unique* to humans. Hence, Dixson (2009) argues, "The concept of *loss of oestrus* as it has been applied to the evolution of Homo sapiens, as distinct from other anthropoids, is flawed, and its use should be discontinued" (p. 479).

The Graded Sexuality Explanation of Preference Shifts Women's sexual preferences shift across the cycle. Can a view that shifts fundamentally consist of changes in *levels* of sexual motivation explain changes in the male features that evoke sexual interest? So long as one assumes that sexual interests are not indiscriminant, yes. Consider a female with classic estrus. She is *only* sexually interested when fertile. As a result, she *only* experiences differential sexual responses to males she prefers when she is fertile; she makes no such discriminations when infertile. The same general point holds when sexual interests vary with fertility in relative, not absolute, terms. Hence, women prefer some male phenotypes over others. As the ease and intensity with which sexual interests are experienced changes across the cycle, then, so, too, may the strength of these preferences.

This thinking underlies Dixson's (2009) proposal that women's shifts in preferences across the cycle reflect general preferences, considered earlier. Though his specific argument—that heightened preferences for masculine traits reflect selective mechanisms for *long-term* mate choice—is not compatiable with evidence, the graded sexuality model could, in principle, explain preference shifts in a more general way. Again, one merely assumes that fertile-phase sexual interests have been extended throughout the cycle, but at weaker levels of intensity.

A Variation on the Graded Sexuality Model Estrous sexuality is generally presumed to function to promote adaptive behavior and sire choice because the estrous *phase* is conceptive. Roney and Simmons (2008) propose an alternative view: that estradiol has been selected to promote female sexual interests and preferences during fertile *cycles* rather than phases, with changes across phases within cycles being by-products of these effects. The idea is grounded in the fact that mid-cycle estradiol surges are strong during fertile phases and weak during nonfertile phases. Roney and Simmons (2013) sought to test this idea and found evidence against it. As they note, progesterone reduces sexual interest, yet progesterone also reaches relatively high levels during fertile cycles. More generally, in our view phylogenetic data argue against this notion. Species with classic estrus (including ones ancestral to humans) are sexually active only when fertile within cycles, and estradiol functions to promote *within-cycle* estrus. Why would within-cycle functionality be lost in our lineage, only to be replaced by a process through which within-cycle changes are mere by-products?

At the same time, we note that a design in which estradiol promotes fertile-phase sexual interests and progesterone suppresses them will also, not incidentally, lead females to experience weak fertile-phase sexual interests during infertile cycles. Fertile-phase sexuality functions when copulation is potentially conceptive, both within and across cycles.

THE DUAL SEXUALITY MODEL

Benefits From Nonfertile Sexuality To propose that females need not derive benefits from nonfertile sexuality for nonfertile sexual activity to evolve is not to deny that, in certain species, they *do* derive such benefits. For instance, black-capped capuchins are fertile about 5–6 days per cycle, the luteal phase lasting about 12 days. Females characteristically initiate copulation with a single dominant male during the fertile phase. As it ends, they may initiate nonconceptive sex with multiple subordinate males. Quite possibly they derive a benefit from doing so (see Dixson, 2012).

This example illustrates two related important points. First, nonconceptive sexuality may serve functions different from those served by conceptive sexuality. Second, nonconceptive sexuality may hence be shaped to be distinct from conceptive sexuality, with interests evoked by different contexts, potentially by different males, with different corresponding responses. Naturally, if nonconceptive and conceptive sexuality serve different functions, then nonconceptive sexuality should not simply be a diminished form of fertile-phase sexuality. It should have been shaped to serve its distinct functions.

Dual Sexuality These points constitute the foundations of the *dual sexuality model*. In this view, variations across the cycle do not merely reflect changes in ease or intensity with which sexual motivation is aroused. Rather, women's sexual psychology during conceptive and nonconceptive phases differs. Accordingly, circumstances that give rise to sexual interest during the fertile phase may fail to do so during nonfertile phases, and *vice versa*.

Dual Sexuality in Common Chimpanzees Humans' closest relatives, chimpanzees, illustrate dual sexuality. Females are sexually receptive and proceptive about 10 days out of each 30-day cycle, but fertile only 2–3 days. They are highly promiscuous, mating with all adult male residents of a group each cycle, purportedly to not allow any male to rule out his own paternity, as those that do so may harm or kill offspring (e.g., Hrdy, 1979). But patterns of female proceptivity and receptivity vary across the sexual phase. Females are least promiscuous during the fertile phase (Stumpf & Boesch, 2005). They reject the advances of an increased proportion of males in the group, and their sexual advances are more selective, converging on males that fertile females consensually prefer—in this study, up-and-coming dominant males. Fertile-phase sexuality purportedly biases sire choice. Females are most promiscuous when nonfertile, during which they purportedly confuse paternity. (See also Matsumoto-Oda, 1999; Pieta, 2008; cf. Muller, Thompson, Kahlenberg, & Wrangham, 2011.)

Extended sexuality in certain other primate species may similarly function to confuse paternity, for example, Hanuman langurs (Heistermann et al., 2001), Phayre's leaf monkeys (Lu, Beehner, Czekala, & Borries, 2012), and white-handed gibbons (Barelli, Heistermann, Boesch, & Reichard, 2008). Orangutan females resist coercion by nondominant males less during extended sexuality (Knott, Emery Thompson, Stumpf, & McIntyre, 2010). Mountain gorillas, who characteristically live in single-male harems, engage in sex infrequently, and almost exclusively during the fertile phase (e.g., Czekala & Sicotte, 2000); they lack extended sexuality during the luteal phase, although females may engage in sex when pregnant, perhaps to draw attention or sperm away from other mating females (Doran-Sheehy, Fernández, & Borries, 2009).

Estrus and Extended Sexuality Thornhill and Gangestad (2008) label fertile and infertile sexual interests estrus and extended sexuality, respectively. Extended sexuality was borrowed from Rodriguez-Girones and Enquist (2001). Classically, estrus, as noted, is a distinct fertile phase sexuality occurring during the fertile phase of the cycle in species lacking any meaningful level of nonfertile sexuality. By this stipulative definition, estrus is "lost" once females become sexual during nonconceptive phases (hence, Dixson's claim that estrus was lost in an early anthropoid primate). By Thornhill and Gangestad's usage, estrus is a distinct fertile-phase sexuality, even in species also possessing functionally distinct extended sexuality. Thornhill and Gangestad proposed that females with extended sexuality typically did not "lose" a distinct fertile phase sexuality; they still possess it, even if in modified form. Rather, a functionally distinct form of sexuality interests prominent during nonfertile phases, extended sexuality, was *added on* and shaped over evolutionary time. Using the term *estrus* in this way captures this thrust of the dual sexuality model.

Women's Extended Sexuality Do women also possess functionally distinct extended sexual interests? And if so, what are they? One can first ask whether they bear any similarity to those of primates confusing paternity: Do women experience more indiscriminant and promiscuous sexual desires during nonconceptive phases? Not surprisingly, it appears not. We asked romantically involved women how frequently they were sexually attracted to their partner and, separately, someone other than their partner both when fertile (as verified by a luteinizing hormone surge) and during the mid-luteal phase. Compared to the fertile phase, nonfertile women reported less sexual interest in men other than their partners, but just as much sexual interest in primary partners (Gangestad, Thornhill, & Garver, 2002; Gangestad, Thornhill, & Garver-Apgar, 2005; cf. Pillsworth, Haselton, & Buss, 2004). Other studies have found that, when women's primary partner is someone who they do not find especially sexy, they report greater attraction to men other than their partners when fertile, but not when infertile (Haselton & Gangestad, 2006; Larson, Pillsworth, & Haselton, 2012). Romantically involved women appear to be more focused on their primary partners during the luteal phase.

Possibly, then, women's extended sexuality has been shaped within the context of pair bonding to bolster benefits delivered by primary partners. Recall Strassman's (1981) explanation of concealed ovulation: By preventing dominant males from monopolizing fertile phase copulations, it permitted nondominant males to attend to specific females, engage in paternity assurance behaviors, and then invest in resulting offspring, contingent on paternity certainty. Paternity assurance, however, involved regular copulation with partners throughout the cycle. From a female's point of view, if male partner investment in offspring is contingent on paternity assurance, itself a function of regular sexual access across the cycle, extended sexuality may function to increase male investment by enhancing male perceptions of paternity assurance, offering partners regular sexual access. By this view, extended sexual interests *should* be directed toward primary partners.

Based on these ideas, Grebe, Gangestad, Garver-Apgar, and Thornhill (2013) proposed that romantically involved women are sexually proceptive—will initiate sex—with primary partners during the luteal phase when they themselves are highly invested in their relationship, but, relatively speaking, partner investment is lacking. In such circumstances, female proceptivity could encourage greater male interest and, ancestrally, paternity assurance. As predicted, discrepancy between female and male relationship investment predicted frequency with which women initated sex with their partners during the luteal phase, but not the fertile phase. (See also Sheldon, Cooper, Geary, Hoard, & DeSoto, 2006, for evidence that women express greater desire for sex for intimacy during extended sexuality. For an alternative view that extended sexuality draws male attention and possibly sperm away from other females in polygynous relationships, see Geary, Bailey, & Oxford, 2011.)

Much more research examining the design of human extended sexuality is clearly needed.

HAS WOMEN'S ESTROUS SEXUALITY BEEN SHAPED BY SELECTION ON HOMININS?

A PHYLOGENETIC PERSPECTIVE ON ESTRUS REVISITED

Estrus has very deep evolutionary roots. If one traces the human lineage back in time, one finds a distinct fertile-phase sexuality in females far more distant in the past than our common ancestor with chimpanzees, apes in general, primates more generally, or even all mammals. Thornhill and Gangestad (2008) proposed that, in fact, the common ancestor to all vertebrates, dating to ~400 mya, may have possessed estrus.

At the same time, features may be modified within particular lineages through secondary adaptation. All simian primates possess five-fingered hands, for instance, but the precise configuration, musculature, and neural control of the hand has been modified within specific lineages.

Human extended sexuality appears to be distinct from that of any other extant ape species. Though the root ancestor of all apes may have possessed extended sexuality, *human* extended sexuality may well function differently from that of all other ape species, possibly because it was modified in the context of pair bonding and biparental care. But what of estrus? Has it, too, been modified by selection introduced by pair bonding and biparental care?

POSSIBLE MODIFICATION OF ESTRUS IN HUMANS: THREE SCENARIOS

No Important Modification One possibility is no: Human estrus has not been importantly modified in the context of pair bonding. Naturally, the precise features preferred have been modified; for example, behavior that asserts influence in humans, which may be preferred by fertile women, differs from dominant behaviors in, say, chimpanzees. But these alterations have not been selected in response to pair bonding.

Two subvariants are possible. First, human estrous motivations may have been maintained because they have also been adaptive within ancestral humans. Second, estrous motivations may have not been adaptive in recent human history (e.g., because they lead to conflicts of interest between pair-bonded partners, disrupting cooperative parenting; see Gangestad, Garver-Apgar, Cousins, & Thornhill, 2014) but persist because selection has not completely eliminated them. That is, estrous motivations may be weak and vestigial.

Estrous Sexuality Has Been Co-Opted to Promote the Stability of Good Relationships As noted earlier, perhaps in almost all cases, the optimal sire of a female's offspring is her primary social partner, even if she could find a sire more genetically fit. Detection of nonpaternity could lead to losses in investment that more than offset the gains of extra-pair sireship. Eastwick (2009) proposed that human estrous sexual motivation has been co-opted to strengthen sexual attraction to men with whom women are strongly bonded—"good," highly compatible and investing partners—during fertile periods: "adaptations linked to fertility and the menstrual cycle are rechanneled toward the new adaptive purpose of protecting and strengthening the pair-bond" (p. 812). Consistent with this proposal, Eastwick and Finkel (2012) found that women's bondedness to partners moderated the impact of fertility status on physical contact motivated by intimacy. Women highly bonded to partners experienced greater emotional connection during sexual contact during the fertile phase, relative to infertile phases.

Though intriguing, this idea requires additional tests. Tests to date have not examined overall sexual contact, simply contact motivated by desire for closeness. In unpublished work, bonding has not moderated attraction to partners or extra-pair men during the fertile phase (Gangestad, Eaton, Garver-Apgar, & Thornhill, unpublished data; Grebe, Emery Thompson, & Gangestad, unpublished data).

Lancaster and Alvarado (2010) note that, ancestrally, women's conceptions typically would have occurred when they were breastfeeding a previous offspring (first borns being obvious exceptions). As lactation entails high levels of prolactin and oxytocin, fertility status would have occurred with a different hormonal milieu than examined in virtually all research on changes in women's interests across the cycle. Perhaps lactational hormones suppress interest in extra-pair men during the fertile phase. That said, the one study linking oxytocin with preferences actually found that it enhanced female interest in male facial masculinity (Theodoridou, Rowe, Rogers, & Penton-Voak, 2011). Additional research on the impact of these hormones is needed.

Estrous Motivations Have Been Shaped to Promote Adaptive Extra-Pair Mating Finally, perhaps estrous motivations have been modified to motivate contingent extra-pair mating. In particular, when partners lacked dominance, indicators of genetic fitness, or genetic compatibility, ancestral women perhaps could have benefited from choosing a sire other than their partners. Naturally, for such behavior to be adaptive, the benefits garnered from an extra-pair sire would have to offset, on average, costs of potential loss of an in-pair partner's parental investment, should he detect nonpaternity. Hence, if adaptive, extra-pair mating should be highly contingent, for example, based on assessments of a primary mate's genetic fitness and compatibility, as well as the value of a mate's actual or potential investment.

Extra-pair paternity does occur in human societies at rates generally low but variable: 2% in the !Kung, 1%–4% in high-confidence Western samples, 9% in the Yanomamö of Venezuela, and >10% in some Indian, African, and South American samples (see Anderson, 2006). The existence of extra-pair paternity per se does not establish adaptation for extra-pair mating, as it may arise for other reasons (e.g., male coercion, failed attempts at mate-switching, nonadaptive "errors" in mating decisions). Indeed, estrous sexual motivations could give rise to extra-pair mating in the absence of *modification* to promote extra-pair mating.

Some have argued that women's estrous preferences are especially pronounced in women who have primary mates, and diminished in unpaired women, consistent with adaptation for extra-pair mating (e.g., Penton-Voak et al., 1999; Havliček et al., 2005). Other studies, however, have found changes across the cycle in unpaired women just as strong as those in paired women (e.g., Gangestad et al., 2002; Haselton & Gangestad, 2006).

Perhaps a more fruitful way to think about adaptations for extra-pair mating is to, first, recognize that estrous sexual desires originated prior to the evolution of pair bonding and could lead to extra-pair mating and, second, think about how selection could favor ways in which maladaptive extra-pair mating might be inhibited, leaving potentially adaptive extra-pair mating possible. This approach bears similarities, in part, to Eastwick's (2009) proposals that estrous motivations may have been modified to promote pair bonding, but need not entail his specific suggestion that selection favored an "adaptive workaround" per se. As Thornhill and Gangestad (2008) noted,

> [E]strous sexuality should generally function to enhance adaptive sire choice by females. One component of adaptive sire choice is choice of a partner who can deliver genetic benefits to offspring. But in pair-bonded species, in many instances the best sire for a woman's offspring is in fact the pair-bond mate, and not merely in instances in which the mate has good genes; the primary partner delivers non-genetic material benefits in a variety of currencies . . . and loss of those benefits could have a drastic negative impact on a female's fitness. . . . Women's willingness to engage in EPC [extra-pair copulation] should hence be sensitive to factors that affect loss of investment.

Predictably, then, relationship satisfaction is one of the best predictors of women's fidelity (Thompson, 1983), and inversely relates to sexual interests in men other than partners during both the fertile and luteal phases (Gangestad et al., 2005). Some research has explored ways in which women with much to lose if their mate were to detect infidelity suppress or control estrous sexual interests in men other than primary partners (e.g., Durante, Rae, & Griskevicius, 2013).

WOMEN'S ATTRACTIVITY ACROSS THE CYCLE

On average, women clearly experience sexual desires differently when fertile. But do they exhibit any outward cues of fertility status? If so, what are the implications for our understanding of women's concealed fertility?

CUES VERSUS SIGNALS

Even in absence of female sexual swellings, males of many species have access to cues of when females are fertile. Indeed, in primates that exhibit sexual swellings, males are typically more attentive to females when they are fertile, even when sexual swelling intensity does not peak with ovulation (Deschner, Heistermann, Hodges, & Boesch, 2004; Engelhardt, Pfiefer, Heistermann, & Niemitz, 2004). Males likely use scent cues to discriminate female fertility status. Even in primate species without swellings, males can often infer female fertility status from scent (e.g., stump-tailed macaques; Cerda-Molina, Hernández-López, Rojas-Maya, & Mondragón-Ceballos 2006; cotton-top tamirins; Ziegler et al., 1993).

Scent cues are probably not signals of fertility. Most likely, they are by-products of hormonal changes across the cycle (e.g., metabolites of estrogens). Females typically do not produce chemicals *in order to* attract males. Instead, males are attracted to incidental effects produced by female adaptation regulating fertility.

SEXUAL SWELLINGS

Swellings have independently evolved in three groups of primates: caterrhine monkeys (including baboons, macaques, and mandrills), red colobus monkeys, and chimpanzees/bonobos (Pagel & Meade, 2006; though gibbons also display a small sexual swelling; e.g., Barelli et al., 2008). The most widely accepted explanation of the function of swellings is Nunn's (1999) graded signal hypothesis: They manipulate the costs and benefits of male guarding of females in species in which dominant males can prevent submissive males from accessing females. As swelling intensity, probabilistically associated with fertility status, increases, so, too, does the benefit of guarding. Guarding has costs, however. Hence, dominant males guard less when swellings subside, thereby permitting other males to gain sexual access. Swellings hence bias sireship toward dominant males but also permit paternity confusion. As males have other cues of fertility status available to them, one can question whether females should exhibit a *costly* graded signal of fertility (e.g., Pagel, 1994; Thornhill & Gangestad, 2008). Possibly, swellings also convey information about female ability to reproduce or genetic quality, also affecting male benefits to guarding; quality signaling may partly explain the costliness of swellings (e.g., Emery & Whitten, 2003).

Cues of Women's Fertility Status Available to Others

Women lack swellings, but cues to women's fertility status exist.

Women's Scent of Fertility Men can discriminate women's fertile phase from their luteal phase based on scent cues, and prefer fertile-phase scents (Doty, Ford, Preti, & Huggins, 1975; Gildersleeve, Haselton, Larson, & Pillsworth, 2012; Havlíček, Dvoráková, Bartos, & Flegr, 2006; Kuukasjärvi et al., 2004; Miller & Maner, 2010; Singh & Bronstad, 2001; Thornhill et al., 2003; cf. Thornhill & Gangestad, 1999). Futhermore, male exposure to periovulatory axillary and vulvar scents may increase testosterone levels (Cerda-Molina, Hernández-López, de la O, Chavira-Ramirez, & Mondragón-Ceballos; Miller & Maner, 2010; cf. Roney & Simmons, 2012). The precise chemical responsible for men's preference remains unknown at this time. Just as with male chimpanzee detection of female fertility status, incidental outcomes of hormonal changes are likely candidates.

Voice Pitch Women's vocal pitch appears to increase and thereby become more feminine when women are fertile (Bryant & Haselton, 2009; Raj, Gupta, Chowdhury, & Chadha, 2010), perhaps as a function of estradiol levels (Firat et al., 2009).

Attractiveness Evidence addressing whether women are visually more attractive when fertile is mixed: Roberts et al. (2004) claimed to find supportive evidence; Bleske-Rechek et al. (2011) failed to replicate their finding and critiqued their methodology; in a small sample, Cobey, Buunk, Pollet, Klipping, and Roberts (2013) found that men rated partners more attractive when fertile; in a larger sample, we fail to replicate that effect (unpublished data). Women do nonetheless appear to feel more attractive when fertile (Durante & Li, 2009; Haselton & Gangestad, 2006; Roeder, Brewer, & Fink, 2009).

Ornamentation Women tend to dress in more sexy, provocative ways on fertile days (Durante, Li, & Haselton, 2007; Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Fredrick, 2007). Women may be more likely to wear red or pink clothing on fertile days (Beall & Tracy, 2013), though contingent on weather: reliably on cold days, but not warm days, perhaps because women dress provocatively in other ways on warm days (Tracy & Beall, 2014). These effects could be incidental to women feeling more sexual when fertile.

Other Behavioral Cues Miller, Tybur, and Jordan (2007) found that men tip female lapdancers about 30% more on fertile days than nonfertile days. Lapdancers using a contraceptive pill earned about what normally ovulating women earned on nonfertile days. As lapdancers are generally motivated to generate as much tipping as possible, no matter where they are in their cycles, Miller et al. reasonably argue that the difference in income is due to men being more attracted or sexually aroused by fertile lapdancers. Moreover, female features themselves, not dress, likely drive effects. Possibly, fertile women can act in sexually more provocative ways when fertile. (See also Miller & Maner, 2011.)

DO WOMEN SIGNAL FERTILITY STATUS?

Women do not possess fully concealed ovulation: They experience estrous sexuality when fertile, and others can detect cues of fertile reproductive status. As already emphasized, however, the mere presence of cues does not imply that females advertise their fertility status. Most cues of fertility status are by-products of reproductive status, which males have evolved to detect.

Cantú et al. (2014) observed women interacting with both a behaviorally dominant and withdrawn man matched for attractiveness, because they were purportedly twins, on two occasions: once when fertile and once during the luteal phase. When fertile, women were more attracted to and flirted more with the dominant male, which might suggest women selectively signal their fertility status to desired men through targeted flirtation. Alternatively, changes in women's behavior across the cycle need not function to signal; they may reflect changes in women's sexual motivations. Additional work on the potential signaling properties of women's flirtation across the cycle is warranted.

Have Fertility Cues Been Selected to Be Suppressed? Women's fertility status is not completely concealed, which does not imply that women signal fertility. Similarly, it need not imply that selection hasn't favored concealment. Indeed, as women may leverage men's sexual interests during nonfertile periods to gain benefits through extended sexuality, selection may favor suppressed production of by-products serving as cues of fertility status. As incidental by-products can't readily be decoupled from the fitness-enhancing effects of adaptations giving rise to them, however, cues may remain. For example, estradiol has evolved to regulate fertility, and it unavoidably yields estradiol metabolites, which could affect scent. As men appear to be poor at detecting female fertility status compared to most male primates, selection may well have led to cue suppression (Thornhill & Gangestad, 2008).

MALE PARTNER RESPONSES TO WOMEN AS A FUNCTION OF FERTILITY STATUS

If men can detect their mates' fertility status, one might expect them to behave differently toward romantic partners across the cycle. Indeed, men appear to engage in greater levels of "mate-guarding" behavior when partners are fertile (Gangestad et al., 2002; Gangestad et al., 2014; Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006). In turn, women become more self-assertive and resist mate guarding when fertile (Gangestad et al., 2014; see also Haselton & Gangestad, 2006; Larson, Haselton, Gildersleeve, & Pillsworth, 2013). More generally, the dynamic in men's and women's relationships tends to change across the cycle, on average, becoming more conflictual when women are fertile.

Couples vary in the extent to which male partners become proprietary and women become more self-asserting during the fertile phase. Increases in women's attraction to other men when fertile predict these changes in behavior (versus increases in women's or men's attraction to their partners; Gangestad et al., 2002; Gangestad et al., 2014; see also Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006). Conflicts of interest surrounding detection of women's fertility between women and their primary partners—favoring male partners, disfavoring women—may be one reason why incidental cues of women's fertility status have been suppressed.

SUMMARY

Women are sexually active throughout the cycle. Nonetheless, their sexual interests clearly change. The precise nature of these changes, as well as their hormonal underpinnings, require more attention. Both estradiol (positively) and progesterone (negatively) likely affect women's sexual interests. As well, several major theoretical issues remain outstanding: What benefits of fertile-phase sexual interests led them to evolve? Does a functionally distinct form of human extended sexuality exist and, if so, what characterizes it? Has women's fertile-phase sexuality been importantly modified in the context of pair-bonding? How are perceptible changes occur across the cycle to be understood within an adaptationist framework? Multiple theoretically informed and empirically generative solutions to these issues have been proposed. We fully expect, in the near future, much progress toward their resolution.

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CHAPTER 15

Human Sperm Competition

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SPERM COMPETITION WAS first defined as “the competition within a single female between the sperm from two or more males for the fertilization of the ova” (Parker, 1970, p. 527). As a form of sexual selection that occurs after the initiation of copulation (termed postcopulatory sexual selection), sperm competition has caused the evolution of adaptations in many taxa (Birkhead, Hosken, & Pitnick, 2009; Birkhead & Møller, 1998). These adaptations in males increase their probability of fertilization when sperm competition occurs, and in females allow them to bias paternity toward favorable males (Eberhard, 1996).

SPERM COMPETITION IN NONHUMAN SPECIES

Sperm competition has been reported in many species, from molluscs (Baur, 1998) and insects (Simmons, 2001) to birds (Birkhead & Møller, 1992) and mammals (Gomendio, Harcourt, & Roldán, 1998). In species with internal fertilization, sperm competition can occur when a female mates with multiple males within a sufficiently short time period so that sperm from two or more males simultaneously occupy her reproductive tract. Although the outcome of such competition depends on many factors (e.g., mating order, male accessory secretions, and the shape, number, and size of female sperm storage organs), the number of sperm transferred is often the most important factor and, consequently, a male can increase the probability of fertilizing ova by inseminating more sperm (Parker, 1970, 1990a). However, because the costs of ejaculate production are nontrivial (e.g., Dewsbury 1982; Pitnick, Markow, & Spicer, 1995), males must trade off ejaculate production costs against the benefits of delivering more sperm in an ejaculate. Thus, one of the first hypotheses generated by sperm competition theory was that males will deliver more sperm when sperm competition risk is higher (Parker, 1982, 1990a). Across species, therefore, sperm competition risk should predict investment in sperm production, whereas within-species males are predicted to exhibit prudent sperm allocation, inseminating more sperm when the risk of sperm competition is higher (Parker, Ball, Stockley, & Gage, 1997). Consistent with the first prediction, investment in sperm production is greater in species with higher levels of sperm competition (e.g., Gage, 1994; Harcourt, Harvey, Larson, & Short, 1981; Møller, 1988). In nematodes, where sperm size correlates with sperm competitiveness (LaMunyon & Ward, 1998), species with greater sperm competition risk produce larger, more costly, sperm (LaMunyon & Ward, 1999). Moreover, experimental exposure to higher levels of sperm competition leads to the evolution of increased testis size in yellow dung flies within 10 generations (*Scathophaga stercoraria*) (Hosken & Ward, 2001) and experimental removal of sperm competition in fruit flies results in the evolution of lower investment in sperm production (Pitnick, Miller, Reagan, & Holland, 2001).

Within species, individual males in many species are capable of prudent sperm allocation (for reviews, see delBarco-Trillo, 2011; Kelly & Jennions, 2011) and adjust the number of sperm they deliver during each insemination in response to auditory, chemosensory, tactile, or visual *cues* of sperm competition. Prudent sperm allocation has been demonstrated in many taxa, but perhaps rats (*Rattus norvegicus*) are of most relevance to humans. Male rats adjust the number of sperm they inseminate depending on the amount of time they have spent "guarding" a particular female prior to copulation (Bellis, Baker, & Gage, 1990) and when mating in the presence of a rival male (Pound & Gage, 2004). In another mammalian example, male voles (*Microtus pennsylvanicus*) deliver more sperm when exposed to the odor of another male (delBarco-Trillo & Ferkin, 2004).

For males, lack of success in sperm competition means loss of fertilization opportunities. However, in species with substantial paternal investment, males also risk cuckoldry—the unwitting investment of resources into genetically unrelated offspring—and the associated loss of the time, effort, and resources spent attracting a partner (Trivers, 1972). Both males and females of socially monogamous species pursue extra-pair copulations, and female sexual infidelity creates the primary context for sperm competition (Birkhead & Møller, 1992; Smith, 1984). Consequently, selection pressures associated with sperm competition can generate adaptations that function to maximize sperm competition success, thereby minimizing cuckoldry risk.

HAS SPERM COMPETITION BEEN AN ADAPTIVE PROBLEM FOR HUMANS?

Smith (1984) argued that female infidelity was the most common ancestral context for sperm competition in humans, whereas other contexts (e.g., consensual communal sex, courtship, rape, prostitution) may not have occurred with sufficient frequency over human evolution to provide selection pressures for adaptations to sperm competition comparable to female infidelity.

Male anatomy and physiology provide evidence of an evolutionary history of sperm competition. Across primate species, relative testis size and the number of sperm per ejaculate correlate positively with the degree of polyandry, which determines sperm competition risk (Harcourt et al., 1981; Harcourt, Purvis, & Liles, 1995; Short, 1979). As a proportion of body mass, human testes are larger than those in monandrous species such as the gorilla and orangutan but smaller than testes in the highly polyandrous chimpanzee (Harcourt et al., 1995). Similarly, human ejaculates contain an intermediate number of sperm. Smith (1984) argued that these traits indicate polyandry, and, therefore, that sperm competition was an important selection pressure during human evolution.

Do Women Have Adaptations to Induce Sperm Competition?

Evolutionary analyses of human sexual psychology have emphasized the benefits to men of short-term mating and sexual promiscuity (Buss & Schmitt, 1993; Symons, 1979). However, for men to successfully pursue short-term sexual strategies, there must be women who mate nonmonogamously (Greiling & Buss, 2000). Ancestral women may have benefited from facultative polyandry in several ways (reviewed in Greiling & Buss, 2000). First, they may acquire resources, either in direct exchange for sex (Symons, 1979) or by creating paternity confusion to elicit investment (Hrdy, 1981). Second, women may secure genetic benefits for their offspring by copulating opportunistically outside their pair bond with men of superior genetic quality (Smith, 1984; Symons, 1979; reviewed in Jennions & Petrie, 2000).

Multiple mating by women is a necessary—but not sufficient—condition for sperm competition to occur. Women must copulate with two or more men *within a sufficiently short time period* such that there is temporal overlap in the competitive lifespans of the rival ejaculates. Several studies indicate that the length of this competitive window is 5 days (Wilcox, Dunson, Weinberg, Trussell, & Baird, 2001; Wilcox, Weinberg, & Baird, 1998). Using an estimate of 5 days, Baker and Bellis (1995) documented that 17.5% of British women self-report "double-mating" in such a way as to generate sperm competition (in the absence of barrier contraception) at some point during the first 50 copulations in their lifetimes.

Large-scale studies of sexual behavior have not collected data on the frequency with which women double-mate specifically, but many have recorded how often they engage in concurrent sexual relationships, more generally. Laumann, Gagnon, Michael, and Michaels (1994), for example, found that 83% of respondents reporting five or more sexual partners in the past year also reported that at least two of these relationships were concurrent. Moreover, a study of sexual behavior in Britain—the National Survey of Sexual Attitudes and Lifestyles conducted between 1999 and 2001 (Johnson et al., 2001)—revealed that 9% of women overall, and 15% of those aged 16–24 years, reported having had concurrent sexual relationships with men during the preceding year. Not all concurrent sexual relationships involve double matings, but it is likely that many do.

Based on survey findings that women report more frequent double matings when conception rate is higher, Bellis and Baker (1990) argued that women "schedule" their copulations in a way that *actively promotes* sperm competition and thus encourages fertilization by the most competitive sperm. Bellis and Baker argued that this finding cannot be attributed to men's preferences for copulation with women at peak fertility, because it arose from increases in the frequency of extra-pair copulations. A general male preference for copulation at times of high conception risk would be expected to also increase the frequency of in-pair copulations during this time. Bellis and Baker may have been too quick to dismiss the possibility that men prefer to copulate with a woman during peak conception risk, however. If women pursue extra-pair copulations to secure genetic benefits from extra-pair partners (e.g., Gangestad & Simpson, 2000), then, while pursuing extra-pair partners, they should simultaneously avoid in-pair copulations (Gallup, Burch, & Mitchell, 2006). Consequently, the absence of a spike of in-pair copulations at times of high conception risk may not reflect the motivation of the in-pair male.

POLYANDROUS SEX IN WOMEN'S FANTASIES

Sexual fantasy may provide insight into the psychological mechanisms that motivate sexual behavior (Ellis & Symons, 1990; Symons, 1979). Empirical studies have addressed sex differences in sexual fantasy (reviewed in Leitenberg & Henning, 1995), many of which have been guided by an evolutionary perspective (e.g., Ellis & Symons, 1990; Wilson, 1987). Given the asymmetric costs of sexual reproduction, female reproduction is limited by the ability to bear and rear offspring, whereas male reproduction is limited by sexual access to females (Trivers, 1972). Consequently, it has been hypothesized that men more than women will have sexual fantasies that involve multiple, anonymous sexual partners who do not require an investment of time, energy, or resources prior to granting sexual access (Ellis & Symons, 1990), and empirical investigations have confirmed this hypothesis. Indeed, one of the largest sex differences occurs for fantasies about sex with two or more members of the opposite sex concurrently: Men report this fantasy much more than do women (Leitenberg & Henning, 1995).

Tests of the hypothesis that men more than women fantasize about concurrent sex with two or more partners have, nevertheless, provided data on women's polyandrous sexual fantasies. Large-scale surveys indicate that some women report fantasies of polyandrous sex, imagining themselves as a woman having sex with two or more men concurrently: 18% in the United States (Hunt, 1974) and 15% in the United Kingdom (Wilson, 1987). Similarly, smaller studies find that 15% to 41% of women report sexual fantasies involving two or more men concurrently (Arndt, Foehl, & Good, 1985; Davidson, 1985; Pelletier & Herold, 1988; Person, Terestman, Myers, Goldberg, & Salvadori, 1989; Sue, 1979). Rokach (1990) reported that, although sex with more than one partner accounted for 14% of the sexual fantasies reported by a sample of 44 men, it accounted for 10% of the fantasies reported by a sample of 54 women. Price and Miller (1984) report that polyandrous sex was among the 10 most frequently reported fantasies in a sample of college women.

If women's sexual fantasies reflect sexual desires and preferences that might sometimes be acted upon, then polyandrous sex is not an unlikely occurrence, given that women more than men are the "gatekeepers" of sexual access—including when, where, and the conditions under which sex occurs (Symons, 1979). If, as Symons (1979) argued, sexual fantasy provides a window through which to view evolved human psychology, then human female sexual psychology may include mechanisms that motivate polyandrous sex, with the consequence of promoting sperm competition.

MEN'S ADAPTATIONS TO SPERM COMPETITION

There are theoretical reasons to believe that mammalian sperm competition takes the form of *scramble competition* in which sperm are "lottery tickets" for the prize of fertilizing ova, and modeling studies and experimental findings support this view (Gomendio et al., 1998). Male adaptations to scramble competition are likely to take the form of physiological, anatomical, and behavioral features that increase the male's chances of fertilizing ova in a competitive environment in which the ability to deliver large numbers of sperm is a crucial determinant of success.

IS THERE EVIDENCE OF PRUDENT SPERM ALLOCATION BY MEN?

Sperm competition theory predicts that investment in sperm production will vary with sperm competition risk across species (Parker, 1982, 1990a, 1990b), and anatomical, physiological, and behavioral adaptations to *high* levels of sperm competition that deliver large numbers of competitive sperm. Sperm competition theory also predicts that, when sperm competition risk varies between matings, males will allocate resources prudently, adjusting the number of sperm inseminated at each copulation. Prudent sperm allocation occurs even in species in which overall levels of sperm competition are not especially high—but sufficiently variable to select for the evolution of such facultative mechanisms.

Ejaculates are costly to produce for human males. Frequent ejaculation, especially more frequent than every other day, results in decreased sperm counts (Tyler, Crockett, & Driscoll, 1982), suggesting limits to sperm production. Men hardly seem limited by sperm production, however, given the apparent wastage of sperm. Sperm are continuously lost in the urine, and entire ejaculates are lost during nocturnal emissions and masturbation, although masturbatory ejaculates contain fewer sperm than do copulatory ejaculates (Zavos & Goodpasture, 1989). Baker and Bellis (1993a) suggest, however, that these lost sperm are older and less competitive, and that noncopulatory ejaculations increase the number of younger, highly-competitive sperm ejaculated at the next copulation. Given the cost of ejaculates, human males may have evolved the ability to modulate ejaculated sperm numbers depending on sperm competition risk at copulation. The number of sperm in a man's ejaculate varies considerably between ejaculates (e.g., Mallidis, Howard, & Baker, 1991). Although clinicians treat this intra-individual variability as "noise" when determining the "true" values of a man's semen parameters, sperm competition theory predicts that some of this variability might reflect prudent sperm allocation in response to the temporal risk of sperm competition.

Evidence indicating that men adjust ejaculate composition in response to sperm competition risk was first reported in several articles by Baker and Bellis. In the first report for a sample of copulatory ejaculates (Baker & Bellis, 1989), one from each of 10 couples, there was a negative rank-order correlation ($r_s = -0.95$) between "objective" sperm competition risk—the percentage of time the couple had spent *together* since their last copulation—and the number of sperm in the ejaculate. No such relationship was identified for masturbatory ejaculates. Baker and Bellis (1989) argued that objective sperm competition risk indexes risk of female double mating and, therefore, that these findings are consistent with the hypothesis that there is a positive association between the number of sperm inseminated and the risk of sperm competition. Their study was based on a single ejaculate per couple, with the finding that men who had spent the most time apart from their partners since their last copulation produced copulatory ejaculates containing the most sperm. It could be that men who tend to produce larger ejaculates also tend to spend a greater proportion of their time between copulations apart from their partners.

Baker and Bellis (1993a) addressed the aforementioned problems by including in their analyses multiple ejaculates from each participating couple. For a sample of 40 specimens produced by five men, nonparametric analyses indicated a negative association between the number of sperm inseminated and objective sperm competition risk. Although Baker and Bellis argued that these results demonstrated prudent sperm allocation in response to a cue of increased sperm competition risk, alternative interpretations are possible. For example, changes in ejaculate composition may depend on changes in female sexual behavior induced by partner absence providing different stimuli prior to, and at the time of, ejaculation. This may be significant because quality differences between ejaculates obtained via uninterrupted coitus and those obtained via *coitus interruptus* (Zavos, Kofinas, Sofikitis, Zarmakoupis, & Miyagawa, 1994) indicate that sexual stimuli present at the moment of ejaculation may be important determinants of sperm numbers.

PHYSIOLOGICAL MECHANISMS ASSOCIATED WITH PRUDENT SPERM ALLOCATION

Although the findings of Baker and Bellis (1993a, 1995) suggest that men are capable of prudent sperm allocation, the physiological mechanisms involved in the adaptive regulation of ejaculate composition are poorly understood. However, factors known to affect semen parameters may provide some clues. In longitudinal studies, individual men exhibit substantial variability in ejaculate parameters such as volume and sperm concentration (e.g., Mallidis et al., 1991), in part because both parameters are affected by the duration of ejaculatory abstinence (e.g., Blackwell & Zaneveld, 1992). There also is evidence that the context in which an ejaculate is produced is important. For example, ejaculates produced during copulation are superior to those produced via masturbation (Zavos, 1985), having greater volumes, greater sperm numbers, and higher grades of sperm motility (Sofikitis & Miyagawa, 1993; Zavos & Goodpasture, 1989).

The mechanisms that cause copulatory ejaculates to contain more sperm than masturbatory ejaculates are not fully understood, but the greater intensity and duration of precoital stimulation increases the number of motile sperm with normal morphology in copulatory ejaculates (Zavos, 1988). There is mixed evidence on whether sexually stimulating visual material can improve semen parameters for masturbatory ejaculates (Handelsman et al., 2013; van Roijen et al., 1996; Yamamoto, Sofikitis, Mio, & Miyagawa, 2000), but there is a positive association between the duration of pre-ejaculatory sexual arousal and sperm concentration for masturbatory ejaculates when multiple specimens are collected from individual men (Pound, Javed, Ruberto, Shaikh, & Del Valle, 2002) although this is not apparent in between-male studies (Elzanaty, 2008; Handelsman et al., 2013).

Relationships between semen quality and the duration of sexual arousal also have been documented in domesticated farm animals when specimens are collected for artificial insemination (for review, see Pound, 2002). Given the relationship between duration of pre-ejaculatory sexual arousal and variation in ejaculate sperm counts across species, males may achieve adaptive changes in ejaculate composition through behavioral changes that prolong arousal prior to ejaculation (Pham, Shackelford, Welling et al., 2013; Pound, 2002).

PSYCHOLOGICAL MECHANISMS ASSOCIATED WITH PRUDENT SPERM ALLOCATION

Males in many nonhuman species can adjust the number of sperm they inseminate in response to sperm competition risk. Baker and Bellis (1993a) suggest that human males share this capacity. Shackelford et al. (2002) investigated men's psychological responses to sperm competition risk, hypothesizing that psychological mechanisms evolved to motivate male behavior to increase the probability of success in sperm competition. For men, the absence of a regular partner (e.g., objective sperm competition risk) may provide key information processed by psychological mechanisms and which subsequently motivates a man to inseminate his partner as soon as possible, to combat the increased risk of sperm competition (Shackelford et al., 2002). Nevertheless, total time since last copulation might have important effects on a man's sexual behavior, perhaps increasing feelings of sexual frustration whether that time has been spent apart or together.

Shackelford et al. (2002) assessed the relationships between male sexual psychology and behaviors predicted to be linked to objective sperm competition risk, while controlling for the total time since a couple's last copulation. Shackelford et al. suggested that men might respond differently to cues of sperm competition risk depending on the nature of their relationship with a particular woman. Satisfaction with, and investment in, a relationship are likely to be linked, with the result that a man who is more satisfied may have more to lose in the event of cuckoldry. For this reason, when examining the responses of men to increases in the proportion of time spent apart from their partner since their last copulation, Shackelford et al. (2002) controlled for the extent to which the participants were satisfied with their relationships.

Shackelford et al. (2002) and Shackelford, Goetz, McKibbin, and Starratt (2007) found that men who spend a greater proportion of time apart from their partner since their last copulation (and, therefore, faced greater sperm competition risk) rate her as more attractive, report that other men find her more attractive, report greater interest in copulating with her, and indicate that she is more interested in copulating with him, but only among men who perceive that she spends more time *with other men* (Pham & Shackelford, 2013a). Starratt, McKibbin, and Shackelford (2013) documented that men experimentally primed with thoughts of partner infidelity report greater partner-directed copulatory interest. Taken together, these findings suggest that men are sensitive to cues to sperm competition risk and adjust accordingly their partner-directed copulatory interest.

The *cuckoldry risk hypothesis* predicts that men at greater sperm competition risk are more likely to sexually coerce their partner (Goetz & Shackelford, 2006; Lalumiere, Harris, Quincy, & Rice, 2005; Thornhill & Thornhill, 1992; Wilson & Daly, 1992). In socially monogamous birds, forced in-pair copulations often follow immediately a female's extra-pair copulation (Bailey, Seymour, & Stewart, 1978; McKinney & Stolen, 1982). In humans, research documents a positive relationship between men's partner-directed sexual coercion and their partner's infidelity risk. Men who rape their female partners often accuse their partner of infidelity prior to the act (Finkelhor & Yllo, 1985; Russell, 1982). Female victims of intimate partner violence rate their abusers as more sexually jealous when the abuse also includes rape (Frieze, 1983; Gage & Hutchinson, 2006). Men who report sexually coercing their partner are more likely to report perceiving their partners as being unfaithful, and women who report being sexually coerced are more likely to report being unfaithful (Goetz & Shackelford, 2006). Even after controlling for men's dominant personalities and controlling behaviors, men's sexual coercion tactics are positively correlated with their perception or knowledge of partner infidelity (Goetz & Shackelford, 2009). Men's sexual coercion is positively correlated with the occurrence of partner-directed insults involving accusations of their partner's infidelity (Starratt, Goetz, Shackelford, & Stewart-Williams, 2008). The proportion of time spent apart from a partner since the couple's last copulation predicts men's partner-directed sexual coercion, but *only* among men who perceive a greater risk of partner infidelity (McKibbin, Starratt, Shackelford, & Goetz, 2011).

Men's partner-directed copulatory interest in response to sperm competition risk may manifest as frequent copulations. In many socially monogamous birds, males use frequent copulations to increase rates of sperm transfer into the female reproductive tract, thereby increasing their chances of success in sperm competition (Birkhead, Atkin, & Moller, 1987; McKinney, Cheng, & Bruggers, 1984). Similarly in humans, men at greater sperm competition risk (Kaighobadi & Shackelford, 2008; Pham et al., 2014), and men who more frequently perform behaviors to minimize sperm competition risk (Shackelford, Goetz, Guta, & Schmitt, 2006), also perform more frequent copulations with their partner.

THE INFLUENCE OF SPERM COMPETITION ON MEN'S REPRODUCTIVE ANATOMY AND COPULATORY BEHAVIOR

Human testis size suggests an evolutionary history of intermediate levels of sperm competition (Smith, 1984), and other aspects of male reproductive anatomy may provide insights as well. Human males have a penis that is longer than in any other ape (Short, 1979), but in relation to body weight it is no longer than the chimpanzee penis (Gomendio et al., 1998). Several arguments have been offered to explain how the length and shape of the human penis might reflect adaptation to sperm competition. A longer penis may be advantageous in the context of scramble competition, which combines elements of a race and a lottery, because being able to place an ejaculate closer to the cervix may increase the chance of fertilization (Baker & Bellis, 1995; Short, 1979; Smith, 1984).

Gallup et al. (2003) empirically tested Baker and Bellis's (1995) hypothesis that the human penis may be designed to displace semen deposited by other men in the reproductive tract of a woman. Gallup et al. found that artificial phalluses with a glans and a coronal ridge approximating a human penis displaced more simulated semen than did a phallus lacking these features. They suggested that when the penis is inserted into the vagina, space around the frenulum allows semen to flow back under the penis and collect behind the coronal ridge, facilitating its extraction. Displacement of simulated semen only occurred, however, when a phallus was inserted at least 75% of its length into the artificial vagina, suggesting that successful displacement of rival semen may require specific copulatory behaviors. Following allegations of female infidelity or separation from their partners (contexts in which the likelihood of rival semen being present in the reproductive tract is relatively greater), both sexes report that men thrusted more deeply and more quickly at the couple's next copulation (Gallup et al., 2003). Such copulatory behaviors may increase semen displacement.

In an independent test of the hypothesis that displacing rival semen may require specific copulatory behaviors, Goetz et al. (2005) investigated whether and how men under a higher risk of sperm competition might attempt to "correct" a female partner's sexual infidelity. Men in committed, sexual relationships reported their performance of specific copulatory behaviors arguably designed to displace the semen of rival men. As hypothesized, men who mated to women who place them at higher recurrent risk of sperm competition were more likely to perform semen-displacing behaviors, including an increase in number of thrusts, deepest thrust, average depth of thrusts, and duration of sexual intercourse.

Sperm competition theory has informed research on other male sexual behaviors, such as oral sex. Evidence suggests that oral sex was a recurrent feature of human evolution, occurring in most cultures and in several other species (see Pham & Shackelford, 2013a, 2013b). It is frequently depicted in modern pornography (Mehta & Plaza, 1997), and appears in Paleolithic cave paintings (Angulo & Garcia, 2005). However, whether oral sex is an adaptation is unclear. Previous researchers have suggested that men perform oral sex to (a) assess a partner's reproductive health (Baker, 1996), (b) detect rival male semen in the vagina (Baker, 1996; Kohl & Francoeur, 1995; Thornhill, 2006), (c) manipulate female mechanisms that may bias the outcome of sperm competition (Pham, Shackelford, Sela, & Welling, 2013), (d) sexually satisfy the woman, thereby reducing the likelihood of her mating with another man (Pham & Shackelford, 2013c), or (e) increase male sexual arousal and consequent semen quality (Pham, Shackelford, Welling et al., 2013). Additionally, oral sex may facilitate "fertility-detection": Men use olfactory cues to detect women's fertility status (reviewed in Haselton & Gildersleeve, 2011), and men report vaginal fluid is more pleasant smelling when produced at high fertility versus low fertility (Cerda-Molina, Hernández-López, de la O, Chavira-Ramírez, & Mondragón-Ceballos, 2013).

The Influence of Sperm Competition on Men's Mate Selection

To minimize sperm competition risk, men may have evolved mate preferences that function to select as short-term sexual partners women who present a lower risk of sperm competition (Shackelford, Goetz, LaMunyon, Quintus, & Weekes-Shackelford, 2004). Men's risk of sperm competition increases with a prospective short-term partner's involvement in one or more relationships. Women who are not in a long-term relationship and who do not have casual sexual partners, for example, present a low risk of sperm competition. Consequently, such women may be perceived as desirable short-term sexual partners. Women who are not in a long-term relationship but who engage in short-term matings may present a moderate risk of sperm competition, because women who engage in short-term matings probably do not experience difficulty obtaining willing sexual partners. Women in a long-term relationship may present the highest risk of sperm competition. The primary partner's frequent inseminations might, therefore, make women in a long-term relationship least attractive as short-term sexual partners.

As predicted, Shackelford et al. (2004) found that men's sexual arousal and reported likelihood of pursuing a short-term sexual relationship was lowest when imagining that the potential short-term partner is married, next lowest when imagining that she is not married but involved in casual sexual relationships, and highest when imagining that she is not married and not involved in casual sexual relationships. These results suggest that when men are presented with different mating options, they are less sexually aroused by options that reflect higher sperm competition risk. However, exposed to high sperm competition risk—such as when their regular partner commits infidelity—men are more sexually aroused to high sperm competition risk (Shackelford et al., 2002, 2007).

THE INFLUENCE OF SPERM COMPETITION ON MEN'S SEXUAL AROUSAL AND SEXUAL FANTASIES

Men's sexual fantasies often involve multiple, anonymous partners (Ellis & Symons, 1990; Symons, 1979). These fantasies tend to be embodied in pornography produced for men, incorporating multiple, low-investment matings with highly fertile women (Malamuth, 1996). However, much pornography contains visual cues of sperm competition risk. Pound (2002) analyzed pornographic images on Internet sites and showed that depictions of sexual activity involving a woman and multiple men are more prevalent than those involving a man and multiple women. Similar results were found in both an online survey of self-reported preferences and in a preference study that unobtrusively examined image selection behavior. McKibbin, Pham, and Shackelford (2013) reported that the number of images on adult DVD covers depicting multimale interactions with one woman predicted DVD sales rank better than the number of images depicting multifemale interactions with one man. Finally, anecdotal reports from the "swinging" or "partner-swapping" community suggest that men often experience intense sexual arousal in response to the sight of their partner interacting sexually with other men (Gould, 1999; Talese, 1981).

Pound (2002) argued that males should find mate sharing to be aversive because of the potential loss of paternity to a competitor's ejaculate. However, sexual arousal in response to cues of sperm competition risk may be produced by a paternity assurance mechanism because it may motivate earlier or more frequent copulation. Moreover, increased arousal in response to cues of sperm competition risk may play a proximate role in ejaculate adjustment mechanisms (Pound, 2002). Consistent with this hypothesis, Kilgallon and Simmons (2005) reported that men who view pornography depicting two men interacting with one woman (cueing sperm competition), relative to men who view pornography depicting three women (cueing absence of sperm competition) ejaculate a higher percentage of motile sperm. Thus, although men should avoid sexual instances with risk of sperm competition, they may actually prefer the arousal associated with the same instances when experiencing the fantasies involved in viewing pornography.

WOMEN'S ADAPTATIONS TO SPERM COMPETITION

If sperm competition was a recurrent feature of human evolutionary history, women may have adaptations that allow them to influence its outcome. Specifically, women may have evolved mechanisms to determine which men achieve paternity; that is, adaptations for both precopulatory and postcopulatory choice. In this context, "postcopulatory female choice" refers to female influence that follows initiation of copulation (Eberhard, 1996).

PRECOPULATORY FEMALE CHOICE: PROMOTING AND AVOIDING SPERM COMPETITION

Bellis and Baker (1990) documented that women in committed relationships are more likely to double mate when the probability of conception is higher. This observation suggests that women have psychological adaptations that promote sperm competition, with the result that their ova will be fertilized by the most competitive sperm. For example, although women's sexual attraction to their regular partner remains unchanged across their fertility cycle, they are more sexually attracted to, and fantasize about, men *other than* their regular partner during periods of higher conception risk (Gangestad, Thornhill, & Garver, 2002; Pillsworth & Haselton, 2006), suggesting that women may promote sperm competition during these periods. However, under certain conditions, it may be advantageous for women to *avoid* sperm competition. Gallup et al. (2006) documented that women delay copulations with their regular partner following their extra-pair copulation. Favoring copulation with an extra-pair partner to the exclusion of a primary partner reduces competition for the extra-pair sperm when conception is more likely. Thus, women's sexual attraction to and fantasy about men other than their regular partner may qualify as a precopulatory female adaptation. But because men have been selected to be sensitive to their partner's increased interest in extra-pair copulation near ovulation (Gangestad et al., 2002), women may have postcopulatory adaptations that favor sperm from one man over another.

POSTCOPULATORY FEMALE CHOICE: A FUNCTION FOR FEMALE COITAL ORGASM?

One such female postcopulatory adaptation to sperm competition may be orgasm. The human clitoris and penis develop from the same embryonic tissue, prompting Symons (1979) and Gould (1987) to argue that female orgasm is a by-product of male orgasm. Others have hypothesized that female orgasm may be an adaptation (e.g., Alexander, 1979; Baker & Bellis, 1993b; Hrdy, 1981; Smith, 1984). Women experience oxytocin surges during orgasm, which may promote pair bonding and repeated copulations with a man (reviewed in Puts, Dawood, & Welling, 2012). Female coital orgasm also may afford selective sperm retention (Baker & Bellis, 1993b; Smith, 1984). Female orgasm causes the cervix to dip into the seminal pool deposited by the male at the upper end of the vagina and this may result in the retention of a greater number of sperm (Baker & Bellis, 1993b, 1995). Baker and Bellis (1993b) and Smith (1984) contend that by strategic timing of orgasm, women may select preferentially the sperm of extra-pair partners, who are likely to be of higher genetic quality than in-pair partners.

Baker and Bellis (1993b) estimated the number of sperm in ejaculates collected by condoms during copulation and by vaginal "flowbacks" (i.e., ejected seminal and vaginal fluids) when condoms were not used, and documented that women influence the number of sperm retained in their reproductive tract through the presence and timing of coital orgasm. Coital orgasms that occurred between 1 minute before and 45 minutes after their partner ejaculated were associated with greater sperm retention than orgasms that occurred earlier than 1 minute before their partner ejaculated. Baker and Bellis also provided evidence that women with a regular partner and one or more extra-pair partners had fewer high-retention orgasms with their regular partner and more high-retention orgasms with their extra-pair partners.

Missing from Baker and Bellis's (1993b) study, however, was an explicit demonstration of higher sperm retention associated with partners of higher genetic quality. Thornhill, Gangestad, and Comer (1995) established this link and documented that women mated to men with lower fluctuating asymmetry (indicating relatively high genetic quality) reported more copulatory orgasms than did women mated to men with higher fluctuating asymmetry. Women mated to men with lower fluctuating asymmetry did not simply have more orgasms, but specifically reported more copulatory orgasms likely to result in greater sperm retention. Another indicator of genetic quality and related to fluctuating asymmetry is physical attractiveness. Shackelford et al. (2000) found that women mated to more physically attractive men were more likely to report achieving orgasm at their most recent copulation than were women mated to less attractive men.

Although orgasm as an adaptation for postcopulatory female choice between rival ejaculates is plausible, the functional significance of the female orgasm is still hypothetical (Pound & Daly, 2000). Baker and Bellis's (1995) evidence that women retain more sperm if they experience orgasm between 1 minute before and 45 minutes after their partner ejaculates than at other times (or not at all) assumes that the number of sperm ejaculated is identical regardless of whether or when the woman has an orgasm. This assumption may be incorrect, however, because the duration of pre-ejaculatory sexual arousal is positively associated with the number of sperm ejaculated (Pound, 2002; Zavos, 1988).

Men's interest in whether their partner achieves orgasm suggests that female orgasm may be an adaptation (see Thornhill et al., 1995). Consistent with this, McKibbin, Bates, Shackelford, Hafen, and LaMunyon (2010) found that sperm competition risk moderates the association between men's relationship investment and their interest in their partner's copulatory orgasm. In some cultures, men do not appear concerned about whether their partners experience orgasm (Symons, 1979), but these may be cultures where sperm competition risks are lowered through other mechanisms; for example, in many cultures, female sexuality (and female orgasm) is suppressed through punishment of female promiscuity (reviewed in Baumeister & Twenge, 2002).

Women may pretend orgasm to appease their partner, suggesting the existence of female counteradaptations to men's interest in their orgasm (Thornhill et al., 1995). Women may pretend orgasm to signal their relationship satisfaction to their partner, thereby minimizing the likelihood of their partner's infidelity (Muehlenhard & Shippee, 2010). Women who perceive a greater risk of partner infidelity are more likely to pretend orgasm (Kaighobadi, Shackelford, & Weekes-Shackelford, 2012). A tendency to pretend orgasm with a desired partner would seem to be inconsistent with the hypothesized sperm retention function of genuine orgasm. If female orgasm functioned to retain, preferentially, sperm from men of high genetic quality, we might predict that women would pretend orgasm more frequently with men of lower genetic quality to "avoid" retaining his sperm from genuine orgasm, simultaneously satisfying him, possibly to continue securing nongenetic benefits. To reconcile these differences, future research should investigate whether the frequency with which women pretend orgasm correlates with measures of their partner's genetic quality (e.g., masculinity, muscularity, fluctuating asymmetry; Frederick & Haselton, 2007).

Direct evidence of preferential use of sperm by females is absent in humans, particularly because it is difficult to study female influence of sperm behavior within the female reproductive tract. Even in nonhuman animals, evidence of female manipulation of sperm is scarce. Although there have been observations of females discarding stored sperm when mating with a new partner (Davies, 1985; Etman & Hooper, 1979), most studies infer female manipulation based on patterns of sperm storage or offspring paternity (see Eberhard, 1996). Because much of postcopulatory competition occurs in the reproductive tract, it is likely that human females have evolved adaptations in response to sperm competition.

This chapter focuses on men's adaptations, which reflects the historical and current state of research and theory. Intersexual conflict between ancestral males and females, however, produces a coevolutionary arms race between the sexes, in which an advantage gained by one sex selects for counteradaptations in the other sex (Rice, 1996, Shackelford & Goetz, 2012). Thus, men's numerous adaptations to sperm competition are likely to be met by numerous adaptations in women, including female orgasm (reviewed in Puts et al., 2012), and manipulating the timing of their copulations with their regular partner and with a potential extra-pair partner (Gallup et al., 2006).

CONCLUDING REMARKS

We describe the far-reaching consequences of female infidelity and consequent sperm competition. First identified in nonhuman species in the 1970s, and not considered in humans until the 1980s, evolutionary-minded researchers are only beginning to uncover its possible role in shaping human anatomy, physiology, and psychology. Sperm competition may have influenced men's and women's reproductive anatomy and physiology, men's attraction to and sexual interest in their partners, men's copulatory behaviors, men's short-term mate selection, and men's sexual arousal and sexual fantasies, so understanding its role will be challenging but necessary if we are to achieve a comprehensive understanding of human sexuality.

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CHAPTER 16

Human Sexuality and Inbreeding Avoidance

DEBRA LIEBERMAN and JAN ANTFOLK

> It takes, in short, . . . a mind debauched by learning to carry the process of making the natural seem strange, so far as to ask for the *why* of any instinctive human act. To the metaphysician alone can such questions occur as: Why do we smile, when pleased, and not scowl? Why are we unable to talk to a crowd as we talk to a single friend? Why does a particular maiden turn our wits so upside-down? The common man can only say, "*Of course* we smile, *of course* our heart palpitates at the sight of the crowd, *of course* we love the maiden, that beautiful soul clad in that perfect form, so palpably and flagrantly made from all eternity to be loved!"
>
> —William James, *Principles of Psychology*, 1891

> A full causal account of a set of phenomena should explain what is absent, and therefore not observed.
>
> —John Tooby, 1989, p. 14

PSYCHOLOGISTS INTERESTED IN sexual attraction and mate choice, have focused, to a large extent, on the features we find attractive in a mate and the circumstances that promote lust, attachment, and deep engagement. But what about the other side of the coin? What traits do we avoid when selecting a mate? Not as much research has been conducted in this area. One reason could be that we suffer from instinct blindness (see James, 1891). So good are the mechanisms that steer us clear of certain individuals sexually that we rarely recognize the absence of close genetic relatives, the very young, and the very old from discussions regarding mate selection. As an illustration of how family members are often overlooked in the mating literature, consider the three factors social psychologists suggest dictate who one will choose as a sexual partner: familiarity, similarity, and proximity (e.g., Berscheid & Walster, 1978). But who best fits this description? Family members! They are familiar—you have known them your entire life. They are similar—you share the same religion, the same culture, and, in the case they are your blood relatives, a strong physical resemblance. Last, they are close by and easily accessible—perhaps even under the same roof and down the hall. Nevertheless, nuclear family members are, typically, the last group of individuals considered as appropriate sexual partners.

Why is this? Intuitively, the answer to this question is that the thought of having sex with close kin is disgusting and repugnant. As James (1891) might say, *of course* we aren't attracted to close genetic relatives! But *why* do most people across diverse cultures feel this way rather than perceiving sexual behavior with a close family member as exciting and erotic? One answer is that humans and many other species evolved robust inbreeding avoidance systems that function to identify close genetic relatives and then disqualify them, depending on circumstance, from the list of potential mates. Because relatives typically do not appear on the sexual radar, when researchers think about sexual attraction, kin are commonly not even mentioned.

In this chapter, we address why such powerful inbreeding avoidance mechanisms evolved in humans as well as in other species. We provide a description of what an inbreeding avoidance system might look like in terms of information-processing structure and discuss recent research aimed at uncovering the systems that perform this function. To start, we begin with the critical background condition, sexual reproduction, which created the selection pressures favoring inbreeding avoidance.

SEXUAL REPRODUCTION: LAYING THE GROUNDWORK FOR INBREEDING AVOIDANCE

There have been a number of profound theoretical questions evolutionary biologists have tackled: How did life evolve? How did eukaryotes evolve from prokaryotes? Why did multicellularity evolve? How can altruism evolve?

One question, which eluded researchers until recently, is why did sexual reproduction evolve? As a system of replication, sex seems strange. Specifically, there are a number of biological costs associated with sexual reproduction that could be avoided if organisms reproduced asexually (Maynard Smith, 1978). First, only half of an organism's genes get passed on with sex. Contrast this with asexual reproduction, in which a genetic clone is produced each generation. Second, for sexual reproduction to take place, specialized internal mechanisms and organs are required, all of which take up energetically costly tissue. Third, there are costs in terms of the time and energy required to search for a potential mate, say nothing of the strategic systems (e.g., psychological, chemical, or structural) required to convince another individual to engage in reproductive activities. As became evident during early forays into a theoretical account for why sex evolved (e.g., see Ridley, 1993), any explanation for the evolution of sexual reproduction required an account for how the benefits of sex outweigh these costs of meiosis, recombination, and mating, respectively.

As Ridley (1993) discusses in *The Red Queen*, there were many candidate explanations for why sex evolved, including to aid in the evolution of the species (e.g., Crow & Kimura, 1965), to repair or edit the genome (e.g., Bernstein, Byerly, Hopf, & Michod, 1985; Muller, 1964), and to generate variability among offspring to increase fitness upon dispersal to novel environments or when remaining in saturated environments (e.g., Bell, 1982; Williams, 1975). However, these early candidate explanations for why sex evolved failed on theoretical grounds and/or on the ability to explain the ecological distribution of sexual versus asexual species.

In the 1980s a number of researchers provided an answer to the question why sex (Bremermann, 1980; Hamilton, 1980; Tooby, 1982; and, more recently, Morran, Schmidt, Gelarden, Parrish, & Lively, 2011). Sex thwarts the transmission of pathogens from parent to offspring and further interferes with pathogen adaptation, and hence replication (Tooby, 1982). Long-lived multicellular organisms live in a sea of pathogens—on the skin, in the body, in food, and in the air. For an idea of how prevalent potential pathogens are, it has been estimated that there are approximately 10^6 bacteria in one mL of ocean water (Whitman, Coleman, & Wiebe, 1998).

Pathogens can exert intense selection pressures on hosts with comparatively longer rates of reproduction. The greater the difference in the rate of replication between host and pathogen, the more deleterious the effect of pathogens can be. In long-lived multicellular species, like humans, this difference can be quite large allowing for fast adaptation of the pathogen to the host. "Micro-organisms can go through as many generations in a week as humanity has gone through since the Neolithic revolution" (Tooby, 1989, pp. 108–109).

Not surprisingly, when they have a constant background against which to evolve, pathogens can wreak havoc on their hosts. Consider a human that reproduced asexually: A mass of cells fissions from the body and develops into a clone. Pathogens that got transmitted to the clonal offspring would have another entire generation to become even better adapted to its internal biochemical environment—evolving better strategies for obtaining host resources and evading destruction by the immune system. Each generation, pathogens would become more deleterious to that clonal lineage. If, instead of cloning, one recombined genomes with another organism *likely to possess different alleles*, this would create a novel internal biochemistry and place pathogens back at square one, having to re-solve the problems of resource acquisition and immune evasion. Pathogens' old keys to locks present in the parent would not work as well (if at all) to unlock the new locks present in the offspring. In general, then, sexual reproduction interferes with the process of pathogen adaptation.

SELECTION PRESSURES LEADING TO THE EVOLUTION OF INBREEDING AVOIDANCE SYSTEMS

With sexual reproduction came selection pressures regarding the choice of suitable mates. Recombining genomes with an individual who does not possess the same genetic "parts" (e.g., an individual of another species) would render offspring unviable (Tooby & Cosmides, 1990). On the other hand, recombining genomes with someone genetically identical defeats the purpose of sex. On the continuum of genetic similarity among humans, it would have been critical to avoid individuals sharing similar alleles, especially those governing immune defense as they govern the battlefront between pathogens and host. One class of individuals with an increased probability of sharing similar genes is kin—individuals who share genes by virtue of common descent. The closer the genetic relationship to another person is, the greater the probability of sharing similar alleles. Thus, evolution is expected to have led to systems that reduced the probability of selecting a close genetic relative as a sexual partner.

In addition to pathogens, a second selection pressure leading to the evolution of inbreeding avoidance mechanisms was the presence of deleterious recessive mutations. To understand why recessive mutations played an important role in the evolution of inbreeding avoidance mechanisms, it is first necessary to understand how the human genome is organized (see Lewin, 1999, for a review).

Humans are a diploid species, which means that they possess two parallel, homologous sets of chromosomes. One set is inherited from the mother, and the other is inherited from the father. The gene at each location (locus) along a given chromosome can be matched up to a corresponding or homologous gene on the chromosome inherited from the other parent. As a result, each individual possesses two copies of each gene (with the exception of genes located on the sex chromosomes, and extranuclear genes).

Functional genes at a given locus typically provide the sequence information required to build one of the tens of thousands of different proteins necessary for the structure, development, health, and activity of the organism. The two corresponding genes at the same locus can be identical in their DNA sequence, or they can have different forms. These alternative forms of the same gene are called alleles. When the alleles inherited from the maternal and paternal lineage are the same, they are called homozygous, and when dissimilar, they are called heterozygous. When two different alleles are present, it is often the case that the product of one allele masks the phenotypic expression of the other. The allele whose phenotype is expressed is said to be dominant, whereas the allele whose phenotypic expression is masked is considered recessive.

Various biological processes and entropic forces continually interject random mutations into the genome, usually transforming functional alleles into damaged or deleterious alleles. Errors can be made during DNA replication, and background radiation, heat, chemical agents, and other environmental factors can also cause changes. Mutations come in a variety of types (point mutations, frame shifts, deletions, etc., see Lewin, 1999 for a taxonomy of mutations that occur in the human genome). These mutations can disrupt a gene-product's ability to function properly. For example, a DNA replication error may lead to a mutation in an allele coding for an enzyme necessary for the neutralization of commonly encountered dietary toxin. Depending on the exact base changes caused by the mutation, the enzyme may, for example, (a) not be affected at all and, therefore, function properly, (b) have a slight change in the charge or shape of the binding site leading to a reduction in function, or (c) not function at all. If the enzyme is not produced, or no longer functions adequately, this can lead to harmful or even lethal consequences for the bearer. These negative mutations accumulate in the population until the rate at which they enter matches the rate at which they are expressed and selected out. The point at which entry matches exit is called equilibrium. Lethal dominant genes are always expressed, and so they are selected out rapidly after entering the population, staying at very low frequencies at equilibrium. As such, they play no special role in selecting against inbreeding.

In contrast, when a detrimental mutation is recessive, it has a much less harmful effect whenever it is matched with its undamaged dominant counterpart. Such a heterozygous individual expresses a normal phenotype, and her or his fitness is uninfluenced by the presence of the unexpressed injurious mutation. For this reason, deleterious recessives can accumulate until they reach relatively high frequencies in the population. The same negative trait that, if it were dominant, would stabilize at a frequency of roughly 1 in 1 million would approach a frequency of 1 in 1,000 if it were recessive—that is, 1,000 times more frequent. Indeed, it is only when the same recessive damaged allele is supplied from both the mother and the father, creating a homozygous individual, that the damaging trait is expressed, impeding the survival and reproduction of that individual.

Selection only acts against deleterious recessives when they are expressed and, according to Bittles and Neel (1994) "all of us are thought to carry in the heterozygous condition 'several' rare recessive genes which, if rendered homozygous, would result in a significant medical handicap, ranging from severe defects of vision and hearing to disorders incompatible with survival beyond childhood" (p. 17). The estimated number of rare lethal genes in a genome is termed *lethal equivalents* (Cavalli-Sforza & Bodmer, 1971; Crow & Kimura, 1970). Data from a number of studies suggest that each of us possess, on average, somewhere between two (Bittles & Neel, 1994; Carter, 1967; May, 1979) and six (Kumar, Pai, & Swaminathan, 1967) lethal equivalents: alleles that, if homozygous, would cause death before an individual reached reproductive age (Burnham, 1975; Morton, Crow, & Muller, 1956). We are not dead many times over because at the great majority of these loci, we are heterozygous, and the intact gene masks the damaged gene.

What influences the probability that the same deleterious recessive will be supplied from both the mother and the father? If the two parents are unrelated, then these recessives come together by chance. For example, if you have a lethal (or otherwise detrimental) recessive allele at one locus (Aa) and the recessive allele (a) exists in the population at a frequency of 1 in 1000 and you have a child with a random nonrelative, this child has a 1 in 4000 chance of being homozygous (aa) for this particular harmful trait. This is because it is a $1/1000 \times 0.25$ chance the child has two copies of the recessive allele (it is a 0.75 chance the child inherited at least one dominant allele). In contrast, mating with close kin increases the likelihood that two rare recessive alleles will meet each other at any given loci (Cavalli-Sforza & Bodmer, 1971; Charlesworth & Charlesworth, 1987; Tooby, 1977). Being genetically related means that the two individuals share common ancestors, and so the same deleterious recessives that show up in one relative are also likely to show up in others descended from the same common ancestor. What is a 1 in 4,000 risk in mating with a nonrelative becomes, when mating with a brother or sister, 1 in 8. If you have a hidden recessive allele at one locus, assuming that only one of your parents had this recessive allele (as described earlier, given no prior inbreeding in your family, there is only a 1 in 1,000 chance that both your parents had the allele), the chance is 0.50 that your sibling also has a nonexpressed copy of that allele. The chance for your child to be a homozygote expressing this detrimental recessive allele is then 1 in 8 (0.50×0.25). This means, that in this example, the risk of expressing a lethal recessive allele increases no less than 500 times when comparing a sibling union to a union between nonrelatives.

Therefore, if two close genetic relatives mate with one another, there is a greatly increased chance that the resulting offspring will be homozygous for many deleterious recessives, leading to decreased chance of survival and reproduction. The more closely related the parents, the greater the likelihood that the offspring will suffer a decrease in health and viability, and the selection pressures become very intense whenever the two parents are siblings, or parent and child. For this reason, deleterious recessive mutations posed a strong selection pressure against close-kin matings.

In summary, there were at least two recurring selection pressures that would have strongly selected against inbreeding among our hominid ancestors: (1) an increased susceptibility to disease-causing organisms, and (2) the generation of defects through making deleterious recessive genes homozygous. The cost in terms of damage to the offspring resulting from matings between close genetic relatives is called inbreeding depression (Wright, 1921). These two selection pressures would have selected for design features that reliably and cost-effectively caused a reduction in the probability of mating and conceiving with close, fertile relatives. Those individuals who carried such design features would have produced offspring more likely to survive, reproduce, and pass on those design features than individuals who did not.

EVIDENCE OF INBREEDING DEPRESSION

Evidence from nonhuman species and humans alike illustrates that inbreeding leads to an increased risk of infection and mortality (nonhuman evidence: Acevedo-Whitehouse, Gulland, Greig, & Amos, 2003; Coltman, Pilkington, & Pemberton, 1999; human evidence: Adams & Neel, 1967; Bittles & Neel, 1994; Carter, 1967; Schull & Neel, 1965; Seemanova, 1971). Inbreeding leads to an increased probability of the expression of recessive deleterious genes leading to a greater incidence of major congenital malformations and postnatal mortality (Bittles, Mason, Green, & Rao, 1991). Many studies in humans have focused on offspring of first cousins since this form of marriage is quite common in many cultures around the world (Bittles, 2005). Though the effects of inbreeding depression in offspring of first cousins ($r = 0.125$) are expected to be much less severe than in offspring of individuals related at an $r = 0.5$ (parents, offspring, and siblings) there have, nevertheless, been reports of various deformities and deficiencies. Across a variety of populations, compared to unrelated parents, parents that were first cousins produced offspring with *twice* the population baseline probability of congenital malformation and/or genetic diseases (Norway: Stoltenberg, Magnus, Lie, Daltveit, & Irgens, 1997; Turkey: Demirel, Katlanoglu, Acar, Bodur, & Padak, 1997; Israel: Jaber, Merlob, Bu, Rotter, & Shohat, 1992; Pakistan: Hussain, 1998). In addition to increased probabilities of mortality and congenital malformations and diseases, children of first cousins have been shown to have cognitive impairments (Bashi, 1977, Cohen, Block, Flum, Kadar, & Goldschmist, 1963; Schull & Neel, 1965).

Studies focusing on the effects of inbreeding between siblings have found substantially increased risks when compared with first-cousin matings. Compared to inbreeding depression rates of 2%–6% in offspring of first cousins (compared to population baseline), it has been estimated that sibling matings lead to an inbreeding depression of 45% (Aoki & Feldman 1997; Ralls, Ballou, & Templeton, 1988; Seemanova, 1971). Moreover, since spontaneous abortion—a likely consequence of expressed detrimental alleles or decreased immunological functioning in the embryo/fetus—may go undetected, the effects of consanguineous marriages may be significantly underestimated (Bittles et al., 1991). There have been a handful of studies documenting the fitness consequences of offspring born of two siblings. In all studies, there was an increased risk of mortality, mental deficiencies, congenital malformations, and disease (Adams & Neel, 1967; Carter, 1967; Schull & Neel, 1965; Seemanova, 1971).

Perhaps one of the best studies on the effects of inbreeding depression was by Seemanova (1971) on a Czech population of women who had children fathered by both a close genetic relative (i.e., father or brother) and an unrelated male. The children of nonincestuous matings provided a perfect control group to investigate the deleterious effects of inbreeding between close genetic relatives. Considering only those females who were of normal intelligence ($N = 44$), 92 offspring were produced with an unrelated father and 50 offspring were produced with the female's father or brother. Of the nonincestuous children, 5.2% died within the first 5 months and 3.4% of the surviving children had impairments or deformities. There were no mental deficiencies found in these children. In comparison, of the incestuous children, 12% died with major deformities, and 45.4% of the surviving offspring were either severely mentally retarded, had major congenital deformities or impairments, or both. So, compared to nonincestuous offspring, the incestuous offspring were roughly 13 times more likely to die or have severe birth defects, an increase similar to that found in a study by Adams & Neel (1967) who looked at the consequences of brother/sister and father/daughter matings. In more recent studies, it has been found that offspring of closely related parents are smaller and weaker (Fareed & Afzal, 2014), suffer reduced fertility (Beer, Quebbeman, Ayers, & Haines, 1981; Schmiady & Neitzel, 2002; Thomas, Harger, Wagener, Rabin, & Gill, 1985), have cognitive impairments (Roberts, 1967; Rudan et al., 2002), and have autosomal recessive diseases, leading to hearing impairments (Zakzouk, 2002).

In summary, studies in humans and comparable nonhuman species have illustrated the deleterious consequences associated with mating with a close genetic relative. These recurring decrements in fitness would have selected for systems that enabled organisms to avoid mating with close genetic relatives. However, the costs of inbreeding are not identical for everyone, nor for the same person across time. Before describing what a system for avoiding inbreeding might look like in terms of information processing, we discuss additional design criteria regarding opportunity costs.

OPPORTUNITY COSTS: IS INBREEDING ALWAYS A BAD STRATEGY?

For long-lived species, such as humans, who interact with close genetic relatives throughout periods of sexual maturity, the recurring deleterious consequences of inbreeding as outlined earlier would have led to the evolution of psychological mechanisms for a sexual preference for nonkin. The strength of this preference, however, should depend on the different costs and benefits associated with the choice of one mate over another. To the degree that an individual forgoes an opportunity to mate with a nonrelative by engaging in inbreeding, inbreeding incurs an opportunity cost (e.g., Dawkins, 1983; Haig, 1999). Instead of having a healthy outbred offspring, inbreeding produces an offspring with a greater probability of inbreeding depression, δ. The decreased fitness in inbred offspring can be defined as x ($x = 1 - \delta$). But δ is likely larger than zero but less than one, meaning that some, but not all inbred offspring fail to survive and propagate genetic material to future generations. Thus, depending on circumstance (e.g., pathogen load of the environment; available mating opportunities) inbreeding is a better option than not reproducing at all, but inbreeding is never as good as optimal outbreeding (Antfolk, 2014a).

In addition to inbreeding depression, one has to take into account opportunity costs. Because the number of offspring an individual can successfully produce and raise is limited, producing an inbred offspring and raising this offspring to nutritional independence will affect the possibility of producing and raising outbred offspring. Adding this opportunity cost (c) to the equation, inbreeding becomes costly when the opportunity costs outweigh the relatively decreased reproductive benefit of an inbred child, or ($x - c < 0$).

Opportunity costs are not equally distributed across groups, situations, and individuals. Opportunity costs are generally higher for females than for males. Because males invest less metabolic energy than females in the production of gametes, a male's reproductive success depends more on his ability to fertilize an egg than on his ability to produce gametes. Conversely, a female's reproductive success depends more on her ability to produce eggs than on her ability to get them fertilized (Bateman, 1948). This notion led Robert Trivers (1972) to establish a theory on how sex differences in the time and energy invested in reproduction leads to different reproductive strategies. Trivers defined parental investment (PI) as any investment an individual directs toward a particular offspring that precludes investment in other offspring. Investment thus includes everything from bestowing sex cells or sacrificing metabolic energy during copulation to risking one's life while guarding offspring. The critical factor is the *minimum level* of parental investment required to successfully produce an offspring capable of surviving and the minimum for men and women differs drastically. In humans, a male's minimum PI is the time and energy required for copulation, whereas a female's minimum PI is gestation (9–10 months) and would, in ancestral conditions, almost certainly include lactation (2–3 years). During these respective time periods, males and females cannot engage in alternative or additional sexual activities that would enhance their reproductive success. Males can inseminate one female at a time, and females don't ovulate during pregnancy and throughout periods of enduring on-demand breastfeeding. Given the much larger minimum level of investment by females as compared to males, females are expected to be more selective in their choice of a sexual partner and evidence suggests this is indeed the case (Clark & Hatfield, 1989).

Returning to inbreeding, because investing in one child decreases the possibility to invest in another child, and more so for females than males, the opportunity costs of inbreeding are higher for females than males ($c_F > c_M$). Although males suffer less direct costs from inbreeding than do females, the cost to a female relative needs to be accounted for when estimating the consequences inbreeding has to a male. This is because an individual's reproductive success is not limited to the number or the biological fitness of his or her *own* offspring. Rather, reproductive fitness is measured by the total number of allele copies that an individual transmits to subsequent generations, either through direct descendants or indirectly, through offspring of relatives. These relatives naturally include the relative with whom inbreeding takes place. Thus, the fitness consequences of inbreeding to the male can be expressed as $(x - c_M) + r_{MF}(x - c_F)$, where r_{MF} is the coefficient of relatedness between the male and the female. From the point of view of the female, the fitness consequences can be modeled as $(x - c_F) + r_{FM}(x - c_M)$. In the case of brother-sister incest, r would be 0.5, meaning that half of the cost to the female is added to the direct cost to the male in the first example. In the second example, half of the cost to the male is added to the direct cost to the female (Antfolk, 2014a; Dawkins, 1983; Haig, 1999). The different levels of costs associated with inbreeding for men and women should be observable in how objectionable inbreeding is thought to be. Indeed, several studies show that human females react more strongly than males to the thought of having sex with close kin (Antfolk, Karlsson, Bäckström, & Santtila, 2012; Antfolk, Lieberman, & Santtila, 2012; Antfolk, Lindqvist, Albrecht, & Santtila, 2014; Lieberman, Tooby, & Cosmides, 2003).

Furthermore, the effect gender has on preferences to tolerate or object to inbreeding should be moderated by the probability of conception. For example, compared to the days in the menstrual cycle when fertility is low, women in the fertile period of the menstrual cycle have more to lose from sex with a relative. Indeed, women who are fertile have a stronger inbreeding aversion (Antfolk, Lieberman, Albrecht, & Santtila, 2014) and are less likely to associate with fathers, a behavior that can decrease the likelihood of inbreeding (Lieberman, Pillsworth, & Haselton, 2011).

Another variable that affects the opportunity costs of inbreeding is access to other mates. The capacity to acquire sexual access to females is unevenly distributed among males, with some males experiencing much greater reproductive success than others. Indeed, Bateman's early studies on sexual selection in fruit flies demonstrated that, whereas most females were successful in producing offspring, only 20% of males sired offspring for the next generation. The greater variation in male reproductive success should have led to adaptations that sensed one's potential success obtaining a high value mate (or a mate at all) and then activated the appropriate mating strategy. For males with high mate value and a pool of potential mates, inbreeding might not be the first strategy employed. But for low status males who detected they were unsuccessful on the mating market, widening the pool of potential mates to include sisters might be a strategy considered. Should a male with no other options engage in inbreeding, he would suffer only the inclusive costs incurred by his female relative, with whom he reproduces, while possibly gaining the benefit, albeit potentially low, of an inbred offspring. Therefore, one might expect males with few mating opportunities and males with no mating partner to be more inclined (or less resistant) to engage in inbreeding than other men. Indeed, a recent study found that individuals who are single (versus married), who have never had sex (versus have had sex), or have a low (versus high) mate value are more inclined to engage in inbreeding (Antfolk, Lieberman, et al., 2014). Moreover, this effect is more pronounced in men compared to women.

Taken together, humans modulate their inclination to engage in inbreeding depending on the perceived opportunity costs associated with having sex with a relative. For this to be possible, the inbreeding avoidance system must take as input variables such as fertility status, mate value, and opportunity costs.

INFORMATION PROCESSING ARCHITECTURE OF INBREEDING AVOIDANCE

To solve the problem of avoiding close genetic relatives as sexual partners, a system would need first to estimate the probability that another individual is a close genetic relative, and then, second, to inhibit sexual contact with that person as a function of this probability. But how do we detect kin? There are a number of constraints that confine the set of cues selection might have favored to engineer kin detection systems. For instance, barring recent medical technology, we are not able to directly compare genomes to assess kinship. However, other possible kinship cues exist. One possibility includes the use of more evolutionarily novel cultural information such as linguistic kin terms. But these are unlikely to be the primary cues used to detect kin because kin terms can blur genetic boundaries (e.g., *aunt* in our culture refers both to a parent's sister, a blood relative, and a parent's brother's wife, a nonblood relative). Furthermore, it is unlikely that phylogenetically prior kin detection mechanisms that functioned in the absence of linguistic information were overwritten by more variable and potentially less reliable cultural information.

Rather, it is likely we rely on ecologically valid cues that correlated with genetic relatedness in human ancestral environments. The stable patterns of genetic similarity created by events of sexual reproduction led to "categories" of individuals: mothers, fathers, offspring, siblings, aunts, uncles, nieces, nephews, and so forth. A system that identified recurring attributes unique to each category of "genetically similar other" and reduced the probability of selecting these individuals as sexual partners in a manner that reflected the costs of mating would have conferred a strong selective advantage. Importantly, the cues mediating kin detection might differ depending on the category of kin in question. To the extent that different cues signaled an individual was a specific type of close genetic relative (e.g., mother, father, offspring, or sibling), different detection mechanisms are likely to exist. Additionally, males and females might use distinct cues to identify the same type of kin. For instance, because men can never be fully certain of their relatedness to potential offspring, the cues signaling that an infant is indeed one's own are likely to differ for men and women. That is, ancestrally, a female was always certain (before the miracles of modern medicine) that the child coming out of her was indeed her own. The cue "birth" would have accurately identified offspring. But men don't give birth. Instead, men need to rely on information regarding the probability that the child of a particular female is indeed their own. If a man never had sex with a woman, the probability is zero. If a man did have sex with a woman, then issues such as timing of intercourse relative to birth and fidelity arise. To date, we do not know how men compute paternity and so this is a question ripe for research.

Evolutionary biologists have identified a range of kinship cues by investigating inbreeding avoidance and altruism in nonhuman species (for review, see Hepper 1991). For instance, early association, a spatial cue that identifies likely siblings in species in which offspring require extended maternal care, predicts patterns of social preferences and mate choice in species such as voles, mice, macaques, and chimps. In some species, chemical cues guide kin detection and associated kin-directed behaviors. Studies on house mice, for example, show that mate preferences are guided by assessments of similarity at loci controlling the major histocompatibility complex (MHC). That is, males and females prefer to mate with individuals who are MHC dissimilar from them, a preference thought to protect against the negative effects of pathogens. For MHC disassortative mating to occur, however, individuals require a referent, either themselves or a close relative, to determine what counts as MHC dissimilar. A series of cross-fostering experiments in which individuals were raised by MHC-dissimilar parents showed that individuals preferred to mate with others who were dissimilar from their foster parent's MHC composition. Thus MHC-guided mate preferences appear to use parental phenotypes as referents of one's own genetic composition (e.g., Penn & Potts, 1999). Of course, one should be careful in translating the MHC/HLA observations from nonhuman animal studies to humans. Few studies have used genotyping for humans so it is unclear whether MHC serves as a kinship cue for humans or functions more broadly to promote genetic diversity across kin and nonkin alike.

In the human evolutionary literature, the majority of research has focused on the detection of siblings and the associated development of sexual aversions and sibling-directed altruism. Next, we briefly discuss some recent findings from this literature.

SIBLING DETECTION: EXPOSURE TO MOTHER-INFANT ASSOCIATION AND CORESIDENCE DURATION

The ancestral social environment of humans was such that a likely reliable cue to siblingship would have been seeing one's own mother caring for (e.g., breastfeeding) a newborn. Indeed, the intense mother-child association that typically occurs surrounding the natal period and continues throughout the first few years of life would have served as a stable anchor point for others to infer relatedness. Thus, if an individual observed an infant receiving care from the individual's own mother (at least the female categorized as one's own mother), then it was highly probable that that infant was the individual's sibling. Further, exposure to this cue would have signaled genetic relatedness regardless of coresidence (or association) duration. That is, regardless of whether one was 5, 10, or 15 years old, maternal-infant directed care would have cued probable genetic relatedness.

However, as potent a cue as mother-infant association might be, it is available only to older siblings already present in the social environment; the arrow of time prevents a younger sibling from having seen his or her older sibling born and cared for as an infant. For younger siblings, then, what cue or cues might evolution have used to identify probable older siblings?

One solution is to track the flow of parental effort. Any child regularly receiving care from one's own mother and father had a higher probability of being kin than children receiving care from other individuals. Moreover, the longer the care, the more likely the individual would have been a sibling. This cue, operationalized as childhood co-residence duration, was first proposed by Edward Westermarck, a Finnish social scientist who noted that children reared in close physical proximity during childhood tend to develop a sexual aversion toward one another later in adulthood (Westermarck, 1889/1891; see also Antfolk, 2014b). This idea, known as the *Westermarck hypothesis*, has received support from various anthropological and psychological investigations (see review in Lieberman et al., 2003). Perhaps most notable are the cases of the Israeli kibbutzim and Taiwanese minor marriages, two natural experiments inadvertently created by cultural institutions in which unrelated children were reared in close physical proximity throughout childhood. As the Westermarck hypothesis predicts, children reared together throughout childhood rarely marry one another (Israeli kibbutzim: Shepher, 1983), and if forced to marry suffer decreased rates of fertility and increased rates of divorce and extramarital affairs (Taiwanese minor marriages: Wolf, 1995). Together, these studies point to early coresidence as one cue our mind uses to assess relatedness and to dampen sexual desires.

However, they also raise many questions. For example, does coresidence duration predict sexual aversions differently for the younger and older sibling in a sib pair? As suggested earlier, older siblings might rely on a different cue to identify probable younger siblings, one that operates independent of coresidence duration. Also, do the same kinship cues that regulate inbreeding avoidance also regulate kin-directed altruism, the other suite of behaviors relying on assessments of relatedness?

PSYCHOLOGICAL INVESTIGATION OF KINSHIP CUES

It is not ethical to subject humans to the life-altering experiments used by evolutionary biologists to study kin recognition in nonhuman animals. For this reason, scientists have either had to look for natural experiments, such as those mentioned earlier, or take advantage of the natural variation that exists in families composed of actual genetic relatives. To investigate whether a proposed cue serves as a signal of relatedness, it is possible to match individual variation in exposure to the specific cue (e.g., coresidence duration, maternal-infant association) to behaviors and reactions relating to sexual behaviors with family members. Converging lines of evidence that we use a particular cue to categorize individuals according to genetic relatedness can be found through investigations of altruism. If the same kin detection mechanism serves to regulate both sexual avoidance and altruism, then a cue to kinship should show parallel effects across these two distinct motivational systems.

Using surveys to collect information, Lieberman, Tooby, and Cosmides (2007) found that individuals not exposed to their mother caring for their sibling as a newborn (as it is typically for the younger sibling in a sib pair), their duration of coresidence with an opposite sex sibling predicted aversions to sibling incest, as measured by disgust at imagining sex with one's own sibling and moral sentiments relating to third-party sibling incest. By contrast, for individuals exposed to their mother caring for their sibling as an infant (the older siblings in a sib pair), coresidence duration with an opposite sex sibling *did not* predict aversion to incest. When measures of altruistic attitudes and behavior were analyzed, the same pattern emerged. That is, coresidence duration with a sibling predicted altruism more strongly for individuals without access to the more potent cue of seeing their mother caring for their sibling as a newborn. These data provide compelling evidence that the mind uses two different cues for identifying older versus younger siblings and for regulating sexual aversions and altruistic motivations.

Upon inspecting the levels of aversions and altruistic inclinations reported, Lieberman et al. (2007) found that older siblings exposed to the cue of seeing their mother care for a younger sibling as a newborn reported intense levels of disgust toward sexual acts with that sibling as well as increased levels of altruism across all durations of coresidence. That is, regardless of whether a subject resided for 15 or only 3 years with their younger sibling, the level of sexual aversion reported in response to sibling incest and altruistic inclinations were close to the maximum. In contrast, for subjects for whom this cue was not available and who relied on coresidence duration as a cue to siblingship (the younger siblings in the dataset), disgust at sexual acts with their older sibling and sibling-directed altruism were low for shorter periods of coresidence and gradually increased with extended periods of coresidence. In fact, data suggest it takes approximately 14–15 years of coresidence for younger siblings to reach the same level of sexual aversions and altruistic effort reported by older siblings who were exposed to the cue of seeing their mother care for their sibling as a newborn.

Taken together, these data provide a first glimpse into the cognitive procedures governing kin detection and kin-directed behavior in humans. The findings indicate that the mind uses at least two cues to detect siblings and mediate inbreeding avoidance and kin-directed altruism: exposure to maternal investments in a newborn (used by older siblings to detect younger siblings) and duration of coresidence throughout periods of shared parental investment (typically used by younger siblings to detect older siblings). Because these same cues were found to regulate aversions and altruism in the same way, it suggests the existence of a single set of kinship-estimating procedures that feed motivational systems guiding mate choice and, separately, altruistic effort. Importantly, additional cues might also play a role in sibling detection. For example, facial resemblance and olfactory cues such as those derived from the major histocompatibility complex (MHC) predict preferences in mate choice (e.g., DeBruine, 2005; Wedekind & Füri, 1997). No matter the cue, if the model of kin detection and kin-directed behaviors outlined earlier is correct, a particular cue to kinship should regulate both sexual aversions and altruism.

Many questions remain unanswered. For example, if coresidence duration mediates sibling detection, is a specific period of coresidence (e.g., ages < 5) required, as some have suggested (Shepher, 1983; Wolf, 1995)? Or does each year of coresidence contribute in equal increments to a computed kinship estimate as research by Lieberman et al. (2007) suggests? Furthermore, what cues might distinguish a full biological sibling from maternal and paternal half siblings? Are the cues used to identify siblings the same as those used to identify parents and offspring? In the coming decades, research in evolutionary psychology can start to answer these and other questions.

THIRD-PARTY INBREEDING: ADAPTATIONS AND BY-PRODUCTS

Interestingly, humans also display an aversion toward others engaging in incest (Antfolk, Karlsson, et al., 2012; Antfolk, Lieberman, et al., 2012; Antfolk, Lindgvist, et al., 2014; Fessler & Navarrete, 2004; Lieberman et al., 2003; Lieberman et al., 2007; Royzman, Leeman, & Sabini, 2008). This reaction to third-party behavior has been explained as an adaptation, and also, as a by-product. Reactions to third-party inbreeding might merely reflect the activation of one's own inbreeding aversions. That is, when asked to think about an unknown brother-sister pair having sex, the strength of one's opposition could be a function of how opposed one would be to having sex with one's own sibling. There is evidence that this is indeed one source of third-party attitudes as the cues that predict disgust toward engaging in sex with one's own sibling also predict opposition toward third-party sibling inbreeding (Lieberman et al., 2007; Lieberman & Lobel, 2012). Thus, reactions to third party incest might be a by-product of the activation of personal inbreeding avoidance mechanisms.

But reactions to third-party inbreeding could also be an adaptation. The actions and decisions of close genetic relatives can greatly impact one's inclusive fitness. This holds for the decisions close genetic relatives make with respect to their mate choice. Not only are instances of inbreeding potentially costly to the individuals engaging in the act (see earlier discussion), they also impose large fitness costs on their close genetic relatives. Indeed, for each individual within the family, there is an expected inclusive fitness matrix of the costs and benefits associated with the different incestuous unions within the family. Consider an example that illustrates how an instance of inbreeding between a brother and sister not only bears fitness costs to the individuals engaged in the sexual liaison, but also to their sister. Although the sister of the sibling pair does not herself engage in inbreeding, she suffers inclusive-fitness costs by losing outbred nieces/nephews via her brother and via her sister. Extending the mathematical model discussed earlier, we can describe the fitness consequences to a related bystander (a common sister S). From the perspective of S, the fitness costs of inbreeding between a related male and female can be modeled as $r_{SM}(x - c_M) + r_{SF}(x - c_F)$, where the costs to the sister and the costs to the brother are first weighted by the degree of relatedness of the sister to the male and the degrees of relatedness of the sister to the female respectively, and then summed.

To the extent that close genetic relatives *could* have pursued one another as a sexual partner in ancestral environments (an almost certain possibility, considering that humans lived in small groups), design features that motivated the interference of sexual unions between one's close relatives in a manner consistent with the costs and benefits associated with each particular incestuous dyad would have become more frequent in the population compared to design features that did not care whether family members mated with one another. That is, in addition to specialized systems for detecting close genetic relatives for the purpose of guiding one's own mating decisions, specialized systems are hypothesized to exist that assess the costs and benefits of other incestuous dyads within the family and motivate the active interference between those dyads imposing elevated costs to one's inclusive fitness (Lieberman, Tooby, & Cosmides, 2001). Intensity of interference should depend on a number of factors including mutation load, pathogen load, and available opportunities to secure unrelated mates (Tooby, 1977).

There is empirical evidence of a third-party aversion to related individuals engaging in incest mirroring the inclusive-fitness costs this behavior potentially has. Antfolk, Lieberman, and Santtila (2012) showed that regardless of a participant being described as involved in incest or not, incest between individuals related to a participant predicted the strength of aversion each incestuous situations elicited in the participant. Lieberman et al. (2001; unpublished data) showed that mate-child sexual behavior was the most objectionable followed, in order, by father-sister sex, son-daughter sex, mother-brother sex, and brother-sister sex. Certainly more work is needed in this area, but thus far, data suggest that humans possess cognitive adaptations for regulating the sexual behavior of family members. A system that used the computed kinship estimates that function to guide one's own sexual motivations to also assess the costs and benefits of particular unions within the family would be on its way to solving this adaptive problem.

INBREEDING AVOIDANCE AND THE INCEST TABOO

There is one question that has been a topic of interest, particularly to sociologists and anthropologists (see Wolf & Durham, 2005): If there is an innate aversion that develops among close genetic relatives, then why do we need rules proscribing incest? There might be many reasons that norms regarding incest exist. Here are two: First, kinship cues are not always present. Siblings might be separated during childhood and, therefore, not observe one another being cared for by the same mother and father. Likewise, men might lack paternity certainty (e.g., because they question the fidelity of their mate or because they rarely witnessed their mate caring for her child) and, therefore, men will be more likely to find a daughter sexually attractive. These events, though likely rare, would have occurred from time to time leading, in some cases, to inbreeding. As discussed earlier, incest within the family carries costs to the inclusive fitness of other relatives. Thus, third parties might be motivated to prohibit certain sexual unions and this prohibition could manifest as cultural norms.

A second reason that norms proscribing incest might exist relates to the evolution of morality and social norms. DeScioli and Kurzban (2009, 2013) proposed a provocative account explaining why humans evolved adaptations to create and spread moral norms. To succinctly paraphrase, one adaptive problem humans faced was choosing sides when a conflict erupted. Costs are minimized to the extent that everyone chooses the same side to support in a conflict. But how does one decide which side to choose? Norms provide one solution: They solve the coordination problem a priori. If it is agreed upon beforehand that stealing is wrong and warrants punishment, then individuals can cost-effectively identify who they support. (Tooby & Cosmides, 2010, offer a slightly different view on the evolution of morality, one that focuses on the adaptive problems that arise once coalitions can form around a common goal, including the exploitation and extermination of less powerful others.)

But which norms to select? Regardless of whether the selection pressure leading to the evolution of social norms was signaling one's alliance in a particular social conflict or group exploitation, there is the problem of content. DeScioli and Kurzban (2009, 2013) suggest that strategically, it makes sense for an individual to support norms that do not impose on personal preferences. That is, to the extent that a moral norm prohibits behavior that one is not inclined to perform, then there is little cost associated with supporting such a norm. Disgust is an emotion that indicates the fitness value of performing particular behaviors relating to pathogen transmission and mate choice and thus might be a privileged emotion when making decisions about candidate moral norms. To the extent that one is disgusted by ingesting certain foods, physically contacting nonhumans or particular groups of humans, or having sex with particular people, these are the behaviors that, if prohibited, would not be felt as curtailing one's preferred course of action. So, one answer to why there exist norms proscribing incest is that inbreeding is a behavior that few people engage in (e.g., because of the fallibility of kinship cues or because of substance abuse, which could impair aversion systems). Given that the majority of people (or people in power capable of enforcing norms) find incest disgusting, proscribing incest is not felt as limiting personal preferences in terms of mate choice and thus would solve the problem of coordination, either for the purpose of choosing sides during a conflict as proposed by DeScioli and Kurzban (2009, 2013) or targeting groups vulnerable to exploitation as suggested by Tooby and Cosmides (2010). Certainly more research will need to be done to test between these alternate functional explanations.

LOOKING AHEAD

There are many questions still left unanswered. Here we have raised a few of these questions about how humans detect their kin and the cognitive systems that perform the function of inbreeding avoidance. We conclude by emphasizing the need to take seriously the information-processing level of description when describing psychological adaptations. Evolutionary psychology has brought to the study of humans an ultimate level of explanation, that is, *why* certain attributes exist. In addition, researchers within evolutionary psychology have made much progress in documenting *what* phenotypes exist (e.g., behavior, preferences, etc.) and connecting them back to ultimate causal processes. In general, however, researchers in the field tend to overlook the intermediate level connecting why and what: how. Developing a cognitive model, no matter how rudimentary, can help clarify the function in question, identify potential moderators, and help direct programs of research. The information-processing model of kin detection discussed herein was a critical tool for thinking about how cues to kinship out in the real world could impact internal sexual preferences. This model also has helped to think about how kinship is integrated with the other attributes guiding mate choice (e.g., health, age, and status) and generated additional hypotheses about how kinship might be traded off against other attributes. Developing a cognitive model starting from inputs to internal computations to behavior can help identify the scope of one's research and help to overcome any instinct blindness that masks the existence and complexity of our evolved psychology.

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CHAPTER 17

Sexual Coercion

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ALTHOUGH ACTS OF sexual coercion have been reported throughout human history, recently this topic has garnered much public attention. For example, President Obama has expressed great concern and taken important steps to reduce such acts on college campuses and in the military (Calmes, 2014). There has even recently emerged a new area of public health concern labeled technology-based sexual coercion (Thompson & Morrison, 2013).

In this chapter, we discuss evolutionary psychological (EP) perspectives on sexual coercion, defined as acts that involve sexual behaviors whereby one of the individuals does not fully consent to the acts. These typically include some use of physical force, threat, deception, or some other form of coercion. Rape is an extreme form of sexual coercion.

EP perspectives seek to identify ultimate causes of behavior, complementing the focus on proximate causes characteristic of other psychological theorizing. In addressing ultimate causation, evolutionary psychologists have often asked whether the ability to inflict sexual coercion or to avoid it contributed to reproductive success in our species' ancestral history, possibly giving rise to dedicated psychological mechanisms pertaining to coercive sex. Although addressing such questions is standard in EP theorizing, some critics have raised concerns that this might imply that sexual coercion is "natural" in the sense of inevitable or morally neutral, an implication we clearly wish to avoid (i.e., the naturalistic fallacy).

In applying the EP paradigm, we begin by considering clues to motivational differences between men and women that may set the stage for the potential occurrence of sexual coercion. Differences in minimal parental investment (Trivers, 1972) contribute to a greater likelihood that a man will be motivated to have sex with certain women than vice versa and that, for men, sex may be more easily separated from emotions associated with long-term mating (Buss & Schmitt, 1993). Such differences create conflicts that can result in some men using coercion to overcome female reluctance and resistance (Gorelik, Shackelford, & Weekes-Shackelford, 2012). Consistent with the predictions derived from parental investment theory is the finding that across various societies and recorded human history, as well as across virtually all species where sexual coercion occurs, there are large sex differences in the use of sexual coercion. Males are typically the perpetrators and females are victims. If one examines criminal statistics, the sex differences are huge. The U.S. Bureau of Justice Statistics reported in the late 1990s that 99% of those imprisoned for rape were men (Greenfeld, 1997). Moreover, there are sex differences in the type of coercive methods used. For example, Hines and Saudino (2003) found that "unlike men who were sexually coercive, sexually coercive females did not use threats or force to make their partners have sex with them; they insisted on the acts instead [when their partners did not want to have sex]" (p. 214).

Although there are cultural differences in the frequency of sexual coercion, large sex differences are found even in the most egalitarian and low general violence nations. For example, Lottes and Weinberg (1996) reported that among Swedish college students, 41% of women and 22% of men reported being subjected to some form of nonphysical coercion to engage in sex by a member of the opposite sex. The rates for U.S. college students are much higher: 69% and 50%, respectively, as presented in the same research.

Much EP theorizing on sexual coercion has focused on models that implicate condition-dependent psychological mechanisms affecting an individual's propensity to coerce. Environmental experiences, particularly in critical early stages, are said to result in the *calibration* of mechanisms at relatively fixed values, which can lead to lifelong differences in thresholds for evoking sexual coercion. Whereas EP theorizing typically has not stressed direct links between genetic differences and sexual coercion, it has considered the possibility that genetic differences may underlie certain personality and other characteristics (e.g., general aggressive tendencies, responsiveness to socialization and peer influences) that affect the propensity to sexually coerce (e.g., Lalumière, Harris, Quinsey, & Rice, 2005; Waldman & Rhee, 2006; Westerlund, Santtila, Johansson, Jern, & Sandnabba, 2012). Lending support to the potential usefulness of also considering genetic factors is evidence of the ability to genetically breed mice that are either more or less sexually aggressive (Canastar & Maxson, 2003). Human twin studies also support the influence of genetic effects on sexual coercion, although researchers caution that this does not mean that there are genes affecting only sexual coercion (Johansson et al., 2008).

In this chapter, we focus on the male perpetrator's psychology but we also consider aspects of relevant female counteradaptation to the risk of male sexual coercion. In the past few years, this has been an area of emphasis of EP rape research. One reason may be that it is more likely that specialized mechanisms for avoiding sexual coercion evolved in women than that specialized mechanisms for engaging in sexual coercion evolved in men. This assumes that the reproductive costs to ancestral women of losing the ability to choose among mating partners due to sexual coercion would have been greater than the reproductive increase to men of, at times, using coercive sex.

SEXUAL COERCION IN OTHER SPECIES

Physical force, harassment, and other intimidation to obtain sex have been reported in many species. Based on a review of the literature on forced copulation among nonhumans, Lalumière et al. (2005) identified specific characteristics in those species that exhibit sexual coercion. Across all nonhuman species forced copulation is always perpetrated by males on females. Despite the tendency of females in some species to be assertive in the mating process, the authors could not find one instance of a female forcing sex on a male. Further, males are more likely to target fertile than infertile females for forced copulation. Relatedly, forced copulation does occasionally result in insemination, fertilization, and offspring. Also, males of most species tend not to engage solely in coercive sexual behaviors. In fact, most males that engage in forced copulation at other times court females. Finally, Lalumière et al. (2005) recognized the role of individual differences in sexual coercion. Certain males are more likely than others to engage in forced copulation. Some males are more successful at sexual coercion than others. Lalumière et al. conclude that sexual coercion (particularly in the form of forced copulation) "is a tactic used by some males under some conditions to increase reproduction" (p. 59).

A particularly interesting species is the orangutan, one of the few nonhuman primates for which sexual coercion is common. There is evidence for two distinct classes of orangutan males: large males and small males. Both types are sexually mature, though the onset of sexual maturity can be highly variable. Large males typically weigh over 80 kg in the wild, about twice the size of the small males (Knott, 2009; Knott & Kahlenberg, 2007). Although both types resort to forced copulations, they are more often perpetrated by small males, who force more than 80% of their total copulations at some orangutan sites, although only about half or fewer of their copulations are forced at other sites, suggesting the role of environmental contingencies such as population density and sex ratio (Knott, 2009; Knott & Kahlenberg, 2007).

The evidence from orangutans can be contrasted with other similar species in which forced copulation has not been reported, Bonobos and common chimpanzees (Stumpf, Emery Thompson, & Knott, 2008). This suggests the importance of factors such as the isolated social system unique to orangutans among the apes (see Smuts, 1995, and Smuts & Smuts, 1993, for analyses emphasizing the importance of female coalitions as a deterrent for male sexual aggression across various primate species and potential implications for humans). Chimpanzee males, however, do use less direct sexually coercive strategies such as harassing and intimidating females. These tactics can manipulate the future rather than the immediate behavior of the target. For example, long-term data from a study of wild chimpanzees showed that a female's willingness to initiate copulation with a male is positively correlated with how frequently the male has been aggressive toward her, suggesting that female mate preferences are constrained by sexual coercion (Muller, Emery Thompson, Kahlenberg, & Wrangham, 2011). A related study (Muller, Kahlenberg, Emery Thompson, & Wrangham, 2007) found that male chimpanzees achieved more matings with females toward whom they were more aggressive, and directed more aggression toward more fecund females.

SEXUAL COERCION IN HUMANS

An issue relevant to an evolutionary-based model of sexual coercion is its frequency in human history, because regularly occurring events are more likely to have a "logic embedded in the dynamics of natural selection for reproductive success" (Wrangham & Peterson, 1996, p. 138). Sexual coercion does appear to have occurred throughout human history (e.g., Chagnon, 1994), and cross-cultural surveys reveal that it occurs in most societies today (Basile, 2002; Broude & Greene, 1978; Fulu, Jewkes, Roselli, & Garcia-Moreno, 2013; Levinson, 1989; Monson & Langhinrichsen-Rohling, 2002). Moreover, even relatively rape-free societies described in such surveys (e.g., Sanday, 1981) have social rules intended to counter male sexual aggression, suggesting that there is universal risk for such behavior.

When fear of punishment is reduced, signaling conditions in which the costs of sexual coercion are low or the perpetrator has anonymity, many men do rape. This is evident in times of war (see Allen, 1996; Stiglmayer, 1994). At least one-third of men admit some likelihood of sexual coercion if they could be assured that they would not suffer negative consequences (e.g., Malamuth, 1989). In addition, sexually coercive fantasies are common among men (Greendlinger & Byrne, 1987, 54% of college men "fantasize about forcing a woman to have sex"; Crèpault & Couture, 1980, 33% of a community sample of men sometimes or frequently fantasize a scene "where you rape a woman"), and imagined sexual aggression is a key predictor of actual sexual aggression (e.g., Dean & Malamuth, 1997; Malamuth, 1981, 1988; Knight & Sims-Knight, 2003; Seto & Kuban, 1996). Aggressive sexual fantasies also covary with measures of high sexual preoccupation, high sexual compulsivity, and hypersexuality (Knight, 2010a). Imagined aggression may reveal important information about evolved mental mechanisms (B. Ellis & Symons, 1989; Kenrick & Sheets, 1993).

ADAPTATION, BY-PRODUCTS, OR NOISE

R. Thornhill and Palmer (2000) presented the most controversial evolutionary analysis of rape. They addressed whether sexual coercion is produced by adaptations or as a by-product of adaptations designed to solve other problems. Adaptations are naturally selected (i.e., they resulted in increased ancestral reproductive success). Criteria for establishing adaptation within evolutionary science include attributes of economy, efficiency, complexity, precision, reliability of development, and functionality in solving a specific problem (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; see also Tooby & Cosmides, 1992). By-products are incidental characteristics that did not evolve because they solved adaptive problems. For example, male nipples, which have no design functionality, are by-products of the adaptive value of nipples in women (Symons, 1979).

Symons (1979) first discussed extensively whether rape is produced by adaptations or by-products of adaptations. He concluded that the available data are insufficient to conclude that rape is a facultative adaptation in humans. Rather, rape may be a by-product of male adaptations that produce sexual arousal and adaptations that motivate coercion to secure desired goods. Later evolutionary models of rape have extended Symons's proposal to include rape as a by-product of both sexual desire and a generalized possessiveness or desire to control others (L. Ellis, 1989). Still other evolutionary models conceive of rape as a manifestation of an alternative strategy, for example, psychopathy, whereby rape is a by-product of the use of coercion in other areas (Mealey, 1995).

THE ADAPTATION HYPOTHESIS

The adaptation hypothesis suggests that in ancestral environments, being sexually coercive under some circumstances (and, particularly for women, having the capacity to avoid being sexual coerced) contributed to reproductive success sufficiently frequently to have resulted in some change in the evolved psychological architecture that would not have occurred without the recurring fitness consequences of sexual coercion. Therefore, this hypothesis posits specific psychological mechanisms pertaining to sexual coercion. Such specialized mechanisms might include reactions such as emotions or arousal patterns that, in the proximate environment, mediate between relevant environmental cues and behaviors.

From an EP perspective, the question is not whether sexual coercion is a better strategy for males than engaging in consensual sex but whether for some ancestral males, under some circumstances, it may have been reproductively effective to use sexual coercion as compared to not using it. In other words, did recurrent ancestral conditions exist under which for some men, some of the time, an overall fitness increase resulted from sexual coercion? Although the hypothesis that sexual coercion contributed to reproductive success has been criticized on grounds that rape rarely leads to conception, Gottschall and Gottschall (2003) estimated pregnancy rates resulting from penile-vaginal rape among women of reproductive age to be twice that of consensual per-incident rates (6.4% to 3.1%). Controlling for age, rape pregnancy rates per incident remained 2% higher than consensual rates (see also Holmes, Resnick, Kilpatrick, & Best, 1996, indicating a rape-related pregnancy rate of 5.0% per rape or 6.0% per victim in a national sample of reproductive age women; for indirect corroboration, see Beirne, Hall, Grills, & Moore, 2011, in a sample of 105 normally ovulating sexual assault victims, identifying "a trend and a distinct rise in the number of assaults when the victims were in the middle of their cycle" [p. 315], that is to say at peak fertility).

Also relevant to the potential fitness outcomes of sexual coercion is the fact that a substantial minority of women continues to have sex with the men who sexually assault them (Koss, 1988). This is particularly true of completed sexual assault, pointing to the use of sexual coercion as a tactic to secure subsequent copulations. From a comparative perspective, this is consistent with forms of sexual coercion in wild chimpanzees used to manipulate the female's future rather than her immediate behavior. Illustratively, Ellis, Widmayer, and Palmer (2009) identified more than two thousand North American undergraduate women who reported having been sexually assaulted, dividing victims into two groups: assault blocked (59.4%) and assault completed (40.6%; i.e., sexual intercourse occurred). A sizable number of women in both groups indicated future intercourse at least one time with the assaulter, with more women in the assault-completed group (27.2%) than in the assault-blocked group (19.4%) reporting this outcome. Overall, these results indicate that, "at least a minority of men may have evolved tendencies to use assaultive tactics to secure mating opportunities beyond those obtained by men who only employ 'voluntary' tactics" (p. 461) (see also Wilson & Durrenberger, 1982; 39% of rape victims had another date with their assaulters, compared to 12% of victims of attempted rape). Ellis, Widmayer, and Palmer hypothesized that completed assault may more readily secure subsequent copulations due to greater experienced female trauma or a felt need for support in the event of pregnancy.

Relatedly, in Holmes et al.'s (1996) study, 41.2% of rape-related pregnancy cases involved repeated assaults, one of which was assumed to result in the pregnancy. Although the data are unclear about what percentage of these women endured multiple assaults from a single perpetrator (indicating only that for these victims, rape-related pregnancy occurred in a context of ongoing abuse), it does point to the possibility that sexual coercion may have increased the likelihood of future copulations with the victim.

For their model, R. Thornhill and Palmer (2000) proposed various possible adaptive mechanisms. These included mechanisms designed: (a) to evaluate women's vulnerability to sexual coercion, theoretically functioning to direct rape toward cost–benefit scenarios most favorable to the prospective rapist; (b) to identify cues associated with fertility (e.g., age, ovulation status), so that men might preferentially target the most fertile women as rape victims; (c) to optimize sperm counts produced during rape; (d) to increase the probability of rape under conditions of sperm competition, when men would be vying most fervently with one another for valued insemination opportunities; (e) to potentiate rape in men who lack sexual access to females (the "mate deprivation" hypothesis); and (f) to produce arousal specific to opportunities of rape. These theories of adaptation as they relate to sexual coercion have been further elaborated and expanded elsewhere (see Camilleri, 2012; Camilleri & Stiver, 2014). In this chapter, we evaluate theory and data specially pertaining to sexual arousal specific to forced sex, showing how such an adaptive decision rule might be selectively constituted.

SEXUAL AROUSAL TO FORCE

One hypothesized candidate for a specialized psychological mechanism motivating sexual coercion that has received focused attention is sexual arousal specific to forced sex, referred to here as *sexual arousal to force* (SAF). Such arousal may be a manifestation of a broader category of sexual arousal generated by controlling or dominating women, which can be accomplished by the use of force.

Using an adaptation model, R. Thornhill and Thornhill (1992) discussed SAF and argued that higher sexual arousal to coercive sex among men should be associated with greater success with coercive sexual tactics, thereby contributing to ancestral reproductive fitness under some circumstances. They noted that given the costs of forced mating in ancestral environments, including possible loss of status or life, men might be expected *not* to have evolved preferences for forced sex and, therefore, *not* to evidence SAF. If, however, under some recurrent ancestral environments, the reproductive benefits of forced mating outweighed the costs, psychological mechanisms enabling sexual arousal despite a woman's lack of consent may have evolved. Harris, Rice, Hilton, Lalumière, and Quinsey's (2007) selectionist hypothesis of psychopathy provides an example of a model suggesting that SAF could reflect a design feature of a rape adaptation. This hypothesis asks: "Do psychopaths respond more to sexual stimuli depicting violence, coercion, and rape simply because they are indifferent to the suffering of others, or does psychopathy entail a mechanism promoting coercive sex?" (p. 20). Harris et al. (2007) suggest that sexual coercion could be a fundamental feature of psychopathy.

Buss (1994/2003) suggests that the model pertaining to SAF and the data presented by Thornhill and Palmer (2000) do not enable differentiating among alternative hypotheses. In consideration of such criticisms, we elaborate both theoretically and empirically on the possibility that SAF might have evolved as a conditional specialized mechanism for sexual coercion in a manner that enables better testing of alternative explanations. Hagen (2004) argues that specialized mechanisms pertaining to rape would not be expected unless the problems involved in "successfully" committing such an act in ancestral environments were not the same problems as with the use of aggression in other contexts. The occurrence of sexual arousal in the context of coercive acts may be an important distinguishing characteristic. For most aggressive acts, sexual arousal would be irrelevant or even detrimental. Because the preferred sexual strategy for most men in most circumstances is to pursue consensual sex, the most common calibration of sexual arousal mechanisms should be to become sexually inhibited by indications of lack of sexual receptivity by women. However, if an individual is to effectively rape in ancestral environments, such aggression may require reversing of the default arousal pattern. This may be hypothesized as a unique adaptive problem associated with sexual coercion as contrasted with the use of coercion in nonsexual contexts.

In evaluating empirical data, we rely on studies that measure SAF (often by direct genital measures), and we contend that studies using related measures, such as reported dominance as a motive for sex (Nelson, 1979) and rape fantasies (Greendlinger & Byrne, 1987), assess closely related constructs that are also relevant to the present analysis.

PROPOSED EVOLVED FUNCTION OF SEXUAL AROUSAL TO FORCE

Within some ancestral circumstances, the inhibition or activation of sexual arousal in response to cues associated with using force might have affected the likelihood of successfully dominating and exerting sexual control over an unwilling woman. Some emotions motivate avoidance of particular stimuli, whereas others motivate approaching or pursuing particular stimuli (for an overview see Elliot, 2008). Just as fear of spiders motivates avoidance of specific threats, sexual arousal cued to the use of force may motivate sexual coercion. This hypothesis is supported by the meta-analysis of Allen, D'Alessio, and Emmers-Sommer (2000), which documented that sexual arousal is associated with positive psychological affect, a precursor of approach or pursuit.

This hypothesis that sexual arousal cued to the use of force may serve as an approach emotion designed to increase the likelihood of engaging in sexually coercive behavior may be contrasted with nonevolutionary hypotheses of SAF. For example, Marshall and Fernandez (2000) hypothesized that SAF is not designed to facilitate sexual coercion, but instead that the causal connection is in the opposite direction. Marshall and Fernandez argue that SAF and other forms of "deviant" sexual arousal are the result of repeated sexual offending. This model suggests that because the offender lacks the requisite social skills and confidence to engage in consensual sex, he uses coercive tactics repeatedly, eventually resulting in the conditioning of SAF (but see, e.g., Ellis et al., 2009; men who commit sexual assault have sex with more women than do men, in general). Other hypotheses have also conceptualized such arousal as an abnormality that is likely to be evidenced by a small percentage of men (e.g., Abel, Barlow, Blanchard, & Guild, 1977). Representative of the abnormality hypothesis, the *Diagnostic and Statistical Manual of Mental Disorders* (5th ed.; *DSM-5*) Paraphilias subworkgroup recently proposed the introduction of a new psychiatric diagnosis, paraphilic coercive disorder, in which the diagnostic criteria featured sexual arousal from nonconsent, struggling, or resisting.

An evolutionary-based model uniquely suggests that, due to calibrating mechanisms grounded in the consequences in ancestral environments, a substantial percentage of "normal" men evidence the sexual arousal pattern that facilitates sexual coercion. How might such calibration occur? In keeping with the proposition that humans share a common evolved psychology that enables relevant developmental experiences to "set" mechanisms at different levels (Belsky, Steinberg, & Draper, 1991; Draper & Harpending, 1982; Trivers, 1972), the model we outline here (which we label the *evolutionary functional* [EF] model) emphasizes some relevant perceived negative experiences with women that may set the sexual arousal versus sexual inhibition to force mechanism more in one direction or the other. Although full testing of such a process would require a longitudinal study that would be difficult to conduct, it may be possible to prime similar processes to create a *state condition* related to the *trait condition.* Yates, Marshall, and Barbaree (1984) found that college men who were insulted by a woman were more sexually aroused by rape portrayals as compared to portrayals of consensual sex. Creating general arousal by physiological exercise instead of an insult by a woman did not result in a similar increase.

Other relevant findings pertain to the trait rather than the state of anger and hostility toward women. These studies indicate that men who are hostile to women, typically on measures that include items referring to perceived rejection from women (e.g., Check, Malamuth, Elias, & Barton, 1985), show relatively high SAF as contrasted with men who are relatively low on such measures of hostility toward women. For example, many studies focusing on the *confluence model of sexual aggression* (Malamuth & Hald, in press) have found a strong connection between measures of individual differences in men's hostility toward women and their SAF or similar constructs such as dominance as a motive for sex and rape fantasies. Other studies examining differences between behaviorally sexually nonaggressive men and sexual aggressors (some of whom are likely to have the relevant calibration of increased SAF) have found similar results (e.g., Murnen, Wright, & Kaluzny, 2002). Several priming studies have revealed that sexually aggressive men may be more prone to automatically associate women with hostility, sex, and power (Bargh, Raymond, Pryor, & Strack, 1995; Leibold & McConnell, 2004). Barbaree (1990) reported a study with a rapist who was asked to imagine raping women for whom he held different emotional feelings. He found that the greater the hostility to the woman, the greater the sexual arousal to rape cues. Forbes, Adams-Curtis, and White (2004) found that the key component linking various measures of male dominance ideology (e.g., attitudes supporting aggression or sexism) to aggression against women is hostility toward women. Baumeister, Catanese, and Wallace (2002) have summarized many studies indicating that experiencing rejection by women, particularly by men who are relatively narcissistic, contributes to sexually coercive behavior. Taken together, these findings provide some support for the hypothesis that perceived blocked access to desired women and associated hostility toward women may affect the calibration of men's sexual arousal patterns in ways that could affect the likelihood of committing sexually coercive acts.

How might a mechanism of SAF operate to affect the likelihood of committing sexually coercive acts? Consider a simple distinction between two types of men: one for whom the best prospects involve mating only with a consenting partner and the other a man whose prospects could be augmented by using sexual coercion. (Rather than a simple dichotomy, we prefer a more dimensional conceptualization but use a dichotomy to facilitate explication.) If we were to design a psychological mechanism that provided the best decision rule (for total ancestral fitness) for each of these men, what might be its properties? For the first man, there would be sensitivity to cues when a sexually desired female indicated disinterest, disgust, or other negative responses. This would be an effective mechanism for inhibiting approach tendencies where persisting in sex with an unwilling female would have high costs compared to pursuing consensual sex with alternative mating prospects. However, for the second type of individual, it could have been ancestrally adaptive to have this inhibiting mechanism disengaged. Potentially, for this latter type, there may even have been fitness benefits to increased SAF relative to consenting sex because engaging in coercion may require relatively greater persistence and energy to overcome the resistance of an unwilling partner. Consistent with this hypothesis, Bernat, Calhoun, and Adams (1999) found that the penile tumescence of self-identified sexually aggressive men who also held callous sexual beliefs (e.g., "Get a woman drunk, high, or hot and she'll let you do whatever you want," "Prick teasers should be raped") increased when force was introduced into a sexual scenario (see also Lawing, Frick, & Cruise, 2010, who found that adolescent sexual offenders high in callous/unemotional traits showed more sexualized aggression and had a greater number of victims than other adolescents with a sex offense).

Our analysis suggests that type 1 men should show inhibited SAF, whereas type 2 men should show at least equal sexual arousal to consensual and coercive sex (i.e., the shutting off of the inhibiting mechanism) or even greater arousal to some types of coercive sex (the activation of a mechanism creating greater sexual arousal). The distinction between two types of men bears some similarity to the distinction between large and small orangutans insofar as that distinction may serve as a useful illustration of how differently situated individuals may respond based on their unique developmental and current circumstances. In summary, if there were ancestral conditions in which, for some men, some of the time, there was an overall fitness increase resulting from sexual coercion, then for these men it may have been important not to be inhibited by cues of a woman's unwillingness and to potentially be sexually aroused by dominating and controlling the victim.

CONVICTED RAPISTS AS GENERALISTS AND DIFFICULTIES IN MAKING PROPER GROUP COMPARISONS

How might we select two groups of men for comparison purposes to correspond to the hypothesized two types described earlier? Previous researchers have compared convicted rapists to other men (e.g., N. Thornhill & Thornhill, 1992; R. Thornhill & Palmer, 2000). This is not the ideal comparison, however (e.g., Lalumière, Quinsey, Harris, Rice, & Trautrimas, 2003; Marshall & Kennedy, 2003). Convicted rapists include men who are "generalists" vis-à-vis antisocial behavior and men who are "rape specialists." The latter group would have the mechanisms calibrated to increase the likelihood of sexual coercion. The former group may include individuals who have not had the relevant mechanisms calibrated but may use sexual coercion due to the workings of other mechanisms. These men engage in various antisocial acts because they differ from other men not necessarily on the specific mechanism of SAF (or other specialized mechanisms for sexual coercion) but on mechanisms underlying general antisocial behaviors (e.g., lack of inhibitory self-control, high impulsivity, low empathy, and/or callousness). They may be more likely to steal or to use coercion for obtaining any desired goal. Accordingly, convicted rapists are comparable to other types of violent criminals on most measures of antisocial traits and behaviors (Lalumière et al., 2005), most rapists have a history of nonsexual offenses (Kingston, Seto, Firestone, & Bradford, 2010), and the criminal records of rapists often resemble those of other offenders (Serin & Mailloux, 2003).

Using data from a large sample of prisoners released in 1994, Miethe, Olsen, and Mitchell (2006) found that rapists display less specialization (i.e., repetition of the same offense) than other offender types. Even within a subset of serial sex offenders "[o]nly a modicum of specialization was embedded in otherwise versatile criminal careers" (p. 221). A recent study of 170 rapists referred for civil commitment also highlights that, contrary to some social constructions, convicted rapists are versatile offenders (Harris, Mazerolle, & Knight, 2009; see also Harris, Smallbone, Dennison, & Knight, 2009). Using a commonly accepted definition that declared specialization if more than half of a rapist's offenses were sexual in nature, only 18 (11.8%) were rape specialists.

Whereas most convicted rapists may be criminal generalists, some rapists do appear to be rape specialists. The Massachusetts Treatment Center (MTC) Rapist Typology, which defines rapist subtypes structured in relation to three (previously four) motivational themes (see Knight, 2010b; Knight & Prentky, 1990; Knight & Sims-Knight, in press), includes two types, sadistic and sexual nonsadistic, more motivated than nonsexual subtypes by a paraphilic interest in rape and sexual gratification. The evidence for such a typology is not strong, however (see, e.g., Looman, Dickie, & Maillet, 2008, who find no between-group differences between sexual subtypes and rapists deemed nonsexual in responses to rape depictions; Kingston et al., 2010, find no evidence of sexual specialization in a sample of sadistic sex offenders; Healey, Lussier, & Beauregard, 2012, note a lack of consensus by the scientific community about what sexual sadism is and how it is defined). As Knight (2010b, p. 17-7) has acknowledged, "The validity data on the sexual types constitute one of the more problematic areas of the typology." Beyond the nettlesome task of reliably grouping different types of sexually coercive men, difficulties with data interpretation add to the troubles (see Harris, Lalumière, Seto, Rice, & Chaplin, 2012, and Seto, Lalumière, Harris, & Chivers, 2012, suggesting a meaningful distinction between rapists and self-identified sexual sadists in the cues that elicit penile responses to rape scenarios; but cf. Knight, Sims-Knight, & Guay, 2013, who find more similarity than difference between these two groups after evaluating the same research).

Knight and colleagues, who developed the original MTC typology, in the latest data-driven revision of the typology, have suggested a structural reconceptualization that provides a more integrated approach. It orders individuals on a single continuum according to the gravity of the coercive sexual behaviors (e.g., Knight, 2010b). Severe forms of sadistic arousal, for example, occupy the high end of the continuum (Knight et al., 2013). The new structural model, which departs from earlier typological attempts to categorize rapists by interrelated but purportedly more discrete distinguishing characteristics, can "best be described as a modified, dimensional, circumplex model, replacing and restructuring the linear configuration proposed in its predecessor" (Knight & Sims-Knight, in press). Because the new model describes men as differing in the traits they possess in degree (rather than in kind) on a univariate dimension, it is consistent with an EP approach in which proximate factors (such as repeated rejections from desired women and a history of exploitative relationships) interact with universal psychological mechanisms to influence the expression of sexually coercive behaviors.

SPECIALIZATION AND COERCIVE POTENTIAL

Classifying rapists according to the MTC Rapist Typology provides a potentially valuable means to identify men who may engage in sexual coercion partly because of the activation of specialized psychological mechanisms, but excludes most men from inclusion. The data indicate that it is among noncriminals, particularly those drawn from college populations, that specialization may be most evident. In general community samples, men who self-identify as having committed sexual coercion show more evidence for "specialization" than convicted rapists. Ronis, Knight, Prentky, and Kafka (2010) found that self-identified sexually coercive community men exceeded incarcerated rapists on diverse measures of sexual and paraphilic fantasies, including sadism, sexual preoccupation, and bondage. Self-identified sexual coercers among criminals who had not been convicted of sexual crimes also showed higher scores on such sexual and paraphilic fantasy than convicted rapists, suggesting that, even among criminals, self-identification might be a better way to identify specialists for sexual coercion than only considering the crime for which the person was convicted. Although there were no significant differences between the community and criminal self-identified sexual coercers on these sexual and paraphilic fantasy measures, the community sample evidenced the highest scores. Overall, these data support the conclusion that most of those currently identified by the judicial system and convicted of acts of sexual coercion display less evidence of specialized psychological mechanisms than other self-identified sexually coercive men. However, caution is necessary in interpreting the data provided by convicted rapists, who might seek to portray a positive image because of the belief that this will increase their likelihood of being paroled.

Researchers focusing on noncriminal samples generally have not addressed whether sexually aggressive men engage in other forms of antisocial behavior (Lalumière et al., 2005). We conducted analyses focusing on this issue in our longitudinal database of close to 150 men (Malamuth, Huppin, & Bryant, 2005). We administered several measures to the same men at about age 20 years (Time 1) and then again 10 years later (Time 2). Examining whether measures assessing SAF showed a pattern supporting specialization, we found support for such a specialized mechanism. Other findings provide corroboration for such a specialized mechanism (for a discussion see Malamuth et al., 2005). Malamuth and Impett (1999) conducted a series of mediational analyses to directly test the hypothesis that high SAF is a specific mediator of forced sex. They found evidence supporting SAF as a specific mediator of coercive sexual behavior.

FEMALE COUNTERADAPTATIONS TO THE RISK OF RAPE

Because rape is a traumatic event for women, and likely to have been a recurrent problem over evolutionary time, it may be more plausible that women have evolved counteradaptations designed to minimize their experience with male sexual aggression, than it is that men have evolved rape-specific adaptations. Negative fitness consequences of sexual assault for women include serious injury or death, partner abandonment, disruption of a woman's parental care, and circumvention of mate choice (Symons, 1979; R. Thornhill & Palmer, 2000). Even if male sexual coercion is a by-product of other adaptations these costs are no less traumatic, meaning that the argument for female counteradaptations is independent of causal explanations for men's behaviors.

Researchers have reported purportedly rape-avoidance behaviors that imply the existence of evolved mechanisms, although most arguments in favor of specificity presently constitute tentative hypotheses. One example is Wilson and Mesnick's (1997) "bodyguard hypothesis," which offers that anti-rape adaptation may have produced women's mate preferences for physically and socially dominant men. Evidence suggests that women may be especially attracted to such men when the risk of sexual aggression from other men is higher (see also Mesnick, 1997). Smuts (1992) cites benefits of protection against potential rapists to help explain patterns of female social relationships, including strategies of forming long-term relationships with particular males, forming strong female–female bonds, and mustering support from relatives. Of course, one can imagine these behaviors having evolved due to the broader benefits they provided, including protection from nonsexual assault and predation.

Also in accord with the hypothesis of female anti-rape adaptation is research on the effects of ovulatory cycle status. This line of research assumes that rape is most costly when pregnancy is most likely, specifically during the ovulatory phase of the menstrual cycle. Bröder and Hohmann (2003), for example, found that, during the ovulatory phase, naturally cycling women reduced risky behaviors and increased nonrisky behaviors, whereas women using hormonal contraceptives that suppress ovulation did not show either effect. This study replicated earlier research that found reduced risk-taking during the fertile phase of the cycle (Chavanne & Gallup, 1998). Both of these studies relied on potentially unreliable self-report methods for identifying ovulatory cycle status, however. The results of both studies are also difficult to reconcile with the results of studies using luteinizing hormone tests to verify ovulation; those latter studies show that women are not risk averse during high fertility. For instance, when asked to illustrate what they would wear to a social event, undergraduate women indicate that they prefer more sexy and revealing clothing around high fertility as compared to low fertility. In the same set of experiments, women who had previously experienced sexual intercourse (but not those who had not) showed more skin and wore sexier outfits to a lab session at high fertility than at low fertility (Durante, Li, & Haselton, 2008; see also Haselton, Mortezaie, Pillsworth, Bleske, & Frederick, 2007). Relatedly, Gangestad, Thornhill, and Garver-Apgar (2010) found that partnered women were more likely when in the fertile phase to report greater willingness to pursue sexual opportunities, including a greater willingness to have sex with unfamiliar men.

An intriguing subset of ovulatory cycle studies relates to physical strength. Petralia and Gallup (2002) showed that, in response to a sexual assault prime, naturally cycling women demonstrate greater handgrip strength than baseline, but only in the fertile phase. By comparison, naturally cycling women in other phases and women using hormonal contraceptives showed no effect of imagined sexual assault on handgrip strength. Neither did a control group exposed to a neutral prime show effects that differed from baseline. Similarly, Prokop (2013) found that women at high conception risk score higher than women at low conception risk on a measure of perceived physical condition (e.g., "I am physically stronger than other people of the same age and sex"). These results support the possibility that specially designed mechanisms may mobilize resistance to rape when conception risk is higher.

Other research consistent with activation of dedicated perceptual mechanisms specially designed to limit the incidence of male sexual coercion includes a study that exposed women to taped short interviews of men. Fertile-phase women rated the men as more sexually coercive than did comparable nonfertile women, whereas fertility status did not affect ratings of traits hypothesized to be less clearly related to sexual coercion, such as kindness, commitment, and faithfulness (Garver-Apgar, Gangestad, & Simpson, 2007). Navarrete, Fessler, Fleischman, and Geyer (2009) found that White women demonstrated greater out-group bias against Black men when in the fertile phase, which the authors interpreted as consistent with a "coercion avoidance perspective" (p. 664). This interpretation assumes that group membership is a feature relevant to assessing risk of sexual coercion.

McKibbin, Shackelford, Miner, Bates, and Liddle (2011) tested the impact of a woman's relationship status, self-perceived physical attractiveness, and proximity to kin as they relate to anti-rape adaptation. Given that would-be rapists should prefer and target more attractive women (e.g., McKibbin, Shackelford, Goetz, & Starratt, 2008; R. Thornhill & Palmer, 2000), the authors predicted that a woman's attractiveness would correlate positively with frequency of rape-avoidance behaviors. Because mated women may experience greater losses from rape than do unmated women, including partner abandonment, they also predicted that mated women would perform more rape-avoidance behaviors. Finally, because a woman's relatives should be motivated to guard her from rape-related harm, the authors predicted that frequencies of rape-avoidance behaviors would increase with the number of family members living in close proximity.

Each of the predictor variables correlated positively with total scores on a rape-avoidance inventory. The authors also reported results according to the inventory's four subscales: (1) *avoid strange men,* (2) *avoid appearing sexually receptive,* (3) *avoid being alone,* (4) *awareness of surroundings/defensive preparedness.* Self-perceived attractiveness correlated with the third and fourth subscales, relationship status with the second and third, and total number of family members residing in close proximity with the second and fourth. However, in multiple regression analyses for the predictor variables on the total scale and its component parts, only a woman's relationship status consistently predicted her rape avoidance (see Snyder & Fessler, 2012, for purported failures to replicate several of these findings; see McKibbin & Shackelford, 2013, for criticisms of Snyder & Fessler).

Lastly, R. Thornhill and Palmer (2000) discussed evidence for anti-rape adaptations involving degrees and types of psychological pain experienced by rape victims. Unfortunately, as Ellsworth and Palmer (2011, p. 359) recently remarked,

> instead of following Thornhill and Palmer's call for new and better research on this crucially important topic, the interest in [antirape adaptations] has been focused primarily on searching for flaws in the original data . . . and its interpretation. . . . We know of no recent evidence on psychological pain of rape victims related to the variables of age, marital status, and type of behavior, and we strongly encourage future research on these areas.

Further investigation would likewise be useful to reconcile studies showing increased mate seeking during high fertility (with results lending support to the "good-genes" hypothesis of sexual selection) with studies providing evidence consistent with anti-rape adaptation. In sum, although promising avenues of exploration into female anti-rape adaptation do exist, more research is needed.

CONCLUSIONS

EP theory and research seek to better understand the ultimate causes and the design of evolved psychological mechanisms underlying manifest behavior. In addressing sexual coercion, there has been considerable focus on whether there may have been, on average, fitness consequences in recurring ancestral environments of the ability to successfully avoid and/or inflict sexual coercion. The growing body of research in the past few years suggests that indeed there may be evolved specialized mechanisms in females designed to avoid being sexually coerced.

The discussion in this chapter focusing primarily on perpetrators suggests three competing models:

1. There were no recurring fitness consequences of using sexual coercion; therefore, the mind does not include mechanisms relevant to sexual coercion.
2. Fitness consequences were a function of the ability to selectively use coercion in various arenas, with sexual conflict being one of many, but no specific adaptive problems existed unique to using coercion in the sexual arena. The mind, therefore, includes mechanisms designed specifically to motivate coercion in various arenas, including but not limited to sexual coercion.
3. Because there were unique adaptive problems associated with the use of coercion in the sexual context (e.g., how to maintain an erection and subdue a victim who is fighting back), specialized mechanisms evolved that enabled the effective use of such coercion in that sexual context. Such specialized modules evolved because there were fitness benefits in ancestral environments specific to the selective use of sexual coercion that differed from the use of coercion in nonsexual contexts.

In seeking to identify potential candidates for specialized mechanisms, it is useful to reiterate that sexual coercion may be produced by differing motivations and antecedents. Rapists identified by the legal system are typically generalists who commit various types of antisocial behavior and often may not reveal the activation of specialized mechanisms motivating sexual coercion. In contrast, among sexual aggressors in the general population, a larger percentage of men are specialists who may be particularly useful for studying such mechanisms. We explored the possibility that SAF may be an evolved specialized mechanism for engaging in sexual coercion. The viability of the EF model for such arousal must be determined by its ability to generate testable predictions. It is important, therefore, to examine how this model has fared in its predictions in contrast to other models. The following is a summary of our conclusions in comparing the EF model to others focusing only on proximate causes, as well as to a by-product evolutionary model.

FREQUENCY

How many men in the general population would be expected to show relatively high SAF? In conceptualizing sexual coercion as either the result of sexual pathology or general antisocial characteristics, proximate models typically predict that only the few "sick" or "antisocial" would fail to inhibit SAF and/or show increased arousal by the inclusion of force. It is not clear whether a by-product model would make any predictions regarding the expected frequency of differing sexual arousal patterns.

The EF model suggests that some psychological mechanisms may have evolved that, when activated by environmental conditions (e.g., repeated rejection from desired women, early experiences with exploitative relationships, and environmental messages via the mass media that communicate favorable images of sexual violence), increase the likelihood of effectively implementing a coercive sexual act. Although the calibration of their arousal mechanism would not depend only on these experiences, and the relevant environmental conditions would need to be better described, within the general population a substantial minority of men would show lack of inhibition and/or increased SAF. The various sources of data described earlier appear to indicate that a substantial minority (e.g., as much as one-third of the population) reveal the type of arousal pattern that indicates the disengagement of the inhibitory mechanism and/or increased arousal to force and are, therefore, arguably most consistent with the EF model.

CORRELATES WITH OTHER CHARACTERISTICS OF MEN

In addition to the expectations regarding frequency of sexual arousal patterns, various models may have differing expectations about which characteristics of men will be associated with the differing arousal patterns. Proximate models typically predict that men who show greater SAF will reveal general sexual deviance, a lower threshold for sexual arousal in general, and/or general antisocial characteristics. The data do not support these predictions: SAF is not associated with increased antisocial or deviant characteristics and behavior, and neither is it fully explainable by a lower threshold for becoming sexually aroused. A by-product model might not predict any systematic association between SAF and any characteristics or behaviors.

The EF model predicts that the degree of perceived blocked sexual access to desired women and resultant emotional responses (e.g., anger, hostility) will be relevant to the development of SAF. The data pertaining to correlates of SAF described earlier and elsewhere are consistent with the EF model by showing strong connections with hostility to women and perceived rejection.

CORRELATES WITH BEHAVIOR

Different predictions arise from the various models regarding the function of SAF and, therefore, its association with sexually coercive behaviors. Some nonevolutionary proximate models argue that responses such as fantasies of rape and SAF have no association to behavioral inclinations. Similarly, a by-product model would not make any clear predictions one way or the other about an association between SAF and actual coercion. The EF model suggests a direct role of SAF for energizing behavioral tendencies. Inhibited arousal would be expected to discourage sexual persistence in response to a woman's lack of sexual responsiveness; in contrast, the disengagement of such inhibition and increased arousal would be expected to facilitate sexually aggressive tendencies and, under some conditions, increased sexual aggression. The data showing that SAF is a key predictor of reported likelihood of raping and of actual sexual coercion, as well as the findings that such arousal is a critical mediator between hostile masculinity characteristics and sexual aggression, are consistent with the EF model.

Further theoretical development and empirical testing are needed to assess the viability of the EF model we have described. The difference in the type of questions raised by such a model is apparent when we contrast it to those raised by proximate models. For example, Barbaree and Marshall (1991) published a thorough attempt to compare differing models focusing on SAF. Although they describe the purpose of the models as designed to "account for men's sexual arousal to descriptions of rape" (p. 621), all six models provide descriptive analyses designed to identify the critical features distinguishing sexual aggressors from nonaggressors (e.g., the ability to suppress sexual arousal or the augmentation of sexual arousal by other emotional states such as hate). None of these models address why there might be certain design features that lead to observed recurring patterns of individual differences in SAF (e.g., Why it is that some men, but not others, who perceive rejection from desired women develop a pattern of SAF, whereas women who are similarly rejected by men do not show such a pattern?). Although we recognize that such questions should be asked with sensitivity to their potential misunderstanding and misuse within certain political contexts, we believe that they may provide useful insights into acts most people consider morally repugnant and consequently yield better preventative policies.

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CHAPTER 18

Love and Commitment in Romantic Relationships

LORNE CAMPBELL and TIMOTHY J. LOVING

In every known culture, formal marriage arrangements between men and women exist (Brown, 1991; Buss, 1985; Daly & Wilson, 1983). An analysis of 166 societies by Jankowiak and Fischer (1992) concluded that romantic love is found worldwide, and over 90% of people in the world will marry at least once (Buss, 1985). Whereas a large proportion of cultures permit polygyny (i.e., having more than one wife; van den Berghe, 1979), the majority of men in these cultures tend to pair with one partner at a time (Lancaster & Kaplan, 1994). Less than 1% of cultures permit a woman to take more than one husband at a time (i.e., polyandry), and this practice is extremely rare (van den Berghe, 1979). It appears, therefore, that the existence of close affectional bonds in romantic relationships, typically, but not always, involving two people is a universal feature of human existence.

Drawing on the power of evolutionary theory to explain behavior across cultures and species, particularly in the domains of sex and reproduction, evolutionary psychology has emerged as a major perspective in the study of intimate relationships (Fletcher, Simpson, Campbell, & Overall, 2013, 2015). At the same time, intimate relationships have been studied in depth by disciplines not traditionally guided by evolutionary theory (e.g., social psychology, communications, sociology). One common theme across these different literatures is that feelings of love function as a commitment device that joins together intimates in long-term pair bonds. Thus, there is much overlap between the ideas presented across these distinct, albeit related, disciplines. With this overlap in mind, we first discuss social psychological approaches to the study of love and then transition to evolutionary psychological approaches that build on this research by emphasizing possible functions for the existence and experience of love. We end by suggesting other topics of relationship functioning that have been much investigated by traditional psychological approaches but have not been systematically explored through the lens of evolutionary perspectives. It is our belief that there is significant value in exposing mainstream evolutionary psychologists to relevant research in the relationship-science domain more generally, and vice versa, as it is this type of cross-talk that will be most advantageous for spurring mutually beneficial collaborations (Loving & Huston, 2011).

A SOCIAL PSYCHOLOGICAL PERSPECTIVE ON LOVE AND RELATIONSHIP GROWTH

Prior to the 1970s most research on interpersonal relationships focused on identifying factors that increase interpersonal attraction (Berscheid & Walster, 1969). An assumption inherent in this research was that the development of strong feelings for another person and the eventual establishment of a serious romantic relationship begins with initial liking and grows from there. To understand love, therefore, it was believed that we first needed to understand why we begin to like other people. Challenging this assumption, Rubin (1970) conceptualized romantic love as a set of positive thoughts and feelings directed toward opposite-sex peers that could potentially lead to marriage. Liking, in contrast, was conceptualized as having a healthy respect for another person and finding the company of that person very rewarding. Indeed, self-reports of liking and loving on Rubin's newly developed scales designed to tap these different sentiments proved to be only moderately correlated. Liking is, therefore, a part of loving, but Rubin exposed the need for research on the distinctive experience of romantic love.

Over 40 years of research following Rubin's conceptualization has increased our knowledge of love, although the bulk of this research was not guided by the goal of identifying possible (adaptive) functions for love in relationships; rather, this research almost exclusively described the different types of love that may exist between intimates. The culmination of this research identified two types of love that are important for understanding pair bonding behavior in humans: passionate love and companionate love. Passionate love tends to focus the attention and sexual desires of intimates, particularly early in relationships. Companionate love, on the other hand, is presumed to take time to develop and represents strong emotional bonds between intimates.

PASSIONATE LOVE

Passionate love is best described as a state of intense longing for union with another, a feeling that is aroused particularly early in a romantic relationship. When falling in love—a relationship transition characterized if not defined by increasing passion—there is generally a heightened sense of excitement associated with experiencing new activities with a partner. There is also an air of uncertainty in new relationships, of not knowing what the future holds. Obsessively thinking of partners, of when you will be together next, and hoping that the relationship continues indefinitely are all hallmarks of passionate love.

Individuals who experience passionate love, and who spend a lot of time thinking of their partners each day, also have significantly higher circulating levels of hormones and other biological compounds, including cortisol, a stress hormone (Emanuele et al., 2005; Marazziti & Canale, 2004). For example, in a laboratory experiment in which women experiencing passionate love were asked to think of their partners and relationships in detail (e.g., to recall when they met their partners and how they fell in love), individuals exhibited a spike in cortisol that was not observed when participants were asked to think of an opposite sex friend (Loving, Crockett, & Paxson, 2009). Through the process known as gluconeogenesis, cortisol subsequently increases blood sugar which presumably provides the body with energy to confront the instigating stressor (e.g., "fight" or "flight"). Does this mean, therefore, that falling in love is a highly stressful experience that can be detrimental to our health? Not necessarily. In the field of stress and health research "starting a love relationship" and "begin to date" are believed to represent positive forms of stress (Reich & Zautra, 1981). In fact, both positive and negative life events can generate a similar physiological response generally recognized as a "stress" response (e.g., elevated cortisol levels; Rietveld & van Beest, 2007), but the effects of these events on an individual's health outcomes largely depends on the subjective interpretation of those events. Even though falling in love can seem to be experienced as stressful physiologically, it is subjectively perceived as a positive life event that tends to be associated with favourable health outcomes (Brand, Luethi, von Planta, Hatzinger, & Holsboer-Trachsler, 2007). In support of this interpretation, in a recent study both women and men showed acute increases in blood glucose levels following partner-reflection; increases in blood glucose in the partner-reflection condition were associated with concomitant increases in positive affect (Stanton, Campbell, & Loving, 2014). It is perhaps because of the influence of romantic attachments on individuals that even those who have been through a romantic rejection (i.e., unrequited love) continue to experience brain activation in neural reward centers similar to what is seen in those with more successful attachment experiences (Fisher, Brown, Aron, Strong, & Mashek, 2010).

COMPANIONATE LOVE

In contrast to passionate love, companionate love is experienced less intensely. It combines feelings of intimacy, commitment, and deep attachment toward others, romantic or otherwise, that occupy an important part of our lives (Walster & Walster, 1978). If you ask individuals to list all the types of love that come to mind, companionate types of love will dominate the list (Fehr & Russell, 1991). Companionate, or friendship-based love, develops across a wide spectrum of important relationships in our lives and is rooted in trust, caring, mutual affection, supportiveness, and friendship, among other things (Fehr, 1988).

Reis and Shaver's (1988) interpersonal process model of intimacy focuses on the role of self-disclosure, or sharing personal information with another person, and how interaction partners respond to such self-disclosures, in the development and maintenance of intimacy. According to this perspective, early relationship self-disclosure alone is not sufficient for intimacy to grow. An additional process crucial to building intimacy is the perception that the relationship partner (e.g., friend, sibling, romantic partner) reacts to the self-disclosure with a warm and sympathetic response that indicates a positive evaluation of the content of the disclosure. This response, in turn, should make the discloser feel validated, understood, and cared for, setting the stage for increasing levels of connectedness and intimacy to develop within the relationship. Feeling close and intimate with someone is based at least in part, then, on how close and intimate you perceive that person feels toward you (see also Reis, 2007). Laurenceau, Feldman Barrett, and Pietromonaco (1998) asked individuals to report on interactions lasting more than 10 minutes they had with others each day for a 1- or 2-week period to see how intimacy develops over short periods of time. Consistent with Reis and Shaver's model, participants felt closer and more intimate with interaction partners when their interactions involved more self- and partner-disclosure *and* when the participants felt that their interaction partners responded positively to their self-disclosures.

LINKS BETWEEN PASSIONATE AND COMPANIONATE LOVE

Romantic relationships often contain a mix of both passionate and companionate love, but the absence of companionate love in particular can spell trouble for the stability of relationships. John Gottman has been studying the predictors of marital success and failure for many years, and his observations led him to conclude that a solid friendship between spouses is the strongest possible foundation for successful marriages (1999). For example, in samples of both older married couples and dating couples recruited from a university population, Grote and Frieze (1994) observed that overall relationship satisfaction in both samples was more strongly related to perceptions of greater companionate compared to passionate love. Therefore, even though sexuality is an integral part of most romantic relationships, and societal norms emphasize marriage as the main dyadic relationship within which sex occurs (Sprecher, Christopher, & Cate, 2006), developing a strong friendship with romantic partners may ultimately be more important for the long-term success of the relationship than is hot sex. Evidence of this assertion comes from additional fMRI work on couples whose long-term relationships continue to be characterized by relatively intense levels of passionate love (which may describe upward of 40% of long-term married couples; O'Leary, Acevedo, Aron, Huddy, & Mashek, 2012). Acevedo, Aron, Fisher, and Brown (2012) asked 17 individuals who were married on average 21 years to undergo the same general procedure utilized in the fMRI passionate love studies of new relationships. As with those experiencing the rush that accompanies falling in love, those in long-term marriages also showed activation in dopamine-rich reward centers of the brain when viewing pictures of their spouses. But, interestingly, this long-term married sample also showed activation in oxytocin- and vasopressin-rich areas of the brain as well, the very same regions identified as linked to long-term pair bonds in other species, as well as activation in the globus pallidus, a brain area the authors note is implicated in general liking of reward sources.

Summary Romantic love contains both passionate and companionate types of love. Whereas passionate love may be a force directing attention to a particular partner, particularly in the early stages of relationship formation, companionate love may play a critical role in keeping partners together over relatively long periods of time. Although the body of research reviewed earlier was not guided by an evolutionary perspective, and did not assume particular functions for love in relationships, it does suggest love as being largely responsible for drawing partners together initially and keeping them together over time (Le, Dove, Agnew, Korn, & Mutso, 2010).

AN EVOLUTIONARY PSYCHOLOGICAL PERSPECTIVE ON THE ETIOLOGY AND FUNCTIONS OF LOVE

Consistent with these social psychological approaches to the study of love, some evolutionary perspectives explicitly view the role of love as drawing partners together and keeping them together over time (i.e., pair bonding). For example, many theorists have posited that romantic love evolved as a commitment device to maintain relational bonds between mothers and fathers and to facilitate mutual investment in offspring (e.g., Frank, 1988; Kirkpatrick, 1998; Mellen, 1981). Over evolutionary time, increased infant dependency placed greater burdens on human mothers and increased the value of paternal support in feeding and protecting young. Given that men have a genetic interest in the survival of their offspring, fathers were able to benefit reproductively by forming committed, investing relationships that would have reliably increased the probability of offspring survival (e.g., Barash, 1977; Fisher, 1998; Kenrick & Trost, 1997).

The formation of pair bonds, therefore, should translate into fitness, and an excellent review of the literature on paternal investment by Geary (2000) provides a great deal of evidence in support of this claim (but see Sear & Mace, 2008). For instance, paternal investment in the form of pair bonds has been linked in preindustrial times with increased infant health and decreased infant mortality (e.g., Hed, 1987), not only because a working father allowed a mother to spend more time with a young infant that required breastfeeding (Reid, 1997) but also because a couple with a working father enjoyed a relatively higher socioeconomic status (SES) and thus was able to provide better food and shelter for his offspring (Schulz, 1991). Paternal investment is also related to improved social competitiveness for children, such as higher SES in adulthood (e.g., Kaplan, Lancaster, & Anderson, 1998) and increased educational achievement for adolescents (e.g., Amato & Keith, 1991). Children born and raised within pair bonds have, therefore, been more likely to survive to reproductive age and to be more socially competitive later in life when they are attempting to attract mates (Geary, 2000).

Among the biological substrates linked to pair formation and paternal investment, testosterone has been implicated as a key regulator of both processes. Just as men show an increase in testosterone in competitive settings (e.g., Van der Meij, Buunk, Almela, & Salvador, 2010), men's sexual interest in women is positively associated with testosterone levels (but only after habituation to sexual stimuli; Rupp & Wallen, 2007). These findings replicate conceptually in more naturalistic settings. For example, in a study by van der Meij, Buunk, van de Sande, and Salvador (2008) heterosexual male's testosterone levels increased significantly within 5 minutes of interacting with a woman (but not after interacting with a man). Other work demonstrates similar effects (Roney, Lukaszewski, & Simmons, 2007) and indicates that women rate men as more outgoing to the extent that the men's testosterone increases. Roney and colleagues suggest such testosterone increases in these male-female interaction paradigms may motivate behaviors in males that promote attracting a mate, particularly a mate with more feminine features (e.g., Welling et al., 2008).

Whereas high testosterone appears to motivate men to seek and attract mates (and compete with others males for said mates), such efforts and competitive orientations could presumably undermine relationship stability (e.g., via increased extrapair copulation attempts) and eventual demands of the fatherhood context (i.e., nurturance versus dominance striving). Indeed, a number of studies report lower levels of testosterone in paired (i.e., those in a committed, romantic relationship) versus single men (e.g., Burnham et al., 2003; van Anders & Watson, 2007). Higher testosterone is also associated with a lower likelihood of partnering or marriage (Booth & Dabbs, 1993; van Anders & Watson, 2006), as well as decreases in relationship quality and increases in divorce (Booth & Dabbs, 1993).

More recent work suggests that sociosexuality and sexual frequency moderate the link between relationship status and testosterone in men (Edelstein, Chopik, & Kean, 2011; Maestripieri, Klimczuk, Traficonte, & Wilson, 2014; see also van Anders & Goldey, 2010). Importantly, such effects extend across the transition to parenthood. Fathers typically have lower levels of testosterone relative to non-fathers, and this pattern is especially strong for men that demonstrate stronger commitments to their partners or to parenting more generally (e.g., Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002; Jasienska, Jasienski, & Ellison, 2012; Kuzawa, Gettler, Muller, McDade, & Feranil, 2009; but see Mazur, 2014). Collectively, these lines of work indicate that elevated testosterone (within and between subjects) promotes pair formation attempts, whereas lower testosterone, typically observed in long-term pair bond relationships, promotes relationship stability and investment in offspring, at least until offspring reach reproductive age (although the exact causal direction of this link is unclear).

The prevalence of sexually transmitted diseases (STDs) may have created another selection pressure for the formation of long-term pair bonds. At least 50 STDs have been documented, ranging from viruses, bacteria, fungi, protozoa, and ectoparasites, and it is estimated that nearly 20 million new sexually transmitted infections occur each year in the United States, particularly within the 15- to 24- year-old age group (see Centers for Disease Control and Prevention, 2002). Although many of these STDs have been recently introduced to humans (e.g., AIDS), Mackey and Immerman (2000) suggest that humans have been vulnerable to these types of diseases over evolutionary history. The fertility of women in particular is severely compromised when they contract an STD, and oftentimes the disease can spread to the fetus, or to the infant as he or she passes through the birth canal. For example, women with syphilis have a heightened risk of miscarriage, premature delivery, stillbirth, and infant death, and, if left untreated, the chances that the fetus will contract the disease are almost 100% (e.g., Schulz, Murphy, Patamasucon, & Meheus, 1990). The strongest predictor of contracting STDs is the number of sexual partners (e.g., Moore & Cates, 1990); therefore, the best way to limit the risk of contracting a disease that could have lethal effects on reproductive success is to limit one's number of lifetime sexual partners. Because women are much more susceptible than men are to contracting STDs (e.g., Glynn et al., 2001; Moore & Cates, 1990), ancestral women would have differentially benefited from a more restrictive attitude toward uncommitted sex. If more inhibited women contracted less STDs and experienced greater reproductive success, they would have been more attractive as long-term mates, thus selecting for the proclivity to desire fewer sexual partners. In short, STDs may have been an important factor in the development of pair bonds over evolutionary history by enhancing the benefits associated with sexual exclusivity and increasing the reproductive success of both men and women (Mackey & Immerman, 2000).

LOVE AS A COMMITMENT DEVICE

In light of the clear evolutionary benefits conferred by long-term pair bonding, one would expect that humans have developed specific psychological and biological characteristics that promote the development and maintenance of pair bonds. Fisher posits that mating behaviors are guided by three distinct emotion systems—lust, attraction, and attachment—and that behaviors related to each set of emotions are governed by a unique set of neural activities (Fisher, 1998, 2000). The *lust system* is proposed to motivate individuals to locate sexual opportunities and is mainly associated with estrogens and androgens in the brain. The *attraction system* directs individuals' attention toward specific mates, makes people crave emotional union with these targets, and is associated with high levels of dopamine and norepinephrine and low levels of serotonin in the brain (i.e., passionate love). The *attachment system* is distinguished by the maintenance of close proximity, feelings of comfort and security, and feelings of emotional dependency (i.e., companionate love), and is associated with oxytocin and vasopressin (Carter, 1998; Insel, Winslow, Wang, & Young, 1998). Additionally, when both men and women who are deeply in love are asked to think of their partners while their brain is being scanned, regions of the brain that are associated with reward become activated, whereas they do not become activated when thinking of an acquaintance (Bartels & Zeki, 2000).

Interestingly, Fisher's attraction and attachment systems are conceptually similar to features of Bowlby's attachment theory (1969). Bowlby proposed that the process of evolution by natural selection equipped infants with a repertoire of behaviors that serve to facilitate proximity to caregivers, particularly in situations when support is required, and that these behaviors are essential for survival. Bowlby believed that the bond forged between mother and infant in childhood provides a cognitive and affective foundation for later attachments, and that as adults the attachment system serves an affect-regulation function similar to what is seen in infancy. Zeifman and Hazan (1997; see also Shaver, Hazan, & Bradshaw, 1988) have proposed that attachment is one of the psychological mechanisms that evolved to solve the adaptive problem of keeping parents together to raise offspring. The secure feelings that partners experience in each other's presence, the lonely feelings experienced while they are apart, and the desire to be together after separations are all emotional hallmarks of the attachment system and serve to keep people together in committed relationships. The hormone oxytocin plays a central role in the formation of attachment bonds between mother and infant (see Hrdy, 1999, for a review), as well as between romantic partners (Carter, 1992; Behnia et al., 2014), suggesting a mechanism that functions to promote attachments at all stages of life.

Gonzaga, Keltner, Londahl, and Smith (2001) also argued that feelings of love promote commitment to one's partner. Specifically, they proposed two psychological mechanisms that link love to commitment. First, the experience of love motivates individuals to approach their intimate partners and thus to move away from tempting alternative partners (e.g., in response to activation of the brain's reward centers). Second, the expression of love in various forms (e.g., telling your partner you love him or her, providing help and support for your partner, or gazing into your partner's eyes and smiling), communicates that you are committed to your partner and the relationship you have formed together, which serves to further strengthen the bond between individuals. Testing these ideas, the researchers asked both partners of a number of couples to answer some questions about their relationships and to engage in some videotaped laboratory interactions. Individuals reporting more love for their partners also reported desiring their partners more, were relatively happier with their relationships, spent more time in the physical presence of their partners, and engaged in a number of unique behaviors while interacting with their partners. Interestingly, these individuals were also observed to be particularly likely to nod their heads in agreement while talking to their partners and to exhibit Duchenne smiles (i.e., a type of smile that uses the orbicularis and zygomatic major muscles and is associated with positive emotional states and is almost impossible to fake). Both of these nonverbal displays reflect spontaneous behaviors linked with positive interpersonal interaction and convey important information to partners and others. In fact, when an independent group of raters was asked to watch the *soundless* videotaped interactions between couple members, the raters were able to accurately determine which individuals felt more love for their partners simply by observing the expression of nonverbal displays of love (i.e., head nods and Duchenne smiles). It appears, therefore, that intimates can decipher the amount of love felt for each other by observing each other's nonverbal behavior while they interact. Moreover, these findings suggest that humans are capable of tuning in to such displays even when they have no vested interest in the status and or outcome of specific relationships, providing preliminary evidence that identification of love relationships, so to speak, is a natural (and presumably advantageous) aspect of social nature.

Love is correlated with self-reports and interpersonal behaviors associated with high levels of commitment, but as already discussed there are likely biological markers of love and commitment. Addressing this possibility further, Gonzaga, Turner, Keltner, Campos, and Altemus (2006) measured the amount of oxytocin in the blood of a number of women after they had recounted positive emotional experiences regarding love or infatuation (study 2). Oxytocin is linked to commitment and long-term pair bonding; when released, it evokes feelings of contentment, reductions in anxiety, and feelings of calmness and security around a mate. The women in this study were also videotaped while reliving their positive emotional experiences, allowing the researchers to measure the degree to which women spontaneously displayed nonverbal signs of love and affiliation (i.e., head nods and Duchenne smiles) when thinking of their partners. Consistent with prior research, women reporting more love for their partners were observed to display more head nods and Duchenne smiles. The expression of these behaviors was significantly associated with higher levels of oxytocin in the blood. Peripheral oxytocin was not associated with displays of sexual cues (e.g., lip licks) or self-reports of love. The former finding is particularly interesting as it is in line with Fisher's distinction between the lust and attachment systems. This is the first research with humans demonstrating a link between behavioral and biological cues of love and commitment.

MAINTAINING LOVE IN THE FACE OF ALTERNATIVES

Perhaps the biggest threat to the love and commitment people feel toward their current partners is the presence of desirable alternative partners. In modern society, individuals are exposed to myriad attractive potential partners on a daily basis, including television, magazines, the Internet, and of course in person. Does this exposure to attractive alternatives to a current relationship partner undermine feelings of love for that partner? Or, do feelings of love for a partner somehow protect individuals from the lure of attractive alternatives?

Testing these competing possibilities, Kenrick, Gutierres, and Goldberg (1989) asked a sample of men to view a series of *Playboy* centerfolds (physically attractive nude women), and a sample of women to view a series of *Playgirl* centerfolds (physically attractive nude men). After viewing the nude photos of beautiful women, men reported being less attracted to their current partners; however, a parallel effect did not emerge for women viewing *Playgirl* centerfolds. Additional research by Kenrick, Neuberg, Zierk, and Krones (1994) that had romantically involved men and women view profiles of opposite sex others that varied on physical attractiveness and social dominance continued to demonstrate that men rated their current relationships less favorably after being exposed to physically attractive, but not socially dominant, profiles. Women, on the other hand, reported less positive feelings toward their partners after viewing a number of profiles of men described as being high in social dominance. Overall, people tend to feel less positively, including less love, for their current partners after exposure to attractive alternative partners.

A logical question to ask, therefore, is how do individuals in satisfying and committed relationships maintain their affections for one another in a world filled with attractive alternatives? Love may direct our attention to the target of our affections, but does it direct our attention away from potentially appealing others as suggested by Gonzaga and colleagues (2001)?

Researchers have identified at least two psychological processes that serve to buffer established relationships from the lure of attractive alternatives. First, individuals in established relationships, compared to their less committed or single compatriots, tend to perceive attractive opposite sex individuals as less appealing. For example, in a series of studies, Johnson and Rusbult (1989) reported that individuals more committed to their current partners and relationships were more likely to derogate (i.e., put down or devalue) potential alternative partners on a number of traits (e.g., intelligence, sense of humor, faithfulness, dependability). People feeling less committed to their current partners and relationships, however, not only failed to derogate potential alternative partners, but they were also less likely to remain in their relationships over time. Simpson, Gangestad, and Lerma (1990) had samples of dating and single individuals review a number of magazine advertisements that ostensibly were being considered for use in a marketing campaign. Of the 16 advertisements presented to participants, only 6 of them contained pictures of attractive opposite sex models. After viewing each advertisement, participants were asked to rate the physical and sexual attractiveness of each model. Both men and women involved in dating relationships rated the physical attractiveness of the opposite sex individuals in the advertisements much less positively than did single participants. In other research testing individual's motivation to derogate the attractiveness of potential alternative partners, participants in committed relationships were led to believe that an attractive opposite sex individual was attracted to them, thus providing the participants realistic alternatives to their current partners (Lydon, Meana, Sepinwall, Richards, & Mayman, 1999). Those in committed relationships, however, subsequently rated the potential alternative partner as less attractive, presumably to defuse the threat posed by having a realistic alternative to approach. Perceiving potential opposite sex alternative partners as less appealing, therefore, helps individuals maintain the love and commitment they feel toward their current partners.

Second, people in established relationships do not always have to go through the process of devaluing the attractiveness of opposite sex alternatives. Instead, they can simply not pay attention to attractive opposite sex individuals in the first place. For example, Miller (1997) asked dating participants to inspect an array of photographs presented on a screen via a slide projector. Included in the series of slides were pictures of physically attractive members of the opposite sex. Participants controlled the amount of time they spent viewing each picture with a remote control, and the viewing time for each photo was privately recorded by the experimenter. Miller found that individuals that reported being more satisfied and committed to their partners reported spending less time viewing the photos of attractive opposite sex pictures, and, indeed, they were observed to click through the pictures of attractive others more quickly than other photos. Interestingly, spending less time viewing the attractive opposite sex photos was also linked with a lower likelihood of the relationship ending at a 2-month follow-up. Similarly, research by Gonzaga, Haselton, Smurda, Davies, and Poore (2008) established that relatively strong feelings of love for a partner can assist individuals in suppressing thoughts and feelings they may have for attractive alternative partners. In their study, participants were asked to select the picture of an opposite sex individual out of an array of pictures that they found most appealing, and then to write a short essay on (a) why the person in the picture was attractive, and (b) the ideal way to be introduced to this person. Participants were then randomly assigned to write an essay about their love for their current partner, their sexual desire for their current partner, or their current stream of consciousness. Only participants induced to feel love for their partners reported fewer thoughts of the attractive alternative partner during a subsequent task (again providing support for Fisher's three-system model). Feelings of love for a partner, therefore, can reduce temptation to view images of attractive alternative partners as well as ruminate or daydream about the allure of alternative mates.

Does being inattentive to potential alternative partners have to be a conscious choice made by people in loving, committed relationships? Or can these "decisions" be made automatically, thus requiring little if any deliberation? To address this question, Maner, Gailliot, and Miller (2009) used what is known as an implicit measure of (in) attention to alternatives. Maner and colleagues studied participants who were either single or currently in a relationship. They were asked to view a computer screen, and, unbeknownst to them, a word (i.e., prime) either directly related to mating goals (e.g., kiss), or relatively neutral in nature (e.g., floor), was presented under conscious awareness. A picture of an attractive opposite sex individual would then appear in one quadrant of the computer screen for a brief period of time in the trials of interests. After the picture was removed from the screen, a categorization object (a circle or square) would appear on the opposite side of the screen (called the "attention shift trials"). The participants then needed to press a button as fast as possible to categorize the picture as a circle or square. As predicted, participants in committed relationships were able to complete attention shift trials much faster than single individuals, but only when those in relationships were primed with mating-relevant words. The authors suggested that being exposed to mating-relevant words primed the importance of the relationship to the dating participants, thus making them pay less attention to the attractive photo and enabling them to shift their attention away from the photo very quickly during the categorization task. The same pattern of results, using a different method of priming thoughts of romantic love, was also reported by Maner, Rouby, and Gonzaga (2008).

The importance of these studies is that they convincingly demonstrate that individuals can reduce their attention to attractive alternatives at a very early stage of visual processing. That is, inattention to attractive alternatives can be an automatic process for individuals in established relationships, helping them maintain feelings of love and commitment for their partners. In fact, the process may be so automatic that disrupting the process, unbeknownst to subjects, results in greater attention to alternatives. DeWall, Maner, Deckman, and Rouby (2011) demonstrated this paradoxical effect in three experiments in which they interfered with participants' abilities to freely limit their attention to alternatives. Over a series of trials, participants were presented with two faces simultaneously, one more attractive than the other, outside of conscious awareness. Participants were subsequently asked to type a letter that appeared on the screen where one of the two faces had appeared. In one condition, participants were consistently asked to type a letter that appeared where the less attractive face had been whereas participants in the other condition typed a letter that appeared randomly across trials over one of the two faces. Afterwards, participants indicated their degree of satisfaction and commitment toward their relationships as well as their general attitudes about infidelity. Participants in the former condition, what the research team referred to as "attention limiting," subsequently reported lower relationship satisfaction and commitment and more positive attitudes toward infidelity (study 1) as well as better memory for the attractive faces (study 2). In other words, implicitly limiting the attention individuals can give to alternatives actually causes them to attend to and remember those very same attractive alternatives better and undermines their own relationship evaluations. Interestingly, when attention is left unabated and individuals are given time to closely attend to attractive others, attached women remember an encountered attractive face, but remember the face as being less attractive than it actually was (Karremans, Dotsch, & Corneille, 2011). Collectively these studies suggest that we have evolved complex cognitive processes designed to maintain and promote romantic connections in the face of possible alternatives.

MATE-RETENTION STRATEGIES

For successful mate retention to occur, however, individuals must avoid tempting alternatives *and* engage in mate-retention strategies in contexts that actually provide attractive alternatives to their partners. For example, Buss and Shackelford (1997) suggested that situations more closely aligned with the relationship goals of men and women should be related to their mate-retention behaviors. For instance, men and women rely on different qualities of their partners to aid in their own reproductive success. Men are capable of producing sperm from puberty until well into old age, whereas women are born with a limited number of ovum that can be fertilized only during a circumscribed period of time, with fertility peaking in the mid-20s and decreasing significantly over time to essentially zero in the later 40s. Younger women are, therefore, more reproductively valuable relative to older women. Also, physical features related to increased fertility (e.g., low waist-to-hip ratio, Singh 1993) are rated as universally attractive to men (Buss, 1989; Symons, 1979), making physical attractiveness—in addition to age—another component of women's mate value. Younger, more physically attractive women are more desirable mates because of their increased fertility, but are also more attractive to potential "mate poachers" who may attempt to woo them into extrapair copulations, or to leave their partner. Men married to women higher in mate value (i.e., younger, more physically attractive women), should, therefore, devote more time to mate-retention behaviors.

Men's mate value as long-term partners, on the other hand, rests largely on their ability and willingness to provide external resources to the partner and relationship (Buss, 1989). Men that possess many resources, or have the ability to acquire resources, and are more willing to share these resources (Graziano, Jensen-Campbell, Todd, & Finch, 1997), should be more desirable as mates, and may be the target of "mate poaching" tactics of other women. Women married to men with more resources should, therefore, devote more time to mate-retention behaviors.

Buss and Shackelford (1997) tested these hypotheses with a sample 107 married couples. Participants completed Buss' (1988) scale of mate retention that contains 19 different mate-retention acts, as well as various other measures associated with the perceived mate value of partners, and satisfaction with their marital relationship. In general, men, relative to women, reported using resource display as a mate-retention tactic; women, on the other hand, reported using appearance enhancement more as a mate-retention tactic than did their husbands. Importantly, men's use of mate-retention tactics was strongly related to the youth and perceived physical attractiveness of their partners, whereas women's mate-retention behaviors were weakly related to their husband's age and perceived physical attractiveness. However, women's mate-retention behaviors were positively correlated with their husbands' income and husbands' reported status striving behaviors, whereas men's mate-retention behaviors were not related to their wives' income or status striving behaviors. Confirming predictions, men and women appeared more motivated to maintain their relationships, and thus prevent the interference of their relationship goals, when they had partners that possessed the qualities most closely aligned with the success of their relationship goals.

The experience of jealousy is a negative emotional experience resulting from the potential loss of valued relationships to real or imagined rivals (Salovey, 1991) that is closely related to the enactment of mate-retention behaviors. Buss (2000) suggests that, over evolutionary history, individuals that were vigilant to interlopers experienced greater reproductive success compared to those who were less concerned about rivals. If jealousy has played an important role in the evolution of human relationships, it should be a universal human emotion. Indeed, that appears to be the case (Buss et al., 1999). Additionally, men and women do not differ in the frequency or intensity of their jealousy (e.g., Buss, 2000; Buunk, 1995; Shackelford, LeBlanc, & Drass, 2000), suggesting that jealousy has played (and continues to play) an important role in the retention of partners and relationships for both sexes.

There are differences, however, between men and women in their experiences of jealousy, and these differences neatly overlap with their different goals in relationships. Whereas women can be confident that they are in fact the mothers of their children, men cannot be certain that they are the father. Paternity uncertainty should make men more sensitive to cues of sexual infidelity of their partners, and wary of rivals that are friendly or flirtatious with their partners (Symons, 1979). Natural selection may have even favored men who have a low threshold to cues of sexual infidelity, as the benefits of being cautious outweigh the costs of not being cautious enough (e.g., Haselton & Buss, 2000). Although maternity uncertainty has not been an issue for women, securing the resources necessary to raise highly dependent offspring was a challenge for ancestral women. The ability to raise offspring to reproductive age would be severely compromised if paternal investment were to be directed elsewhere, and, therefore, women should be sensitive to cues indicating emotional infidelity of their partners. If a man "falls in love" with another woman and subsequently leaves the relationship to form another, his resources will be largely directed away from the abandoned woman. Natural selection may have, therefore, favored women who underestimate the amount of commitment men have to relationships, and are particularly sensitive to signals that their partners are forming emotional bonds with other women (Haselton & Buss, 2000).

To date, a great deal of research supports the notion that men's jealousy is particularly responsive to cues of sexual infidelity, whereas women's jealousy is principally related to cues of emotional infidelity (for a review, see Buss, 2000; but see DeSteno, Bartlett, Braverman, & Salovey, 2002, and Harris, 2003, for challenges to these data). For example, Buss, Larsen, Westen, and Semmelroth (1992) asked men and women to imagine a close romantic relationship, and then to imagine the partner becoming involved with someone else. When asked what sort of involvement would bother them the most, men selected imagining their partner enjoying passionate sexual intercourse with another person, whereas women selected imagining their partner forming a deep emotional attachment to another person. This basic pattern of effects was replicated with physiological data showing that men displayed greater electrodermal activity (EDA) and increased pulse, as well as greater muscular tensions measured by EMG activity of the *corrugator supercilii* muscle (a muscle associated with "furrowing" of the brow, and expressing negative emotion), when imagining a partner's sexual relative to emotional infidelity, whereas the pattern was reversed for women. Men also report more difficulty in forgiving a sexual infidelity than did women; men also report a greater likelihood of ending a relationship following a partner's sexual rather than emotional infidelity that did women (Shackelford, Buss, & Bennett, 2002). Further, evidence from cross-cultural research suggests that husbands are more likely to divorce wives who have engaged in sexual infidelities, whereas wives are less likely to divorce husbands who have engaged in similar behaviors (Betzig, 1989). This general pattern of results is not surprising given that men's relationship goals center on directing resources to their own, and not somebody else's, children, whereas women's relationship goals center on retaining resources to direct to offspring.

CONCLUSIONS AND FUTURE DIRECTIONS

Overall, there seems to be a great deal of empirical evidence—spanning cognitions, behaviors, and physiology—for the argument that love is a commitment device that brings intimates together and helps keep them together for relatively long periods of time (see Fletcher et al., 2013, 2015). Interestingly, this evidence is consistent regardless of the theoretical perspective guiding the research (e.g., social psychological theories focusing on proximate causation, or evolutionary perspectives focusing on ultimate causation, of behavior). Whereas the social psychological research reviewed has done an excellent job of describing different types of love and discovering the importance of love in the development of romantic relationships, the evolutionary psychology research reviewed has played a critical role in understanding the etiology and functions of love and pair bonding in humans. Considered collectively, a more holistic view of love in human romantic relationships is achieved.

Where do we go from here? A large number of topics of investigation in the field of relationship science (e.g., relationship maintenance, conflict resolution, sexual intimacy, dissolution, attributions, interdependence) are the focus of relatively less research guided by evolutionary theory (but see Meltzer, McNulty, Jackson, & Karney, 2014, for recent research on marital satisfaction over time and wives' physical attractiveness). As one example, research on links between passionate and companionate love do not make predictions regarding specific types of "shared novel activities" that should heighten passion. It is quite possible that novel activities that have served important adaptive functions are particularly profound inducers of passion. Additionally, research on conflict in romantic relationships typically focuses on how to best manage conflict and on ways to "fight fairly," but does not always make specific predictions regarding issues that are likely to be the target of difficult conflicts. Further, we still need to do more work on identifying exactly what specific hormone changes that accompany relationship formation and maintenance actually mean and whether such changes involve neuroendocrine systems implicated in older versus newer neurological structures. These are areas of research in which evolutionary perspectives can assist in making more fine-grained hypotheses and provide more nuanced interpretations of empirical findings. Given the large body of existing research on these topics, there are, therefore, many opportunities for relationship research to view these topics through an evolutionary lens, as was done with the topics of love and commitment.

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PART IV

PARENTING AND KINSHIP

MARTIN DALY

PSYCHOLOGY NEEDS DARWIN, AGAIN

Few topics demonstrate psychological science's desperate need for evolutionary theory as starkly as parenting and kinship. Lacking a Darwinian perspective, mainstream psychologists had no idea how to approach these central domains of human existence, and simply neglected them. If you can somehow collect a valid, representative sample of human social interactions, I guarantee you that close genetic relatives will be prominent in your data, but no social science has paid less attention to "blood ties" than social psychology. And although parental care consumes an immense proportion of human time, energy, and attention, psychologists have had little more to say about the psychology of parenting.

Google "parenting" plus "psychology" and what you'll find is pep talks encouraging you to be more child-centric and advice about how to prepare your kids for success. (Should you be more of a "tiger mother"?) How parents actually feel and behave surfaces mainly in taxonomies of parenting styles, which are discussed only with respect to their alleged impacts on child development. Well, that's pop psychology, but the academic literature, except for that which is explicitly evolutionary, yields scarcely more. Consult a general motivation textbook or treatise, for example, and you may find, at best, a page or two on how to induce the "maternal state" in a virgin rat, or whether maternal "drive" results from pressure in the mammary glands. And yet the theory required to generate a rich set of well-founded and well-supported hypotheses about the sources of variability in women's and men's parental efforts and inclinations has long been available. As the six ensuing chapters, comprising Part IV of this handbook, all demonstrate, the theory that psychologists have so desperately needed was and is Darwin's. All motivational mechanisms, including those modulating parental efforts, are products of natural selection, and can, therefore, be understood as strategic means to the end of genetic posterity.

As regards kinship, genealogical relatedness has been central to evolutionary biology's analysis of social phenomena since Hamilton (1964), whose seminal theory of inclusive fitness is introduced in Chapter 19 by Hames and informs all six chapters in Part IV. Because Hamilton's theory identifies what it is that any species' social psychology has evolved to accomplish, it is generally recognized by biologists as the essential framework for analyzing social evolution (West & Gardner 2013). But you don't need math to recognize the centrality of kinship in human affairs. Anthropologists just had to watch people and listen to them. According to the eminent British social anthropologist Edmund Leach, "Human beings, wherever we meet them, display an almost obsessional interest in matters of sex and kinship" (Leach 1966, p. 41).

Ask any sample of people who they feel closest to, care the most about, would sacrifice the most to help, and the bulk of the nominees will be either close genetic relatives or the romantic partners of your respondents. It is, therefore, scandalous that experimental social psychology remains overwhelmingly a science of stranger interactions, a state of affairs that I blame mainly on an addiction to the convenient "pool" of captive undergraduate research participants. As I write, the most recent complete volume of the *Journal of Personality & Social Psychology*, considered by many to be the field's top journal, is Volume 106, January–June, 2014; the 58 primary research reports therein include just six that are about social interaction with anyone other than strangers. Only one treats genealogical kin as a meaningful social and mental category.

JOINING FORCES WITH ANTHROPOLOGISTS

Fortunately, the evolutionary psychologists who have tackled these neglected topics have had a lot of help from evolutionary biologists, and from anthropologists, many of whom are contributors to this handbook. Attending to and collaborating with anthropologists is a psychologist's best defense against making the ethnocentric error of imagining that the familiar practices of her own culture provide a direct window onto human nature. So it is a heartening sign of synthesis in the community of scientists who study "evolution and human behavior" that four of the five chapters in this *Handbook*'s Part I (Foundations of Evolutionary Psychology) have been authored or coauthored by anthropologists. And here, in Part IV, we have three new chapters, all by anthropologists, in addition to three chapters that constitute updated versions of contributions to this *Handbook*'s first edition, one of which is again by anthropologists.

In Chapter 19, Raymond Hames, an evolutionary anthropologist with extensive field experience among tribal horticulturalists in Amazonia, provides a brisk review of Hamilton's inclusive fitness theory, and of some of the many ways in which it has begun to elucidate human affairs.

The most striking peculiarity of human family life, in comparison to the behavior of other living hominids, is the parental participation of men, so in Chapter 20, David Geary provides a thorough and thoughtful review of the ideas and evidence bearing on why paternal investment evolved in our lineage, and why it nevertheless remains spotty. This review updates Geary's treatment of the same topic in this *Handbook*'s first edition, incorporating new evidence on the endocrinology of paternal behavior, on fathers' impacts on child outcomes, and on how boys' childhood experiences affect their subsequent behavior as fathers. Almost half of the 120 references cited in this revised chapter are new.

Like Geary, Catherine Salmon has updated her treatment of parental investment and parent-offspring conflict in Chapter 21. Since the seminal paper by Trivers (1974), formal models of parent-offspring conflict have proliferated, but Salmon is able to convey the essential ideas with admirable clarity while eschewing mathematics. One novel topic is the initially puzzling phenomenon of systematic disagreement between young adults and their parents about the offspring's mate-selection criteria, and Salmon briefly introduces the new thinking and findings.

Chapter 22, by anthropologist Ruth Mace, is a new addition to the *Handbook*. Mace endeavors to integrate many important topics of relevance to human social evolution and cross-cultural diversity, including the peculiarities of our species' evolved life history, with its prolonged prereproductive phase and its even stranger postreproductive phase; how different modes of subsistence, property ownership, and heritable wealth affect and are affected by family structure and family relations; and why fertility has declined in a context of relative abundance (the demographic transition), in seeming defiance of a Darwinian imperative to maximize reproduction.

Chapter 23, by anthropologists Coren Apicella and Alyssa Crittenden, is another new addition to the handbook, zeroing in on what we know about parenting and kinship among hunter-gatherers. Evolutionary psychologists have long stressed the importance of hunter-gatherer lifeways as the crucial social and material environment of evolutionary adaptedness (EEA) in which our species' attributes evolved. This view has sometimes been criticized as unduly essentialistic on the grounds that hunter-gatherer societies are diverse, that contemporary hunter-gatherers have been affected by their agricultural neighbors, and that the hallmark of human success has been flexibility of social practices. Apicella and Crittenden are fully cognizant of these complications, but make a convincing case that hunter-gatherer studies do indeed provide crucial evidence bearing on hypotheses about the nature of human sociality and about how and why it evolved.

Chapter 24, by anthropologists Mark Flinn and Carol Ward, is another update, with the central topic being the peculiarities of the human family, human development, and social endocrinology. In reviewing the latest information and ideas on these topics, Flinn and Ward maintain a strong comparative focus, and thereby make it evident that a number of aspects of human family life and sociality more generally are true evolutionary novelties.

While celebrating this interdisciplinary synthesis, we mustn't forget that convincing anthropocentric social scientists that they need a Hamiltonian overview is a long, uphill struggle, and one that is far from over, as will be apparent to anyone who peruses recent issues of the many journals that include the word *family* in their titles. Anthropology had a head start over psychology in its attention to kinship, but influential figures like Marshall Sahlins and David Schneider naively insisted that cross-cultural diversity proves that human kinship has no biological basis, and the bankrupt biology-culture dichotomy still bedevils the extensive, stagnant backwaters of cultural anthropology. We're all in this together.

INCLUSIVE FITNESS ISN'T (QUITE) EVERYTHING

In my opinion, there is one substantive challenge to the proposition that Hamilton's inclusive fitness theory has given us the essential metatheory for social evolution, and hence for evolutionary social psychology. None of the six chapters in Part IV mention it, so I feel I should. No, it's not any of the multilevel selection models that have tried to give between-group selection new life as an explanatory principle. Even their proponents admit that multilevel models are simply alternative accounting practices that are interchangeable with inclusive fitness accounting, and I am not aware of any cases in which they have yet been shown to yield more fruitful insights. The substantive challenge to which I refer is one "from below" rather than "from above": the issue of intragenomic conflicts.

Imagine a woman with a novel mutation on one of her two X chromosomes. There is a 50% chance that her X (like any of her autosomal genes) will be transmitted to each child, regardless of its sex, but what of her grandchildren? Her daughter's children of either sex have a 25% chance of inheriting the mutant, but if her son has a daughter, that granddaughter will definitely get her father's maternal-origin X (the only one he has) and thus has a 50% chance of carrying the mutant, whereas a son's son has a 0% chance. Now imagine that the mutation's phenotypic effect is to bias investment toward sons' daughters at the expense of sons' sons. *Any* resultant gain in the son's daughter's fitness, however small, at the expense of a loss in the son's son's fitness, however large, would be sufficient to give the mutant X a selective advantage! This situation, dubbed "sexually antagonistic zygotic drive" (SAZD) by Rice, Gavrilets, and Friberg (2010) is not simply hypothetical (Friberg, Stewart, & Rice, 2011).

One might imagine that SAZD couldn't possibly be important in creatures like ourselves, given both the competing interests of the rest of the genome and the fitness interests of other relevant persons besides paternal grandmothers. But if costs to male children were offset by benefits to female children, selection for suppressors would be weak until the sex ratio became seriously unbalanced. Interestingly, there are data that have been interpreted as indicative of SAZD in humans (Fox et al., 2010), and the case is open.

SAZD is an intriguing idea, but its relevance in human social evolution, if any, is still up in the air. However, we already have plenty of convincing evidence that genes whose transmission dynamics make their fitness interests distinct from the inclusive fitness interests of their organism have important phenotypic effects on intrafamilial interactions, especially imprinted genes (Crespi, 2011; Haig, 2002, 2009). During the sociobiological revolution that began in the 1960s, as it became increasingly clear that one had to think about the "fitness interests" of genes in order to understand social evolution, it was Hamilton's concept of inclusive fitness that allowed us to retain our focus on the organism as an actor with an integrated agenda. But the many forms of intragenomic conflict oblige us to acknowledge that the apparent integrity of the individual is to some degree illusory (Burt & Trivers, 2008).

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CHAPTER 19

Kin Selection

RAYMOND HAMES

INTRODUCTION

When Hamilton (1964) published his theory of inclusive fitness it had no immediate impact in the social and behavioral sciences, even though ethnographers knew kinship to be a universally fundamental factor in human social organization, especially in egalitarian societies in which humans have spent nearly all their evolutionary history. In many ways, it was a theory that perhaps anthropologists should have devised: Anthropologists knew kinship fundamentally structured cooperation, identity, coalition formation, resource exchange, marriage, and group membership in traditional societies. It was not until 1974 with the publication of Wilson's *Sociobiology* (1975) and especially Richard Alexander's *The Evolution of Social Behavior* (1974) that evolutionary social scientists began to take note of the potential of kin selection as a powerful theory that could revolutionize the study of human social behavior. Alexander was the first to comprehensively demonstrate that ethnographic and psychological evidence provided strong support that hypotheses drawn from kin selection would be a productive area of investigation. His review of the anthropological literature on kinship, especially of the Human Relations Area Files (HRAF), was elaborated more fully in *Darwinism and Human Affairs* (1979). For example, Alexander's prediction that paternity uncertainty would skew nepotism matrilaterally (1974, pp. 373–374; 1979, p. 169) is now well documented. In addition, he provided important preliminary evidence that suggested that kin selection would help us understand food transfers and cooperative economic activities (Alexander, 1979, pp. 144–161), and that kin selection and reciprocal altruism would be closely linked (1979, pp. 52–58).

Meaning and Measurement in Kin Selection

What has become known as Hamilton's rule is at the heart of kin selection theory and it states that helping or cooperative behavior between any two individuals can evolve so long as benefit to the recipient's fitness is greater than the cost to the donor, devalued by the coefficient of relatedness between donor and recipient, or $Br - C > 0$. Although the general implications of the theory are relatively easy to comprehend, there have been a number of misunderstandings of its technical elements. Chief among them is that belief that relatedness refers to the proportion of genes shared, when, in reality, it is the probability that two individuals have genes in common as a consequence of immediate descent. This error and others are discussed by Dawkins (1979) and Queller (1996), whereas Park (2007) reviews erroneous or problematic characterizations of kin selection in social psychology text books. There is a growing literature on joint or coordinated behavior that may appear to be examples of kin-based nepotism but, in fact, may be instances of reciprocal altruism, mutualism, coercion, or manipulation (Clutton-Brock, 2009).

THE STATUS OF KIN SELECTION IN NONHUMANS

Cooperation and helping behavior among kin is well documented in a variety of animal species especially those that live in small, stable breeding groups with high degrees of relatedness. In a general review of kin selection in nonhumans, Griffin and West (2002, p. 1) assert:

> Hamilton's inclusive fitness theory represents one of the most important developments in evolutionary biology. In particular, the idea that individuals benefit from the reproduction of relatives (kin selection) has been extraordinarily successful in explaining a wide range of phenomena, especially cases of supposed altruism.

The evidence for kin selection in primates, largely through maternal links (reviewed by Silk, 2009), has been documented in baboons, macaques, vervets, gorillas, and red howlers. Kinship is crucial for social networks, grooming, coalitions, and dominance relationships.

In chimpanzees there is some evidence of reciprocal altruism in a variety of behaviors such as grooming, coalitionary support, and meat and sex exchanges (Gomes & Boesch, 2009). However, only very recently has kin selection been reasonably well established as a mechanism for cooperation among chimpanzees. Langergraber, Mitani, and Vigilant (2007) showed that maternal brothers were more likely to associate, groom, maintain proximity, support one another in conflicts, share meat, and jointly patrol. These patterns were not found for paternal brothers because of promiscuous mating among chimps. However, in a study based on 14 years of observation Lehmann, Fickenscher, and Boesch (2006, p. 931) found that chimp fathers spent more time playing with their own offspring and conclude that "our data show for the first time that wild chimpanzee males can recognise their own offspring." However, consistent with Langergraber et al. (2007), they found affiliative matrilateral links to be far stronger.

RECIPROCAL ALTRUISM AND KIN SELECTION

In many instances, reciprocal altruism (Trivers, 1971) is an alternative or even complementary model to explain cooperation. The general difference is that relatedness is zero and the payoff to the helper occurs in the future. Clutton-Brock's (2009) review of reciprocal altruism in nonhuman species shows that we have few examples of nonhuman intra-specific reciprocal altruism even though allogrooming in primates come close. Clutton-Brock draws several important conclusions: (a) most cases of purported reciprocal altruism can be explained as either examples of mutualism (simultaneous gain by both interactants) or manipulation, and (b) apparently convincing cases of reciprocal altruism may involve kin selection. He concludes that reciprocal altruism exists in humans because of language to communicate long-term intensions of interactants and "social norms" that prevent or discourage cheating.

Human Evolutionary History and Why Kin Selection Should Be Important

Humans, until quite recently, lived for much of their history in hunting and gathering bands of about 50 individuals (Binford, 2002). Hill et al. (2011) have recently investigated the degree to which kin relatedness structured bands in a comparative analysis of 32 hunter-gatherer societies. On average only about 10% of an adult (age >15) individual's primary adult kin (parents, siblings, or offspring) will be coresidents and about 25% of coresidents will be made up of close and distant kin. Mean relatedness of all adult Ache and !Kung band members to one another is 0.054 (slightly less than a half cousin). These measures should be viewed as underestimates because measuring relatedness only among adults hides the fact that an individual's subadult grandchildren and nephews and nieces are related by 0.25 were not counted, even though in hunter-gatherer groups subadults comprise about 50% of band members. Quarter relatedness kin ties are important because, as will be shown later, kin altruism tends to flow from senior (aunts, uncles, and grandparents) to junior kin (nephews, nieces, and grandchildren) as a consequence of differences in reproductive value. Hill and colleagues do note that historical factors such as pacification and the influence of colonial power and trade relations at the time kinship data was recorded could have altered the kin structure in these bands. Be that as it may, because of this alleged low level of relatedness, the authors declare, "These patterns produce large interaction networks of unrelated adults and suggest that inclusive fitness cannot explain extensive cooperation in hunter-gatherer bands" (Hill et al., 2011, p. 1286). They are unclear what extensive cooperation is and who one could rely on for critical cooperation. A similar but more detailed analysis was done on the Hadza drawing this conclusion "Although the Hadza have a preference for kin as both campmates and gift recipients . . . the Hadza also actively form many ties with non-kin" (Apicella et al., 2012, p. 500).

APPROACHES TO THE STUDY OF KIN SELECTION

Evolutionary psychology and behavioral ecology are the two broad approaches taken in the study of kin selection in humans, although there can be considerable overlap. In part, the differences revolve around the kinds of questions asked, which often lead to different methodological approaches. Evolutionary psychology generally focuses on elucidation of mental modules that produce attitudes, expectations, orientations, and emotions toward kin and how kin are recognized. Most of the work is done through surveys and experiments. In contrast, behavioral ecologists who are mostly anthropologists observe behavior and fitness outcomes or associated proxies in naturalistic settings. The emphasis is on what subjects actually do and the reproductive impact of behavior. In many instances researchers in both camps overlap methodologically especially in the use of survey instruments to collect nonobservational, informant-generated data such as reproductive histories on fertility and survivorship, bequests in wills, and characterization of patterns of interaction with kin.

Another general contrast is the behavioral ecologists' study of traditional non-Western populations who live in social conditions that more closely approximate the environment of evolutionary adaptedness. In contrast, evolutionary psychologists more frequently study Western, educated, industrial, rich, and democratic or WEIRD peoples (Henrich et al., 2010). In some instances there is a point of tension over evolutionary predictions can be best tested by demonstrating the design features of mental modules in terms of how they lead to adaptive behaviors or how these behaviors actually affect measurable proxies of fitness such as growth, survivorship, and fertility (see Daly & Wilson, 1999 and a response by Smith, Borgerhoff Mulder, & Hill, 2001). Notwithstanding, both approaches are complementary because they work at different levels of analysis such that both approaches are required to gain a complete picture of the dynamics of kin selection or any evolved human behavior.

The balance of this chapter is organized by topics covered by researchers in the study of kin selection. I begin with topics that have been dominated by evolutionary psychologists and then move to topics that increasingly are dominated by behavioral ecologists.

THE EVOLUTIONARY PSYCHOLOGY OF KINSHIP

As recently as 1997, Daly, Salmon, and Wilson (1997) declared that psychologists had made few contributions to the study of kinship even though their research agenda encompasses interpersonal relationships. As Daly and Wilson (2005) now note, this situation has improved significantly with considerable research on kin recognition, emotional closeness, empathy, and kin support reviewed next.

KIN RECOGNITION

Kin recognition is widely studied in animals and reveals that multiple mechanisms are employed such as olfaction, cosocialization, habituation, and phenotypic matching (Park, Schaller, & van Vugt, 2008). For nepotism to function effectively, an organism has to be able to reliably distinguish between close, distant kin, and nonkin. All cultures have culturally based kinship classification schemes that distinguish between near and distant kin (based on genealogical closeness) and specify mutual expectations about helping behavior, coalition membership, marriage, mutual rights and obligations, and affective ties. Jones (2004, p. 214) notes that universal features of kinship terminological systems include genealogical distance, social rank, and group membership. From an evolutionary psychological perspective, Lieberman, Tooby, and Cosmides (2007) argue that humans have special mental circuitry to detect cues of kinship and compute them through a kinship estimator that gives us an idea of how close or distant the relationship is. This estimator generates appropriate emotions such as disgust in relation to contemplation of sex with close kin to a willingness to assist kin depending on their degree of relatedness. Lieberman, Oum, and Kurzban (2008) argue that kinship along with sex and age may be universal social categories people employ to guide their social interactions.

Phenotypic Matching The degree to which individuals are phenotypically similar may be a signal of genetic kinship. The research to date focuses on facial similarity, attitude similarity, and common surnames. One study uses self-assessed overall physical similarity (Bressan & Zucchi, 2009) based on 12 physical traits, whereas all other studies are based on single phenotypic attributes such as facial similarity. Very useful reviews of this literature can be found in Park et al. (2008) and Arantes (2012).

Facial Similarity Considerable research has been done on facial similarity although much of it focuses on mate choice and paternity determination (DeBruine, Jones, Little, & Perrett, 2008). In an interesting marriage of behavioral economics and evolutionary psychology, several studies of facial similarity show enhanced cooperation in a public goods game (DeBruine, 2002; Krupp, DeBruine, & Barclay, 2008) and perceptions of trustworthiness (DeBruine, 2005), and altruism toward children who resemble adult subjects (DeBruine, 2004).

Association Patterns The widely known Westermarck hypothesis (see Wolf & Durham, 2004, for a review) posits a relationship between intimate patterns of childhood association (or cosocialization) leading to an absence of sexual attraction and even disgust at the very idea of sexual relations among individuals who have been reared together as siblings or as if they were siblings. Lieberman, Tooby, and Cosmides (2003, 2007) argue that sibling childhood association (or cosocialization) and maternal perinatal association are key elements of kin recognition that not only lead to incest avoidance but also to sibling altruism. The addition of maternal perinatal association (observing one's mother caring for an infant) is an important advance because it is a mechanism that prevents older siblings who might spend little or no time growing up with younger siblings from having a sexual interest in them. It is unclear whether the maternal perinatal association can be extended to account for grandparental altruism and whether there are other associative cues for kin identification.

EMOTIONS UNDERLYING KIN ALTRUISM

A number of researchers have attended to the possible emotional mechanisms such as emotional closeness, emphatic concern, and empathy that underlie kin relationships. It is an area that has been less well studied compared to research on willingness to help, patterns of interaction, and actual patterns of help. According to Park and Schaller (2005), the altruistic mechanisms that trigger assistance to friends and kin may be very similar, and there may be sexual differences in how these mechanisms are activated (Ackerman, Kenrick, & Schaller, 2007).

Korchmaros and Kenny (2001, p. 262) use a measure called emotional closeness defined as "a sense of concern, trust, and caring for another individual and enjoyment of the relationship with the individual." They asked college students to choose which of their family members they would most likely provide with life-saving assistance. They found that emotional closeness and kinship independently predicted altruism, and kinship was strongly associated with emotional closeness. A later study by Neyer and Lang (2003) found that measures of subjective closeness (those who one could not live without) and support received on a regular basis (daily assistance, encouragement, and social support) was significantly correlated with kinship even after controlling for proximity and age. Maner and Gailliot (2007) posit that empathic concern (concern for the welfare of others) more strongly motivates altruism toward kin compared to strangers. Finally, Jeon and Buss (2007) show that empathic concern and emotional concern are correlated and both have independent effects on kin altruism toward cousins.

Kruger (2003) examined the psychological constructs of oneness (a sense of self–other overlap) and empathy representing something akin to the concept of emotional closeness. His research failed to show that subjects felt these emotions more strongly toward kin than toward friends. However, he did find that subjects strongly expected assistance from kin. Park et al. (2008, p. 220) importantly note that empathy ought to be the appropriate emotion to elicit because it is a demonstrated mediator of altruism. They note that "A subjective sense of closeness is not an emotion, per se" (Park et al., 2008, p. 219). At this point, which emotions influence altruism toward kin are poorly understood.

The work of Curry, Roberts, and Dunbar (2013) and Pollet, Roberts, and Dunbar (2013) invokes the concept of a "kinship premium" and points to a deeper understanding of how kinship is an independent factor in altruism. Both studies replicate previous research showing that emotional closeness is important to maintain helpful relationships (such as willingness to donate a kidney or travel a great distance to maintain contact) among friends and kin through reciprocation. However, both studies showed that close kinship (but not distant) had an independent contribution to altruism, hence the "kinship premium."

WILLINGNESS TO HELP

A number of studies have focused on willingness to help kin and friends. Perhaps the first study of kinship and willingness to help is found in Essock-Vitale and McGuire's survey (1980, p. 1985) of 300 women in the Los Angeles area. They found that close kin were more likely to help than distant kin and close kin bias increased with the cost of the assistance. In addition, help from friends was balanced in returns, whereas this was not the case for kin. These patterns have been replicated and elaborated in subsequent research. The pattern we see emerging is that, although friends may help more frequently as a consequence of proximity, kin become more important as the costs or benefits to helping increase.

Several studies show that, on a daily basis, we may depend on nonkin more frequently, but when the benefit for help to the recipient or the cost to the donor increases, then we increasingly rely on kin. Burnstein, Crandall, and Kitayama (1994) did the first such study and found that when the costs and benefits to kin were great (based on hypothetical scenarios of saving someone in a burning house at some risk to themselves compared to helping them find a lost personal item and being late to a meeting as a result) close kin were more likely to be helped. Fitzgerald (2009) replicated these results by distinguishing between everyday altruism (driving someone to the store), extraordinary altruism (giving a large loan), and life-threatening altruism (risking one's life).

Stewart-Williams (2007, 2008) administered surveys to undergraduates about their helping and exchange behavior toward friends, kin (siblings and cousins), and mates. For siblings, cousins, and acquaintances, greater relatedness was associated with more frequent levels of helping. Friends were an exception because they received as much or more help than kin. However, as shown in other studies, as the cost of helping increased, kin became strongly favored over friends, even though subjects felt closer to friends and mates. He contrasts his second survey (2008) with the results from Neyer and Lang (2003) who found that individuals in their sample felt closer to kin than friends and received more help from kin. He speculates that the difference in results are likely a consequence of age differences in subjects. The older subjects in Neyer and Lang (2003) had married, whereas Stewart-William's subjects were college students. These different results may reflect life historical changes in the development and maintenance of helping relationships. It may also reflect differences in mobility and wealth, as well as mature adults probably have established long-term friendships and familial relationships in contrast to college students who have just left home and are rapidly acquiring a new set of relationships.

SEX DIFFERENCES IN NEPOTISM

It seems reasonable to predict that men and women may have different strategies when it comes to nepotistic effort. One would hypothesize that these differences are determined by local reproductive opportunities. For example, where marriage is dependent on accruing cattle to pay bride price, men might use that wealth for themselves instead of assisting a son or nephew (Borgerhoff Mulder, 1987; Mace, 1996). In contrast, additional mating effort for women may have a much lower payoff, leading them to allocate more energy to parental and kin effort. This is especially true for women after menopause, which informs Hawkes' (Hawkes, O'Connell, & Blurton Jones, 1989) grandmother hypothesis. The same sort of life historical change may occur for men, especially in societies where polygyny is uncommon or prohibited (Winking, Kaplan, Gurven, & Rucas, 2007).

Salmon and Daly (1996) refer to Western women as "kin keepers" because, compared to men, they have greater interest in the welfare and activities of their kin, are more likely to identify themselves in kinship relation terms, more likely to maintain contact, felt closer to kin, and can recall more relatives (see Chagnon, 1988 for non-Western exception). However, both males and females were just as likely to nominate a kinsperson as the most significant person in their lives. These differences and others are also documented by researchers who take a nonevolutionary approach (see Dubas, 2001, p. 480 for a review). Benenson et al. (2009) note that the cross-cultural literature shows that men from childhood to adulthood form larger and more inclusive and interconnected nonkin networks than women, whereas women focus more strongly on maintaining family ties. Neyer and Lang's (2003) research measured these differentials in different age categories. As demonstrated in other studies (Essock-Vitale & McGuire, 1985; Euler & Weitzel, 1996), women felt closer to kin than men, and women were more likely to assist kin; these differences became more pronounced in middle and old age, which has implications for understanding menopause as a possible adaptation. In the grandparental solicitude literature, the female of a grandparental pair always engages in more altruistic acts toward grandchildren than her male counterpart (Euler & Weitzel, 1996). Females are much more likely than males to engage in the care of young, dependent kin through direct care, such as holding, feeding, babysitting (Huber & Breedlove, 2007) or economically through food production. Perhaps the most dramatic sex difference in nepotism is seen in alloparental care by siblings (Hames & Draper, 2004) and in the extensive grandmothers' literature.

BEHAVIORAL AND ETHNOGRAPHIC APPROACHES TO KIN SELECTION

This section reviews research by anthropologists, psychologists, and others who evaluate kin selection hypotheses in naturalistic or seminaturalistic settings, measure the consequences of kin altruism through fitness differentials or their proxies, or measure actual instances of kin altruism. A striking feature of this literature is the enormous range of human behavior that kin selection theory can help us understand ranging from the evolution of homosexuality, labor and food exchanges, and political coalitions.

HOMOSEXUALITY

Decades ago Wilson (1975, p. 279) speculated that homosexuality is maintained via kin selection. Given that male homosexuals in the West have about one-tenth the fertility of heterosexuals (Vasey & VanderLaan, 2009; King et al., 2005) it would seem that investment in kin would be their only road to fitness. In the West, evidence for high kin investment by gays is negative (Rahman & Hull, 2005). However, Vasey and VanderLann's meticulous examination of the transgendered androphiles in Samoa clearly demonstrates that an EEA-like culture may make a difference in altruism of androphilic males toward kin. The Samoan status *fa'afafine* means "in the manner of a woman" and it represents a third gender. Vasey and VanderLann (2009) show that Samoan *fa'afafine* invest more heavily in closely related younger kin (siblings, nephews, and nieces) compared to heterosexual kin who have no children. It is important to understand that *fa'afafine* are what Vasey and VanderLaan term transgendered androphilic males who are present in many ethnographic tribal and traditional populations in contrast to what they call sex-gender congruent androphiles (or egalitarian homosexuals) found in the West. *Fa'afafine* are expected to excel in feminine tasks such as the care, nurturing, and support of children and devotion to the home and domestic tasks. VanderLaan, Ren, and Vasey (2013) argue that the transgendered form is the norm in egalitarian populations, and it is in that social context that this behavior is adaptive.

ECONOMIC COOPERATION: FOOD AND LABOR EXCHANGE

A considerable amount of research has been done in evolutionary economic anthropology on how kin selection might influence interhousehold transfers of food and assistance. Although much of the research has entertained multiple hypotheses of transfers such as reciprocal altruism, costly signaling, tolerated scrounging, as well as kin selection (see Gurven, 2004, pp. 545–546 for definitions), I largely focus on the rather mixed research results relative to kinship. If we begin with Gurven's (2004, p. 558) comparative survey, food transfers appear to be more frequently regulated by reciprocal altruism than kin selection among foragers and other subsistence-based peoples. Although there is ample evidence, reviewed later, that kin selection can be important in particular ethnographic instances, it is becoming increasingly clear that food transfers are regulated by a variety of mechanisms.

Studies showing relatedness is the likely mechanism to account for food exchange is documented among the Ifaluk (Betzig & Turke, 1986), Hiwi (Gurven, Hill, Kaplan, Hurtado, & Lyles, 2000), Dolgan (Ziker & Schnegg, 2005), in a mixed tribal Peruvian community (Patton, 2005), and among settled Ache (Gurven, Hill, & Kaplan, 2002). These studies show that kinship predicts the frequency of exchange between households. Kinship also is negatively correlated with imbalance in exchange. That is, close kin tolerate greater one-way flows of resources with little or no reciprocation, whereas distantly related households seem to be in balance, suggesting a tit-for-tat form of reciprocal altruism. In contrast, research on the Yanomamö (Hames, 2000), Ye'kwana (Hames & McCabe, 2007), Tucker on the Mikea (Tucker, 2004) and forest Aché (Kaplan & Hill, 1985) show that relatedness does not predict transfers, whereas reciprocal altruism does. Noting these complex results, Allen-Arave, Gurven, and Hill (2008) persuasively argue that the Ache tend to set up reciprocal relations with close kin because they are better known, likely to be near-neighbors, and can be trusted to reciprocate.

In contrast to food transfers, cooperative labor has received relatively little recent study even though it was one of the first issues economic anthropologists examined to test kin selection predictions. These studies examine whether close kin are more likely to engage in joint labor such as working in each other's gardens or to work together as boat crews in marine hunting. Hames (1987) used an observationally based study of labor exchanges between Ye'kwana households and found strong support for kinship in a variety of ways. He found that mean relatedness between households predicted how frequently individuals would work in one another's gardens, that close kin were likely to have large imbalances in their labor exchanges while distant kin seem to pursue a closely regulated tit-for-tat strategy, and that those households that had more kin in the village were more likely to engage in cooperative garden labor.

A major problem in many of these economic studies is that the problem that food sharing or cooperative labor is designed to overcome (Hames & McCabe, 2007) is not addressed before predictions about the mode of exchange (e.g., kin selection or reciprocal altruism). For example, one might predict that food exchange is designed to reduce the variance in daily intake of critical food resources (Gurven, 2004, p. 544). Consequently, in small bands, one would predict that all hunters would contribute, regardless of their relatedness, and reciprocal altruism would be the mechanism. In contrast, if sharing were designed to help those who fell on hard times because of garden failure (Hames, 1987) or physical incapacitation (Sugiyama & Chacon, 2000), then strong kin biases would be predicted.

INHERITANCE

In the modern context, allocating all of one's worldly assets in a last will and testament is the ultimate opportunity to benefit kin. In many instances it is likely to be the largest investment individuals can make in kin and offspring. Straightforward predictions would be that close kin would receive more than distant kin and that reproductive value would also be important such that younger kin (nephews and nieces and grandchildren) would receive more than equally related older kin, such as grandparents, aunts, and uncles, and offspring should receive more than siblings of a testator. These predictions were generally borne out in analyses of wills in British Columbia (Smith, Kish, & Crawford, 1987) and California (Judge & Hrdy, 1992). In a series of laboratory studies Webster (2004) and Webster, Angela, Crawford, McCarthy, and Cohen (2008) students were asked to allocate fictional lotteries to blood relatives along with an examination of 1,240 probated wills with 4,819 beneficiaries in British Columbia. Although there was a strong correlation between relatedness and proportion of estate given, several new results emerged. First lineal relatives were biased over collateral relatives. This bias occurred even after controlling for age, since lineal kin of equal relatedness tend to be younger than collaterals and thus have greater reproductive value. Second, wealthy benefactors more strongly adhered to relatedness than poor benefactors. And third, among the wealthy group, younger relatives were favored over older relatives, whereas among the less wealthy, older kin were favored over younger. Why there is a bias toward lineals over collaterals is unknown, and Webster et al. (2008) pose a number of different hypotheses, such as paternity certainty and differences in the number of lineal and collateral kin. Finally, female testators more closely adhered to relatedness than males, a finding paralleling Judge (1995).

POLITICS AND COALITIONS

In perhaps the first use of inclusive fitness theory from a behavioral ecological perspective, Chagnon found that village fissioning was linked to biological kinship (1975). The problem revolved around how a village could maintain large size giving them an advantage in a milieu of chronic intervillage warfare. Within-village disputes are normal in any society, but in egalitarian societies, dispute-settlement mechanisms employ the authority of senior kin and the strength of their kinship ties to amicably settle disputes. As Yanomamö villages grow, disputes increase and mean village relatedness declines, thereby reducing the effectiveness of kinship in dispute settlement. After fissioning, new villages have greater mean relatedness than in the prefission village, and disputes are rarer and are more easily reconciled when they surface.

Using a filmed analysis of an ax fight among 30 Yanomamö in the village of Mishimishimaböwei-teri, Chagnon and Bugos (1979) showed that the side selected by the participants corresponded to their degree of relatedness to the two principle combatants, and members of each faction were more closely related to themselves than they were to the other faction. A later reanalysis by Alvard (2009) using more sophisticated statistical tools showed that the initial results stood up and, in addition, showed that lineage membership disappeared when relatedness was controlled for and that affinal links also played a role in coalition alignment.

ADOPTION, FOSTERAGE, AND STEP-RELATIONS

In a series of articles on anthropological populations by Silk for Oceania (1980), the Arctic (1987), and in Africa and elsewhere (1990) she tested a variety of standard cultural anthropological hypotheses (need for labor, sex-ratio balance) and found that close kin are the most frequent adopters. Silk also found biological parents monitor the welfare of their adopted children, place their children in households that are wealthier than theirs or offer advantageous social ties, and children are given up for adoption when parents feel they cannot adequately care for them. Although these patterns appear to fit derivable inclusive fitness predictions, often, adopted children are not treated as well as biological children. Realizing this, biological parents apparently strive to give their children to the closest biological kin available to mitigate this problem and actively monitor their treatment.

Adoption is an area of research that has direct social policy implications because in the United States, Canada, Great Britain, and elsewhere foster care and adoption institutions now bias placement with kin (Daly & Perry, 2011), and, in the United States, federal law encourages kin fostering (Herring, 2005). Such laws and policies encouraging kin placement were developed without reference to inclusive fitness theory. Herring, Shook, Goodkind, and Kim (2009) review a number of studies querying whether foster care placement with kin generally leads to better outcomes compared to placement with nonkin. Overall, as reviewed by Herring et al. (2009), a number of studies consistently, but not invariably, find that kin placements are more stable (i.e., they last longer) than nonkin placements. Of course, stability does not necessarily mean good treatment or outcomes (Perry, Daly, & Kotler, 2012).

Some researchers have examined the psychological consequences of kin versus nonkin fostering. Lawler (2008) examined foster-care outcomes using measures of emotional availability, for children who had been diagnosed with disruptive behavior, and found no difference between kin and nonkin fostered children. Testa (2004, cited in Herring et al., 2009, p. 10) used the construct of permanence to study the well-being of fostered children. Permanence consists of three components: "intent that the family relationship lasts indefinitely, continuation of the relationship despite geographic moves and temporal change; and belongingness. . . ." The concept of permanence was strongly correlated with kinship and increased with closeness of kinship. Despite these positive results, many studies do not control for important confounds such as income, education, and school and neighborhood environments that have independent effects on adoptee outcomes (Perry et al., 2012).

Pollet and Dunbar (2007) examined a large public database of 13,935 families compiled in 1910. They predicted that childless couples would be more likely than couples with children to have a household with a nephew or niece in them. Given that nephews and nieces had much higher reproductive value than other close kin (e.g., siblings), such households would better deploy their kin effort to younger categories of kin. After controlling for a variety of factors, they found that childless couples were 3.5 more times likely to have a nephew or niece in their household. Due to limitations in the database, there is no indication that any of these nephews and nieces were legally adopted but, given that they live in the households of their aunts and uncles, one can regard this as adoptive behavior.

ALLOPARENTING: HELPERS AT THE NEST AND THE GRANDMOTHER HYPOTHESIS

There is now a large literature on alloparental care or cooperative breeding that encompasses helpers at the nest (care by siblings) and the grandmother hypothesis. Important reviews have been made by Sear and Mace (2008), Coall and Hertwig (2010), and Sear and Coall (2011) on the grandmother hypothesis, whereas Hames and

Draper (2004), Hrdy (2005), and Kramer (2012) cover the more general topic under the rubric of cooperative breeding. Most reviews examine the factors of paternity certainty, genetic relatedness, reproductive value, and sex biased investments. The potential utility of alloparents stems from a combination of derived life-history traits in humans including short interbirth, "reproductive stacking," or parents caring for multiple, dependent offspring, and long dependency where subadults are typically unable to produce as much as they consume until they reach the age of 16 years or more (Kramer, 2010).

The earliest evolutionarily informed research on human alloparenting (Turke, 1988) was inspired by the avian "helpers at the nest" literature and was firmly grounded in kin selection theory. Turke documented the positive effects of older siblings, particularly girls, on a mother's fertility or the survivorship of her children, behavioral measures of child care, and labor effort of older siblings. Hames (1987) showed a moderate correlation between alloparental relatedness and time expended in childcare among the Ye'kwana. This pattern of heavy investment in allocare by close kin is also noted in hunting and gathering groups such as the Efe (Fouts and Brookshire, 2009), Hadza (Crittenden and Marlowe, 2008), and the Martu (Scelza, 2009). Research by Ivey (2000) on the Efe shows that relatedness is a consistent and powerful predictor of allocare and similar findings are made for the Toba (Valeggia, 2008), Aka (Meehan, 2005), Hungarian Gypsies (Bereczkei, 1998), and Maya (Kramer, 2008). The dominant alloparents in roughly rank-order providing direct care were female siblings, grandmothers, aunts, cousins, and distant or nonkin.

The focus on the grandparental dimension of alloparenting was inspired by Williams' queries on menopause (1957) and became a well-researched area following Hawkes' innovative research on Hadza grandmothers (Hawkes et al., 1989) that revolve around grandmothers as reliable investors in conjunction with the evolution of longevity and menopause. The overwhelmingly consistent pattern in grandparental investment is maternal grandmothers invest most because they have no uncertain links to their grandchildren, followed by maternal grandfathers and paternal grandmothers who have one uncertain link to their grandchildren, and paternal grandfathers who have two uncertain links. However, socioecological differences do matter. For example, among Greeks paternal grandparents engage in more caretaking than maternal grandparents in rural farming communities where farmland is inherited patrilineally, residence is patrilocal, and paternal grandparents may co-reside with their son and daughter-in-law (Pashos, 2000).

The now voluminous grandparental research can be divided into three kinds of studies: (1) biological and reproductive outcomes; (2) investments, or what alloparents do for kin, and; (3) solicitude and other psychological factors that lead grandparents have greater interest, empathy, or feel closer to grandchildren. In addition, I note studies examining investment from aunts and uncles to nephews and nieces.

Outcomes Outcome research looks at the demographic consequences of grandparents on the fertility of their children and/or survivorship and growth and development of their grandchildren. Sear and Mace (2008) and, more recently, Sear and Coall (2011) summarized the demographic outcomes research. Sear and Mace provide an extensively detailed and critical analysis of studies that document how the presence of four types of grandparents as well as older siblings on child survival. In a comparative analysis of 45 studies, they found that presence of maternal grandmothers improved child survivorship in 69% of studies, whereas paternal grandmothers improved survivorship at a lesser 53% rate. In rare cases, grandmothers were found to actually decreased survivorship. They suggest two reasons why maternal grandmothers were more helpful than paternal: (1) they tend to be younger since females reproduce earlier than males, and (2) maternal grandmothers may have higher rates of paternity certainty. In contrast, maternal grandfathers had no effect on the survivorship of grandoffspring in 83% of the cases, whereas paternal grandfathers had no effect in 50%, a negative effect in 25%, and a positive effect in 25%. The effects of other relatives such as siblings are generally positive (Sear & Coall, 2011). The effects on survivorship tend to be greatest when the child is less than 5 years of age. Since survivorship during this period is highly sensitive to forms of direct care such as child tending, monitoring, and feeding, and women dominate these activities, grandmothers are likely instrumental. However, grandfathers may be valuable later in life when their social influence may be critical to marital and economic success. Finally, see Strassmann and Garrard (2011) for limitations of Sear and Coall's (2011) meta-analysis.

Investments Early research by Hawkes et al. (1989) showed that food production by grandmothers had positive effects on grandoffspring weight maintenance during food-scarce periods of the year. Gibson and Mace (2005) present time-budget data to show that maternal grandmothers spent more time in their daughter's households and were more likely to do heavy domestic labor thus reducing their daughter's labor load. In a more direct accounting, Meehan, Quinlan, and Malcom (2013) found that kin, largely grandmothers, significantly reduced a mother's energetic expenditure by as much as 216 kcal/day. In an interesting study of birthing, Huber and Breedlove (2007) made a distinction between direct care of the mother (assisting in the birthing process) and indirect care (food preparation and other activities to assist the mother after the birth). Using the HRAF Statistical Cross Cultural Sample of 60 societies, they found that relatedness, sex, and paternity certainty affected rendering of assistance. In the area of direct care, aunts provided more care than uncles, grandmothers more than grandfathers. The same pattern held for indirect care except that there was no difference between grandmothers and grandfathers.

Most grandparental research shows that although all grandparents invest, the investment magnitude generally follows female and paternity certainty links noted earlier. Euler and Michalski (2007) summarize numerous studies on contract and interaction frequencies, childcare, gifts received, and adoption. Nearly identical patterns were found for aunts and uncles by Gaulin, McBurney, and Brakeman-Wartell (1997) and their investments in nephews and nieces.

In a large and detailed study, Pollet, Nettle, and Nelissen (2006) found that contact frequency, investment in grandchildren shortly after birth, gifts, and provisioning of essentials was greater for maternal grandparents than paternal grandparents. However, there was no difference between the grandparents in loans, money for childcare, or assisting with household costs. They also noted that frequency of contact was an excellent proxy for financial investment.

Solicitude and Contact A number of studies such as Euler and Weitzel (1996) and Euler and Michalski (2007) show emotional and cognitive differences mirror the investment difference among grandparents. That is, MGM>MGF>PGM>PGF pattern was found in emotional closeness, favorite grandparent, relational closeness, grandparental mourning after the death of a grandchild, and emotionally closest grandparent. A variety of studies have shown matrilateral bias by aunts and uncles toward nephews and nieces (Gaulin et al., 1997). For example, McBurney, Simon, Gaulin, and Geliebter (2002) found matrilateral aunts and uncles had a greater concern for the welfare of their nephews and nieces than patrilateral aunts and uncles in an eastern U.S. sample with high paternity certainty. In addition, Kurland and Gaulin (2005, p. 461) showed the same matrilateral bias in terms of frequency of contact and doing favors for one another for full, half sibs, and cousins. Jeon and Buss (2007) using a formal model predicted that cousins linked though mother's sisters would be most altruistic, whereas those through father's brothers would be least altruistic. Links through mother's brother and father's sister would be intermediate. They found that measures of emotional closeness, empathic concern, and the frequency of contact followed the rank ordering in their model.

SUMMARY, TRENDS, AND CONCLUSIONS

Kin selection has been a potent force in our life history as a species. It plays a significant role in nearly all human social domains from care for subadults, costly investments, food and labor allocations, politics, and daily social interaction, to the ultimate altruistic act of designating recipients of last wills and testaments. In proportion to their degree of relatedness, kindreds feel emotionally close, are concerned about one another's welfare, and are willing to help them at great costs to themselves. Evolutionary anthropologists and psychologists are in the lead of behavioral scientists studying kinship. The following is a summary of what we know so far about kin selection.

WOMEN MORE FREQUENTLY DEPLOY NEPOTISM THAN MEN

Kin investment by post- and prereproductive females provide two lines of clear evidence that females more than males use kinship to enhance their fitness. Demographic analysis of hunter-gatherer life history shows that, on average, women who reach the age of 45 will live an additional two decades (Gurven & Kaplan, 2007). Given that direct reproduction ceases as a consequence of menopause the only avenue open to females is indirect reproduction through the enhancement of the survival and reproduction of their offspring and grandoffspring, and there is considerable evidence for kin effects. Since men do not go through menopause and have options of serial monogamy and polygyny, direct reproduction may be a better option than kin investment in many sociocultural circumstances. However, where polygyny is limited, direct reproduction by men may end for the vast majority with their wives' last reproduction (Winking et al., 2007). Some of the grandparental literature show grandfathers enhance the survivorship of their grandchildren. The second line of evidence comes from the alloparenting literature documenting that girls are much more likely than boys to care for their siblings and other close kin and the presence of girls is more likely to reduce interbirth intervals for their mothers and the survivorship of their younger siblings. Beyond menopause and subadult female alloparenting, there is other evidence such as the kin keeper literature that shows that females are much more likely to keep track of kin and are more concerned about their welfare than men.

KIN SELECTION AND RECIPROCAL ALTRUISM

In the modern context there is considerable research that reveals we rely on friends for everyday forms of assistance with strict balancing, whereas kin are much more likely to assist when the cost is high and balance or reciprocation is not required. It is reasonable to conclude that people use reciprocal altruism for cheap, chronic, and easily tracked altruism; in contrast, they use kin selection for high cost/benefit altruism. Whether this is true in nonstate societies is unclear. In these societies, close kin are frequently coresident for one sex or the other. The flow of everyday assistance in goods and services shows reciprocal altruism is somewhat more important than kin mediated assistance (Gurven, 2004). For example, among the Ye'kwana, garden labor exchanges are strongly determined by kinship ties (Hames, 1987) but meal sharing is based on reciprocal altruism and not kinship (Hames and McCabe, 2007). The difference may be that meal sharing is a regular, nearly everyday event, easy to track, and not very costly (mainly food preparation). However, garden labor (clearing, planting, weeding, and harvesting) is arduous and seems to be a form of insurance for garden failure; if a family's gardens fail they can make up shortfalls by taking food from a kinsperson's garden.

KIN ALTRUISM FLOWS DOWNHILL

The ability of a recipient to parlay assistance into fitness is a crucial factor in the allocation of altruism. Many factors influence these decisions such as current and future needs, phenotypic quality, the ability of other kin to profit from the investment, and reproductive value. Age is a rough index of reproductive value and where research takes this into consideration assistance flows from older individuals to younger individuals. This is obviously evident in the grandmother- and alloparental-care literature as well as research on beneficiaries in wills, adoptions, and gifts.

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CHAPTER 20

Evolution of Paternal Investment

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REPRODUCTIVE EFFORT INVOLVES trade-offs between mating and parenting (Trivers, 1972; Williams, 1966), and the attendant conflicts between the best interests of males and females and between parents and offspring (Krebs & Davies, 1993; Trivers, 1974). Conflicts emerge as each sex and each parent invests limited resources in self-interested ways that are not always in the best interest of the other sex or of offspring. Males and females and parents and offspring also have overlapping interests, and thus the evolution and proximate expression of reproductive effort reflects a coevolving compromise between the best interest of the two sexes and of parents and offspring. For the majority of species, the evolutionary result is that males invest more in mating (typically competition with other males for access to reproductive females) than in parenting, and females invest more in parenting than in mating (Andersson, 1994; Darwin, 1871), although there are readily understandable exceptions (Reynolds & Székely, 1997). Females benefit from male-male competition and the male focus on mating effort, because their offspring are sired by the most-fit males, and successful males benefit because they produce more offspring by competing for access to multiple mates than by investing in parenting.

The basic pattern is especially pronounced in mammals, where male parenting is found in less than 5% of species and where females invest heavily in offspring (Clutton-Brock, 1989). The reasons for these differences are found in the biology of internal gestation and obligatory postpartum suckling, and the associated sex differences in the opportunity and potential benefits of seeking multiple mating partners (Clutton-Brock & Vincent, 1991; Trivers, 1972). Given this pattern, the phenomenon of human paternal investment is extraordinary and the focus of this chapter; extended discussions can be found elsewhere (Draper & Harpending, 1988; Flinn & Low, 1986; Geary, 2000; Geary, Bailey, & Oxford, 2011; Geary & Flinn, 2001).

To understand the evolution and expression of men's parental investment, we must consider both the benefits to children and the costs to men, as well as the cost-benefit trade-offs to women. I begin with an overview of the cost–benefit trade-offs of paternal investment in nonhuman species, and discuss these as they relate to the evolution and proximate expression of men's parenting in the second section. I then turn to the relation between men's investment and women's reproductive strategies, and close with a review of the proximate correlates of men's parenting.

PATERNAL INVESTMENT

Although uncommon in mammals, paternal investment is found in many species of bird, fish, and in some insects (Perrone & Zaret, 1979; Thornhill, 1976; Wolf, Ketterson, & Nolan, 1988). For some species, this investment is *obligate*, meaning that male care is necessary for the survival of his offspring and will thus favor paternal males. For other species, this investment is *facultative*, meaning that it benefits offspring but it is not always necessary for their survival (Westneat & Sherman, 1993). In these species, the degree to which males invest in parenting reflects trade-offs between the costs and benefits of this investment in the contexts in which the male is situated.

TRADE-OFFS

Our focus here is specifically on male facultative investment, because this is the pattern found in humans (Geary, 2010). The trade-offs found with this type of investment are summarized in Table 20.1, and involve balancing the benefits to offspring against the cost of lost mating opportunities and the risk of cuckoldry. Benefits to offspring are lower mortality due to provisioning and protection from predators and may be uncommon in mammals because suckling provides most or all of the offspring's early nutrition (Clutton-Brock, 1991).

As an example of trade-offs, consider that male parenting in fish is most common when males externally fertilize eggs and defend nesting sites from predators (Perrone & Zaret, 1979). Under these conditions, paternity certainty is high and males are able to fertilize the eggs of several females and thus investment does not reduce mating opportunities. Paternal investment is uncommon in fish with internal fertilization, because paternity is not certain and because males can abandon females after fertilization and avoid the cost of investment. Paternal investment does occur in some species with internal fertilization, including most species of bird and a few mammals. Again, the degree of paternal investment varies with potential benefits to offspring, availability of other mates, and paternity certainty.

The trade-offs are illustrated by the relation between level of males' parental investment and the likelihood of paternity or conversely the risks of cuckoldry (Birkhead & Møller, 1996). With facultative male parenting, cuckoldry rates often vary with male quality (e.g., as indicated by plumage color); an example is provided by the barn swallow (*Hirundo rustica*) whereby females often risk loss of male investment and copulate with healthier and more attractive males, if they are paired with a low-quality mate (Møller & Tegelström, 1997). Males counter cuckoldry risk by monitoring their mates' activity and adjusting investment accordingly, as illustrated by Ewen and Armstrong's (2000) study of the socially monogamous stitchbird (*Notiomystis cincta*). In this species, males provide between 16% and 32% of the food to the nestlings. Extra-pair copulations occur in the pair's territory and are easily monitored. Males counter this paternity threat by chasing off intruding males, but extra-pair copulations still occur. In this study, male provisioning of the brood decreased as the frequency of female extra-pair copulations increased ($r = -0.72$).

Table 20.1
Factors Associated with the Evolution and Facultative Expression of Male Parenting

Offspring Survival

1. If paternal investment does not substantially influence offspring survival prospects or quality, then selection will favor male abandonment (Trivers, 1972; Williams, 1966).
2. If paternal investment results in relative but not an absolute improvement in offspring survival prospects or quality, then selection will favor males that show a mixed reproductive strategy. Males can vary in degree of emphasis on mating or parenting, contingent on social (e.g., availability of mates) and ecological (e.g., food availability) conditions (Westneat & Sherman, 1993; Wolf et al., 1988).

Mating Opportunities

1. If paternal investment is not obligate and mates are available, then selection will favor:
    A. Male abandonment, if paternal investment has little effect on offspring survival and quality (Clutton-Brock, 1991).
    B. A mixed male reproductive strategy, if paternal investment improves offspring survival and quality (Perrone & Zaret, 1979; Wolf et al., 1988).
2. Social and ecological factors that reduce the mating opportunities of males, such as dispersed females or concealed ovulation, will reduce the opportunity cost of paternal investment. Under these conditions selection will favor paternal investment, if this investment improves offspring survival prospects or quality, or does not otherwise induce heavy costs on the male (Clutton-Brock, 1991; Perrone & Zaret, 1979; Thornhill, 1976; Westneat & Sherman, 1993).

Paternity Certainty

1. If the certainty of paternity is low, then selection will favor male abandonment (Clutton-Brock, 1991; Westneat & Sherman, 1993).
2. If the certainty of paternity is high, then selection will favor paternal investment, if:
    A. Investment improves offspring survival or quality, and
    B. The opportunity costs of investment (i.e., reduced mating opportunities) are lower than the benefits associated with investment (Dunbar, 1995; Thornhill, 1976).
3. If the certainty of paternity is high and the opportunity costs, in terms of lost mating opportunities, are high, then selection will favor males with a mixed reproductive strategy, that is, the facultative expression of paternal investment, contingent on social and ecological conditions (Dunbar, 1995; Westneat & Sherman, 1993).

Adapted from "Evolution and Proximate Expression of Human Paternal Investment," by D. C. Geary, 2000, *Psychological Bulletin, 126*, p. 60. Copyright 2000 by the American Psychological Association. Reprinted with permission.

Paternity certainty and an improvement in the survival rate of his offspring are not sufficient for the evolution or facultative expression of paternal investment. The benefits of investment must also be greater than the benefits of siring offspring with multiple females (Dunbar, 1995). For instance, social monogamy and high levels of paternal investment are common in *canids* (e.g., coyotes, *Canis latrens*), which tend to have large litters (Asa & Valdespino, 1998). Large litter sizes, prolonged offspring dependency, and the ability of the male to provide food during this dependency (through regurgitation of meat) result in *canid* males being able to sire more offspring with a monogamous, high parental investment strategy than with a polygynous strategy. Paternal investment might also evolve if females are ecologically dispersed and consequently males do not have the opportunity to pursue multiple mating partners, as with *callitrichid* monkeys, such as marmosets (*Callithrix*; see Dunbar, 1995).

HUMAN FATHERHOOD

As noted, men's investment in children is facultatively expressed and thus subject to the same trade-offs found in other species. These are the physical and social benefits to their children balanced against the costs of lost mating opportunities and the risk of cuckoldry.

Physical Well-Being of Children

Mothers invest more in children than do anyone else. Across cultures, maternal investment in children is supplemented by that of other kin (Sear & Mace, 2008). Whether this investment comes from maternal or paternal grandparents or the children's father varies across cultures and contexts (Hrdy, 2009; Sear & Mace, 2008). The focus here is on when and to what extent fathers' investment improves the physical well-being of their children, but unfortunately, information on whether fathers reduce mortality rates in infancy and childhood is scant, in comparison to the literature on the psychological correlates of paternal investment. Fortunately, there is some information on the relation between paternal factors (e.g., occupation) and childhood mortality rates in preindustrial Europe and the United States, and a few studies of this relation in extant developing and traditional societies. The gist is that paternal investment can lower infant and child mortality risks in some human groups, but the magnitude of this effect cannot be determined.

Children's Mortality Risks in Traditional Societies Hill and Hurtado's (1996) extensive ethnography of the Ache (Paraguay) provides one of the most extensive assessments of the relation between paternal investment and child mortality in a traditional society. For forest-dwelling Ache, 1 out of 3 children died before reaching adolescence, with significant differences for father-present and father-absent children. Father absence due to death or divorce tripled the risk of child death due to illness, and doubled the risk of being killed by other Ache men or being kidnapped—and presumably killed or sold into slavery—by other groups. Overall, father absence at any point prior to the child's 15th birthday was associated with a mortality rate of more than 45%, as compared to 20% for father-present children.

Death due to sickness is related, in part, to the adequacy of the child's diet and in many traditional societies paternal provisioning provides an important component of this diet. The Ache share hunting proceeds among all members of the group and thus fathers do not directly provision their children with meat. Nevertheless, the children of skilled hunters have lower mortality rates than children of less-skilled hunters (Hill & Kaplan, 1988); this is also true in other hunter-gatherer societies (Smith, 2004; Wiessner, 2002). It appears that these children are better treated than the children of less-skilled hunters, including greater tolerance "of food begging by the children of good hunters" (Hill & Kaplan, 1988, p. 283), a greater willingness of band members to stay in one location to nurse the ill child of a good hunter, and greater alloparenting of these children.

Across a variety of other cultures, Sear and Mace (2008) found no consistent relation between father's investment and mortality risks for infants and young children. Sometimes fathers mattered, and sometimes they did not. With the death of the father or following a divorce, other kin—typically maternal grandmothers—are often able to compensate for the lost paternal investment (see also Hrdy, 2009; O'Connell, Hawkes, & Blurton Jones, 1999). Moreover, even when a father's skill at provisioning his family is related to child mortality risks, a causal link cannot be made. This is because culturally successful men tend to marry competent women who will improve the well-being of their children and it may be the mother's contributions that have the strongest effects on child mortality (e.g., Blurton Jones, Hawkes, & O'Connell 1997).

Protection from other men may be the one area in which other kin may not be able to compensate for loss of a father. As with the Ache, the presence of a stepfather is associated with increased mortality of young children in some human groups (Sear, Steele, McGregor, & Mace, 2002), and is associated with ongoing low levels of conflict and poor health in many other contexts (Flinn, 1992).

Children's Mortality Risks in Developing Societies In developing countries in South America, Africa, and Asia there is a consistent relation between marital status and infant and child mortality rates; "mortality of children is raised if the woman is not currently married, if she has married more than once or if she is in a polygamous union. . . . Overall, it appears that there is a strong, direct association between stable family relationships and low levels of child mortality" (United Nations, 1985, p. 227). Indonesian children of divorced parents, for instance, have a 12% higher mortality rate than children of monogamously married couples. The same relation was found in 11 of the 14 developing nations surveyed.

The same pattern was evident in preindustrial Europe. During the 19th and early 20th centuries in Sweden, infant mortality rates were 1.5 to 3 times higher for children born to unmarried mothers than children born to married couples (Brändström, 1997). The same was true of the Netherlands from 1885 to 1940 (Kok, van Poppel, & Kruse, 1997). The direct importance of fathers is confirmed by the finding that the mortality of "illegitimate" children was lower if the father provided economic support to the child and mother and by the finding of higher mortality of "legitimate" children if the father died. A relation between paternal provisioning and infant and child mortality risks has in fact been reported throughout preindustrial and industrializing Europe and the United States (e.g., Klindworth & Voland, 1995; Morrison, Kirshner, & Molho, 1977; Schultz, 1991).

Children's Physical Health Even with vastly lower child mortality, the relation between socioeconomic status (SES) and the physical well-being of children remains true in modern societies (Reid, 1998). Adler and her colleagues concluded, "individuals in lower social status groups have the highest rates of morbidity and mortality within most human populations. Moreover, studies of the entire SES hierarchy show that differences in social position relate to morbidity and mortality even at the upper levels of the hierarchy" (Adler et al., 1994, p. 22). The relation between SES and health holds for all members of the family, not just the primary wage earner, and is not simply related to healthcare access. Members of high-status families are treated better than those of lower-status families and they have more control over the activities of everyday life, both of which influence physical health.

In modern societies, paternal income and occupational status are an important, and sometimes the sole, determinant of the family's SES. As a result, paternal investment is correlated with the physical well-being of his children, even in contexts with low infant and child mortality rates.

Flinn and his colleagues provide clues about the potential relation between paternal investment and children's physical health (Flinn & England, 1997; Flinn, Quinlan, Decker, Turner, & England, 1996). In one assessment, family environment and cortisol (a stress hormone) and testosterone were assessed for children and adults in a rural village in the West Indies. Fathers' presence or absence was related to the cortisol and testosterone levels of boys, but not girls. In comparison to boys residing with their biological father, father-absent boys and boys living with a stepfather had either unusually low or highly variable cortisol levels and weighed less. Men who grew up in father-absent homes had higher cortisol levels and lower testosterone levels than did their father-present peers. The endocrine profile of father-absent men suggests chronically high stress levels, which can increase health risks (e.g., Sapolsky, 2005). Related studies suggest that prolonged parental conflict increases girls' and boys' risk for a variety of health problems in childhood and when they become adults (Troxel & Matthews, 2004).

Social Well-Being of Children

Human paternal investment is puzzling when it occurs in contexts with low infant and child mortality. Under these conditions, selection would favor men who reduced or eliminated parental effort in favor of mating effort, but many men still invest in their children. The question is why? Geary and Flinn (2001; also Geary, 2010; Geary et al., 2011) proposed our australopithecine ancestors evolved in a gorilla-like family structure, whereby males maintained long-term polygynous relationships with several females and protected and behaviorally engaged with their offspring. If so, human paternal investment has a very long evolutionary history. Still, even with an evolved bias to provide paternal investment, high-investing men may no longer benefit from this investment, particularly in contexts in which most women only have a few children. All other things being equal, culturally successful high-investment men may be disadvantaged in terms of lost mating opportunities. Another possibility is that paternal investment in low-risk environments provides social-competitive advantages to children–investment designed to improve the "quality" of offspring (Davis & Daly, 1997)—and long-term reproductive benefits (e.g., number of grandchildren) to men.

In modern societies, men's investment—including income, play time, and support of mother—is correlated with better social and academic functioning of their children and higher SES when these children reach adulthood (Kaplan, Lancaster, & Anderson, 1998; Pleck, 1997).

There are also unique relations between men's investment and some child outcomes. Kaplan and his colleagues found that fathers' investment of time (e.g., helping with homework) and income (e.g., paying for college) was associated with the upward social mobility of children, when maternal characteristics (e.g., years of education) were controlled (Kaplan, Lancaster, Bock, & Johnson, 1995; Kaplan et al., 1998). Amato (1998) found a similar pattern. The common finding that withdrawal of paternal investment is associated with decrements in children's later social and cultural success is consistent with these results.

Divorce is the most common reason for reduction or withdrawal of paternal investment. Children from intact families are consistently found to have social and educational advantages over children from divorced families. Many of the differences between children from divorced and intact families are, however, found before the divorce (Cherlin et al., 1991). Still, some differences emerge, after controlling for predivorce levels of family functioning. It appears that divorce results in small to moderate increases in aggressive and noncompliant behaviors in boys, and an early onset of sexual activity and lower educational achievement for both sexes (Amato & Keith, 1991; Belsky, Steinberg, & Draper, 1991). Genetically informed studies confirmed a likely causal effect of divorce on these outcomes, although some of the effects were smaller with control of genetic factors (see D'Onofrio et al., 2006). These findings are consistent with the view that paternal investment can improve children's later social competitiveness, given the strong relation between delayed sexual activity, educational outcomes, and later SES in these societies (Belsky et al., 1991).

Fathers can also directly influence the social and psychological well-being of children. Children with fathers who regularly engage them in physical play are more likely to be socially popular—chosen as preferred playmates by their peers—than are children who do not regularly engage in this type of play (Carson, Burks, & Parke, 1993; Parke, 1995). In a longitudinal study, Lindsay, Colwell, Frabutt, and MacKinnon-Lewis (2006) found that boys with a high-quality father-son relationship reported more friends and better relationships with these peers than did other boys. Other qualitative features of fathers' relationships with their children, such as affection, are also associated with greater social and academic competencies in children (Parke & Buriel, 1998), and with fewer behavioral (e.g., aggression) and psychological (e.g., depression) difficulties (e.g., Sheeber, Davis, Leve, Hops, & Tildesley, 2007).

Many of the relations are, however, confounded by genetic and child evocative effects, in addition to maternal effects (Park & Buriel, 1998; Scarr & McCartney, 1983). Motivated and intelligent children are more likely to receive education-related paternal investment than are other children (Kaplan et al., 1998), and even these effects might simply be related to shared genes (e.g., for intelligence). Studies that incorporate genetic influences and simultaneously assess maternal and paternal effects are needed to more firmly establish a causal relation between paternal investment and child outcomes (Parke & Buriel, 1998; Rowe, 1994), as D'Onofrio et al. (2006) did for the relation between divorce and child and adolescent outcomes.

In all, it is likely that paternal investment improves children's social competencies and their later cultural success in contexts with low infant and child mortality rates (Nettle, 2008).

In fact, paternal investment may improve the cultural success of children in many contexts, not just modern ones, through payment of dowry and bride price and inheritance of wealth and social title (Hartung, 1982; Irons, 1979; Morrison et al., 1977). For Martu Aborigines living in Australia, fathers contribute substantially to the initiation of their sons into the social structure of adult men, and this is associated with sons' earlier age of marriage and higher reproductive success (Scelza, 2010). Winking, Gurven, and Kaplan (2011), however, found no such effect for the Tsimane (Bolivia). Clearly, much remains to be learned about when, where, and how men can effect the social development and competitiveness of their children.

COSTS TO FATHERS

Reduction of child mortality and improvement of social competitiveness are not sufficient to explain the evolution and maintenance of men's parental investment. As we know from Table 20.1, these benefits have to be balanced against the costs to fathers; specifically, the loss of potential mating opportunities and the risk of cuckoldry.

WOMEN'S STRATEGIES AND MEN'S MATING OPPORTUNITIES

There are several aspects of women's sexual and social behaviors that are potential adaptations that reduce the men's mating opportunities, and thereby decrease the opportunity cost of paternal investment. The first is women's aversion to casual sex (Symons, 1979). Men prefer, on average, more sexual partners than do women (Buss & Schmitt, 1993; Clark & Hatfield, 1989; Ellis & Symons, 1990), meaning that most men have fewer partners than they would prefer. The critical result here is that most men's mating opportunities—and the attendant opportunity cost of parental investment—are substantially reduced by women's aversion to casual sex. A second factor is relational aggression, that is, female-female competition that involves social and psychological harassment of potential competitors (Campbell, 1995, Geary, Winegard, & Winegard, 2014). One function appears to be to exclude potential competitors from the social group, thereby reducing the mating opportunities of men and lowering the opportunity cost of paternal investment.

Relatively concealed ovulation and sexual receptivity throughout the ovulation cycle are other features of women's sexuality that may promote paternal investment. To ensure conception, concealed ovulation requires a longer relationship than is necessary for most other primate males (Dunbar, 1995), but this is not sufficient to ensure paternal investment. Once physical signs of pregnancy are evident, men could easily abandon women and avoid the cost of parenting. The combination of relatively concealed ovulation and continuous sexual receptivity (i.e., frequent intercourse) may foster another proximate mechanism, namely pair bonding (MacDonald, 1992), which maintains men's investment in their partner and children. Pair bonding and women's satisfaction with the relationship are also likely to reduce the risk of cuckoldry; that is, increase paternity certainty.

CUCKOLDRY

It cannot be stated with certainty, but it appears that men may be cuckolded 3% of the time, perhaps slightly less so in some contexts, on average, and more so in others (Anderson, 2006; Bellis & Baker, 1990; Bellis, Hughes, Hughes, & Ashton, 2005). As with other species, cuckoldry rates can vary substantially across contexts and social status. Sasse, Muller, Chakraborty, and Ott (1994) reported nonpaternity rates of 1% in Switzerland, but others have reported rates greater than 20% in low SES settings (Cerda-Flores, Barton, Marty-Gonzalez, Rivas, & Chakraborty, 1999; Potthoff & Whittinghill, 1965). It is, of course, possible that some of these men are aware of the nonpaternity of the children they are raising, and thus have not been technically cuckolded.

Moreover, it remains to be resolved whether women's extrapair relationships are explicitly to cuckold their partners or if cuckoldry results from failed attempts to switch mates. Support for the latter mate comes from Banfield and McCabe's (2001) survey of 112 women, 44 of whom were followed longitudinally. Less than 2% of these women had ever engaged in a purely sexual affair, but 12% reported a sexual affair when romantically attached to the extrapair man; romantic attachment suggests the pair-bonding mechanisms that support long-term relationships and biparental care are operating in these women. The issue is further complicated in contexts with high male mortality. Women in these cultures often maintain sexual relationships with several men, one of whom is considered to be the primary father and the others secondary fathers (Beckerman et al., 1998; Hill & Hurtado, 1996).

PROXIMATE EXPRESSION OF MEN'S PARENTING

Men differ considerably in how much they invest in their children, but this follows naturally from an evolved facultatively expressed bias. The interesting question is why some men invest substantially in their children, whereas others invest little to nothing.

BIOLOGICAL CORRELATES

Most of the research on the biological factors associated with men's parenting is focused on the hormonal profiles that are associated with interest in or reactivity to infants. There is also research on the heritability of men's engagement with children, but this has not yet been well linked with the hormone studies.

Hormones In species in which male parenting is facultative, higher levels of testosterone are associated with a focus on mating effort, and lower levels of testosterone and higher levels of prolactin with a focus on parenting (e.g., Reed et al., 2006). Trade-offs in men's focus on mating or parenting also appear to be reciprocally related to testosterone and prolactin (Delahunty, McKay, Noseworthy, & Storey, 2007; Fleming, Corter, Stallings, & Steiner, 2002; Gray, Parkin, & Samms-Vaughan, 2007). In North American samples, men in long-term committed relationships have lower testosterone levels than other men (Mazur & Michalek, 1998), consistent with the prediction that these men are allocating less effort to competing for mates (Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002). Important tweaks to this relation provide further support: Men in committed relationships but who are open to an extra-pair affair have higher testosterone levels than their monogamous peers (McIntyre et al., 2006).

Men in a committed and monogamous relationship who wish to become fathers may have a different hormone profile than other men, including married men who do not wish to become fathers (Berg & Wynne-Edwards, 2001; Hirschenhauser, Frigerio, Grammer, & Magnusson, 2002). Expectant fathers who respond to infant distress cues (e.g., crying) with concern and a desire to comfort the infant have higher prolactin levels and lower testosterone levels than other men (Storey, Walsh, Quinton, & Wynne-Edwards, 2000). "Men with more pregnancy symptoms (couvade) and men who were most affected by the infant reactivity test had higher prolactin levels and greater post-test reduction in testosterone" (Storey et al., 2000, p. 79). Higher paternal (and maternal) cortisol levels are also correlated with more attentive and sensitive parenting of newborns (Corter & Fleming, 1995).

Cause and effect are not certain, however. Lower testosterone levels are associated with greater sensitivity to infant cries among men who are not fathers, suggesting that hormone levels may influence the tendency toward paternal investment (Fleming et al., 2002). It is also possible that the lower testosterone associated with a committed relationship bias men toward parenting, that men prone to parental investment are preferred as long-term partners, or some combination. The relation between men's parenting and prolactin is also complex. Close contact with infants appears to result in decreased prolactin levels when fathers hold their first-born but not later-born children (Delahunty et al., 2007). A combination of little contact with their infant during the past several hours and stated concern for the infant is related to increasing prolactin levels in men and heightened reactivity to infant crying. On average, men's prolactin levels appear to be more sensitive to development experiences (e.g., having younger siblings) and social context than women's levels (Delahunty et al., 2007), perhaps reflecting the facultative nature of men's parenting.

Genes Kendler (1996) estimated that about half of the variation among fathers in warmth toward their children was due to genetic influences (see also Pérusse, Neale, Heath, & Eaves, 1994). More modest genetic influences were found for parental protection/control and authoritarian parenting (e.g., the parent making decisions for child). There is also evidence that men's (and women's) parenting is influenced by heritable traits of their children and adolescents (Feinberg, Neiderhiser, Howe, & Hetherington, 2001; Neiderhiser, Reiss, Lichtenstein, Spotts, & Ganiban, 2007), as well as by the unique experiences of mothers and fathers, including in their family of origin.

Firm conclusions cannot yet be drawn, but it may be that paternal behavior is more strongly influenced by context, prior experience, and child-evocative effects than maternal behavior, consistent with a facultatively expressed suite of behaviors. Research on heritable and environmental influences on men's basal and reactive (e.g., in presence of children) testosterone and prolactin levels are needed to more fully understand the proximate biological mechanisms potentially linking genetic and environmental influences to the expression of paternal behavior. Studies of the relation between personality and parenting are also needed. This is because the results reported here could reflect genetic influences on personality that are not directly related to the evolution of paternal care but still influence parenting behavior. For instance, individual differences in personality traits, such as conscientiousness are moderately heritable and associated with the stability of long-term spousal relationships and marital quality and could affect responsiveness to children (Graziano & Eisenberg, 1997).

Social Correlates

For men in monogamous relationships in modern societies, the quality of the marital relationship is a critical influence on their engagement with children. Men in these contexts also face a trade-off between focus on cultural success and time with children.

Marital Relationship The quality of the spousal relationship is a key influence on men's parenting (Feldman, Nash, & Aschenbrenner, 1983; Lamb, Pleck, & Levine, 1986). Although the quality of this relationship can influence how both parents interact with their children (Amato & Keith, 1991), "paternal parenting is more dependent on a supportive marital relationship than maternal parenting" (Parke, 1995, p. 37). In a set of observational studies, for instance, Belsky, Gilstrap, and Rovine (1984) and Lamb and Elster (1985) found that fathers' engagement with children was related to the quality of the marital relationship but found little relation between the level of marital interaction (e.g., degree of communication) and mothers' involvement with their children.

The finding that men with satisfying spousal relationships invest more in parenting suggests women's efforts to maintain an intimate relationship with these men is, in part, a strategy to induce more paternal investment. It is also possible that men biased toward paternal investment are more cooperative and prone to monogamy—and thus less likely to incite conflict with their wives—than are other men, and that the relation between martial satisfaction and paternal investment reflects genetic and not social effects. It is most likely that a combination of heritable biases in both parents (e.g., personality; Spotts et al., 2005), reactivity to martial dynamics, and hormonal mechanisms (earlier) influence paternal investment.

Social Status The extent to which fathers' are directly engaged in parenting is also related to the nature of his work and his personal ambition. Fathers in demanding and stressful jobs are less involved in infant caretaking, less playful with their infants, and less engaged with their toddlers than are fathers in less salient occupations (Feldman et al., 1983). Lamb et al. (1986) suggested there is a trade-off between family involvement and commitment to work. In comparison to men who were more focused on work than on family, "family-oriented accommodators . . . [were] more professionally passive and less successful professionally. They also tended to be in less prestigious jobs . . . , although it is not clear whether this was a cause or an effect of the family-oriented accommodative strategies" (Lamb et al., 1986, p. 79).

A similar relation between a man's success in culturally important endeavors and caretaking of children has been found in some traditional cultures (Hewlett, 1988; Hill & Hurtado, 1996). For instance, high-status Aka (west central Africa) men—those with large kin networks and, therefore, high hunting success—hold their infants less than half as frequently as men with few kin: Men without male kin hunt either alone or with their wives and are generally less successful hunters. The less direct care provided by these high-status men appears to be balanced by the provisioning of their families with diets that consist of a high proportion of fat and protein (Hewlett, 1988). It is not clear, however, whether efforts to obtain more income or other indicators of cultural success are components of paternal investment or if they are components of mating effort; successful men have more mating opportunities.

DEVELOPMENTAL CORRELATES

Draper and Harpending (1982), Belsky and his colleagues (Belsky et al., 1991), and Chisholm (1993) proposed that parents' social experiences (e.g., degree of conflict with other adults) and the availability of resources and risks in the wider community influence the attachment between parents and their children. In risky, low-resource environments, the stressors on parents are high and result in less attentive and more conflicted marital and parent-child relationships. These relationships are predicted to increase the risk of insecure parent-child attachments and through this bias the later relationship dynamics of these children. In less risky, high-resource environments, parent-child relationships are warmer and secure parent-child attachments are more common. Secure attachments are predicted to result in a tendency to form trusting and stable relationships later in life, including the spousal relationship. A history of a warm parent-child relationship during development and a stable spousal relationship is predicted to bias men toward higher levels of parental investment (MacDonald, 1992).

Del Giudice and Belsky argued the mechanisms related to later reproductive strategy include the type of parent-child attachment and the age of onset of adrenarche (prepubertal hormonal secretions from the adrenal gland) (Del Giudice, 2009; Del Giudice & Belsky, 2010; also Ellis & Essex, 2007). The combination of a conflicted family life and early adrenarche are associated with heightened risk of ambivalent (e.g., emotionally insecure, dependent) attachment styles in girls and women and avoidant (e.g., emotionally distant) styles in boys and men (Del Giudice, 2008). In adolescence and adulthood, an avoidant attachment style is associated aggression and dominance striving in boys and men, emotionally distant and frequent short-term sexual relationships, as well as little investment in parenting in early adulthood (Del Giudice, 2009).

Conditions in the wider community may also bias reproductive strategy. Wilson and Daly (1997) found age of first reproduction, number of children borne per woman, mortality risks, and local resource availability were all interrelated in Chicago. In neighborhoods with low resource availability, men compete intensely for these resources. The corresponding increase in mortality rates translated into an average lifespan difference of 23 years comparing the least and most affluent neighborhoods. A shorter lifespan, in turn, was associated with earlier age of first reproduction for both sexes and nearly twice as many children borne per woman comparing the least and most affluent neighborhoods. In other words, the early and frequent reproduction of women and men in these contexts might be, at least in part, a facultative response to high mortality rates, or at least a response to the perception that the future is uncertain and not likely to bring a better life (Davis & Werre, 2008).

However, for Ache and Mayan (Central America) men, Waynforth and colleagues found that "measures of family stress and violence were unsuccessful in predicting age at first reproduction, and none of the psychosocial stress indicators predicted lifetime number of partners" (Waynforth, Hurtado, & Hill, 1998, p. 383). Father absence was, however, related to less "willingness to pay time and opportunity costs to maintain a sexual relationship" (Waynforth et al., 1998, p. 383), although this could easily reflect genetic and not psychosocial effects. The final word on these issues will require genetically informed studies conducted in contexts that vary in risk factors (e.g., premature mortality).

CULTURAL AND ECOLOGICAL CORRELATES

The key cultural and ecological influences on men's bias toward parenting or mating are the social constraints on polygyny and the operational sex ratio (OSR), that is, the ratio of women to men seeking romantic relationships.

Father-Absent and Father-Present Societies Father-absent societies are characterized by aloof husband-wife relationships, a polygynous marriage system, local raiding and warfare, male social displays, and little or inconsistent direct paternal investment in children (Draper & Harpending, 1988). These conditions "are particularly prevalent in so-called middle-range societies, that is, those in which agriculture is practiced at a very low level" (Draper & Harpending, 1988, p. 349) and in resource rich ecologies. In the latter, women can often provide adequate care to their children—for example, through small-scale agriculture—without substantial direct contributions from the father (Draper, 1989). If they are able to accumulate resources beyond what is needed to attract a single wife, these are conditions and social mores that allow polygyny and provide men with the opportunity to invest time and wealth into either parental investment or mating effort. Most men opt for the latter.

Father-present societies, in contrast, tend to be found in harsh ecologies and in modern or other relatively large, stratified societies (Draper & Harpending, 1988). These are societies that are sometimes characterized by ecologically—or socially—imposed monogamy (Flinn & Low, 1986). Under harsh conditions, few men are able to acquire the resources needed to support more than one wife and family. The reproductive aspirations of most men are thus ecologically restricted to monogamy. In most modern societies, monogamy is socially imposed; there are formal laws that prohibit polygynous marriages. The result is at least a partial suppression of men's mating efforts, and, through this, reduced opportunity cost to paternal investment. In these cultures, investing "excess wealth" in the well-being of children is a viable reproductive strategy for men, especially when child mortality risks fluctuate greatly and vary inversely with level of paternal investment (e.g., during epidemics).

Operational Sex Ratio The OSR has a strong influence on men's relative focus on mating or parenting (Guttentag & Secord, 1983; Pollet & Nettle, 2008). In modern societies, expanding populations, for instance, result in an "oversupply" of women, because women prefer slightly older marriage partners and men slightly younger ones (Kenrick & Keefe, 1992). With an expanding population, the younger generation of women will be competing for marriage partners from a smaller cohort of older men. The resulting imbalance in the numbers of marriage-age men and women is correlated with changes in divorce rates, sexual mores, and levels of paternal investment (Guttentag & Secord, 1983).

When there is an oversupply of women, men's mating opportunities increase, and these historical periods are generally characterized by liberal sexual mores; high divorce rates; an increase in the number of out-of-wedlock births and the number of families headed by single women; an increase in female participation in the workforce; and, generally lower levels of paternal investment (Guttentag & Secord, 1983). The bottom line is that men are better able to express their preference for a variety of sexual partners and relatively low levels of paternal investment. A very different pattern emerges when there is an oversupply of men (Guttentag & Secord, 1983). Here, women are better able to enforce their preferences for a monogamous, high-investment spouse. As a result, these periods are generally characterized by an increase in the level of commitment of men to marriage, as indexed by declining divorce rates and greater levels of paternal investment.

CONCLUSION

Given the biology of mammalian reproduction, it is unremarkable that mothers throughout the world show a much greater availability for and engagement with their children than fathers. The most remarkable feature of human reproduction is that many fathers show some degree of direct and indirect investment in their children. Although the level of paternal care may not always be satisfactory from the perspective of the wives of these men, it is nonetheless remarkable in comparison to the little paternal care found in most mammals (Clutton-Brock, 1989).

Men's investment or lack of investment in their children reflects the same cost–benefit trade-offs found with facultative paternal investment in other species (Table 20.1). The benefits of paternal investment include reductions in infant and child mortality rates in high-risk environments and improvements in children's later ability to compete for essential social and material resources (Kaplan et al., 1998). As found with other species with high levels of paternal investment, men's parenting is associated with relatively high—roughly 95%—levels of paternity certainty and with restricted mating opportunities. The combination reduces the costs of paternal investment.

The facultative expression of men's parenting is correlated with many factors, including heritable individual differences, hormonal profile, the quality of the spousal relationship, and child characteristics (Neiderhiser et al., 2007; Storey et al., 2000). Childhood experiences may also bias men toward mating effort or parental effort through the nature of the parent-child attachment, the level of parent-parent conflict, and the age of onset of adrenarche (Belsky et al., 1991; Del Guidice, 2009). An insecure, avoidant parent-child attachment and early adrenarche may bias boys and later men to exploit social relationships (Del Giudice, 2009). Among the consequences are an increased frequency of short-term sexual relationships and little parental investment. Wider social and ecological factors, especially laws against polygynous marriages and the OSR, also influence the degree to which men invest in the well-being of their children (Draper & Harpending, 1988; Flinn & Low, 1986; Guttentag & Secord, 1983). The goal for future studies is to uncover the relative contribution of each of these factors in general, and to better understand individual differences in men's responsiveness to factors such as marital quality and the OSR as they influence paternal investment.

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CHAPTER 21

Parental Investment and Parent-Offspring Conflict

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Many species do not engage in parental care (Alcock, 2001). Part of the reason is that parental care is costly. By investing in offspring, parents lose out on resources that could be devoted to themselves, channeled toward securing a larger territory, finding additional mates, or future offspring. Some parents even risk their own lives in an effort to improve the survival of their offspring. So when we do see parental care, the reproductive benefits must have been great enough to outweigh the costs of providing not only the physical means for survival but also fostering the development of the skills required for success across the lifespan.

From the parental perspective, each individual's overall reproductive effort is a combination of mating effort (courtship, etc.) and parental effort or investment. Trivers (1972) defined parental investment as any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive potential) at the cost of the parent's ability to invest in other offspring (either current or future). In many species, it involves such things as food provisioning, and protection from predators. In humans, it involves a great deal more, ranging from providing food and shelter to an education, music lessons, taking the kids to hockey or soccer practice, or providing them with braces. In general, an offspring's fitness increases with the amount of parental investment it receives. We can assume that, in species that have parental care, extremely low levels of parental investment may result in the loss of offspring because a certain amount of investment is required for survival, but a point of diminishing returns is also eventually met at very high levels of parental investment because the offspring are unable to capitalize on investment over and above a certain amount.

Hamilton's rule (1964) can shed light on how parents and offspring behave with regard to parental investment. Hamilton developed the concept of inclusive fitness, noting that when we assess the fitness of a trait or behavior, we need to consider its contribution to the reproduction of that individual and to whether it influences the reproductive prospects of its kin. The inequality that sums up the conditions under which a particular behavior would be expected to spread is $c < rb$, where c equals the fitness cost of the action (such as providing food) to the actor, b is the fitness benefit (getting to eat) to the recipient, and r is the degree of relatedness between the actor and recipient (0.5 for parent-offspring, 0.5 for full siblings, 0.25 for half-siblings, etc.). Obviously, a parent's investment in its offspring provides a benefit to the offspring, which increases the parent's inclusive fitness. As long as the cost of parental investment doesn't begin to outweigh the benefit to the offspring times the degree of relatedness, it should continue.

Similarly, in a brood of two equal siblings, A and B, from Hamilton's rule (1964), A should continue to take resources until its marginal gains drop to one-half those of B, who gets the remainder (Parker, Mock, & Lamey, 1989). For half-siblings, marginal gains drop to one-quarter.

The key to this is the degree of relatedness. A child shares a given gene with itself with a probability of 1.0, but it shares the same gene with its sibling with a probability of only 0.5. For this reason, a child is expected to try to obtain resources (or continue to monopolize them in the case of nursing, for example) unless the value of that resource to that child drops below the value, multiplied by the degree of relatedness, of giving that resource to its sibling. Parents, in contrast, are equally related (0.5) to each of their offspring. As a result, they are motivated to distribute resources equally unless one child is better able to benefit from the resources than others. Our offspring are the way our genes get into the next generation but not all offspring are equally good fitness vehicles. Some offspring will be better able to survive or be more likely to mate. Certain offspring may be more likely to benefit from some forms of parental care than others (an infant compared to a teenager, perhaps). As a result, selection has favored mechanisms of parental care that have the effect of increasing the fitness of the parent by favoring offspring who are likely to provide a higher reproductive return on their parents' investment (Daly & Wilson, 1995). But the costs, degree of relatedness, and benefits to parents can be influenced by a variety of factors that, in turn, influence the amount of parental investment given. The conflict this can cause between parent and offspring will be discussed later.

FACTORS AFFECTING THE AMOUNT OF PARENTAL INVESTMENT

Factors influencing the amount of parental investment include the costs to parents, the benefits to parents, the circumstances influencing costs and benefits, and the degree and probability of relatedness to offspring.

Factors Influencing Costs to Parents

Parental age is one factor influencing maternal investment. In species in which the probability of death increases systematically with age, a parent is selected to give an increasing proportion of parental investment to older offspring. And some data shows that older parents do invest more than younger parents (Salmon & Daly, 1998; Voland & Gabler, 1994). This is often particularly true of older mothers who face more of a reproductive constraint due to menopause. In humans, the age of the mother is also a significant factor in the likelihood of perpetrating maternal infanticide (Daly & Wilson, 1988). Young women, those likely to have many future opportunities to reproduce, might be expected to be more willing to sacrifice a current child when conditions for successfully raising the child are poor. Older women, close to the end of their reproductive years, who pass up the opportunity to invest may never have that opportunity again. As the likelihood of future reproduction decreases, delaying childbirth becomes more costly. Selection should favor substantial immediate investment in children by older more than younger women, rather than delaying investment. The dramatic cross-culturally observed decrease in the rate of maternally perpetrated infanticide with increasing maternal age reflects the change over time of the weight the maternal psyche places on a current offspring versus possible future offspring (Daly & Wilson, 1995; Lee & George, 1999; Overpeck, Brenner, Trumble, Trifiletti, & Berendes, 1998).

The *number of offspring* at any given time is also expected to have an impact on parental investment. As parental investment is a limited resource (food, time, money) that must be allocated among offspring, it seems clear that with the possible exception of protection from predators, most parental resources will be in shorter supply when there are multiple young (not necessarily all the same age) present at the same time (Daly & Wilson, 1995). More children means fewer resources for each one.

Parental resource circumstances are also predicted to have an impact on the amount of parental investment. Clearly, when resources are in short supply or difficult to obtain, any particular investment is more costly from the parent's perspective than when resources are abundant. Davis and colleagues (Davis & Todd, 1999; Davis, Todd, & Bullock, 1999) modeled the success of a variety of parental investment decision rules in the Western bluebird and found that the success of different rules is highly dependent on the amount of resources available to parents. The less parents have, the more biased they ought to be in their allocation of investments. Parents faced with extremely poor resources ought to invest heavily in a single offspring, ignoring the others. As resources become more abundant, parents will do best by becoming more egalitarian. At a very general level, one could argue that the degree to which parents divide current investment unequally among offspring is a function of the amount of resources available to them.

Mating opportunities would also be expected to influence the cost of investing in offspring. Mating opportunity costs are missed mating opportunities resulting from effort devoted to parental care. Females and males experience missed mating costs but they are higher for males due to the fact that male reproductive success is largely limited by access to females, whereas for females reproductive success is not increased by sexual access to a variety of males. As a result, we expect males to provide less parental care, and studies suggest that when mating opportunities are frequent, men invest less (Magrath & Komdeur, 2003).

FACTORS INFLUENCING BENEFITS TO PARENTS

The *age of the child* can have a significant impact on the benefit of investing to parents. In many ways, one would predict a greater payoff from investing in older children. One's expected contribution to parental fitness resides mainly in one's reproductive value (expected future reproduction), and this quantity increases with age until at least puberty, making an older immature offspring more valuable from the parental perspective than a younger one. This increase occurs primarily because in non-technological societies some percentage of children die (Volk & Atkinson, 2013).

As a result, the average 14-year-old, for example, has a higher reproductive value than the average infant, because some infants don't survive to their teenage years. However, the older an individual offspring gets, the less valuable parental investment (especially certain kinds of investment) may be in terms of the offspring's ability to utilize it when compared to its utility to other offspring. In particular, a great deal of parental investment is often critical to the survival and future of young offspring. For them, significant parental investment can make a huge difference.

Parents clearly respond to the changing needs and abilities of their children. But when one child must be sacrificed so others can be saved, it is apparently a cross-cultural universal that the youngest is the likeliest victim (Daly & Wilson, 1984). Data on Canadian homicides also suggest that older children are more highly valued. When Daly and Wilson (1988) looked at the risk of the homicide of a child by a biological parent in relation to the child's age, infants were at a much higher risk of being killed than any other group of children. After 1 year, the rates drop off dramatically until they reach zero at age 17. And it is not only that infants are easier to kill, as the risk of a child being killed by a nonrelative shows a different pattern, with 1-year-olds more likely to be killed than infants, and teenagers being the most likely to be killed.

A *child's expected future prospects* will also be expected to have an impact on the benefits of parental investment. In other words, future survival and reproductive success influence the benefit to parents. If there is unlikely to be a fitness return on their investment, natural selection would be unlikely to favor mechanisms to invest in such offspring. Like offspring age, offspring expected future prospects are related to an offspring's ability convert parental investment into fitness. Thus, one would expect evolved psychological mechanisms of parental care to be sensitive to cues of offspring "quality" or ability to convert parental care into future reproductive success. For example, children who are disabled in some way, all else being equal, are less likely to have future reproductive success than children who are healthy. In humans, poor infant quality clearly has an impact on parental investment. Offspring born with a severe physical deformity are likely to be the victims of infanticide, especially in traditional societies where institutional care of the handicapped is not available (Daly & Wilson, 1984, 1988). Selection favors adaptations for investing where the return on investment will be highest relative to alternative forms of investment. This can shape differential investment between siblings, or it can direct investment toward other kin, or toward mating effort (as seen in some divorced men).

The effect of maternal condition/resources on the sex ratio at birth has received some attention in demographic studies of modern societies (Almond & Edlund, 2007; Gibson & Mace, 2003). Trivers and Willard (1973) argued that when one sex has a greater variance in lifetime reproductive success than the other and parents (specifically mothers) vary in their physical condition or access to resources, differences in preferences for offspring of the two sexes are likely to evolve. And some studies have demonstrated maternal condition predicting sex biases in infant mortality (Almond & Edlund, 2007; Voland, Dunbar, Engel, & Stephan, 1997); however, effect sizes tend to be small and a number of studies have failed to find Trivers-Willard effects (e.g., Beaulieu & Bugental, 2008; Guggenheim, Davis, & Figueredo, 2007). Cronk (2007) has highlighted the difficulties, both theoretical and methodological, of testing the Trivers-Willard hypothesis in large industrialized societies. The strongest evidence for Trivers-Willard effects comes from studies of small-scale societies.

Dickemann's (1979) review of historical data on infanticide and the Indian caste system reveals that infanticide was extremely common among the highest castes prior to the 20th century, with female infants the victims. These daughters had very few marriage options (had to marry within own subcaste). Among high-caste Indian families, investment in males (who could marry females from lower subcastes) paid larger dividends in terms of grandchildren, and parents heavily biased their investment toward males (Gupta, 1987). For lower castes, the tendency toward males marrying down meant daughters out-reproduced sons and parents biased their investment toward daughters (lower rate of female infanticide). Studies in the United States (Gaulin & Robbins, 1991) and Kenya (Cronk, 1989) have suggested that female infants from low-income families are nursed more than infant boys. Hungarian Gypsy populations also show a female-biased sex ratio (Bereczkei & Dunbar, 1997, 2002). Like lower-caste Indians, Gypsies are at the bottom of the social scale in Hungary, and Gypsy women are more likely to marry up the social scale than men and, in doing so, provide their parents with more surviving grandchildren. Gypsy women who marry up have babies with higher birth weights, lower mortality rates, and lower rates of birth defects than Gypsy women who marry within their social group. Bereczkei and Dunbar (1997) found that compared to native Hungarians, Gypsy women were more likely to suckle their firstborn daughters for longer than sons, abort a subsequent pregnancy after a daughter than after a son, and allow their daughters to stay in school longer.

There are also examples in which investment favors sons. In societies where the possession of resources has a significant impact on male reproductive success, a preference for sons will be seen among the affluent. This has been the case in 18th-century northern German villages (Voland, 1998) and has been noted in the records of probated wills among Canadians living in British Columbia (Smith, Kish, & Crawford, 1987). In terms of the parental pay-off, Cameron and Dalerum's (2009) study of Trivers-Willard effects in *Forbes'* list of billionaires indicated that people in the top economic bracket have more grandchildren via their sons than daughters and that mothers at this highest socioeconomic status have more sons.

Offspring need is also a relevant factor. Although offspring prospects, or the ability to turn maternal investment into future reproductive success, has always been assumed to be a strong predictor of maternal care, it has also been suggested that mothers' investment in offspring could be contingent in that high-risk offspring will either receive more or less investment than low risk offspring based on maternal resources (Beaulieu & Bugental, 2008). Beaulieu and colleagues have tested this in several studies (Beaulieu & Bugental, 2008; Bugental, Beaulieu, & Silbert-Geiger, 2010). Their results in samples including preterm babies and children and women with high or low resource availability suggest that mothers with low resources invest more in low-risk children, whereas those mothers with higher resource levels invest more in high-risk children (as they have sufficient resources to care for other children as well).

FACTORS AFFECTING RELATEDNESS

Paternity uncertainty is one of the driving reasons that females invest more in parental care than males. From a genetic perspective, individual males should only invest in an offspring if they can be sure that the offspring is their own. Mammalian females (with internal gestation and fertilization) have always been certain that their offspring are their own. Males do not have such certainty and as a result, should be attuned to signs of paternity and inclined to invest only when such signs are present.

There are a variety of results that suggest that paternity uncertainty does have an impact on human paternal investment. Given the relatively high levels of heritability in many physical traits, the more a child resembles the putative father, the greater the paternity confidence is likely to be. As a result, one might expect that paternal affection and investment will be influenced by paternal perceptions of resemblance. Several empirical studies have demonstrated that perceived father-child similarity is associated with higher degrees of paternal emotional closeness and investment, typically measured as time spent with the child, or involvement in education (Alvergne, Faurie, & Raymond, 2010; Apicella & Marlowe, 2004, 2007; Li & Chang, 2007).

Data also suggest that people pay more attention to a child's paternal resemblance compared to maternal resemblance, despite the fact that the degree of actual resemblance between parents and infants is, in fact, quite low and, if anything, is slightly biased toward mother-child resemblance (Alvergne, Faurie, & Raymond, 2007; Bressan & Grassi, 2004). Greater resemblance to the mother makes sense if paternity confusion is beneficial for offspring (because they might be living with a social rather than biological father). Yet evidence suggests that mothers and maternal relatives are highly inclined to emphasize paternal resemblance in newborns. This is most often interpreted as an attempt to manipulate fathers' perceptions of paternal resemblance, increasing their paternal attachment and investment (Bressan, 2002; Daly & Wilson, 1982; McLain, Setters, Moulton, & Pratt, 2000; Regalski & Gaulin, 1993). For further discussion of paternal investment, see Geary (Chapter 20, this volume).

Stepparenting also obviously affects relatedness in that a stepparent is not related biologically to any stepchildren they may have. In species with biparental care, when one parent dies or disappears and is replaced by a new mate, any preexisting offspring now have a stepparent. As with paternal uncertainty, one would expect mechanisms of parental allocation of investment to be sensitive to whether an offspring is one's biological child, with resources being directed away from stepchildren toward biological children.

Daly and Wilson's (1984, 1988, 2001) studies of discriminative parental solicitude have focused attention on the dynamics of stepparenting in humans. Parental care can be viewed as a continuum with self-sacrifice at one end and acts that inflict costs on the child, including child abuse and homicide, at the other end. Daly and Wilson's study of child abuse in Hamilton, Ontario demonstrated that children living with one genetic parent and one stepparent are about 40 times more likely to be physically abused than children living with both genetic parents. This occurs even when controlling for poverty and socioeconomic status (to control for the higher rate of child abuse in low-income families).

Data on child infanticide tells the same story. The rates of child murder are far higher for stepparents than for genetic parents. The risk is highest for the very young, particularly children under 2 years of age. Daly & Wilson (1988) found that the risk of a preschool-aged child being killed ranged from 40 to 100 times higher for stepchildren than for children living with two genetic parents.

A less extreme example involves amounts of investment, rather than termination. Stepfathers invest fewer monetary resources in their stepchildren. In a study of men living in Albuquerque, New Mexico, Anderson, Kaplan, and Lancaster (1999) reported that genetic children were 5.5 times more likely to receive money for college than stepchildren. On average, genetic children received $15,500 more for college and had 65 percent more of their college expenses paid for than stepchildren. There have also been suggestions that when stepparental investment is seen, it may reflect mating effort on the part of males (intended to make themselves more attractive to their new mate) rather than parental effort (Anderson et al., 1999; Hofferth & Anderson, 2003; Rohwer et al., 1999).

Adoption is another factor that changes relatedness. One needs to distinguish between the adoption of related versus unrelated individuals. With one's own offspring, relatedness is 0.5. The adoption of other kin (niece, cousin's offspring, etc.) would entail a lesser degree of relatedness, but there would still be some genetic common interest. Under these circumstances, one would expect a lesser degree of parental investment than in one's own biological children. From this perspective, one would expect very little to no parental investment in an adopted child as they are not genetically related at all. With stepparent situations, at least one parent is the biological parent; in adopted situations there is no biological parent present.

However, there is little evidence that the adoption of unrelated individuals has ever occurred with any frequency over most of human evolutionary history. Nonhuman primates, who often live in close knit kin groups like humans, tend not to adopt orphaned young (Silk, 1990). Most historical evidence of human adoption and adoption practices in traditional societies has been of genetically related individuals. Those individuals who cannot have their own children have often adopted their siblings' extra children ($r = 0.25$) (Pennington & Harpending, 1993; Silk, 1980, 1987). In Stack's (1974) study of a Chicago urban Black community, most of the fostered children were with maternal kin—either older sisters, aunts, or grandmothers. There's no reason to expect that we would have a mechanism designed specifically to deal with the adoption of unrelated individuals. It may be that, in our current human environment, strong biological desires and cultural expectations lead some individuals to adopt unrelated offspring. Indeed, the relationship between adopted children and parents typically functions in the same way as that between genetic parent and child, particularly when they are adopted as very young infants.

PARENT-OFFSPRING CONFLICT

At the core of inclusive fitness theory is the idea that our kin are valuable, that we share a commonality of interest. In a genetic sense, what enhances the fitness of one's kin enhances one's own fitness. The more closely related two relatives are, the more common their genetic cause. But the inevitable consequence of social living is that at some point, individuals who interact will experience some conflict. Individuals act so as to increase their own inclusive fitness, even when it has fitness costs to others. Parent-offspring interaction can be highly cooperative but it can also involve significant conflict. There may be agreement about the general goal of offspring fitness, but conflict can occur over amounts of investment in one offspring versus another.

Being closely related does not mean that two individuals' interests are identical. As much as the degree of genetic similarity is a source of unity, the degree of genetic difference is a source of possible conflict. This becomes obvious when individuals are competing for scarce resources (mates, food, or territory). Conflicts can also happen when disagreement occurs over the optimal distribution of resources (to shared offspring, offspring of a previous union or mating effort). Such conflicts can also occur between parent and offspring.

Parent-offspring conflict can arise because some actions that advance the fitness of an offspring can potentially reduce the lifetime success of the parent and vice versa. In general, we would expect individuals to allocate their parental investment among their offspring in ways that optimize their own inclusive fitness. All other things being equal, parents are equally related to all their offspring. However, we would expect offspring to have a somewhat different take on that matter. They are more closely related to themselves than to their siblings. (Trivers, 1974). As a result, one might expect each offspring to want to extract more than their share of parental investment. Conflicts arise over the level of investment considered to be appropriate. This zone of conflict can be predicted from kin selection theory. When the costs to parents are less than the benefits, both parents and offspring benefit from parental investment and there is no conflict. When the cost becomes greater than the benefit but not more than twice the benefit, parents lose but offspring still gain, so there is conflict. When the cost becomes greater than twice the benefit, both lose, so there is no conflict, and parental investment ends. (For reviews of parent-offspring conflict in humans and nonhumans, see Maestripieri, 2002; Salmon & Malcolm, 2011.)

MATERNAL-FETAL CONFLICT

Maternal investment begins long before birth. The mother's own resources provide nutrients and a safe environment for the developing child over the 9-month gestational period. Although, at first glance, this would seem a very harmonious relationship with fetus and mother sharing the same goals, the genetic interests of both parties are not identical. Because the fetus is more closely related to itself than either its mother or any future siblings, the process of pregnancy becomes a sensitive balance between the developing fetus' tendency to secure as large a share of maternal resources as possible and the mother's tendency to preserve resources for herself and future offspring. Often this balancing act results in a variety of unpleasant symptoms for the mother and occasionally serious complications. Haig (1993, 1998) has analyzed pregnancy complications from a maternal-fetus conflict perspective, suggesting that such conflicts are responsible for some puzzling aspects of pregnancy and its complications.

WEANING CONFLICT

Conflict over weaning in mammals (Maestripieri, 2002; Trivers, 1974) is a very clear example of parent-offspring conflict. As Figure 21.1 illustrates, parents are selected to continue to invest in their offspring up to the point when the cost in terms of reduced reproductive success (the more a parent invests in a current offspring, the less they have to invest in future offspring) begins to outweigh the benefits of increased survival for the current offspring. Or, as soon as the costs begin to exceed the benefits ($B/C < 1$), parents should stop investing in the current offspring and start to work on the next (Trivers, 1974).

But at this point, the offspring would like investment to continue, being more closely related to itself than to any future siblings, it has been selected to demand investment until the cost–benefit ratio drops below 0.5. After that point, continued demands for investment would lead to a reduction in indirect fitness, since the parent would produce fewer siblings with whom the offspring would share genes. But until that point is reached, offspring should attempt to obtain as much parental investment as possible, enhancing its own reproductive fitness in the process. As a result, weaning conflict tends to involve a gradual shift in parental investment.

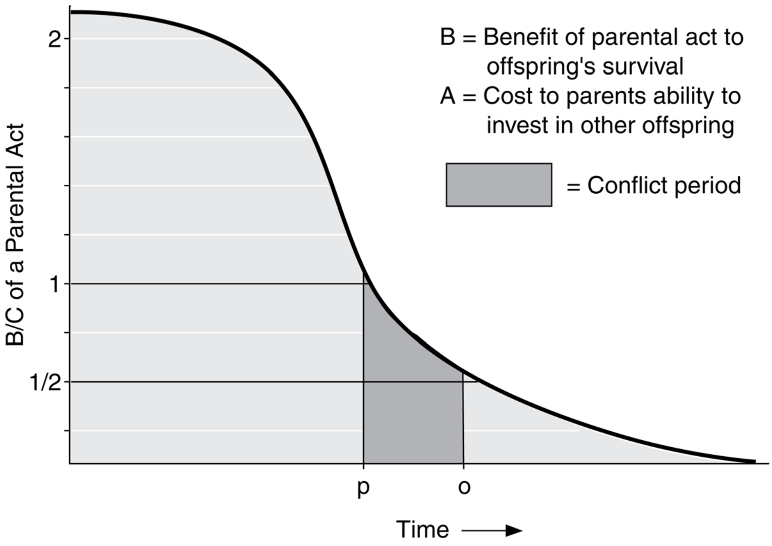

Figure 21.1 Analysis of the Costs and Benefits of Parental Investment and the Parent-Offspring Conflict That Results. Adapted from "Parent-Offspring Conflict," by R. L. Trivers, 1974, *American Zoologist*, *14*, pp. 249–264.

PARENT-OFFSPRING CONFLICT OVER MATING

Another zone of conflict can occur over offspring mate choice. Parental influence over mate choice has been documented in many cultures (Apostolou, 2007a, 2007b) ranging in degree from minimal influence to complete control. Recent studies suggest that parental and offspring mate preferences are often not in sync with parents exhibiting stronger preferences for SES and family background features, whereas offspring focus more on attractiveness and a sense of humor (Apostolou, 2008a, 2008b, 2011; Buunk, Park, & Dubbs, 2008; Perilloux, Fleischman, & Buss, 2011). It has been suggested that conflict over offspring mate choice is driven less by differences in genetic relatedness and more by parent-offspring conflict over resource distribution in that parents can benefit by having more in-law investment allowing them to redistribute their own investments to other offspring (for a model of such conflict over allocation of resources to daughters see van den Berg, Fawcett, Buunk, & Weissing, 2013).

ATTACHMENT

In a sense, attachment type can be seen as the result of the form of parental investment a child receives. Bowlby (1969) characterized attachment as reflecting a child's "internal working model" of the self, others, and relationships, emphasizing the importance of early experience on adult personality and behavior. The central propositions of attachment theory are that: (a) individual differences in the quality of infant-parent attachment relationships are primarily determined by the quality of care provided to the child, and (b) early security shapes later development (Belsky, 1997). It has been suggested that variations in attachment security evolved to serve reproductive fitness goals and that environmentally induced modifications in life history traits tend to be reproductively strategic (Belsky, Steinberg, & Draper, 1991). The argument has been that patterns of attachment evolved as psychological and behavioral vehicles for translating information about prevailing ecological conditions into fitness-enhancing reproductive strategies (Belsky, 2000; Bjorklund & Pellegrini, 2002; Chisholm, 1996; Wiley & Carlin, 1999). This relies on two assumptions: that patterns of attachment are relatively stable from childhood through adolescence and early adulthood, and the relative stability of environmental conditions across the first 20–30 years of human life in the EEA (environment of evolutionary adaptedness).

According to Chisholm's life history model of attachment (1996), the type of attachment seen is a facultative adaptation to the style of parenting. Consistently responsive attentive parenting produces secure attachment because, in the ancestral environment, such parenting was evidence of access to resources and a commitment to provide the necessities of life to that offspring. Nonresponsive or rejecting parenting produces insecure attachment. And in the ancestral environment, such parents would have been unwilling or unable to invest in their offspring. The suggestion has been that insecure-avoidant behavior in offspring represents the facultative adaptation to parental unwillingness to invest, whereas insecure-resistant behavior in offspring is the facultative adaptation to parental inability to invest (Chisholm, 1996).

Attachment is normally classified as secure, insecure-avoidant, and insecure-resistant. If individual differences in attachment organization represent facultative adaptations to conditions of risk and uncertainty that were recurrent in the EEA (Chisholm, 1996), we can examine the nature of styles of attachment in a new light. Secure attachment would develop under ecological conditions that indicated that resources were reasonably abundant and would remain so. This would foster the belief that the world is a relatively safe place, that other people can be trusted, and that relationships last. The result would be the emphasis of parenting over mating.

The psychological and behavioral data on secure individuals is consistent in terms of adult relationships and parenting. Secure men have more positive and supportive interactions with their spouses than insecure men, whereas secure women are more likely to seek emotional support and physical comfort from their male partner when in a stressful situation (Simpson, Rhodes, & Nelligan, 1992). Conflict and negative affect are pronounced in married couples when both are insecure (Cohn, Cowan, Cowan, & Pearson, 1992) but when both partners are secure, negative interactions are rare (Senchak & Leonard, 1992). In general, lower levels of conflict and more skilled ways of managing conflict occur in relationships involving secure individuals. Security facilitates the development of mutually rewarding relationships. Secure individuals report higher levels of satisfaction when dating (Simpson, 1990), married (Kobak & Hazan, 1991), and their romantic relationships are longer lasting (Hazan & Shaver, 1987; Kirkpatrick & Davis, 1994; Shaver & Hazan, 1993). A history of security fosters the development of mutually rewarding and stable pair bonds in the service of promoting high investment parenting (van Ijzendoorn, 1995; Ward & Carlson, 1995). Secure attachment in childhood is a central component of developing a facultative reproductive strategy selected to promote a quality versus quantity orientation toward reproduction.

Belsky et al. (1991) and Chisholm (1996) have suggested that, when the flow of resources is chronically low or unpredictable, it may be (or have been) biologically adaptive to reduce parental investment, to allocate resources not to parenting but to offspring production (Borgerhoff Mulder, 1992). Limited and unpredictable resources would result in a reproductive strategy designed to foster in offspring beliefs and expectations that the world is uncaring, that others can't be trusted, and that relationships are not likely to be mutually rewarding or enduring. As a result, individuals are predicted to pursue interpersonal relationships that are disproportionately self-serving, opportunistic, and exploitative. Under such conditions, individuals will have many partners, and pair bonds will be unstable with many kids and little paternal care, a quantity not quality strategy.

The data suggest that insecure-avoidant individuals are more promiscuous and less committed (Kirkpatrick & Hazan, 1994; Simpson, 1990) and more likely to be involved in a break-up (Feeney & Noller, 1992). As well, avoidant mothers are less responsive (van IJzendoorn, 1995), less supportive and helpful, less concerned, and more remote and controlling (Crowell & Feldman, 1988, 1991).

The insecure-resistant case is a little different. These children tend to exaggerate their need for care and attention (Cassidy & Berlin, 1995) in response to inconsistently responsive care. One suggestion about why this develops has been related to the helpers at the nest phenomenon (Borgerhoff Mulder, 1992; Emlen, Wrenge, & Demong, 1995). Inconsistently responsive parenting seems to produce a dependency in their children that has been suggested to promote the parent's reproductive fitness. Kunce and Shaver (1994) noted that insecure-resistant women are compulsive caregivers, particularly toward younger siblings. Resistant mothers are difficult to separate from their toddlers (Crowell & Feldman, 1988) and doubt their offspring's ability to function away from home (Kobak, Ferenz-Gillies, Everhart, & Seabrook, 1994). These mothers keep their children close while maximizing their own ability to psychologically manipulate the children, perhaps fostering helping at the nest behavior (Belsky, 1997). We might expect that such an attachment style would be seen more in some niches (firstborn females for example) if the mother's ability to care for her offspring is taxed (lack of resources, caregiving help, etc.).

Attachment, whether secure (reliable parental investment) or insecure (the consequences of early stress), might have evolved to function as an assay by which future social relations might be predicted. Data on early menarche, father absence, maternal harshness, and sexual activity (Belsky, Steinberg, Houts, & Halpern-Felsher, 2010; Ellis, Schlomer, Tilley, & Butler, 2012; Graber, Brooks-Gunn, & Warren, 1995; Nettle, Coall, & Dickens, 2010; Surbey, 1998; Wierson, Long, & Forehand, 1993) suggest that this may be the case. When girls grow up in father-absent homes (cues that the local males may be unlikely to stay and invest or that long-term survival prospects are poor), they tend to mature faster and follow a strategy of quantity over quality. Under some circumstances, adaptations are designed to facilitate reproduction early and often. In a similar vein, data suggests that boys that grow up in father-absent homes may exhibit increased promiscuity and criminality as well as a general increase in "macho" behavior (Bereczkei & Csanaky, 1996). Such a strategy of increased aggression might serve under some circumstances to intimidate rivals and attract women interested in protection (Kim, Smith, & Palermiti, 1997).

SIBLING RELATIONS

The other side to parent-offspring conflict is how the battle for resources plays itself out among a group of siblings. Natural selection has shaped strategies for sibling competition just as it shaped mechanisms for discriminative parental solicitude. Many factors play a role in the approach individual siblings may take but two are of particular interest: birth order and birth spacing (interbirth interval).

Birth Order

Theoretical models of the evolution of parental inclinations predict that parents will often treat their offspring differently. However, if one assumes that human parents typically have enough resources available to them to raise all of their children to adulthood (as presumably most do in Western societies), this assumption leads to the expectation that human parents may use a decision rule that divides investment equally among all their children. Such a rule is called the *equity heuristic* (Hertwig, Davis, & Sulloway, 2002).

However, the equity heuristic is not the only model of the allocation of parental investment. There are times when the equal allocation of resources may not provide the optimal result, perhaps because, most of the time, all else is not equal and some offspring may be more valuable fitness vehicles than others.

In addition to enjoying the relative security of parental preference in a pinch (as discussed earlier), firstborn children have always benefited from an early absence of sibling contenders for a share of parental investment (Salmon, Shackelford & Michalski, 2012). Even in the modern West, where parental resources are presumably less stretched than in noncontracepting, premodern societies, firstborn children still receive more parental caretaking and attention in infancy than laterborns (Jacobs & Moss, 1976) and they grow faster, such that despite being smaller at birth, they are larger by 1 year of age (Wingerd, 1970).

There is, however, a counterveiling effect: As parents themselves grow older, the fitness value of an offspring of any given age and phenotype increases relative to the parent's residual reproductive value. Thus, in any species in which expected future reproduction is a declining function of parental age, older parents will have been selected to invest more in offspring, all else being equal, than younger parents. Thanks to menopause, this argument certainly applies to the human female, and dramatic decreases in maternally perpetrated infanticide as a function of maternal age appear to be one reflection of age-related changes in the relative weights that the maternal psyche places on one's infant versus one's future (Bugos & McCarthy, 1984; Daly & Wilson, 1995).

Impact of Birth Order on Personality and Development Sulloway and others (Salmon, 1999, 2007; Salmon & Daly, 1998; Sulloway, 1996, p. 305) have suggested that the favoring of firstborns (due to their greater reproductive value) and lastborns (due to older parents and lack of younger rival) means that middleborns are the birth order that loses out on average in the parental investment game. Certainly middleborns seem to report lesser levels of financial and emotional support from parents (Janicki & Salmon, 2002; Kennedy, 1989; Salmon & Daly, 1998) than firstborns or lastborns (who tend to be more parentally and familially oriented). As a result, they seem to focus more on developing nonkin reciprocal relationships outside the family unit (Salmon, 2003), and their personality traits seem to be a reflection of that. They are often noted for their skills in getting along with other people and in being excellent negotiators, traits that would have tended to serve them well in trying to find their niche within the family and a network of support outside it (Sulloway, 1999).

Sulloway (1996) has summed up many of the birth order differences with regard to personality, shaped by sibling competition and parental investment, in terms of the five-factor model of personality (which posits five basic personality dimensions: conscientiousness, agreeableness, openness to experience, extraversion, and neuroticism). Sulloway's (1995) meta-analysis of those studies that control for related background variables reveals consistent birth order differences across the five-factor model. The big-five trait of conscientiousness is one that shows consistent birth order differences with firstborns tending to score higher than laterborns. In the area of openness to experience, laterborns tend to score higher on risk-taking (Sulloway & Zweigenhaft, 2010).

Even if parents do not actively favor one child over another (Hertwig et al., 2002), siblings compete with each other for a greater share of parental resources. Sulloway (1995) suggested that they do so by carving out unique niches, or roles, within the family that are influenced by their birth order. Secure in their expectation of parental favoritism (and benefiting from an early absence of competitors for parental investment), firstborns tend to have their choice of niches; motivated to fulfill parental expectations, they typically become supporters of parental values and the status quo. Laterborns cannot compete as effectively in the same roles (being smaller in size and less experienced) so they seek out different niches, other routes to sources of parental (or other) investment. Personality traits that facilitate this include openness to experience and unconventionality, traits that sometimes mark them as rebels (Saraglou & Fiasse, 2003). Michalski and Shackelford (2002) have also suggested that firstborns are more likely to follow long-term mating strategies than laterborn children, with laterborn children desiring a greater variety of sexual partners in the future.

Siblings are not only different in the ways they approach parental investment and cultivating niches, but also in the strategies they use in interacting with each other. Human siblings have dominance hierarchies much like that of other mammals (Sulloway, 2001b). Anyone who watches a litter of puppies can observe the largest using physical strength and the threat of it to get their own way. Firstborn humans are very similar, tending to dominate their younger siblings. Smaller siblings (or laterborn humans) have to resort to alternative strategies, finding ways to get parental assistance or forming bonds with other siblings to unite against their oppressor. What eldest sibling hasn't been occasionally frustrated at having their plans thwarted by a junior sibling who has gone whining or crying to a parent?

Only children (those with no siblings) are an example of what happens without sibling competition. In a sense, they are firstborns who never had a sibling come along after them, never had to compete for parental resources. And, like firstborns, they tend to have a drive for success and respect for parental values. But on many other measures, they fall somewhere between firstborn and laterborns (Sulloway, 2001a). Birth spacing can also affect the correlation between birth order and personality as well as levels of parental investment.

BIRTH SPACING

The impact of birth order is decreased when the birth interval is so short that the siblings are on almost equal footing or when the interval is so large that they are not competing for the same resources from parents. For example, a middleborn with a sibling 7 years older and another sibling one year younger, may have a personality more representative of a firstborn than a typical middleborn (Sulloway, 1999).

Parents invest in their offspring based on many things, including offspring quality, reproductive value, their own residual reproductive value, and the amount of available resources. There is a cost–benefit analysis going on. And for siblings, their brothers and sisters also entail costs and benefits, which vary in proportion to the birth interval. Substantially older offspring, no longer dependent on parental care, experience minimal costs from additional siblings (hence their typical protectiveness). Close age spacing increases competition for parental investment, promoting greater parent-offspring conflict as well as increased sibling rivalry. As well, the costs represented by a younger sibling are greatest when both are infants, requiring the same high levels of parental investment. In traditional and low- to middle-income societies, short birth intervals (less than 2–3 years) are associated with increased infant mortality (Kozuki et al., 2013; Lindstrom & Berhanu, 2000).

The influence of birth order on sibling strategies should be greatest for offspring who are spaced within 5 years. Under these circumstances, older siblings should tend to highlight their own worth and run down the value of their younger sibs. Younger siblings should respond by trying to minimize direct comparisons with older siblings, diverging in their interests and perhaps searching out nonparental sources of investment as they get older (Salmon & Daly, 1998). For example, in terms of openness to experience, the greatest disparities are among offspring separated by moderate age differences. Those that are more distant or very close are less polarized (Koch, 1956; Sulloway, 1996). The reasons for this seem clear in terms of large birth intervals but less intuitive for close ones, until we consider the issue of benefit, not just the cost of having a sibling. If we look at the relative differences in the likelihood of survival of offspring, those that are close in age are more equal. The cost of having a sibling may be high but the benefit is also high as you are equally likely to survive. For large intervals, the cost is much less as you yourself need less parental investment, though the benefit may be lower as the younger sibling may be less likely to survive simply by virtue of the fact that it is young. At middle age spacings, the adjusted costs of having a younger sibling are elevated in relation to the benefits. As a result, moderate age gaps result in more polarization between siblings.

CONCLUSIONS

Basic human relationships and characteristic conflicts show a startling consistency across time and space and it is reasonable to expect that psychological adaptations have evolved to deal with them that are particular to each type of relationship. Evolutionary psychology contributes to our understanding of parent-offspring relations, as well as sibling relations, allowing us to predict and explain the behavior of parents and offspring with regard to social and ecological variables.

A number of factors influence the degree of parental investment. Females invest substantially more than males, the amount of investment given is influenced by the availability of resources and the likelihood of their successful use, and male investment reflects genetic certainty of paternity. Human children require greater investment than other primate offspring and, in particular, fathers must contribute more than they do in many species. Maternal investment begins in utero as do conflicts over levels of investment. Conditions like preeclampsia can be seen as the result of a tug of war between mother and fetus over the amount of fetal growth that is appropriate. Differential investment in offspring is quite common and reflects the factors that affect the costs and benefits of parental investment to parents including: parental age, number of offspring, parental resources, age of offspring, offspring's expected future prospects, paternity certainty, and stepparenthood. Sibling conflict can be seen as an extension of parent-offspring conflict and the degree of conflict is influenced by birth spacing (exacerbated by small intervals) and birth order (in that parents may bias their investment toward a particular birth order).

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CHAPTER 22

The Evolutionary Ecology of the Family

RUTH MACE

INTRODUCTION

Humans live in families. A central relationship in virtually all human social systems is that between husband and wife, although there are relatively few systems where a pair-bonded couple live entirely independently (Harrell, 1997). Hunter-gatherers mostly had (serially) monogamous marriage, no heritable wealth of consequence, and relatively egalitarian social systems. Hunter-gatherer bands were relatively fluid associations of groups of nuclear families that could be based on matrilateral or patrilateral or mixed kinship, friendship, or convenience (Apicella, Marlowe, Fowler, & Christakis, 2012; K. R. Hill et al., 2011; Marlowe, 2005). Changes in subsistence strategy were instrumental in many of the major evolutionary transitions in human evolution, including in the family; particularly important was the advent of agriculture. Access to heritable resources, that greatly influences the future reproductive success of descendants, generates inequalities in wealth and political power (Kaplan, Hooper, & Gurven, 2009). Fertility increased and population densities increased with the advent of agriculture; more complex political systems emerged, correlating with ethnolinguistic groups becoming larger (Currie & Mace, 2009; Johnson & Earle, 2000). Patterns of marriage, residence, descent, and inheritance became both more formalized and probably more diverse and with much more sex-biased dispersal. Thus, understanding human families involves understanding their biological and cultural evolution. The framework of evolutionary ecology has been used to investigate both these aspects and their coevolution.

Ruth Mace's research is funded by the ERC (AdG 249347). All the issues discussed have benefited from discussion and collaboration with many people, with special thanks to present and former members of her research group HEEG at UCL Anthropology.

THE COEVOLUTION OF HUMAN LIFE HISTORY WITH SOCIAL ORGANIZATION

Given that humans have lived as hunter-gatherers for most of their evolutionary histories, a large part of our physiology and psychology, including our key life-history traits such as age of onset and termination of fecundity and senescence, presumably arose as adaptations to this form of subsistence. Human female life histories have features that are rather different from that of other apes, including long childhoods, rapid reproductive rate after puberty, and then female menopause followed by a long postreproductive life. Explanations for these patterns are varied, but most are related to the cooperative and competitive relationships in families (Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998; K. Hill, 1993; Mace, 2000). The combination of relatively short interbirth intervals and long childhood means that families include several dependent children at the same time, and that is costly for mothers. The phenomenon of mothers raising children alone is not observed as normative in any traditional human social system; human mothers nearly always rely on help from their husband to a greater or lesser extent, and often also on the extended family, including grandmothers.

Menopause might be selected for because grandmothers were cooperative breeders and grandmothers were helping their daughters reproduce (Hawkes et al., 1998). This hypothesis stimulated a great increase in interest in kin effects on human fertility, providing an example of how evolutionary theories have helped to set the agenda beyond the evolutionary field in areas such as demography. Speculation on menopause goes back to Williams (1957) and (Hamilton, 1966). A more formal "grandmother hypothesis" that human menopause might be selected for by kin selection favoring older mothers investing in their grandchildren rather than continuing to reproduce themselves was developed (Hawkes et al., 1998). There is now considerable evidence that grandmothers enhance the reproductive success of their offspring (reviewed in (Sear & Mace, 2008). Maternal grandmothers benefit grandchild survival across a wide range of societies. Paternal grandmothers may also be of help, especially in hunter-gatherers (Crittenden & Marlowe, 2008), but their effects are more mixed.

Not all researchers agree about whether the grandmother effect, on its own, is enough for menopause to be favored by natural selection. Some favor the view that the effect of mothers on offspring is more important (Pavard, Koons, & Heyer, 2007; Peccei, 2001), often described as the "mother hypothesis." The mother and grandmother hypotheses are adaptive models that are fairly similar in that they both require some benefit for a separation of reproductive aging from somatic aging. In contrast, some contend that menopause is just due to physiological constraints, such as the temporal viability of female ova (K. Hill & Hurtado, 1991). Postreproductive life could then have evolved as the derived trait, with fertility constrained to halt at 50 (Hawkes et al., 1998; Kim, Coxworth, & Hawkes, 2012). Mathematical models informed by data have had mixed results: They either fail to predict any fitness benefit associated with terminating reproduction so long before death (Hill & Hurtado, 1996) or find that benefits of combined mother and grandmother effects on fertility and age-related increases in maternal mortality may be enough to favor menopause (Pavard & Branger, 2012; Shanley, Sear, Mace, & Kirkwood, 2007), but effects are possibly rather marginal.

Implicit in most of the various models of the grandmother hypothesis is the notion that mothers and daughters are in reproductive competition, because it is assumed only nonreproductive grandmothers can really help her daughter's reproduction. It is striking how little human female generations overlap (Figure 22.1); as a daughter

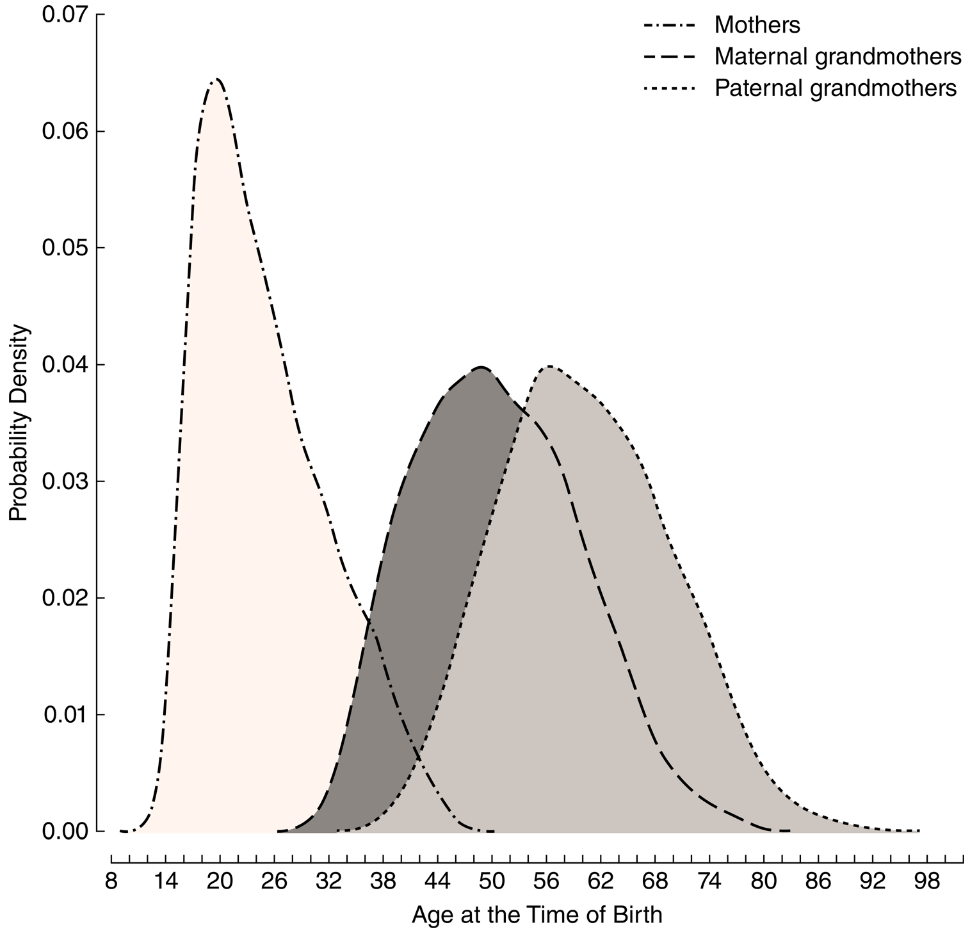

Figure 22.1 Age at Time of Birth for Mothers, Maternal Grandmothers, and Paternal Grandmothers in Rural Gambia. *Source:* From Mace and Alvergne, 2012.

reaches reproductive age, her mother reaches menopause, and as she reaches menopause, her mother dies. However, although reproductive conflict predicts that reproductive generations should reduce overlap, it does not address why it is the older woman that is foregoing reproduction rather than the younger one, as is generally the case in most cooperatively breeding birds or mammals (Clutton-Brock, Hodge, Flower, Spong, & Young, 2010; Hatchwell & Komdeur, 2000). The competition between mothers and grandmothers is particularly intense in species in which females disperse, as female dispersal means that older females are not closely related to younger breeding females in their group (Cant & Johnstone, 2008; Johnstone & Cant, 2010). Female dispersal is unusual among mammals, but is the most common condition in chimpanzees (*Pan troglodytes*) and we assume was the case in ancestral humans, although there is variation in residence patterns of contemporary hunter-gatherers (K. R. Hill et al., 2011). Under patrilocal residence (when females disperse at breeding age and males do not disperse), adult female relatedness to the group will be low at the point of arrival in a new group, and the other females in the group will normally be only distantly related if at all. A female's relatedness to the co-resident group will gradually increase with age as her offspring (particularly sons who do not disperse) are born and then grow up to reproduce themselves. We have shown that this pattern of relatedness does apply in the case of patrilocal compounds (where fathers, sons, and brothers and their families co-reside) in rural Gambia (Mace & Alvergne, 2012). When older women find themselves in competition with their sons' spouse for reproductive resources, there is an essential asymmetry in that the older woman is related to her son's offspring (and thus will suffer a fitness cost in harming her son's wife's reproduction), whereas the son's wife has no relatedness to the older women's offspring, so natural selection does not favor helping her husband's mother reproduce. Evolutionarily stable strategy (ESS) models show that the younger woman is more likely to win the competition, and the older women is destined to become the sterile helper (Cant & Johnstone, 2008). They draw on earlier models that show how reproductive conflict in communally breeding species generally means that, although dominant breeders use more of the resources needed for reproduction than do less dominant ones, it may well be in the genetic interest of less dominant individuals to help more powerful kin reproduce rather than pay the costs of trying to compete with them to reproduce (Reeve, Emlen, & Keller, 1998). Johnstone and Cant (2010) argue that increasing relatedness to the group with age helps explain late life low fertility in whales and primates in which females either disperse or mate outside the group; humans usually fall into the former category. Thus menopause could be linked to sex-biased dispersal patterns. This is interesting, because some had assumed that previous grandmother hypotheses would require matrilocal societies, because maternal grandmothers appear to be the most helpful. This conflict under female-biased dispersal hypothesis suggests the opposite. This theory for menopause only holds if female–female conflict is the main determinant of reproductive schedules. Fathers and sons co-reside in patrilocal societies, and fathers will typically win in conflict with sons, so if males determine the outcome of reproductive conflict, then female dispersal would not predict menopause (Ji, Xu, & Mace, 2014). Dominance and polygyny, not just dispersal, matter in determining patterns of reproduction. Models of genomic conflict between maternally and paternally inherited genes suggest conflict under many circumstances, and predict that fertility could be surpressed by a number of factors, not just sex-biased dispersal (Úbeda, Ohtsuki, & Gardner, 2014). So the evolutionary basis of menopause is still an area of ongoing research.

When wealth from parents or their kin is needed for marriage, parents can control their son's reproductive opportunities, and by delaying their son's marriage, can reduce intergenerational reproductive conflict. In rural Gambian Mandinka (who are farmers), the cultural norm of late male marriage reduces overlap in the reproductive span of mothers and daughter's-in-law almost to zero (Figure 22.1; Mace & Alvergne, 2012). In the very few cases of a daughter-in-law's reproduction overlapping with their mother-in-law's reproduction, the costs seem to be high (Lahdenpera, Gillespie, Lummaa, & Russell, 2012). When daughters move out of the natal household at marriage or shortly after first birth, intergenerational competition between female kin for household resources is presumably reduced by patrilocality (also known as virilocality). Thus fertility patterns could be coevolving with human kinship systems, with earlier female age at first birth and possibly later male age at first birth associated with patrilocal residence (Marlowe & Berbesque, 2012). Kinship, residence, and marriage norms in human societies can themselves be seen as cultural adaptations to reduce reproductive conflict in families (Mace, 2013).

THE COEVOLUTION OF KINSHIP, MARRIAGE, AND SUBSISTENCE SYSTEMS

The cultural norms of marriage, kinship, and descent are in large part products of the socioeconomic system on which societies are based. Hence human behavioral ecology is fundamental to understanding this foundational area of anthropology.

POLYGYNY, MONOGAMY, AND POLYANDRY

As is well known to behavioural ecologists, if males are able to monopolize access to territory that has the resources required for breeding, then that resource can be used to attract females, who will mate polygynously if need be, to acquire that resource. Such resource-defense polygyny, not dissimilar to that described in birds (Orians, 1969), is also common in humans that have heritable wealth or a resource that can be monopolized (Borgerhoff Mulder, 1990). As in other species, such polygynous systems can only really emerge when there are sufficient resources for females to raise their children without a great deal of individual help from fathers. Resources such as livestock are particularly associated with polygynous marriage and male-biased wealth inheritance (Hartung, 1982). Men compete for resources and use those resources to compete for marriage partners. They compete with their own brothers if families are the main source of resources. Polygynous societies contain plenty of unmarried men. Under polygyny, because females are in demand, the parents of daughters can exploit this to demand bride price (a wealth transfer from the groom to the bride's family). Pastoralist systems typically show all these characteristics, because livestock are walking money and not as hard work as extensive crop farming systems for example. Gabbra pastoralists, who herd camels in northern Kenya, can enhance their number of grandchildren more by passing on livestock to their sons (enabling them to marry earlier and more often) than by giving camels to daughters (Mace, 1996); so under resource-based polygyny, patrilineal (male-biased) wealth inheritance norms will maximize the inclusive fitness of the parents.

Monogamy (and occasional polyandry) in hunter-gatherers may relate to resource constraints and difficulty of a male supporting more than one female; one such case is the Inuit of the high Arctic. This is known as ecologically imposed monogamy (Alexander, Hoogland, Howard, Noonan, & Sherman, 1979). But monogamy is also widespread in wealthy societies, especially in Eurasia, including in populations that do not appear to be especially poor, suggesting the need for other explanations. In birds, monogamy is thought to be due to the need for male provisioning, and in primates it is more likely to be related to the avoidance of infanticide (Opie, Atkinson, Dunbar, & Shultz, 2013). Both issues are important in human social evolution. Parental investment, including inherited wealth, is probably key to the cultural evolution of monogamy in agricultural societies. In polygynous societies, the advantages to women of marrying a wealthy male are diluted by the fact that wealth will have to be shared with future co-wives and their offspring; thus male competition for females is much more intense than female competition for males. Yet in monogamous societies, the wife's offspring enjoy sole rights to the inheritance; so females should compete to marry the wealthiest males. This competition generates dowry, that is the payment of money from the bride's family to the groom's family, to make their daughters more attractive enhancing their marriage prospects (Gaulin & Boster, 1990). In parts of India, where dowry is a significant cost to parents required to marry off daughters, females with several older sisters are even at risk of infanticide (Dickemann, 1979). The benefits to males of monogamous marriage are more difficult to explain. Modelling shows that an ESS can emerge if females reward exclusive male investment with their sexual fidelity, but only in ecosystems where the returns on male investment are high with diminishing returns when resources are partitioned (Fortunato & Archetti, 2010). Monogamous marriage is seen where intensive agriculture led to scarcity of land, with depletion in the value of estates through partitioning among multiple heirs.

But the role of infanticide in the evolution of human monogamy cannot be overlooked. It was probably common among hunter-gatherers, in part as a means of controlling fertility rate, when mothers or fathers felt unable to support further offspring. The idea that parental investment is linked to mating strategies, mortality risks, and all other life-history traits was not well understood prior to evolutionary analyses of demographic data. Parental investment cannot be taken as a given and reduced paternal investment is one of the costs of mothers mating with multiple males. The death of the father is a significant cause of infanticide in the Ache (K. Hill & Hurtado, 1996), as other families are not willing to help support orphans or children without fathers. Infanticide of the sort seen in several mammals, such as in langurs (Hrdy, 1990), gorillas, or lions, where incoming males systematically kill infants to induce females to return to oestrus, is not what happens in humans. Nonetheless, one of the most important findings on human parenting was the key work on child abuse and child homicide, which highlighted the role of unrelated partners of mothers in the abuse and neglect or homicide of children from previous relationships (Daly & Wilson, 1988). Since this early study, the results have been replicated in different settings all over the world, with the notable exception of Sweden (Temrin, Nordlund, Rying, & Tullberg, 2011). These findings have clear public-policy implications, not that they have always been given the attention by policy-makers that they deserve (Daly & Perry, 2011). Infanticide is clearly an extreme situation, but the insight that unrelated father-figures are likely to be more of a cause of stress or conflict than genetic fathers applies even in cases where no abuse is involved. In a study of accidental deaths in Australia (ranging from traffic accidents to falling into swimming pools, when no foul play is involved), genetic parents, be they one single parent or two married parents, were less likely to lose their child to such an accident than if young children were living with one genetic parent and one nongenetic parent (Tooley, Karakis, Stokes, & Ozanne-Smith, 2006). In a cohort of normal UK children aged 10, father absence is associated with a tiny reduction in stature over father-present families, and a bit larger reduction in stature is correlated with an unrelated co-resident father figure (Figure 22.2; results from Lawson & Mace, 2009). Some of the costs of a new partnership may be due to the mother diverting her attention toward the new partner, and any new offspring fathered by him, as much as maltreatment being attributable to actions by the new partner himself. There could be additional costs of father absence to older children in terms of monetary investments and wealth inheritance, and hence on marriage prospects, as has been shown in a study of paternal death in India (Shenk & Scelza, 2012). All these effects are relevant to the evolutionary basis of monogamous marriage, and the potential fitness costs to fathers of divorce, as fathers have to trade off the fitness costs of leaving one family against the benefits of starting another.

Only a tiny proportion of human cultures worldwide show polyandrous marriage (Murdock, 1967), which is normally fraternal (two or more brothers marry one wife), no doubt due to the risks of a mother's unrelated sexual partner co-residing with her

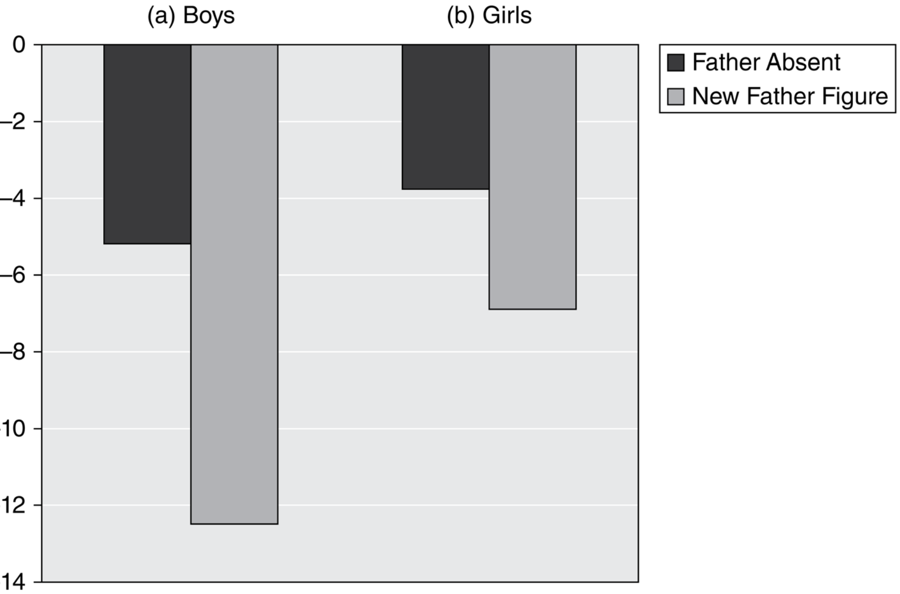

Figure 22.2 Height Difference in mm in Children Aged 10 With Either Father Absent (black bars) or Stepfather Present (gray bars), Relative to Height of 10-Year-Olds Who Live With Both Genetic Parents, for (a) Boys and (b) Girls. *Source:* Data from Lawson and Mace, 2009.

children from another father. In the patrilineal Sherpa of the Himalyas, farming habitat is saturated, as it is restricted to a few river valleys, so there are few opportunities to disperse and set up neolocal farms. It appears that competition between brothers can only be resolved by all brothers marrying the same wife—the ultimate in reproductive sharing. Younger brothers do badly, in terms of direct fitness (Haddix, 2001). But sharing some paternity with a dominant elder brother (albeit the smaller part) can be better than fighting with him for the farm or for more access to their shared wife (Ji et al., 2014). When resource constraints were lifted by the emergence of jobs outside farming, then the younger Sherpa brothers quickly left polyandrous marriages to set up nuclear families (Haddix, 2001).

Residence, Descent, and Wealth Inheritance

Most human societies trace their ancestry predominantly through one side of the family or the other. This is usually reflected in their naming system and frequently prioritizes either the patrilineal or matrilineal line over the other in terms of the inheritance of both titles and material wealth. Within lineal descent systems, patriliny is the most common pattern worldwide. This is because of the benefits to males of controlling resources, particularly important after the advent of agriculture and heritable wealth that has been discussed earlier (in section titled Polygyny, Monogamy, and Polyandry). Patrilineal wealth inheritance and patrilocal residence are usually found together for the same reason. Females in patrilineal, patrilocal, social systems are foregoing the benefits of proximity to their female kin for the advantages of access to male-owned resources, such as land and livestock. The price could be severe female–female conflict, as described in the Dogon in Mali who do not seem to be well-described as cooperative breeders (Strassmann, 2011).

A significant minority (about 17%) of systems described in the *Ethnographic Atlas* (Murdock, 1967) are matrilineal. Marriage bonds are often weak in matrilineal systems, with women frequently having several husbands over the course of their lives; multiple paternity has few implications for heritable resources as wealth and titles are generally passed down the female line. The ecology that is predictive of matriliny is biased toward systems with a lack of resources that can be easily monopolized by males to attract females. In Africa, it is strongly associated with the absence of livestock herding (Aberle, 1961; Holden & Mace, 2003). In other parts of the world, matriliny has been proposed to be associated with high male mortality and/or male absence rates, either because of warfare, as in some matrilineal native American groups (Keegan & Maclachlan, 1989), or with trade networks and ocean fishing as in the Pacific (Hage & Marck, 2003). Whatever the underlying ecology, women in matrilineal systems rely on mothers, daughters, and sisters to support their family, as help from husbands, or any males, is often transitory. Paternity certainty tends to be low in matrilineal systems, although the extent to which this is a cause or consequence of matrilineal descent systems is a matter of debate (Hartung, 1985). Matrilineal systems represent a puzzle to evolutionary (and other) anthropologists, because it is unclear why a male should invest in his sister's offspring rather than that of his wife. Even if paternity uncertainty is at the highest levels observed in human societies (for example as seen in the Himba; (Scelza, 2011), the relatedness to his wife's offspring is higher than to his sister's offspring; this would change only if paternity certainty were less than 0.268 (Greene, 1978), which is unrealistically high. However if sisters are breeding communally, and a male's investment is shared by the communal household, then the fitness payoffs change in favor of matrilineal investment (Wu et al., 2013). Figure 22.3 shows the results of Wu et al.'s model of the optimal allocation of male investment between his wife's household and his sister's household as a function of the number of sisters co-residing in a communal household. In the case of just one breeding female per family, p (paternity certainty) would again have to be less than 0.268 for a male to invest more in the matriline (the same figure Greene predicts); however if two or three sisters co-reside and live communally, then the payoffs quickly change against investing in the wife's household in favor of the sister's household (i.e. the natal household) where all offspring are genetic relatives. The more sisters or female kin breed communally, the more matrilineal investment is favored. Note that the number of communally breeding sisters (n) is a more important determinant of matrilineal investment than is paternity certainty (p) within realistic ranges of p. The Mosuo of southwestern China are one of the most matrilineal societies ever described, as neither sex disperses and brothers and sisters live together throughout life and work on communal farms; household food (mostly grains, pork. and fish) is shared, so males will not gain much fitness by investing in feeding a household full of their wives' sisters offspring (to whom they are unrelated) (Wu et al., 2013). Sexual partnerships in the Mosuo are described as "walking" or "visiting marriages" as males only stay with partners overnight, but return home in the morning; fathers invest little in their offspring. The fact that these traditional unions do not imply exclusivity or co-residence, shows that marriage, as usually understood, is not fundamental to all societies.

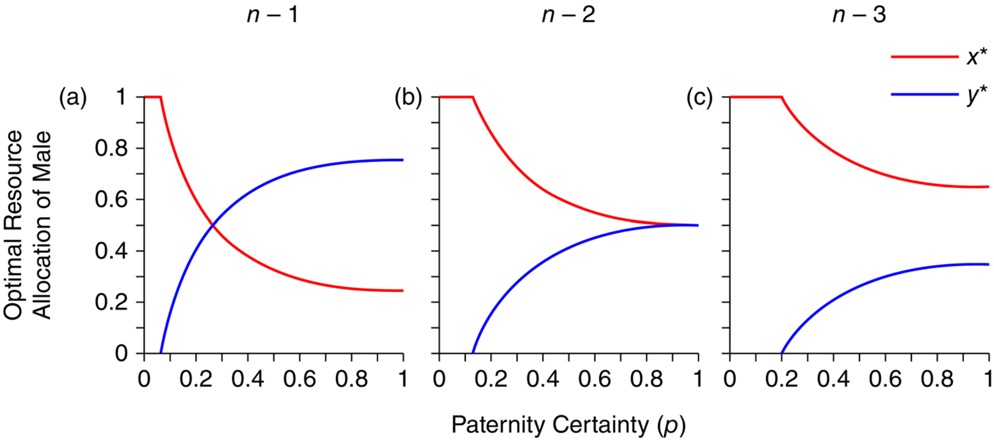

Figure 22.3 Optimal Resource Allocation From Males Choosing Between Natal or Spousal Household. The optimal resource allocation of males' effort to either their sister's farm ($x*$, upper line) or the wife's farm ($y*$, lower line) as function of paternity certainty (p) and the number of sisters that co-reside in a household (n). Note that for nuclear families ($n = 1$) only after $p < 0.268$ does investment in a sister exceed investment in a wife. But when $n \geq 2$ in a communal household, matrilineal investment is increasingly favored. *Source:* From Wu et al. (2013).

Monogamous marriage and neolocal nuclear households are now becoming more common in the Mosuo, in part because it is encouraged by Chinese law and family policy, but also due to economic changes. The emergence of tourism in the Mosuo area has enabled some individuals to raise extra money independent of the farm (through activities such as tourist hotels), making them more likely to leave the communal households and set up neolocal households living as nuclear families (Mattison, 2010). This shows how the communal breeding observed here may be based on constraints on dispersal, as it is believed to be in many communal breeders in the animal kingdom (Hatchwell & Komdeur, 2000). An example of communal breeding by brothers comes from polyandrous Tibetan Sherpa households in the Himalayas (discussed in section titled Polygyny, Monogamy, and Polyandry). Thus, both the matrilineal Mosuo and the polyandrous, patrilineal Tibetans show how communally breeding households can emerge out of constraints on dispersal, and they become unstable when there is a relaxation of these constraints.

Social systems rarely leave any trace in the archaeological record. Sex-specific genetic patterns are often argued to reflect aspects of past human mating systems (Kayser et al., 2003; Seielstad, Minch, & Cavalli-Sforza, 1998), although such inferences are possibly picking up genetic patterns generated after the advent of agriculture and other aspects of population structure (Heyer, Chaix, Pavard, & Austerlitz, 2012; Wilkins & Marlowe, 2006). Most ethnography is confined to the present and recent history relying on living memory or on written or oral histories as sources. Phylogenetic comparative methods provide a powerful set of statistical tools that have been developed by evolutionary biologists for understanding diversity, and these go beyond just seeking correlation to examine a whole host of evolutionary processes and questions, including rates of change, ancestral states, the tempo and mode of evolution, phylogenetic signal, and reticulation (Pagel, 1999). Cultural phylogenetic techniques make use of language phylogenies to do similar analyses across human cultures (Mace & Pagel, 1994) and potentially enable us to put prehistory back into anthropology (Mace, Holden, & Shennan, 2005). These were the methods used to show that in Bantu-speaking populations, patrilineal social systems were associated with pastoralism, whereas matrilineal systems were associated with a lack of cattle-keeping (Holden & Mace, 2003) and the model of direction of change that best fits the data confirmed the hypothesis that a transition to pastoralism precedes a switch to patrilineal descent systems, suggesting causation.

Phylogenetic techniques rely on using the extant distribution of traits, and the phylogeny, to infer which evolutionary processes were most likely to have generated that distribution (Pagel, 1999; Pagel & Meade, 2006). Implicit in the method is the inference of ancestral conditions. We have used these techniques to show that the most likely ancestral condition of Proto-Malayo-Polynesian (~4,500 years ago) was matrilineal and matrilocal, with patrilocal systems evolving later on in the Austronesian family (Jordan, Gray, Greenhill, & Mace, 2009). Similarly we have been able to show that dowry and monogamy were probably ancestral in Indo-Europeans (Fortunato, Holden, & Mace, 2006). Although studies of ancestral condition do not necessarily demonstrate adaptation, they are essential in arbitrating between different causal hypotheses for the origins of cultural traits. For example, if the ancestral Indo-Europeans were monogamous, then monogamy long predates the emergence of Christianity (which is only about 2,000 years old), debunking the common assumption that Christianity is the driving force behind European monogamy. It supports the notion that prevailing local social systems and conventions generally determine religious rules rather than vice versa.

THE PUZZLE OF LOW FERTILITY

Clearly the desire to have children is not hard to explain—it is our *raison d'être* in evolutionary terms. Evolutionary reasons not to have children, therefore, present a very interesting puzzle to an evolutionary anthropologist or psychologist or demographer. The most obvious phenomenon that curtails human fertility is the demographic transition. Voluntary childlessness and homosexuality are other examples of apparently maladaptive behaviors that clearly reduce lifetime reproductive success, but have been the subject of relatively little research by evolutionary scientists.

THE DEMOGRAPHIC TRANSITION TO LOW FERTILITY

A dramatic and near-universal decline in family size was one of the most pervasive social changes of the past two centuries, and one that continues apace around the world. However there is no clear agreement on how to interpret this demographic transition. Demographers have traditionally placed great emphasis on the reduction in infant mortality as the primary causal factor of fertility decline. There is no doubt it is one driver of the transition to low birth rates, but its failure to predict all aspects of fertility decline lead some to propose cultural transmission of a new idea as a major determinant (Coale & Watkins, 1986). Evolutionary demographers and anthropologists have always focused on high parental investment as key (Borgerhoff Mulder, 1998).

It has long been recognized that maximizing reproductive success is not necessarily about maximizing fertility alone, going back to ornithologist David Lack (Lack, 1954). A "Darwinian demon" that reproduced at the maximum rate is unlikely to succeed in the real world because there will be costs of reproduction to the mother (and probably also to the father), and there will competition between the many siblings for limited parental resources. Trading off these costs with the fitness benefits of fertility is known as a "quantity–quality trade-off," and is ultimately what we would predict determines the nature of human reproductive decisions. Reproductive rate can coevolve with wealth transfers (such as gifts at marriage or through inheritance), limiting optimal fertility in circumstances when the costs of these transfers is high (Mace, 1998). It is possible that parental investment can snowball, subject to a runaway process driven by competition between individuals favoring quality over quantity of offspring (S. E. Hill & Reeve, 2005; Mace, 2008). This could potentially make competition between siblings for parental investment more intense, not less, in modern societies. However, the reproductive decisions of those of us with small families do not appear to maximize our genetic fitness, despite the numerous social, financial, health-related, educational, and other individual benefits associated with low fertility (Goodman, Koupil, & Lawson, 2012).

If some aspect of society, or indeed any part of a person's environment, has recently changed in ways that would not have occurred before in human evolutionary history, then evolutionary models will not necessarily predict observed behavior; natural selection takes time to work. This is sometimes referred to as "mismatch" or "evolutionary lag." How quickly individuals respond to changing cues is still relatively unexplored. The society most of us live in has been described as WEIRD: Western, educated, industrialized, rich, and democratic (Henrich, Heine, & Norenzayan, 2010), and the largely urban, industrial, or postindustrial environment where WEIRD societies are found is very different from that in which our ancestors evolved. The very rapid changes in mortality, economy, and nutrition in our recent history has occurred in the blink of an eye on an evolutionary time scale.

Cultural evolutionary models have raised the possibility that low fertility could be the result of prestige-biased copying: In societies in which social success and reproductive success are no longer positively correlated, perhaps due to modern contraception, a predisposition to copying successful people could mean copying low fertility (Boyd & Richerson, 1985). More generally, some cultural evolutionary theorists have argued that models of cultural group selection could ensure that either conformity and/or punishment could lead to the maintenance of cultural differences between groups; competition between these groups could favor cultural behavior that benefits the group (Richerson & Boyd, 2005). Limiting fertility, or any trait that leads to reproductive leveling in groups (such as food sharing), could be an example of a behavior that evolved in this way. In rural Ethiopia, we found little evidence that the decision to start using contraception was spreading by copying friends or family in the immediate proximity or by copying those in your immediate social network, suggesting a limited role for social transmission at this early phase of uptake, although religious affiliation did have an effect (Alvergne, Gurmu, Gibson, & Mace, 2011); this was also the case in rural Bangladesh (Munshi & Myaux, 2006). Meanwhile land inheritance does predict contraceptive uptake in both Ethiopia and Bangladesh, with those with private landholdings to pass on to their children being more likely to use contraception (Gibson & Gurmu, 2011; Shenk, Towner, Kress, &

Alam, 2013). This suggests low fertility is coevolving with wealth inheritance as behavioral ecological models predict (Mace, 1998). A dichotomy between explanations based on culture and cost/benefit is somewhat unrealistic. Local cultures impose local costs and benefits, and cultural transmission is one of the ways that humans learn that costs and benefits have changed, or perhaps might change in the future. So costs and benefits and cultural transmission are both important and have complementary effects. The well-known influence of education on women's fertility might be as much a cultural effect as it is an economic effect. It has been argued that education itself enhances the cultural transmission of low fertility norms through populations (Borenstein, Kendal, & Feldman, 2006; Ihara & Feldman, 2004). In villages in rural Poland in the midst of demographic transition, women of similar socioeconomic status have lower fertility in a better-educated village than in a less-well-educated village, providing some support for this view (Colleran, Jasienska, Nenko, Galbarczyk, & Mace, 2014). A preference for wealth and status as achieved by education can thus spread at the expense of fertility, as in this case, but without any evidence that such preferences are maximizing current genetic fitness. If this is some evolutionary lag, natural selection would be predicted to eventually reverse such preferences, but this seems unlikely, so the demographic transition remains something of an evolutionary puzzle.

HOW CAN MALE HOMOSEXUAL PREFERENCE EVOLVE BY NATURAL SELECTION?

Male homosexual preference (MHP) is associated with low lifetime reproductive success, but it is too widespread to be understood as something that does not require an evolutionary explanation. It is not often seen as a stable, persistent trait in wild animals. It is occasionally documented in anthropological studies of hunter-gatherers; Hill and Hurtado describe a homosexual phenotype that was rare but observed in Ache hunter-gatherers, of effeminate behavior in males who do not reproduce, but who did not engage in homosexual sex until after exposure to Paraguayans (Hill & Hurtado 1996). Several traditional societies acknowledge the existence of a third gender. It seems the phenotype is too common worldwide to not have been subject to natural selection (2%–6% in Western societies). There is little evidence that homosexual brothers are of direct benefit to their kin by helping them out (Bobrow & Bailey, 2001; Vasey, Pocock, & VanderLaan, 2007); but they may be of indirect benefit to their kin, for example by reducing competition between the other siblings for parental resources. There is good evidence that male homosexuality shows a birth-order effect, with each elder brother (but not sister) significantly increasing the likelihood of homosexuality in males (Blanchard, 2001). Sisters of homosexuals appear to be more fertile than those who do not have homosexual brothers (Camperio-Ciani, Corna, & Capiluppi, 2004). This could be due to shared genetic effects such as feminine beauty (which could, for example, be advantageous to fertility in females but has disadvantageous pleiotropic effects in males). Alternatively this could be simply a side effect of both large family size being heritable, combined with the higher incidence of male homosexuality in younger brothers, but further analysis does suggest a sex-linked sexual antagonistic effect (Camperio-Ciani & Pellizzari, 2012). A model for the evolution of male homosexual preference shows that, in a stratified society, a relatively high frequency of MHP could be maintained as a result of the social ascension (or up-migration through social strata) of females signaling high fertility (hypergyny) (Barthes, Godelle, & Raymond, 2013). Their prediction that MHP is more prevalent in stratified societies was significantly supported in a sample of 48 societies for which the presence or absence of MHP has been anthropologically documented. They argue that any traits associated with up-migration are likely to be selected for in a stratified society and will be maintained by frequency dependence even if they induce a pleiotropic cost, such as MHP. This insight applies to the evolutionary basis of any trait that lowers fertility but increases social upward mobility. This explanation cannot, of course, explain female same-sex preferences, the explanation for which must lie elsewhere. Other evolutionary reasons for childlessness other than homosexuality have not been greatly studied, but may in many cases to be related to failures in mate choice. Ultimately, any evolutionary explanation for a behavior associated with reduced fertility, that is not due to constraints, is either a short-term maladaptive outcome that will only persist long enough for evolution to remove it; or it is a stable feature in a given population and thus can only be explained as an adaptation in evolutionary terms if it is associated with indirect benefits to existing children or other kin.

CONCLUSIONS

Human behavioral ecology has proved an essential framework within which to understand human kinship and family systems. Behavioral ecologists start from the premise that natural selection works on behavior to maximize fitness. They use three main approaches to test adaptive hypotheses about the evolution of behavior: experimentation, testing the predictions of theoretical models, and the comparative method (Krebs & Davies, 1993). When a particular adaptive model fails to explain observed phenomena, the usual modus operandi is to seek a better model, assuming that some vital cost or benefit has been overlooked; hence, our understanding of the evolutionary basis of that behavior is enhanced by ruling out multiple alternative explanations. Human behavioral evolutionary studies are often described as falling roughly into three main schools of thought: evolutionary psychology (often experimental studies seeking universal psychological adaptations), gene culture or cultural evolution (generally focused on theoretical models of cultural evolution), and human behavioral ecology (Laland & Brown, 2002). The last two are primarily interested in explaining variation in human behavior. Although sometimes taking different approaches, often generating different conclusions, these fields are becoming similar and sometimes indistinguishable (Mace, 2014).

Family systems have been the traditional obsession of anthropologists since the inception of the field. How families influence our reproductive and other behaviors is now a subject of interest across the full range of human sciences. Understanding the evolutionary basis of human families illustrates the usefulness of a range of evolutionary approaches, as well as the central importance of ecology. Although all human societies base social organization around the building block of families, the nature of those families do vary through history and around the world. I have outlined here how evolutionary ecology provides a framework that can be used to explain a range of phenomena to do with our social organization, reproductive physiology, cultural norms, and parenting behavior, and how they coevolve to generate the diversity that we observe, both within and between cultures, in human family life.

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CHAPTER 23

Hunter-Gatherer Families and Parenting

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OUR SPECIES IS characterized by remarkable biological success. In the past 10,000 years, since the advent of agriculture, our population has increased over 1,000-fold (Coale, 1974; Westing, 2013). We have successfully populated all reaches of the planet, calling the most extreme of habitats, *home*. This remarkable success is largely a consequence of our extraordinary ability to cooperate with one another. While cooperation is observed in many other species, human cooperation is anomalous in both scale and nature. Humans are unique in that they form long-lasting, nonreproductive ties with genetically unrelated individuals. Social learning in humans further accentuates the utility of cooperative ties by allowing adaptive information to accrue over many generations (Boyd & Richerson, 2009). It was these cognitive and social processes that enabled us to adapt to a wide range of environments and ultimately led to our unsurpassed success (Tennie, Call, & Tomasello, 2009). Possibly the biggest challenge faced by our Pleistocene ancestors, who lived roughly 2.5 million years ago until the advent of agriculture, was how to raise energetically expensive, big-brained children in unpredictable and changing climates. The solution to this problem was to extend cooperation beyond the pair bond and nuclear families (Emlen, 1995; Hill & Hurtado, 2009; Hrdy, 1999). Thus, in order to understand hunter-gatherer families and parenting, one must consider the reproductive challenges faced by our ancestors, as well as the larger social context in which they unfolded.

Although the traditional emphasis in the study of hunter-gatherers has focused on the nuclear family, with extended social networks being largely conceived as modern constructs, the importance of more diffuse cooperative networks, concerning food sharing, provisioning, child care distribution, and labor are increasingly being stressed (Apicella, Marlowe, Fowler, & Christakis, 2012, Crittenden & Marlowe, 2013; Hrdy, 2009; Kramer, 2011). Specifically, it has been reasoned that cooperation beyond immediate families evolved in response to the high reproductive burden that human children place on their parents. Humans are characterized by a unique pattern of reproduction and childrearing—delayed maturity and prolonged dependence of children. As a result, human families are often comprised of multiple children, all of whom require high amounts of care and provisioning. Thus, without a large constellation of helpers—without extended cooperative networks—the demands of rearing hunter-gatherer children would have been hard to meet.

This chapter provides an overview of hunter-gatherer families and parenting within the context of larger groups and social networks. First, we discuss what it means to be a hunter-gatherer and why understanding the problems faced by contemporary foragers is important to the study of evolutionary psychology. We then provide a brief outline of human life history, focusing on adaptive features of human reproduction and parenting. We do this by contrasting humans to our closest living primate relatives in order to highlight the unique reproductive obstacles faced by families and emphasize how support from others would have been critical in overcoming these obstacles. We then discuss the properties of hunter-gatherer social life at both the dyadic and macroscopic level that were designed to support reproduction and parenting. Much of our discussion focuses on Hadza hunter-gatherers, a population that we have both worked with extensively, and when possible we broaden our discussion to other foraging populations. We do this to address population variation and to situate the Hadza data cross-culturally. We conclude the chapter with a discussion of the role that extended networks, including children, grandmothers, and nongenetic relatives, play in supporting the human family.

HUNTER-GATHERERS AND EVOLUTIONARY PSYCHOLOGY

The discipline of psychology has often been criticized for its overreliance on Western college populations (for review, see Henrich, Heine, & Norenzayan, 2010). Since evolutionary claims about the origins of psychological phenomena are largely thought of as claims about a universal nature (Cosmides & Tooby, 1994), the study of evolutionary psychology necessitates cross-cultural comparisons. Such work not only helps to recognize the diversity present in our species but also aids in identifying the behaviors and traits that unite us. While some studies of small-scale societies have helped to identify human universals, other work suggests that some psychological phenomena may instead be artifacts of our postindustrialized life (e.g., Apicella, Azevedo, Christakis, & Fowler, 2014; Henrich et al., 2010).

Cross-cultural research aimed at uncovering universals is often criticized on the grounds of common exposure to Western life. Since many foragers remain relatively geographically isolated, they may be particularly useful for tests of universality. The more isolated a population, the stronger the case for a culturally invariant human psychology. The appeal of studying hunter-gatherers also lies in the fact that their way of life is evolutionarily relevant. For the vast majority of time that humans have populated the planet, they have been hunter-gatherers (Lee & Daly, 1999). For this reason, most evolutionary psychologists believe the mind is adapted to a hunter-gatherer way of life (Barkow, Cosmides, & Tooby, 1992). From this perspective, understanding the functional relevance of various psychological mechanisms requires consideration of the challenges faced by our ancestors and to better understand these challenges, researchers may look to hunter-gatherers. Though the extent to which current hunter-gatherers can be used as a model for understanding our past is debated, they provide some of the best direct observations of behavior in the absence of agriculture.

Much of evolutionary psychology rests on the assumption that some psychological traits observed today evolved because they, on average, enhanced the fitness of our ancestors. One way to identify an adaptation is to examine the effect of variation in the said trait on fitness outcomes and to do so in the environment in which it is assumed to have functioned as an adaptation (West-Eberhard, 1992). Since hunter-gatherer societies have limited access to medical and reproductive technologies, including birth control, they can be useful for tests of Darwinian fitness (Apicella, 2011).

It is important to recognize that not all evolutionary psychologists confine their research to Western populations. One of the most esteemed and widely cited papers in evolutionary psychology involved the study of mate preferences in 37 different cultures (Buss, 1989). Today, a growing number of evolutionary psychology studies are conducted among hunter-gatherers and other small-scale societies (e.g., Apicella, Little, & Marlowe, 2007; Sugiyama, Tooby, & Cosmides, 2002). While it is true that studies involving Western populations provide an economical and efficient first pass for testing evolutionary hypotheses, they are also important in their own right. It is also unreasonable to expect that all evolutionary psychology research be replicated in hunter-gatherers. If hunter-gatherers did not exist, which is the most likely future that we are facing, we would certainly not eliminate the discipline. Similarly, if for some reason we lost sequencing technology, the field of genetics would continue. It is possible to conduct a fruitful evolutionary psychology research program without collecting forager data. With a solid understanding of the hominin ancestral environment and the problems faced by our ancestors, testable hypotheses can be readily generated regarding the properties that an adaptation should have in order to solve the problem well (for discussion, see Cosmides & Tooby, 2013) and these adaptations can be studied in a multitude of settings and with many methods. That said, hunter-gatherers potentially offer researchers a rare glimpse into how humans have lived for many thousands of generations.

HUNTER-GATHERERS OF THE WORLD

WHAT IS A HUNTER-GATHERER?

Defining "hunter-gatherers" is not an easy task. To some, this way of life represents a mode of subsistence entailing the collection of wild foods, including fish, game meat, and plants with "no deliberate alteration of the gene pool of exploited species" (Panter-Brick, Layton, & Rowley-Conwy, 2001, p. 2). Although this definition appears straightforward, some populations practice mixed-subsistence regimes that can include varying degrees of farming and animal husbandry. Some populations also receive food subsidies from governments and aid organizations. Thus, there is debate as to how many of the calories consumed must come exclusively from foraging in order to be classified as a hunter-gatherer. If it were 100%, no contemporary foraging population would meet the designation. Some anthropologists contend that classification should be based on more than just mode of subsistence. Specifically, consideration should be paid to the unique social and economic lives of hunter-gatherers, which include high mobility, egalitarianism, and lack of property rights (Lee & Daly, 1999). Again, each of these features occurs on a spectrum and so drawing strong distinctions can be problematic. In this section, we provide a general overview of some key properties of social life in hunter-gatherers as well as a more in-depth discussion of the relevancy of the Hadza for understanding human evolution.

HUNTER-GATHERER SOCIAL LIFE

Anthropologist Frank Marlowe (2005) attempted to characterize general hunter-gatherer social life using ethnographic data from 437 different past and present foraging societies. Such data are useful for building evolutionary models as they provide parameter estimates for how our ancestors likely behaved. Marlowe found that the vast majority of forager societies live in small groups or "camps" and practice central place foraging and food sharing. This means that acquired foods are brought back to a central location and shared widely among group members. Moreover, many explanations for the evolution of cooperation have highlighted the importance of food sharing (Kaplan, Gurven, Hill, & Hurtado, 2005; Lancaster & Lancaster, 1983). Cooperative hunting is observed in some foragers such as the Ache of Eastern Paraguay (Hill, 2002) and the Aka of the Western Congo Basin (Hewlett, 1992), however solitary hunting is more common in the ethnographic record (Marlowe, 2010).

A sexual division of labor characterizes most hunter-gatherer populations in which men primarily target animal-based foods and women target plant-based foods. This is, however, not a rule, because men may target plant foods, as seen among the Hadza with baobab fruit, and women in some tropical and subtropical foraging populations routinely hunt. For example, Martu aboriginal women in Australia regularly hunt for small burrowed game (Bird, Bird, & Parker, 2005) and Agta women in the Phillipines often hunt for medium to large sized game (Goodman, Griffin, Estioko-Griffin, & Grove, 1985). In some populations, including the Aka, both women and children are involved in net hunting (Hewlett, 1992).

Foragers also exhibit flexible residence patterns with fission-fusion grouping and are multilocal (Marlowe, 2004b), meaning that couples may live with the wife's family, the husband's family, a combination of the two, or without either family. A recent analysis examining residence patterns among 32 present day foragers confirms this pattern (Hill et al., 2011). The resulting implication is that individuals frequently end up co-residing with siblings.

THE HADZA

Despite the diversity characterizing contemporary foragers, it is worth noting that the Hadza are typical in many key traits. Like most foragers, the Hadza practice bilateral decent, central-place foraging, and they are egalitarian (Marlowe, 2010). Frank Marlowe (2010) compared the Hadza to 237 warm-climate, nonequestrian foraging societies. We echo Marlowe's decision to exclude equestrian foragers from analysis, as they have larger home ranges and group sizes than their nonequestrian counterparts. Furthermore, they have lowered travel costs and higher rates of hunting success (Shimkin, 1983), making them less relevant for discussions of foraging behavior prior to the introduction of the horse. Warm-climate foragers are often considered to be the most relevant for making inferences about human evolution since their environment best approximates the environment of our earliest ancestors. Marlowe found that the Hadza fall at or near the median value on many key demographic traits, including the percentage of calories that men and women contribute to the diet, age at weaning, total fertility rate, interbirth interval (IBI), and infant mortality. These data suggest that the Hadza are not an unusual group of foragers.

There is debate about the extent to which we can use the Hadza and other contemporary foragers as a model of our preagricultural past, as many foragers practice mixed subsistence strategies and have had varying degrees of contact with neighboring populations (see Wilmsen, 1989). The Hadza are, by no means, completely isolated. Much interaction occurs with neighboring groups of pastoralists, agropastoralists, and small-scale horticulturalists. Despite this, there is much evidence to suggest that Hadza social and family life remains largely uninfluenced by neighboring tribes. Comparisons of the earliest ethnographic descriptions and photographs of the Hadza (see Obst, 1912) to current descriptions, suggest that their daily lives have changed very little over the past century (Marlowe, 2010). The Hadza have maintained their language (Hadzane) and have experienced very little change in their mobility and residential patterns, diet composition, and mating system (e.g., high levels of monogamous pair bonding; Blurton Jones, Hawkes, & O'Connell, 2005). The total population size (~1,000) of the Hadza has stayed relatively constant over the past 100 years, though it is estimated that only 300 Hadza continue to practice a forager way of life (Marlowe, 2010). This subset of the Hadza may represent the only contemporary population where more than 90% of calories consumed come from hunted and gathered foods (Crittenden, 2014).

In general, common sense should be applied when using any hunter-gatherer group to make inferences about the past. Specifically, it is important to consider traits on an individual basis (Foley, 1995) as some behaviors and traits may be more recent (e.g., bow and arrow hunting technologies) than others. However, with respect to many social and economic behaviors, there is reason to think that the Hadza may be a useful analog of humans further back in history.

THE CHALLENGES OF HUMAN REPRODUCTION AND PARENTING

Since our divergence from the great apes roughly 7 million years ago, humans have accumulated a number of distinct features associated with reproduction and parenting. Here, we draw comparisons of humans to other primates in order to highlight our unique reproductive obstacles and the resulting implications for familial and social life.

Compared to other primates, humans begin reproducing late. Even chimpanzees, also late bloomers among the primates, experience first parturition 5–7 years earlier than humans (Nishida et al., 2003). Cross-culturally, ages of first reproduction range between 18 and 20 years (Bogin, 2009), which is largely due to the late age at which foragers reach menarche. For instance, Hadza girls reach menarche at 16.5 years of age (Marlowe, 2010). By delaying reproduction, humans are able to grow to a size large enough to successfully support the birth of large-bodied, large-brained infants.

Among primates, humans are the most encephalized species. Significant increases in brain size have occurred during several points in human evolution (Ruff, Trinkaus, & Holliday, 1997) and tripled in the past 2 million years (Lee & Wolpoff, 2003). Likewise, body size increased markedly with the appearance of *Homo* (Ruff et al., 1997). These increases have had profound implications on the birth process, so much so, that it has led to what is known as the "obstetric dilemma" (Rosenberg & Trevathan, 2002). In fact, childbirth has been described as the most dangerous thing that a woman will do in her lifetime (Trevathan, 2011). This contrasts to the birthing experience of other primates, who all give birth unassisted and with relatively little difficulty. Evolution was less kind to human mothers as they faced trade-offs between having a pelvis built for efficient bipedal locomotion and the need to accommodate the birth of infants with large heads and wide shoulders (Rosenberg & Trevathan, 1995, but see Warrener, Lewton, Pontzer, & Lieberman, 2015, for an alternative hypothesis on locomotor mechanics). These trade-offs resulted in a very tight squeeze. As a result, human mothers must obtain assistance from others during labor and delivery. This species-specific characteristic has led many notable scholars (e.g., Rosenberg & Trevathan, 2002) to argue that obstetrics is the true "oldest profession." We have witnessed childbirth among the Hadza, and female relatives and friends are always present to assist.

Giving birth among cooperative conspecifics would have been critical for our ancestors. Assistance during birth has a significant effect on birthing outcomes even in medicalized settings with the best technology available (Sauls, 2002). It has been reported that one in every 55–75 pregnancies result in maternal death among the Hiwi foragers of Venezuela (Hill, Hurtado, & Walker, 2007). Of 34 female deaths among the Hadza that were attributed a cause during a 12-year period, 14.7% of them occurred during childbirth (Blurton Jones, Hawkes, & O'Connell, 2002). Maternal mortality is similarly high in the world's poorest countries with a lifetime risk of ~17% (Ronsmans & Graham, 2006). Since this is an event where both survival and reproduction are at stake, small differences in behaviors could lead to big differences in outcomes. The significance of this is further underscored by the fact that birth happens multiple times in a woman's life. Among the Hadza, for example, women give birth roughly six times in their lives (Marlowe, 2010). Finally, since the exact timing of birth cannot be predicted, even with the most advanced technology, having constant and reliable access to helpers would have resulted in better reproductive outcomes. Selection would likely have favored women who had a desire to be around potential helpers.

While it is true that we give birth to big-brained babies, their brains could have been bigger. Length of human gestation compared to that of other primates remains average (Martin, 2007, but see Dunsworth et al. 2012 for alternative suggestion that human gestation may be longer than expected), meaning that much of growth occurs outside of the womb. The adult human brain is approximately 3 times as large as the brain of an adult chimpanzee (Rilling & Insel, 1998), and while there is considerable postnatal brain growth in both species, the human infant brain is not 3 times larger than a chimpanzee infant brain. This led the zoologist Adolf Portmann (1941) to suggest that if humans were born as developed as chimpanzees, they would need to gestate for an additional 12 months. He went on to describe humans as "secondarily altricial," arguing that postnatal growth in humans is an extension of the growth that should have taken place in the womb. The dominant view is that maternal pelvic constraints necessitate early birth, however, an alternative hypothesis suggests that maternal metabolic constraints may be to blame (Dunsworth, Warrener, Deacon, Ellison, & Pontzer, 2012). That is, mothers may not be able to keep up with the caloric demands of the growing infant. Whatever the reason may be, human infants enter the world early and, therefore, require extensive postnatal care.

Early weaning is another key distinction in humans. The majority of mammalian infants are weaned when their first permanent molar erupts or when they reach approximately one-third of their mother's body weight (Charnov & Berrigan, 1993; Lee, Majluf, & Gordon, 1991). If humans followed this pattern, the average age at weaning would be between the ages of 6 and 6.5 years (Smith, 1992). Rather, the cross-cultural average suggests that weaning typically occurs between 1.5 and 2.5 years old (Kennedy, 2005). For instance, Hadza children are weaned around 2.5 years (Marlowe, 2010) and, like all weaned infants, they require transitional foods that their immature digestive tracts and dentition can process (Sellen, 2007). The early weaning of infants has direct reproductive consequences for the mother, in that it allows her to resume ovulation more quickly and reproduce sooner (Kaplan, Hill, Lancaster, & Hurtado, 2000). The average IBI among foragers is approximately 3.5 years (Marlowe, 2005). This is relatively short compared to gorillas, chimpanzees, and orangutans who have IBIs of 4, 6 and 8 years, respectively (Alvarez, 2000; reviewed in Robson & Wood, 2008). Although a shortened IBI allows women to rear a larger percentage of offspring to adulthood (Bogin, 1999), it also means that they give birth to new infants while current children are still nutritionally dependent. As a result, early weaning and shortened IBIs may not have been possible without assistance from others.

The human life-history pattern is also unique in that it includes an extended period of juvenile dependency. Prolonged dependence may be due to the extended time that children need to learn and accrue a lot of information prior to adulthood (Kaplan, Hill, Hurtado, & Lancaster, 2001), or it may be a by-product of selection for longer life spans (Charnov & Berrigan, 1993). Whatever the reason, children require prolonged and extensive investment in the form of provisioning and care. Data from the Machiguenga and Piro people of Southeastern Peru, two largely horticultural populations, and the Ache, showed that children, on average, accumulate a 10–13 million calorie deficit from birth to adulthood (Kaplan, 1994), far surpassing what mothers can provide alone. In some forager societies infants are held almost continuously throughout the day. For instance, Aka infants are held or touched more than 90% of the time in a 24-hour period (Hewlett, Lamb, Leyendecker, & Schölmerich, 2000).

In short, human offspring require a high degree of behavioral and nutritional investment. As a result, mothers are faced with a distinct and unique reproductive challenge—caring for and supporting overlapping nutritionally dependent children. Forager mothers would have met this challenge only by relying on the assistance of others (Hrdy, 2009). The remainder of the chapter is devoted to how hunter-gatherer family and social life work to support these parental demands.

SUPPORTING HUMAN REPRODUCTION AND FAMILIES

MOTHERS, FATHERS, AND THE PAIR BOND

Leo Tolstoy famously wrote that *everything depends on upbringing* (1868). Perhaps this could not be more true than in hunter-gatherer life where child mortality risk is remarkably high. One-third of Ache children die before reaching 15 years of age (Hill & Hurtado, 1996). Among the Hadza, the risk is even higher with nearly half (46%) of children dying before the age of 15 (Blurton Jones et al., 2002). The rate is similarly high among other warm-climate nonequestrian foragers (Marlowe, 2010). Consequently, forager children not only necessitate high levels of investment but their outcomes are remarkably variable. For these reasons, it has long been suggested that monogamous pair bonding and paternal investment evolved because the marginal payoffs to investing in offspring outweighed the payoffs to seeking additional mates (Geary, Chapter 20, this volume; Lancaster & Lancaster, 1983; Lovejoy, 1981). Tied closely to the evolution of the pair bond is the view that the sexual division of labor serves to maximize the efficiency by which parents can provision their children. Despite the long-term appeal of this interpretation, the significance of paternal provisioning and human pair bonding has not gone unchallenged.

There continues to be considerable debate on how to best characterize the human mating system. The notable reduction in body size dimorphism during human evolution (McHenry, 1992; Plavcan, 2001) suggests a decline in male–male competition consistent with a reduction in polygyny. Across animals, high levels of size dimorphism, such as that observed in gorillas, are typically associated with polygynous mating systems. Likewise, humans also have relatively small testes, a characteristic routinely associated with reduced sperm competition and monogamous mating (Harcourt, Purvis, & Liles, 1995). Based on these observations alone, one might assume that humans are largely monogamous. However, when we look across the ethnographic record, the picture becomes more complicated. Roughly 85% of societies in the anthropological record permit some degree of polygyny, though most individuals in these societies are monogamous (Murdock & White, 1969). This pattern largely holds for foragers. Approximately 10% of foraging societies maintain strict monogamy and 60% of forager societies are classified as slightly polygynous (Marlowe, 2003). In only 30% of foraging populations sampled, do more than 20% of married men have more than one wife (Marlowe, 2003). It is also important to note that these data reflect marital arrangements and exclude other channels through which polygyny may occur, such as extra-pair and serial matings (see Low, 1988 for discussion on problems with measures of polygyny). Nevertheless, these data suggest that humans have developed a varied behavioral repertoire when it comes to mating and may be adapted for more than one strategy (Buss, 1998; Buss & Schmitt, 1993).

Opportunities for polygynous matings are also largely tied to resource holding. For example, in many preindustrial societies, such as the Kipsigis, wealth is the main determinant of the number of wives a man has (Borgerhoff Mulder, 1988). In foraging societies in which men's foods are largely shared and wealth not accumulated, the threshold for which a woman would choose to marry an already mated man may not be met (Marlowe, 2003). Interestingly, an association between hunting ability and reproductive success has been reported in a number of forager societies, including the Hadza (Apicella, 2014; Marlowe, 1999), the Ache (Hill & Hurtado, 1996; Kaplan & Hill, 1985) and the !Kung (Wiessner, 2002). Although better hunters may enjoy increased mating opportunities, other explanations for this pattern are possible. For instance, better hunters can improve their reproductive success by provisioning their wives and children (see Smith, 2004 for discussion).

In almost all human societies, males provide some degree of parental investment, (Geary, 2000) though mothers tend to be the primary caregiver. This system of "maternal primacy" (Konner, 2005) is seen among the Hadza (Crittenden & Marlowe, 2008), the Martu of Australia (Scelza, 2009), the Efe of the Ituri rainforest (Morelli & Tronick, 1992), the Aka (Hewlett, 1993), the Ache (Kaplan & Dove, 1987), and the Agta of the Phillipines (Griffin & Griffin, 1992). While mothers provide the majority of infant care, fathers in foraging populations can also invest heavily in their offspring. Aka fathers for instance, provide some of the highest levels of direct care to their offspring. It is estimated that just over 20% of men's time in camp is devoted to holding infants (Hewlett, 1992). Among the Hadza, fathers are the second most important caregivers after the mother (Crittenden & Marlowe, 2008). Ache fathers also provide substantive care and infants are in tactile contact with their mother or father 93% of daylight hours (Hill & Hurtado, 1996). This contrasts with other societies, such as the Agta, where fathers spend only 4% of time in childcare (Early & Headland, 1998). Among the !Kung San, approximately 2% of men's time is allocated to holding infants (West & Konner, 1976). Nevertheless, additional lines of evidence suggest that !Kung fathers are still typically more involved than fathers from the United States and Europe (Blurton Jones & Konner, 1973). Although most forager fathers do participate in some amount of childcare, the majority of their investment may take the form of provisioning.

The importance of hunted food in the evolution of the human family has long been considered. Meat is a high-quality food and, as such, may be critical for the growth of large brains (Milton, 2003). Across tropical foragers, however, women typically bring in more calories than men (Marlowe, 2005). Marlowe (2010) reports that the median proportion of the diet in warm-climate foragers that comes from gathering, hunting, and fishing is 53%, 26%, and 21%, respectively. In most African foragers there is little fishing, and for these populations the median values for gathering and hunting are 67% and 32%, respectively (Marlowe, 2010). Since hunting, on average, brings in fewer calories than foraging and because hunted foods are often distributed to individuals outside the nuclear family, the importance of big game hunting in familial provisioning has been questioned (Hawkes, O'Connell, and Blurton Jones, 2001). It has been argued that hunting may serve as a costly signal for advertising mate quality (Hawkes & Bliege Bird, 2002; Smith, 2004) and/or as a means of establishing reputations for generosity (Gurven, Allen-Arave, Hill, & Hurtado, 2000).

The importance of male provisioning has also been stressed. Among the Hadza, it has been shown that women experience a reduction in food returns when they are lactating and pregnant and their husbands make up this deficit by bringing in more food (Marlowe, 2003). In another study, Hadza men reported that they would prefer to join a group of good hunters rather than a group of bad hunters, which is consistent with a strategy for familial provisioning rather than showing off (Wood, 2006). More recent research also suggests that, although meat is shared widely, the amount of meat the hunter's family receives can still be higher than other group members (Wood & Marlowe, 2013).

The importance of childcare and provisioning to both men and women may also be reflected in their choices of long-term mating partners. For Hadza women, both character traits and foraging ability ranked highest in their criteria for husbands; for men, in contrast, foraging ability ranks only third after character and physical appearance (Marlowe, 2004a). These findings suggest that women want good providers for their children, although women may be using hunting ability as a signal for genetic quality. If the latter were true, one might expect physical appearance to rank as high, if not higher, than hunting ability if women are primarily in search of good genes. There is much research in evolutionary psychology that suggests that appearance is commonly used as a cue of genetic quality. In our own research with the Hadza, we asked 112 men and women whether they would prefer a husband (or wife) who was attractive or one who was a good hunter (or gatherer); only 6.25% preferred the attractive mate. Similarly, when we asked them to choose between physical attractiveness and good parenting, only 9.1% chose attractiveness ($n = 66$). This is not to say that physical attractiveness is not important to the Hadza. Indeed, a number of studies suggest that the Hadza do discriminate between individuals on a number of measures of attractiveness such as symmetry (Little, Apicella, & Marlowe, 2007), averageness (Apicella, Little, et al., 2007), voice pitch (Apicella & Feinberg, 2009) and waist-to-hip ratio (Marlowe, Apicella, & Reed, 2005). Attractiveness may be an important criterion for selecting short-term mates. To our knowledge, we know of no studies that have examined short-term mating preferences among foragers.

The evolution of monogamous pair bonding as one mating strategy also rests on the assumption that male care and provisioning results in increased reproductive success by reducing offspring mortality, increasing their wife's fertility, or both (Gray & Anderson, 2010). Across foraging societies, a higher mean male contribution to the diet predicts both younger age at weaning and greater reproductive success of the wife (Marlowe, 2001). The effect of father-absence on child survivorship has also been examined in a handful of populations. Ache children with absent fathers are three times more likely to die of illness and twice as likely to be murdered (Hill & Hurtado, 1996). Among the Hiwi, however, child survival is not impacted by father absence (Hurtado & Hill, 1992). Sear and Mace (2008) report that in the majority of subsistence populations (between 54% and 68%) with available data on the effects of father absence, death of a father is not associated with increased child mortality. Nevertheless, father death does compromise child survivorship in at least one-third of populations studied.

Father effects on children's outcomes have also been assessed indirectly. If father effects are important, one might assume that polygyny, as compared to monogamy, would reduce positive outcomes in children since men in polygynous relationships (a) tend to have more children, thus reducing the average investment per child and (b) divert more resources that could be used for parenting to obtaining additional long-term mates (Henrich, Boyd, & Richerson, 2012). While there is little available evidence on whether forager children with polygynously married mothers fare worse, this has been examined in other populations (for review, see Henrich, Boyd, & Richerson, 2012). In general, children with fathers who have multiple wives have worse health outcomes and elevated mortality. One might also expect better child outcomes when the mating system is reversed and children have multiple fathers from which to receive investment (Hrdy, 2000). In a few societies, the belief that men who have sex with a woman around the time of conception share in the paternity of the child is widely held. Ache children who have more than one "biological father" have better outcomes compared to children with only one "biological father" (Hill & Hurtado, 1996).

In summary, the majority of forager men provide some form of care and investment to their children and spouses. The significance of human fathers may be contrasted with the near lack of paternal investment in most other mammals, including our closest primate relatives. This suggests that at some point during human evolution, the benefits to parenting began to outweigh the benefits of seeking additional mates, at least in the short-term (for review, see Gray & Crittenden, 2014). We specify short-term, because a strategy involving serial monogamy may still best enhance men's reproductive success in the long-term (Winking & Gurven, 2011). Nevertheless, we still do not fully understand the selection pressures that favored paternal investment. Male investment may lead to better outcomes for children and increased fertility of wives, but there may also be other advantages. By providing paternal investment, men may enjoy increased paternity confidence, be able to attract higher quality mates, and build larger coalitionary networks through their affinal kin.

CHILDREN

The relationship between infants and mothers is fairly straightforward—infants consume. Though they require high levels of behavioral and nutritional assistance, when they survive, they increase the reproductive success of the mother (Kramer, 2011).

Juveniles are a special case because they are both dependents and providers. Although adults may assist children, they also contribute by providing labor and resources (Bock, 2002; Hames & Draper, 2004; Kramer, 2005). This "twofold" nature of human juvenility is an often overlooked, yet critical, dimension of human life history and the evolution of cooperative breeding (Kramer, 2014).

Cross-cultural data confirms that children can spend considerable amounts of time in daily food collection, as long as the risk of predation and getting lost are low and access to drinking water is available (Blurton Jones, Hawkes, & Draper, 1994). Among the Meriam foragers of the Eastern Torres Strait, children are avid foragers and participate in hand-line beach fishing, spear fishing, and shellfish collection (Bird & Bird, 2002). Young Mikea foragers of Madagascar collect significant amounts of tubers and foraging is considered an extension of play (Tucker & Young, 2005). Although young foragers may not consistently collect their total daily caloric requirements, their contribution significantly reduces the high costs of raising children to nutritional independence. This is true among the Hadza where one of the most recognized characteristics of childhood is foraging productivity. Even the earliest Hadza ethnographies provided rich anecdotes of foraging by Hadza children (e.g., Bleek, 1931; Woodburn, 1968).

Hadza children either accompany their mothers on foraging excursions or forage with their peers without adult supervision. Blurton Jones, Hawkes, and O'Connell (1989) estimated return rates per hour for three types of children's food—baobab, tubers, and berries. Their data suggests that children and adolescents are capable of collecting up to 50% of their daily energy requirement above the age of 5 years, depending on the season and availability of certain resources. These high levels of productivity have been reconfirmed with detailed long-term foraging data that focused on the whole repertoire of juvenile diet (Crittenden, Conklin-Brittain, Zes, Schoeninger, & Marlowe, 2013). These data suggest that children primarily collect fruit (64%), followed by birds (16%), tubers (9%) and other plants, and small game animals. While older children target harder to obtain foods, such as tubers and meat, children aged 3–5 years primarily target fruits, and collect an average of 458 kilocalories per foraging day. Although there is also wide variation in the food return rates, the majority of children consistently collected a large portion of their daily caloric requirements (Crittenden et al., 2013). Furthermore, these collected foods are routinely distributed to others, including other children (Crittenden, Zes, & Marlowe, 2010).

Children also provide much assistance in the arena of child-care (Lancy, 2012). Among the Agta, about 10% of the direct care provided to infants comes from female siblings (Goodman et al., 1985). Among the Hadza, child allomothers represent over 60% of all childcare providers and spend large percentages of their day in active child care (Crittenden & Marlowe, 2008). When adults are out foraging, teenage girls are also responsible for resolving conflicts between children. The forager record suggests that children take an active part in subsidizing their own cost and even provide to the household or group economy providing food, domestic services, and childcare to others.

GRANDMOTHERS

The "grandmother hypothesis," although originally proposed by George Williams (1957), entered the mainstream lexicon of evolutionary anthropologists when revisited and expanded upon by Kristen Hawkes and colleagues at the University of Utah in the 1980s and 1990s. This hypothesis suggests that the characteristically long post-menopausal lifespan seen in human females was favored because of the fitness enhancing benefits of grandmaternal investment over maternal investment (Hawkes, O'Connell, & Blurton Jones, 1997). When a woman shifts her investment from her own children to her grandchildren, she is effectively contributing to her daughter's fertility, enabling her to have shortened IBI and ultimately produce more children. Despite the widespread traction of this hypothesis, some have argued that the greater fitness benefits of grandmaternal investment over maternal investment have yet to be supported (Kachel, Premo, & Hublin, 2011). Regardless of why menopause exists, we acknowledge the important role that grandmothers play in the lives of forager children.

Grandmothers have been shown to positively affect outcomes, such as the survivorship and growth of their grandchildren, in a number of populations (Bereczkei, 1998; Hawkes et al., 1997; Leonetti, Nath, Hemam, & Neill, 2005). Their assistance also functions to reduce maternal workload (Meehan, Quinlan, & Malcom, 2013) and maternal time spent in child-care (Crittenden & Marlowe, 2013). Conversely, an alternative study found that paternal grandmothers have a negative effect on infant mortality in a German population, potentially due to tense relationships between mother and daughters-in-law (Voland & Beise, 2002). Evolutionary theory predicts lower investment by paternal grandmothers compared to maternal grandmothers because of lowered paternity confidence (Euler & Weitzel, 1996), yet among foragers, the effects of paternal grandmothers have largely been positive (but see Sear, Mace, & McGregor, 2000 for differential effects in a rural Gambian population). Among the Hadza, for instance, paternal grandmothers invest as heavily as their maternal counterparts, a finding that may reflect either high paternity confidence among the Hadza or the residence choices of paternal grandmothers who choose to live with sons who have high paternity confidence (Crittenden & Marlowe, 2008).

The model population for Hawkes and colleagues' initial iteration of the grandmother hypothesis was the Hadza. Early work suggested that grandmothers' foraging yield predicted childhood growth of her grandchildren (Hawkes et al., 1997). More recently, the "demographic effect" of Hadza grandmothers has been highlighted. Not only do grandmothers choose to reside with daughters who require more assistance (Blurton Jones et al., 2005), but grandmothers also tend to reside in camps when their daughter's husband is not present (Crittenden & Marlowe, 2008).

Grandmothers may also provide substantial amounts of childcare. After fathers, they represent the category of allomother who spends the most time in direct childcare (Crittenden & Marlowe, 2013). These results map on to the data in other foraging populations, in which grandmothers play a special role. Among the Aka of the Central African Republic, fathers and grandmothers also provide the second and third highest rate of direct care (Meehan et al., 2013). Similarly, among the Martu of Australia, grandmothers represent the category of allomother most likely to provide care, such as bathing and feeding (Scelza, 2009). A recent study examining the flow of food resources among Hiwi and Ache hunter-gatherers, however, provides alternative data suggesting that grandmothers are not the main source of food subsidies for a reproductive pair (Hill & Hurtado, 2009).

Despite the debate over the impact of grandmothers, they continue to receive much attention in evolutionary anthropology (Hawkes & Coxworth, 2013; Mace, 2013). Increasingly, however, focus has shifted to the large constellation of helpers available to a recipient mother. The emphasis on widespread networks of care includes both related and unrelated helpers, and is yielding robust results cross-culturally and across subsistence regimes (Bell, Hinde, & Newson, 2013; Hrdy, 2014; Meehan, Helfrecht, & Quinlan, 2014). It is these widespread networks to which we turn now.

DISTANT KIN AND SOCIAL NETWORKS

One of the most striking features of human sociality is the existence of cooperative social ties within and between unrelated individuals and groups. It is possible that this unique pattern of social behavior evolved, in part, in response to the high demands and costs of human reproduction. Indeed, sharing food and childcare is widespread in many hunter-gatherer societies. Data from foraging populations around the world supports the notion of humans as a cooperatively breeding species that invest calorically, in terms of distributed food sharing, and behaviorally, in terms of distributed childcare.

Long-term data collected among the Aka (Meehan, 2005), the Efe (Ivey Henry, Morelli, & Tronick, 2005), the Ache (Hill & Hurtado, 2009), and Hiwi (Hill & Hurtado, 2009) suggest that unrelated individuals spend considerable amounts of time providing childcare. Among the Hadza, unrelated allomothers provide over 12% of all holding and carrying of infants (Crittenden & Marlowe, 2008). Hunter-gatherer food sharing is also widely characterized as "camp wide" because the pooling and distribution of game resources occurs between all related and unrelated individuals who reside together. This pattern is well documented among several populations, including the Ache (Kaplan & Hill, 1985), Hiwi (Gurven, Hill, Kaplan, Hurtado, & Lyles, 2000), and the Hadza (Hawkes et al., 2001).

We know of no work that has explicitly used social network analysis in hunter-gatherers to test theories of cooperative breeding in humans; however, the significance of distant kin, affines, and nonkin has been repeatedly stressed (Hrdy, 2009, Sear & Coall, 2011). In the Lamalera, a whale hunting population of villagers in Indonesia, a social network analysis of household food transfers suggest that although kinship is an important criterion in food sharing, unrelated households also share food with one another (Nolin, 2010). Among the Ache, kin are preferred recipients of food transfers, yet sharing patterns map more readily onto reciprocal altruism theory than kin selection (Allen-Arave, Gurven, & Hill, 2008). Among the Aka, degree of relatedness did not determine frequency or amount of meat shared (Kitanishi, 1998) though widespread sharing of meat beyond close relatives tends to correlate with the size of animals (Bahuchet, 1990). This pattern has also been observed in other foragers (Gurven, 2004).

A recent social network study of the Hadza revealed that adults with more children were given more honey in a gift-giving network (Apicella et al., 2012) possibly due to the increased needs of these parents. In this same network study, Hadza individuals were asked to nominate people that they would like to live with in the future. Although genetic relatedness was important in selecting residence partners, a non-trivial proportion of nominations included affines and friends (Apicella et al., 2012). Interestingly, individuals reported wanting to live with affines from past relationships, possibly due to the genetic relatedness of these affines to their children. Affinal kinship appears to be an important and original feature of human sociality (see Chapais, 2013). It is possible that cooperative affinal relationships represented the first step in the extension of cooperation beyond immediate kin, and from there it was generalized to other genetically unrelated individuals.

Humans not only recognize affines, but they also recognize both their maternal and paternal kin. This has likely led to the increased flexibility in residence patterns observed in foragers (Hill et al., 2011). Because humans can trace descent bilaterally, the risk of inadvertent incest with a sibling is low (Perrin & Mazalov, 2000). This ability to trace descent bilaterally affords a number of social advantages. It allows individuals to move freely about social space, thus maximizing choice in residence partners (Apicella et al., 2012). It also facilitates family connections between groups and increases the number of kin available for help support (Marlowe, 2005). Increased familial relations between groups may have, in turn, fostered multigroup coordination and cooperation. This particular feature may be the very definition of human social structure (Chapais, 2013).

The advantages of cooperation to foragers are obvious given the high demands of reproduction and the benefits that sharing food and labor provide. It is less clear how cooperation was maintained in light of the fact that free riders may benefit from defecting. This is particularly bewildering given that hunter-gatherer residence patterns are dynamic, with group membership in constant flux and large numbers of unrelated individuals living together (Hill et al., 2011). When one considers that cooperation in humans occurs at both a group and network level, it may be easier to understand how cooperation can be sustained. All explanations for the evolution of cooperation rely on some degree of assortativity. That is, natural selection is argued to support cooperation under conditions in which cooperators can get together and benefit from that cooperation. Theorists have hypothesized that group structure (e.g., Bowles, 2006) and social networks (e.g., Ohtsuki, Hauert, Lieberman, & Nowak, 2006) are essential for the evolution of cooperation because they allow for assortativity. Until recently, however, this had not been empirically demonstrated in real-life networks, let alone among hunter-gatherers. A recent sociocentric network analysis of the Hadza revealed assortativity in cooperation at the group and network level (Apicella et al., 2012). The analysis also revealed greater variance between camps and less variation within camps in levels of cooperation, as measured using a public goods game with real economic consequence. More simply put, individuals were living with similarly cooperative people. At the network level, similarity in public good donations predicted ties between people. This similarity in cooperation extended up to two degrees of separation. Importantly, social ties explained the similarity above and beyond genetic similarity, shared environment, and physical proximity. These data suggest that social networks, not simply groups, may be key in sustaining cooperation.

CONCLUSION

A rapid increase in brain size occurred with the emergence of *Homo* around 1.7 and 1.9 million years ago. This larger brain size had important implications for human evolution because it came at a high metabolic cost. This cost was offset, in part, by shifts to more energy and nutrient-rich diets. Nevertheless, achieving a high degree of encephalization in adulthood necessitated higher rates of growth over long periods of development. Consequently, the total time and cost needed to raise a child from birth to nutritional independence increased dramatically. Despite these increased demands, early *Homo* mothers, through early weaning and shortened interbirth intervals, were more reproductively successful than earlier australopithecines (Aiello & Key, 2002). The data reviewed here on hunter-gatherers suggest that this life-history strategy would have been impossible without subsidies from alloparents. Rather, a social system, with a wide range of helpers to tend to children's nutritional and behavioral needs, would have helped to relieve mothers from the energetic burden of raising overlapping, dependent children. In fact, this ability to rely on assistance would have permitted hominid mothers to thrive in a multitude of settings, a characteristic of human behavioral diversity.

The old adage that "it takes a village to raise a child" appears to have deep evolutionary roots. Across hunter-gatherer societies, children receive support not only from their parents, but also their siblings, grandparents, extended kin, and unrelated individuals. We suggest that human social structure, characterized by lifelong, cooperative bonds that exist within and between groups, may have evolved, in part, to support the needs of the human family. The unique ability of humans to recognize both their maternal and paternal kin, as well as their affinal kin, not only increased the pool of available caregivers, but also may have marked the first steps in the transition to cooperative breeding among unrelated individuals. Although much work has examined the role of specific categories of helpers, future work should examine how social networks themselves may play a role in supporting children. Such work not only increases our understanding of the evolution of the human family, but may also inform our understanding of contemporary family formation in its various forms.

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CHAPTER 24

The Role of Hormones in the Evolution of Human Sociality

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THE HUMAN FAMILY seems to follow a typical mammalian pattern: intense maternal care including breastfeeding of an altricial (helpless) offspring, with some support from an assortment of other relatives—siblings, aunts, fathers, and the like. Beyond the shared mammal/primate commonality, however, humans have some highly unusual traits. The extent and duration of offspring care is exceptional, and unique in the huge informational transfer via language. We are the only species characterized by the combination of stable breeding bonds, extensive paternal care in multimale groups, extended bilateral kin recognition including life-long brother-sister relationships, grandparenting, and controlled exchange of mates among kin groups. These characteristics are important for theoretical and pragmatic understanding of family relationships and child development; their evolution presents one of the great challenges for science. Here we consider clues from the fossil record and the physiological mechanisms that underpin central aspects of our sociality.

Hormones and neurotransmitters help shape important aspects of our lives, including growth, differentiation, sexuality, physiology, emotion, and cognition. From romantic thoughts to jealous rage, from the release of gametes to lactation and parent-offspring bonding, the molecules produced and released by tiny and otherwise seemingly insignificant cells and glands orchestrate our reproductive strategies in extraordinary ways (see Roney, Chapter 46, this *Handbook*, Volume 2).

Our endocrine and neuroendocrine systems may be viewed as complex sets of mechanisms designed by natural selection to communicate information among cells and tissues. This chapter focuses on an area of particular importance for evolutionary psychology: the behavioral endocrinology of human sociality. Steroid and peptide hormones, associated neurotransmitters, and other chemical messengers guide mating and parental behaviors of mammals in many important ways (Bridges, 2008; Curtis & Wang, 2003; Rosenblatt, 2003; Young & Insel, 2002). Cross-species comparisons among primates require careful analysis (Bercovitch & Ziegler, 2002; Fernandez-Duque, Valeggia, & Mendoza, 2009) because of the apparent rapid evolutionary changes in patterns of reproductive behaviors and increased phenotypic flexibility involving intricate mental processes. *Homo sapiens* present special problems in these regards (Fisher, 2004; Maestripieri, 1999; Marler, Bester-Meredith, & Trainor, 2003; Rilling, 2013; Wynne-Edwards, 2001, 2003).

Here we first provide a theoretical scenario for the evolution of human patterns of mating and parenting behaviors. We test our model by examining the phylogenetic trajectories of associated traits such as sexual dimorphism and life history stages from the hominin fossil record. We then turn to a description and functional analysis of the endocrine mechanisms that may influence these remarkable reproductive behavioral characteristics of our species.

EVOLUTION OF THE HUMAN FAMILY

Human childhood may be viewed as a life history stage that is necessary for acquiring the information and practice to build and refine the mental algorithms critical for negotiating the social relationships that are key to success in our species (Geary & Flinn, 2001; Hrdy, 2009; Konner, 2010; Muehlenbein & Flinn, 2012). Mastering the social environment presents special challenges for the human child. Social competence is difficult because the targets (other children and adults) are constantly changing and similarly equipped with theory of mind and other cognitive abilities (Flinn, 2006c; 2013b; Flinn & Alexander, 2007).

The family environment is a primary source and mediator of the ontogeny of information processing abilities, including social competencies and group cooperation. Human biology has been profoundly affected by our evolutionary history as unusually social creatures, immersed in networks of family, kin, and dynamic, intercommunity coalitions. Human kinship systems appear unique in the universal recognition of both bilateral (maternal and paternal) and multigenerational structure, with a general trend for co-residence of male kin, but a dozen or more major variants (Chapais, 2008, 2013; Davis & Daly, 1997; Flinn & Low, 1986; Walker, Flinn & Hill, 2010; Walker, Hill, Flinn & Ellsworth, 2011). These aspects of human kinship link families into broader cooperative systems, and provide additional opportunities for alloparental care during the long social childhood. Five species-distinctive characteristics stand out as unusually important in this regard: (1) fathering, that is, extensive and specific parental investment by males; (2) life-long sibling bonds, including sister-brother relationships; (3) complex pair-bond relationships between mates; (4) grandparenting; and (5) networks of kinship that extend among communities and involve affinal (ties by marriage) and consanguineal (ties by blood) relationships. These five distinctive social characteristics appear linked with a suite of other unusual human traits, including concealed (or "cryptic") ovulation, physically altricial but mentally precocial infants, lengthy child development, female orgasm, and menopause (Flinn, Quinlan, Ward, & Coe, 2007).

Hormones are involved in the development (ontogeny) and regulation of these and other components of reproduction, including the neurobiology that underpins the associated psychological competencies (e.g., Bartels & Zeki, 2004; Donaldson & Young, 2008). Understanding the proximate causes, phylogenetic relations, and adaptive functions of the hormonal and neurotransmitter mechanisms may provide important steps toward reconstructing the evolutionary history of our (human) unusual patterns of mating and parenting and their variability in different environmental contexts.

The altricial (helpless) infant is indicative of a protective environment provided by intense parental and alloparental care in the context of kin groups (Alexander, 1987; Chisholm, 1999; Flinn, 2004, 2006b; Flinn & Ward, 2004; Hrdy, 1999, 2004). The human baby does not need to be physically precocial. Rather than investing in the development of locomotion, defense, and food acquisition systems that function early in ontogeny, the infant can work instead toward building a more effective adult phenotype. The brain continues rapid growth, and the corresponding cognitive competencies largely direct attention toward the social environment. Plastic neural systems enable adaptation to the nuances of the local community, such as its language (Alexander, 1990a; Bjorklund & Pellegrini, 2002; Bloom, 2000; Geary & Bjorklund, 2000; Geary & Huffman, 2002; Small, 1998, 2001). In contrast to the slow development of ecological skills of movement, fighting, and foraging, the human infant rapidly acquires skill with the complex communication system of human language (Pinker, 1994) and other social competencies such as facial recognition (de Haan, Johnson, & Halit, 2003), eye contact (Farroni, Mansfield, Lai, & Johnson, 2003), and smiling (Bornstein & Arterberry, 2003). The extraordinary information-transfer abilities enabled by linguistic competency provide a conduit to the knowledge available in other human minds. This emergent capability for intensive and extensive communication potentiates the social dynamics characteristic of human groups (Dunbar, 1997, 2004) and provides a new mechanism for social learning and culture. The recursive pattern recognition and abstract symbolic representation central to linguistic competencies may facilitate the open-ended, creative, and flexible information processing characteristic of humans—especially of children (Flinn & Ward, 2004; cf. Ranganath & Rainer, 2003).

The advantages of intensive parenting, including paternal protection and other care, require a most unusual pattern of mating relationships: moderately exclusive pair bonding in multiple-male groups. No other primate (or mammal) that lives in large, cooperative multiple-reproductive-male groups has extensive male parental care, although some protection by males is evident in multimale troops of baboons (Buchan, Alberts, Silk, & Altmann, 2003), and extensive care is provided by males in small monogamous family groups in indris, marmosets, tamarins, night monkeys, titi monkeys, and, to a lesser degree, gibbons (Fernandez-Duque et al., 2009). Although some group-living species of birds have paternal care, there appear to be special mechanisms enhancing confidence of paternity (e.g., mate guarding and the lack of long gestation periods), and they lack the coalitionary cooperation characteristic of humans. Among primates, competition for females in multiple-male groups usually results in low confidence of paternity (e.g., chimpanzees). Males and females forming exclusive pair bonds in multiple-male primate groups would provide cues of nonpaternity for other males and hence place their offspring at higher risk for infanticide (Hrdy, 1999). Paternal care is most likely to be favored by natural selection in conditions where males can identify their offspring with sufficient probability to offset the costs of investment (Alexander, 1974; see Geary, Chapter 20, this volume), although reciprocity with potential mates is also likely to be involved (Buss, 1994; Smuts, 1985). Humans exhibit a unique "nested family" social structure, involving complex reciprocity among males and females embedded in kin networks that restricts direct competition for mates among group members. It is difficult to imagine how this system could be maintained in the absence of the unusual human trait of concealed or "cryptic" ovulation (Alexander, 1990b; Alexander & Noonan, 1979). Although many other primates lack estrus swellings and other obvious visual signals of female reproductive condition (Pawlowski, 1999; Sillén-Tullberg & Møller, 1993), humans appear especially oblivious to the timing of ovulation, although frequency of intercourse (Wilcox et al., 2004), mate-guarding activities (Flinn, 1988), and mate choice discrimination (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004; Gangestad, Thornhill, & Garver-Apgar, Chapter 14, this volume) may be higher during midcycle in some conditions.

Human social relationships are especially complex because they involve extensive coalitions. We are extraordinarily cooperative, most exceptionally and importantly in regard to competition with other groups (Alexander, 2006; Bowles, 2009; Flinn, Geary, & Ward 2005). Humans are unique in being the only species that engages in group-against-group play (Alexander, 1990b) including team sports. This trait is cross culturally universal, emerges early in child development, and often is the object of tremendous collective effort. Human groups tend to be male philopatric (men reside in the group in which they were born, although they may also emigrate), resulting in extensive male kin alliances, useful for competing against other groups of male kin (Chagnon, 1988; Flinn, Ponzi, & Muehlenbein, 2012; LeBlanc, 2003; Macfarlan, Walker, Flinn, & Chagnon, 2014; Wrangham & Peterson, 1996). Patterns of kinship residence, however, are variable (Murdock, 1949) and associated with different aspects of mating and marriage systems (Flinn & Low, 1986; Rohner & Veneziano, 2001; Walker et al., 2013). Females also have complex social networks, but usually are not involved directly in the overt physical aggression and alliances characteristic of intergroup relations (Campbell, 2002; Geary & Flinn, 2002; for an insightful case of indirect competitive activities by females, see Biella, Chagnon, & Seaman, 1997; for comparisons with other primates, see Bissonnette et al., 2015).

Across extant primates, a long developmental period and intensive parenting are associated with a long life span (Allman & Hasenstaub, 1999; Leigh, 2004; van Schaik & Deaner, 2003). One unique feature of the life history and long life span of women is menopause. Menopause results in an extended period during which women can invest in the well-being of their later born children as part of a potential adaptation that enables the long-term investment in a smaller number of children and other relatives such as grandchildren. It allows them to focus on children they have already produced, avoiding the costs of additional pregnancies at a time when their health and the likelihood of their survival to the end of later-born children's dependency are diminishing (Alexander, 1974; Hawkes, 2003; Williams, 1957). The increasing probability of mother's death with age has especially significant effects on the reproductive value of later-born children if long-term maternal investment is important. Orphans have low reproductive value in many societies. A parallel is found in some preindustrial societies, whereby parents sometimes commit infanticide to reduce the risks to their older children (Daly & Wilson, 1988; Hill & Hurtado, 1996). Infanticide, as well as reduced fertility associated with breastfeeding and increasing age (Ellison, 2001) enables parents to reduce the number of dependent offspring and direct more parental investment to older children. When this pattern is combined with a substantial increase in the length of the developmental period, menopause follows as a logical evolutionary adaptation that serves the same function, that is, to reduce the number of dependent children and thus free parental resources that can be invested in a smaller number of children and other kin. Empirical tests demonstrating such advantages, however, have proven difficult (Hill & Hurtado, 1996; Hill & Kaplan, 1999; cf. Hawkes, 2003; Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998).

Men, with different, less risky parental activities, would not have been subject to the same selective pressures for terminating reproductive potential, although they, too, may have been selected to adjust reproductive behavior from mating to parenting with increased age (Draper & Harpending, 1988). From this perspective, older females may have had important effects on the success of their developing children, perhaps in part because of the importance of their accumulated knowledge for negotiating the social environment. Socially skilled and well-connected older mothers and grandmothers may have been especially valuable teachers of social and political wisdom, with associated reproductive benefits (Alexander, 1990b; Caspari & Lee, 2004; Coe, 2003; cf. O'Connell, Hawkes, & Blurton Jones, 1999). In short, the doubling of the maximum life span of humans, involving an increased period of prereproductive development on the one hand and an increased period of postreproductive parental and kin investment on the other, suggests the importance of parent-offspring relationships for acquiring and mastering sociocompetitive information (Bjorklund & Pellegrini, 2002; Flinn & Ward, 2004; Geary, 2005).

These characteristics of the human family—extensive biparental and kin care, physically altricial but linguistically and cognitively precocial infants, lengthy childhood and adolescence, concealed ovulation, variably exclusive pairbonds in multiple-male coalitionary groups, and menopause—are a unique combination of traits with associated morphological, physiological, and psychological mechanisms (Flinn, Geary, & Ward, 2005). In the following section, we review the paleontological evidence of the selective pressures that produced this complex set of adaptations.

THE FOSSIL RECORD

The temporal sequence of changes in hominin anatomy documented in the fossil record provides evidence of the sequence of morphological changes that occurred in human evolution. Unfortunately, it is difficult to directly infer hominin social structures and associated neurobiological and endocrinological mechanisms from fossils. Some evidence comes from changes in the pattern of human sexual dimorphism and shifts in life-history strategies that would impact social interactions, in particular, reduction in the magnitude of body size sexual dimorphism, threefold increase in brain volume, near doubling of the length of the developmental period, and disappearance of related species of hominins. Covariation among these variables and social and ecological differences across living primates provide data from which inferences can be made about the nature of social dynamics in human evolution (Alexander, Hoogland, Howard, Noonan, & Sherman, 1979; Anton, 2003; McHenry, 1994a, 1994b; Dunbar, 1998; Foley, 1999; Plavcan, van Schaik, & Kappeler, 1995), although associated models may not be definitive (Plavcan, 2000; 2012a).

The best indicators of the increasing stability of male-female pair bonds and associated male coalitionary behavior in the fossil record are sexual dimorphism and life-history patterns. Reduced body size dimorphism is associated with both monogamy (Plavcan, 2000, 2001) and male coalitionary behavior (Pawlowski, Lowen, & Dunbar, 1998; Plavcan & van Schaik, 1997; Plavcan et al., 1995) in extant primates. Although the large canine size dimorphism that characterizes all living and fossil great apes had greatly diminished in *Australopithecus* (Manthi, Plavcan & Ward, 2012; Ward, Leakey, & Walker, 2001; Ward, Walker, & Leakey, 1999), the reduced body mass dimorphism typical of modern humans did not occur until sometime during the evolution of *Homo erectus* (Antòn, 2003; McHenry, 1992a, 1992b, 1994a, 1994b; Plavcan, 2012a, 2012b; Rightmire, Van Arsdale, & Lordkipanidze, 2008).

It is tempting to assume that the behavioral characteristics of the ancestor common to the australopithecine species and humans were similar to those observed in modern chimpanzees or bonobos (de Waal & Lanting, 1997; Kano, 1992; Wrangham, 1999; Wrangham & Peterson, 1996; Zihlman, Cronin, Cramer, & Sarich, 1978). This appears a reasonable assumption in some respects, as relative brain sizes of chimpanzees, bonobos, and australopithecines are very similar (McHenry, 1992a, 1992b). In addition, sexual dimorphism in body weight is about 20% for chimpanzees and bonobos (Goodall, 1986; Kano, 1992), as are lean mass and skeletal size dimorphsim in humans (Plavcan, 2012a). Thus, it might appear that the large multimale, multifemale group structures characterizing all three species would have been found in the last common ancestor and thus in earliest hominins. Chimpanzees and humans display coalitional aggression (Wrangham, 1999), and although this is not documented for the less studied bonobos, it has been hypothesized to be a homologous trait shared with the common ancestor of chimpanzees and humans (Wrangham & Peterson, 1996).

Size dimorphism was substantially greater in *Australopithecus* than in *Pan* or *Homo*, although less than in gorillas and orangutans (Gordon, Green & Richmond, 2008; Harmon, 2006; Kimbel & Delezene, 2009; Lockwood, 1999; Lockwood, Richmond, Jungers & Kimbel 1996; Lockwood, Menter, Mogg-Cecci & Keyser, 2007; McHenry, 1992b; Plavcan, 2012b; Richmond & Jungers, 1995; Ward et al., 1999, 2001; Wood & Constantino, 2007; but see Reno, Meindl, McCollum, & Lovejoy, 2003; Reno, McCollum, Meindl & Lovejoy, 2010 for an alternate interpretation of *A. afarensis,*). The contrast suggests that reproductive strategies of australopithecines may have differed in important respects from that of male chimpanzees, bonobos, and humans. *Australopithecus* body mass dimorphism suggests that these early hominins were polygynous, as significant mass dimorphism is not associated with monogamy in any extant primate (Plavcan, 2001). Body mass dimorphism is inconsistent with both monogamy and extensive coalitionary behaviors in extant primates (Plavcan, 2000; Plavcan & van Schaik, 1997). Therefore, the social structure of *Australopithecus* was unlikely to have been characterized by either monogamy or extensive male coalitions (Plavcan, 2012b).

At some point during the evolution of *Homo erectus*, body-size sexual dimorphism became reduced to near-modern human levels. The reduction in sexual dimorphism resulted in spite of a slight increase in male size, because of an even more substantial increase in female body size (McHenry, 1994a; Plavcan, 2012a). Body mass dimorphism in early *H. erectus* is difficult to estimate accurately, but disparities in size and robusticity among even early *H. erectus* crania are less than in australopithecine species, signaling a reduction in body size sexual dimorphism. By the early mid-Pleistocene (approximately 800 k), body mass dimorphism was similar to that found in modern humans (McHenry, 1994a; Ruff, Trinkaus, & Holliday, 1997), consistent with either an increase in pair bonding and/or male coalitionary behaviors.

Changes in social behavior accompanying the shift in mating and parenting strategies are likely to have presented novel cognitive challenges involving complex reciprocity among coalition members. Unlike gorillas, with one-male breeding groups, and chimps, with promiscuous mating and little male parental behavior, at some point, the evolving hominids were faced with the difficulties of managing increasingly exclusive pair bonds in the midst of increasingly large coalitions of potential mate competitors. These behavioral changes would be consistent with the documented decreases in dimorphism.

Prolongation of childhood, including secondarily altricial infants born early in their ontogenies coupled with extended juvenile periods, an adolescent growth spurt, and delayed maturation relative to apes (Bogin, 1991, 1999), seems to have broadly coevolved with changes in sexual dimorphism and reproductive behaviors. The first major changes in hominin infant altriciality probably occurred in later *Homo erectus*, possibly concurrent with changes in sexual dimorphism and cranial capacity—that is, more recently than 1.5 mya (Antòn & Leigh, 2003; Nelson, Thompson, & Krovitz, 2003). Female pelvic dimensions are constrained by mechanical-locomotor as well as thermoregulatory constraints, so birth canal size was not greatly expanded over australopithecine levels (Begun & Walker, 1993; Ruff, 1995), yet adult brain sizes were nearly doubled even in early *Homo*. This means that, to have appropriate neonatal proportions relative to the size of the mother's pelvic inlet, infants must have been born at a relatively small size and were relatively altricial early (Martin, 1990; Portman, 1941; Rosenberg & Trevathan, 1996) with rapid rates of brain growth (Antòn & Leigh, 2003; Martin, 1983). They do not appear to have attained large adult brain size simply by prolonging overall growth (Deacon, 1997; Dean et al., 2001; Leigh, 2004). Increasingly altricial infants would have required more intensive parenting by the mother, and, given the decrease in sexual dimorphism occurring at this time, which may indicate pair bonding, perhaps parental care by the father and/or alloparents (Flinn & Ward, 2004; Rosenberg, 1992; Rosenberg & Trevathan, 1996).

Despite these ontogenetic shifts associated with the timing of birth, delayed maturation does not appear to have occurred until later in human evolution (summary in Nelson et al., 2003). Dental development is coupled to life history variables such as age at sexual maturity, and thus can be used to infer the timing of important life history stages. Early *Homo erectus* appears to have had relatively rapid development, similar in rate to *Australopithecus* and great apes, whereas that of modern humans is much slower (Dean et al., 2001). Rates of development of the dentition as determined by studies of tooth calcification patterns support the hypothesis that all Pliocene and Pleistocene hominin growth was rapid, more similar to that of apes than of modern humans (reviews in Lacruz & Ramírez Rossi, 2010; Smith, 2008, 2012), until very recently, possibly even until the appearance of anatomically modern *Homo sapiens* (Smith et al., 2010). However, it is important to note that the relation between dental development and development of the brain and other aspects of hominin biology are uncertain (Smith, 2012). Coincident with its rapid rate of development, early *H. erectus* is predicted to have lacked a humanlike adolescent growth spurt, based on the fact that the single known juvenile skeleton, KNM-WT 15000, appears to have had a more rapid rate of dental development than that of his postcranial skeleton when compared with humans (Antòn & Leigh, 2003; Smith, 1993). There are no comprehensive data on rates of child development for hominins between 1.6 million and 60 thousand years ago, but the single Neandertal specimen examined by Dean and colleagues (2001) was modern in its developmental trajectory, indicating a humanlike extended childhood had occurred by this time. A modern human pattern of dental development was present by 800 k (Bermudez de Castro, Rosas, Carbonee, Nicolás, Rodríguez, & Arsuaga, 1999; Bermudez de Castro, Ramírez Rossi, Marinón-Torres, Sarmiento Pérez, & Rosas, 2003), but this may or may not imply a similar rate (Dean et al., 2001). Relatively large brains in some Neandertals compared to their dental development stages (Dean, Stringer, & Bromage, 1986) may reflect the overall larger brains of at least some individuals, rather than significant maturational differences. If it does, it might be reasonable to hypothesize that the human adolescent growth spurt was already in place by this time as well (Bermudez de Castro et al., 2003). Neandertals and modern humans probably shared similar stages of development, including an adolescent growth spurt that would have been present in their mutual ancestry, perhaps by 500 kya (Krovitz, 2003). Still, their dental development patterns are more similar to those of earlier hominins than modern humans (Smith, 2008, 2012; Smith et al., 2010). Longevity appears to have gradually increased from *Australopithecus* to modern humans with a higher proportion of individuals living to old age in the past 50,000 years (Caspari & Lee, 2004). If ecological dominance reduced mortality from extrinsic causes, this would allow for selection for delayed reproduction and extended life histories (Chisholm, 1999; Stearns, 1992; Williams, 1957). Taking all the data together, it appears that the evolution of altriciality may have begun after the initial brain expansion but that delayed maturation and an adolescent growth spurt may have evolved later in human evolution, perhaps as brain size increase continued throughout the Pleistocene.

Thus, it appears that modern human social structures, and likely human family structures, developed gradually during the early to mid-Pleistocene. Integrated adaptations included more altricial infants, delayed maturation, increasingly stable mating relationships between males and females, increasing paternal and alloparental care of offspring, and more significant nonkin coalitionary behaviors. All of these changes roughly co-occurred with brain size expansion, which began increasing with early *Homo* and continued through the mid-Pleistocene where it reached modern human levels (Lee & Wolpoff, 2003). Evidence for coevolution among all these variables broadly supports a model in which increasing social complexity favored sociocognitive competencies, necessitating a longer childhood and more parental care of children (Figure 24.1).

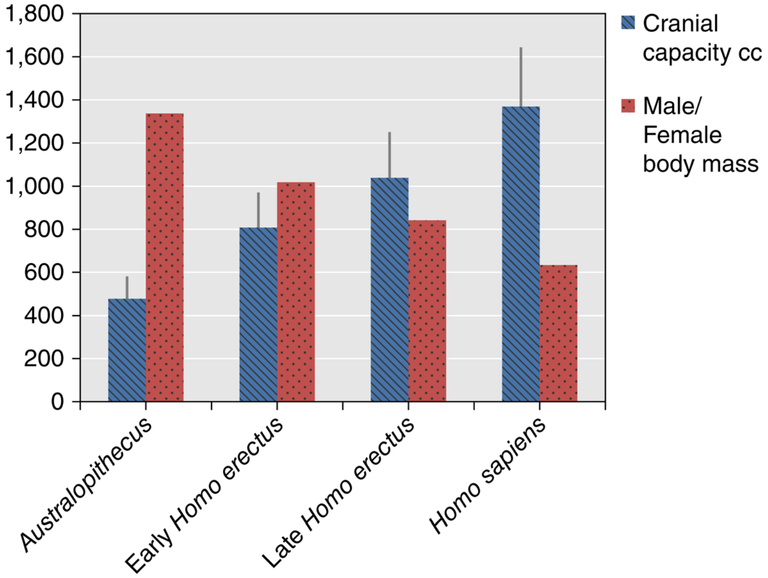

Figure 24.1 Cranial Capacity (cubic centimeters) and Ratio of Male-to-Female Body Mass in Hominins.

In the following sections, we examine the hormonal mechanisms that may be involved with the ontogeny and regulation of this unique combination of life history, reproductive, and social traits suggested by the fossil and comparative primate evidence.

HORMONAL AND NEUROTRANSMITTER MECHANISMS

The constellation of behaviors associated with the human family and the dynamics of social competition described in previous sections require complex regulatory systems. In this section, we first briefly review the potential mechanisms for human pairbonding, maternal and paternal attachment to offspring, kin attachment, and male coalitions. We then turn to a more detailed analysis of how the neuroendocrine stress response system functions to enable acquisition of social competencies during childhood in the context of the human family environment.

The chemical messenger systems that orchestrate the ontogeny and regulation of sexual differentiation, metabolism, neurogenesis, immune function, growth, and other complex somatic processes tend to be evolutionarily conservative among primates and more generally among mammals. Hence rodent and nonhuman primate models provide important comparative information about the functions of specific human neuroendocrine systems, for which we often have little direct empirical research. It is the particular balance of human mechanisms and abilities that is unique and reflects the history of selection for complex social interactions that shaped the human lineage.

THE CHEMISTRY OF AFFECTION

Some of the most precious of all our human feelings are stimulated by close social relationships: a mother holding her newborn infant for the first time, brothers reunited after a long absence, or lovers entangled in each other's arms. Natural selection has designed our neurobiological mechanisms, in concert with our endocrine systems, to generate potent sensations in our interactions with these most evolutionarily significant individuals. We share with our primate relatives the same basic hormones and neurotransmitters that underlie these emotional gifts. But our unique evolutionary history has modified us to respond to different circumstances and situations; we are rewarded and punished for somewhat different stimuli than our phylogenetic cousins. Chimpanzees and humans delight in biting into a ripe, juicy mango. But the endocrine, neurological, and associated emotional responses of a human father to the birth of his child (e.g., Storey, Walsh, Quinton, & Wynne-Edwards, 2000) are likely to be quite different from the responses of a chimpanzee male. Happiness for a human (Buss, 2000) has many unique designs, such as romantic love (Fisher et al., 2002), that involve shared endogenous messengers from our phylogenetic heritage.

Attachments are central in the lives of the social mammals. Basic to survival and reproduction, these interdependent relationships are the fabric of the social networks that permit individuals to maintain cooperative relationships over time. Although attachments can provide security and relief from stress, close relationships also exert pressures on individuals to which they continuously respond. It should not be surprising, therefore, that the neuroendocrine mechanisms underlying attachment and stress are intimately related to one another. And although more is known about stress response systems than affiliative systems, some of the pieces of the puzzle are beginning to fall into place.

The mother-offspring relationship is a core aspect of mammalian social life. The biochemistry of this intimate bond was also selected to serve in primary mechanisms regulating bonds between mates, paternal care, the family group, and even larger social networks (Fisher et al., 2002; Hrdy, 1999). Although a number of hormones and neurotransmitters are involved in attachment and other components of relationships, the two peptide hormones, oxytocin (OT) and arginine-vasopressin (AVP), appear to be primary (Carter, 2002; Curtis & Wang, 2003; Lim et al., 2004; Young & Insel, 2002), with dopamine, cortisol, and other hormones and neurotransmitters having mediating effects.

The hypothalamus is the major brain site where OT and AVP, closely related chains of nine amino acids, are produced. From there they are released into the central nervous system (CNS) as well as transported to the pituitary where they are stored until secreted into the bloodstream. OT and AVP act on a wide range of neurological systems, and their influence varies among mammalian species and stage of development. The neurological effects of OT and AVP appear to be key mechanisms (e.g., Bartels & Zeki, 2004; Donaldson & Young, 2008) involved in the evolution of human family behaviors. The effects of OT and AVP in humans are likely to be especially context dependent, because of the variable and complex nature of family relationships.

PARENTAL CARE

Along with OT and AVP, prolactin, estrogen, and progesterone are involved in parental care among mammals (Insel & Young, 2001). The involvement of these hormones varies across species and between males and females. The effects of these hormones are influenced by experience and context. Among rats, for example, estrogen and progesterone appear to prime the brain during pregnancy for parental behavior. Estrogen has been found to activate the expression of genes that increase the receptor density for OT and prolactin, thus increasing their influence (Young & Insel, 2002).

Experience also influences parental behavior and the hormonal activity associated with it. In animal studies, a significant body of evidence demonstrates that early life experience influences later parental behavior (Champagne & Meaney, 2001; Fairbanks, 1989). And a number of studies demonstrate that this experience influences the neurohormonal biology involved in the expression of maternal care (Barrett & Fleming, 2010; Fleming, O'Day, & Kraemer, 1999). The hypothalamic-pituitary-adrenal (HPA) system of offspring during development is influenced by variation in maternal care, which then influences their maternal behavior as adults. Such changes involve the production of, and receptor density for, stress hormones and OT.

HPA-modulated hormones and maternal behavior are related in humans during the postpartum period (Fleming, Steiner, & Corter, 1997). During this time, cortisol appears to have an arousal effect, focusing attention on infant bonding. Mothers with higher cortisol levels were found to be more affectionate, more attracted to their infant's odor, and better at recognizing their infant's cry during the postpartum period.

fMRI studies of brain activity involved in maternal attachment in humans indicate that the activated regions are part of the reward system and contain a high density of receptors for OT and AVP (Bartels & Zeki, 2004; Fisher, 2004). These studies also demonstrate that the neural regions involved in attachment activated in humans are similar to those activated in nonhuman animals. Among humans, however, neural regions associated with social judgment and assessment of the intentions and emotions of others exhibited some deactivation during attachment activities, suggesting possible links between psychological mechanisms for attachment and management of social relationships. Falling in love with a mate and offspring may involve temporary deactivation of psychological mechanisms for maintaining an individual's social "guard" in the complex reciprocity of human social networks. Dopamine levels are likely to be important for both types of relationship but may involve some distinct neural sites. It will be interesting to see what fMRI studies of attachment in human males indicate because that is where the most substantial differences from other mammals would be expected. Similarly, fMRI studies of attachment to mothers, fathers, and alloparental caretakers in human children may provide important insights into the other side of parent-offspring bonding.

Paternal Care Paternal care is not common among primates or mammals in general (Fernandez-Duque et al., 2009; Geary, Chapter 20, this volume). It is, however, found among some rodent and primate species, including humans. The extent and types of paternal care vary among species. The hormonal mechanisms for parental care among males appears to differ somewhat from that found among females. Vasopressin appears to function as a co-factor to OT in males (Young & Insel, 2002). Along with prolactin and OT, vasopressin prepares the male to be receptive to and care for infants (Bales, Kim, Lewis-Reese, & Carter, 2004; Bridges, 2008; Rilling, 2013).

Paternal care is more common in monogamous than polygamous mammals and is often linked to hormonal and behavioral stimuli from the female. In the monogamous California mouse, disruption of the pair bond does not affect maternal care but does diminish paternal care (Gubernick & Alberts 1989). In other species with biparental care, however, paternal care is not as dependent on the presence of the female (Young & Insel, 2002). Experience also plays a role in influencing hormonal activation and paternal behavior. Among tamarins, experienced fathers have higher levels of prolactin than first-time fathers (Ziegler & Snowdon, 1997).

Pair Bonding Like male parental care, bonding between mates is also uncommon among mammals but has been selected for when it has reproductive advantages for both parents (Carter, 2002; Clutton-Brock, 1991; Young, Wang, & Insel, 2002). Monogamy is found across many mammalian taxa, but most of the current knowledge related to the neuroendocrine basis of this phenomenon has been obtained from the comparative study of two closely related rodent species. The prairie vole (*Microtus ochrogaster*) mating pair nest together and provide prolonged biparental care, whereas their close relatives, the meadow vole (*Microtus pennsylvanicus*), do not exhibit these behaviors (Young et al., 2002). As with other social behaviors in rodents, OT and AVP have been found to be central in the differences these related species exhibit with respect to pairbonding.

The receptor density for OT and AVP in specific brain regions might provide the basis for mechanisms underlying other social behaviors. Other neurotransmitters, hormones, and social cues also are likely to be involved, but slight changes in gene expression for receptor density, such as those found between the meadow and prairie voles in the ventral palladium (located near the nucleus accumbens, an important component of the brain's reward system), might demonstrate how such mechanisms could be modified by selection (Lim et al., 2004). The dopamine D2 receptors in the nucleus accumbens appear to link the affiliative OT and AVP pair-bonding mechanisms with positive rewarding mental states (Aragona, Liu, Curtis, Stephan, & Wang, 2003; Wang et al., 1999). The combination results in the powerful addiction that parents have for their offspring.

Given the adaptive value of extensive biparental care and prolonged attachment found in the mating pair and larger family network, it is not surprising that similar neurohormonal mechanisms active in the maternal-offspring bond would also be selected to underlie these other attachments. Though there is some variation among species and between males and females, the same general neurohormonal systems active in pair bonding in other species are found in humans (Wynne-Edwards, 2003). The challenge before evolutionary psychologists is to understand how the general systems have been modified and linked with other special human cognitive systems (e.g., Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001; Blakemore, Winston, & Frith, 2004; Feldman et al., 2012; Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010) to produce the unique suite of human family behaviors and sociality.

THE CHEMISTRY OF STRESS, FAMILY, AND THE SOCIAL MIND

The evolutionary scenario proposed in previous sections posits that the family is of paramount importance in a child's world. Throughout human evolutionary history, parents and close relatives provided calories, protection, and information necessary for survival, growth, health, social success, and eventual reproduction. The human mind, therefore, is likely to have evolved special sensitivity to interactions with family caretakers, particularly during infancy and early childhood (Baumeister & Leary, 1995; Belsky, 1997, 1999; Bowlby, 1969; Daly & Wilson, 1995; Flinn, 2011a; Geary & Flinn, 2001).

The family and other kin provide important cognitive "landmarks" for the development of a child's understanding of the social environment. The reproductive interests of a child overlap with those of its parents more than with any other individuals. Information (including advice, training, and incidental observation) provided by parents is important for situating oneself in the social milieu and developing a mental model of its operations. A child's family environment may be an especially important source and mediator of stress, with consequent effects on health.

Psychosocial stressors are associated with increased risk of infectious disease (Cohen, Doyle, Turner, Alper, & Skoner, 2003) and a variety of other illnesses (Ader, Felten, & Cohen, 2001). Physiological stress responses regulate the allocation of energetic and other somatic resources to different bodily functions via a complex assortment of neuroendocrine mechanisms. Changing, unpredictable environments require adjustment of priorities. Digestion, growth, immunity, and sex are irrelevant while being chased by a predator (Sapolsky, 1994). Stress hormones help shunt blood, glucose, and so on to tissues necessary for the task at hand. Chronic and traumatic stress can diminish health, evidently because resources are diverted away from important health functions. Such diversions may have special significance during childhood because of the additional demands of physical and mental growth and development and possible long-term ontogenetic consequences.

STRESS RESPONSE MECHANISMS AND THEORY

Physiological response to environmental stimuli perceived as stressful is modulated by the limbic system (amygdala and hippocampus) and basal ganglia. These components of the CNS interact with the sympathetic and parasympathetic nervous systems and two neuroendocrine axes, the sympathetic—adrenal medullary system (SAM) and the HPA. The SAM and HPA systems affect a wide range of physiological functions in concert with other neuroendocrine mechanisms and involve complex feedback regulation. The SAM system controls the catecholamines norepinephrine and epinephrine (adrenalin). The HPA system regulates glucocorticoids, primarily cortisol (for reviews, see McEwen, 1995; Sapolsky, Romero, & Munck, 2000).

Cortisol is a key hormone produced in response to physical and psychosocial stressors. It is produced and stored in the adrenal cortex. Release into the plasma is primarily under the control of pituitary adrenocorticotropic hormone (ACTH). The free or unbound portion of the circulating cortisol may pass through the cell membrane and bind to a specific cytosolic glucocorticoid receptor. This complex may induce genes coding for at least 26 different enzymes involved with carbohydrate, fat, and amino acid metabolism in brain, liver, muscle, and adipose tissue (Yuwiler, 1982).

Cortisol modulates a wide range of somatic functions, including: (a) energy release (e.g., stimulation of hepatic gluconeogenesis in concert with glucagon and inhibition of the effects of insulin), (b) immune activity (e.g., regulation of inflammatory response and the cytokine cascade), (c) mental activity (e.g., alertness, memory, and learning), (d) growth (e.g., inhibition of growth hormone and somatomedins), and (e) reproductive function (e.g., inhibition of gonadal steroids, including testosterone). These complex multiple effects of cortisol muddle understanding of its adaptive functions. The demands of energy regulation must orchestrate with those of immune function, attachment bonding, and so forth. Mechanisms for localized targeting (e.g., glucose uptake by active versus inactive muscle tissues and neuropeptide-directed immune response) provide fine-tuning of the preceding general physiological effects. Cortisol regulation allows the body to respond to changing environmental conditions by preparing for specific short-term demands.

Further complications arise from interaction between HPA stress response and a wide variety of other neuroendocrine activities, including modulation of catecholamines, melatonin, testosterone, serotonin, β-endorphins, cytokines, and enkephalins (de Kloet, 1991; Saphier et al., 1994; Ponzi, Muehlenbein, Sgoifo, Geary, & Flinn, 2014). Changes in cortisol for energy allocation and modulation of immune function may be confused with effects of psychosocial stress. As discussed in the previous section, OT and vasopressin intracerebral binding sites are associated with familial attachment in mammals and may influence distress involving caretaker-child relationships. Other components of the HPA axis such as corticotropin-releasing hormone (CRH) and melanocyte stimulating hormone have effects that are distinct from cortisol.

Relations between family environment and cortisol stress response appear to result from a combination of factors including frequency of traumatic events, frequency of positive "affectionate" interactions, frequency of negative interactions such as irrational punishment, frequency of residence change, security of "attachment," development of coping abilities, and availability or intensity of caretaking attention. Probably the most important correlate of household composition that affects childhood stress is maternal care (Flinn, 2009, 2010). Mothers in socially "secure" households (i.e., permanent amiable co-residence with mate and/or other kin) appeared more able and more motivated to provide physical, social, and psychological care for their children. Mothers without mate or kin support were likely to exert effort attracting potential mates and may have viewed dependent children as impediments to this. Hence co-residence of father may provide not only direct benefits from paternal care but also may affect maternal care. Young mothers without mate support usually relied extensively on their parents or other kin for help with childcare (Flinn & Leone, 2006, 2012/2009).

Children born and raised in household environments in which mothers have little or no mate or kin support were at greatest risk for abnormal cortisol profiles and associated health problems. Because socioeconomic conditions influence family environment, they have consequences for child health that extend beyond direct material effects. And because health in turn may affect an individual's social and economic opportunities, a cycle of poor health and poverty may be perpetuated generation after generation (Flinn, 2006b, 2011b; Flinn, Nepomnaschy, Muehlenbein, & Ponzi, 2011).

CONCLUSIONS

People in difficult social environments tend to be less healthy in comparison with their more fortunate peers (e.g., Cohen et al., 2003; Flinn, 2008; Wilkinson, 2001). Social support may often have reproductive consequences. If the brain evolved as a social tool, then the expenditure of somatic resources to resolve psychosocial problems makes sense. Relationships, especially family relationships, are of paramount importance. They have been a key factor affecting human reproductive success at least for over half a million years, and selection has shaped our hormonal, neural, and psychological mechanisms to respond to this critical selective pressure. Children elevate their stress hormone (cortisol) levels much more frequently and extensively in response to psychosocial stimuli than to challenges associated with the physical environment. The adaptive effects of the major stress hormones (Huether, 1996, 1998) and affiliative neurotransmitters on neural reorganization are consistent with the observation that children are especially sensitive to their social worlds (Flinn, 2006b, 2013a).

Social competence is extraordinarily difficult because the target is constantly changing and similarly equipped with theory of mind and other cognitive abilities. The sensitivity of the stress-response and affiliative systems to the social environment may enable adaptive neural reorganization to this most salient and dynamic puzzle. Childhood is necessary and useful for acquiring the information and practice to build and refine the mental algorithms critical for negotiating the social coalitions that are key to success in our species. The human family provides critical support for the developing child in this regard. Traumatic early environments may result in diminished abilities to acquire social competencies as a consequence of glucocorticoid hypersensitivity disrupting neurogenesis, particularly in the hippocampus (Mirescu, Peters, & Gould, 2004; Weaver et al., 2004). An improved understanding of the hormonal and neurological mechanisms that facilitate the intensive and extensive relationships involved with human families and broader kin coalitions (e.g., Carter, Grippo, Pournajafi-Nazarloo, Ruscio, & Porges, 2008; De Dreu, 2012; Flinn et al., 2012), including comparisons between humans and our close primate relatives, may provide important insights into the selective pressures that shaped human psychology.

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