Male, Female

The Evolution of Human Sex Differences

THIRD EDITION

DAVID C. GEARY

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To Yin and Alexa

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PREFACE

It is surprising that C. Darwin's (1871) discovery of the principles of sexual selection—the evolutionary sources of most sex differences (e.g., male–male competition for mates)—languished in the biological sciences for nearly 100 years (Cronin, 1991), whereas his discovery (with Alfred Wallace) of the principles of natural selection was confirmed and hailed as one of the greatest achievements in the history of science. Despite its slow start, sexual selection is now a vibrant area of research in evolutionary biology, one that explains myriad sex differences across invertebrate and vertebrate species (Andersson, 1994). In the 1970s and 1980s, evolutionary anthropologists and psychologists, including David Buss, Martin Daly, Margo Wilson, and Donald Symons, began to apply the principles of sexual selection to human sex differences, primarily to sex differences in aggression, parenting, and mating strategies. These were significant and groundbreaking achievements, but did not provide an integration of human sex differences across the many domains in which they are found (e.g., in brain architecture and play patterns); this is, in part, because much of what we know about sex differences was still unknown even a few decades ago.

My primary goal in writing the first edition of *Male, Female* was to attempt to provide this integration and, in doing so, to provide the proof that C. Darwin's (1871) big picture of the origin and expression of sex differences was largely correct. In the second edition, I was able to flesh out many of the details with the substantial advances that had occurred, including important advances in population genetics and cognitive neuroscience. The pace of new advances in these and in other relevant areas has accelerated since the publication of the second edition, not just with respect to human sex differences but also in our understanding of the evolution and expression of sex differences in nonhuman species. This latter work is critical because it securely anchors our understanding of our own species. There have also been advances in analyses of the historical record, as related to individual differences in reproductive outcomes, as well as new insights from anthropological studies of people living in more traditional contexts.

All these advances and more can be found in this third edition. In writing this edition, I went through each section of the book, attempted to make the prose more accessible, and included more direct interpretations of the gist of the section. A few sections here and there are largely the same as in the second edition, but most sections have been expanded (or newly added), and many of them have been completely rewritten to accommodate new advances in the area. With the third edition, I was able to add the chapter on "Sex Differences in the Modern World." This last chapter includes updates in many of the topics covered in the first edition (e.g., sex differences in academic competencies). The chapter also includes new discussions of variation in sexual orientation, gender identity, and relationships, as well as sex-specific vulnerabilities to various stressors (e.g., toxin exposure) based on some of my more recent work (Geary, 2015, 2017, 2019).

The most difficult aspect of writing the first edition of *Male, Female* was to develop a model that tied together research on sex differences that are clearly related to sexual selection (e.g., aggression, parenting, mating strategies) with more than a century of research on sex differences that are not obviously related (e.g., play, social development, cognitive strengths and weaknesses). This model—the motivation to control—was developed and later elaborated in the context of brain and cognitive evolution over many years (see Geary, 1998a, prior editions of *Male, Female*, and Geary, 2005). In this third edition, the same general theoretical framework is melded with sexual selection to provide a framework for understanding the evolution and here-and-now proximate expression of sex differences in many traits, from physical and behavioral to cognitive and neural. I have also elaborated on this model by better integrating it with theories of human motivation and with work in systems neuroscience related to self-awareness and the use of mental models for social problem-solving.

In effect, when writing the first edition of *Male, Female*, I was convinced that C. Darwin (1871) was correct and that Buss, Daly, Wilson, Symons, and others were on the right track in using sexual selection as the theoretical framework for understanding human sex differences. I also knew that most social scientists were unaware of the principles of sexual selection and the supporting research in nonhuman species. Even if they were aware of this work, most social scientists preferred to believe that humans were different: specifically, that human sex differences were due largely to socialization. In the two decades since the first edition of *Male, Female* appeared, our understanding of the biology of human sex differences has flourished, but the politics of sex differences has become more heated or at least has not cooled much. The stronger the evidence for biological influences on sex differences, the more strident the arguments that any such influences do not exist or are unimportant. I have chosen not to address these arguments, as this would leave less space for the coverage of substantive work on sex differences. I leave it to readers to decide for themselves the extent to which biology informs our understanding of human sex differences.

In any case, to counter the general bias to discount the importance of evolution as a contributor to human sex differences, in the first edition I included three chapters on the basics of sexual reproduction and sexual selection in nonhuman species (Chapters 1–3). I added a fourth chapter on life history and sexual selection to the second edition to provide a better foundation for understanding human developmental sex differences (Chapter 4). These chapters, along with the chapter on primates and human evolution (Chapter 5), have been retained and thoroughly updated for the third edition. I refer readers to these basics throughout the extensive discussions of human sex differences to make explicit links to patterns found across species. At the same time, the expression of many sex differences can be significantly influenced by social factors, such as marriage rules (e.g., whether polygyny is legal) and levels of intergroup violence, among many other factors. We cannot fully understand human sex differences without consideration of these social and cultural factors. I weave discussion of these factors with biologically based biases throughout the nine chapters devoted to human sex differences (Chapters 6–14).

I note that my referencing is extensive and perhaps excessive at times. I did this to provide a listing of sources for interested readers to pursue, but largely to provide documentation for my claims in light of the highly contentious nature of evolutionary accounts of human sex differences. I also tried to make the writing style more reader friendly (i.e., less academic) than the first two editions but no less scientifically documented. I believe the result is a book that is more accessible and useful for a wider audience, from the educated lay reader to the working scientist.

As when I wrote the first two editions of this book, I asked for feedback on each of the chapters to ensure clarity of the presentation and to ensure that I had not missed an important study or topic. I did the same for this edition and thank all these individuals: Rosalind Arden, Mary Hoard, Ted Koditschek, Joseph LaMendola, John Schofield, and Carol Ward. I further thank John Schofield for preparing some of the brain images found in Chapters 9, 12, and 13, and Carl Gerhardt for the bower photo in Chapter 3. I also thank Chris Kelaher at the American Psychological Association for his persistence that ultimately convinced me to do this third edition, and Beth Hatch, Anna Reinhart, and Joe Albrecht for their assistance during the production process, and the following people for help with the proofs: Kristin Balentine, Mandar Bhoyar, Amanda Campbell, Heather Miller, Lara Nugent, and Madelyn Trost. I am of course responsible for all statements herein. Finally, my deepest thanks go to my wife, Yin Xia, the love of my life. Her continual support and kindness contributed greatly to my ability to focus on and significantly improve this edition of *Male, Female*.

Male, Female

1

Introduction

It is widely acknowledged that Charles Darwin's (1859) *On the Origin of Species by Means of Natural Selection* is one of the most important works in the history of science. The principles of natural selection provide the key for understanding how new species emerge across evolutionary time and the relations among species, among many other facets of the natural world. One of C. Darwin's other pivotal contributions was the discovery of the principles of sexual selection which were detailed in his 1871 book, *The Descent of Man, and Selection in Relation to Sex*. These principles were debated and largely ignored for 100 years (Cronin, 1991), but in recent decades have been confirmed as the key to understanding the evolution and here-and-now proximate expression of sex differences across a vast array of species, ranging from insects and plants to fish and mammals (Andersson, 1994). Despite the widespread acceptance of evolution generally and sexual selection more specifically by biological scientists, the application of these principles to our own species has been and remains a source of vigorous and often heated debate. The reasons for this resistance are multifaceted and the subject of many book length treatments (see Degler, 1992; Segerstråle, 2000), but it is neither my goal nor my interest to detail these reasons.

My goals are more straightforward: to analyze, synthesize, and integrate our vast knowledge of human sex differences in terms of the principles of sexual selection and to integrate this knowledge with my own ideas about the evolution of human social dynamics (e.g., the human family), the architecture of the human mind and brain, the motivational foci of human behavior, and sex-specific vulnerabilities to stressors (e.g., toxin exposure, malnutrition),

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among others. Before beginning, it is helpful to have a big-picture view of the core difference between men and women, a picture that frames the many sex differences described throughout this book.

At its core, men have evolved to attempt to organize their social world and life trajectory in ways that increase their social status and influence within the wider communities in which they live, and they have evolved to attempt to gain access to and control of culturally important resources. In short, men are focused on achieving status and recognition in a niche that is valued in the wider culture (e.g., a respected warrior or physician) and through this obtain some level of social potency and access to resources that are important in that culture (e.g., cows, cash). As we will see in Chapter 8, men who are successful in these endeavors are more likely to marry and have children than are their less successful peers. Women have evolved to attempt to create networks of social relationships that provide them and their children with social and emotional support and that enhance their access to and control of culturally important resources. The nature of these networks can vary from nuclear families (e.g., husband, wife, children) to female-biased families (e.g., mother, grandmother, children), but whatever form they take, women who are successful in developing and maintaining social networks have healthier children and more surviving children.

OVERVIEW OF THIS BOOK

In the following sections, I provide a glimpse at the core topics and ideas covered throughout this book. This overview will give readers a sense of where we are going and why I cover specific topics.

Chapter 2: Natural Selection and the Evolution of Sex

In this chapter, I cover two of the most important, profound, and intriguing issues addressed by biological scientists: the mechanisms that result in the origin of new species and the evolution of sexual reproduction. The former is of course natural selection (C. Darwin, 1859; C. Darwin & Wallace, 1858). Although the term *natural selection* is widely known and is one of the most important discoveries in the history of the natural sciences, most people do not understand or frequently misunderstand how it works (Shtulman, 2006; Sinatra & Danielson, 2016). I provide an overview of how natural selection works and a sampling of the overwhelming evidence that supports this theory. Among other issues, I discuss the difference between microevolution (change within a species) and macroevolution (emergence of new species), and the climatic, ecological (e.g., availability of different food types), and social (e.g., competition among members of the same species for control of limited resources) selection pressures that drive these changes.

Although sex is something most human beings spend a lot of time thinking about (men more than women, as I discuss in Chapter 7) and is obviously related to reproduction, most of us have not considered the deeper issue of how we came to reproduce sexually. In fact, the evolution of sexual reproduction is one of the most pivotal events in the history of life on this planet. The focus here is on the benefits of sexual reproduction. This is a critical issue, because many species can reproduce asexually and, therefore, do not pay the price of giving up half of their genes in the process. Despite the genetic cost of sexual reproduction, it is what we and many other species do. I address the different proposals and corresponding evidence about the initial evolution as well as the maintenance of sex. As I am sure readers are aware, sex complicates our lives and that of all other sexually reproducing species in many ways. The most basic complications and the heart of sexual selection concern competing with others to get access to the mate or mates of choice and choosing the most suitable mate or mates.

Chapter 3: Overview of Sexual Selection

Sexual selection represents the social dynamics that emerge as a result of sexual reproduction and most generally involves *intrasexual competition*, competition with members of the same sex for access to mates or control of the resources that mates need to reproduce (e.g., nesting sites) and *intersexual choice*, discriminative choice of mating partners. These are the processes that C. Darwin (1871) identified and described for a vast array of species, with a focus on male–male competition and female choice. One hundred years later, biologists discovered that sex differences in investment in parenting help to explain why males are more likely to compete for mates and females to choose mates (Trivers, 1972; G. C. Williams, 1966/2008). The sex that invests the most in offspring is a resource over which the lower investing sex competes. In 1991, Clutton-Brock and Vincent provided an answer as to why one sex typically invests more in offspring than the other—specifically, the underlying limit on the potential rate of reproduction.

Because of internal gestation and postpartum suckling, female mammals take much longer to produce offspring than it takes males to sire them. A female African elephant (*Loxodonta africana*) will be pregnant for 22 months and then suckle her baby for several more years. As a result, she can produce only one offspring every 5 or so years. A dominant male African elephant in contrast could, in theory, sire multiple offspring in a very short time. Once they sire an offspring, males can then rejoin the mating pool and find another mate or wait for the calf to be born and then attempt to invest in it. In this situation, male African elephants that rejoin the mating pool and compete for access to other females will sire more offspring than will more dutiful males who stick with the mother. In this species and many others, the result is that the sex with the higher potential rate of reproduction (typically males) is better off investing time and effort competing for mates rather than investing in parenting, and the sex with the slower potential rate of reproduction (typically females) is better off investing more in parenting than in competing.

This dynamic is found in more than 90% of mammalian species (Clutton-Brock, 1989). I also review research on species with sex role reversals, where males invest more in parenting (e.g., protect eggs) and females compete more intensely for mates.

The discussion then turns to the different ways in which females choose one mate over another and the reasons for these choices. Debate over whether the choices reflect good taste (i.e., choice based on attractive males but with limited genetic benefits to offspring) or good genes is titling toward the latter. Good looking males tend to have better functioning immune systems and are generally more vigorous and healthier than are other males (W. D. Hamilton & Zuk, 1982; Weaver, Santos, Tucker, Wilson, & Hill, 2018). Variation in these male traits is partly heritable and is passed on to offspring who in turn are generally healthier than offspring sired by less attractive males. Females may also choose mates on the basis of mating displays or physical stamina or other traits that are not easily faked by less fit males (Zahavi, 1975). In some species, these males also provision the female and their offspring, in addition to providing good genes, and in other species the males only provide genes. Sometimes female choice is not based on male looks or behavioral vigor but occurs through sperm competition. In these species, females mate with several males. Choice emerges through a combination of mechanisms in the female reproductive track that can bias fertilization toward one male or another (e.g., Firman, Gasparini, Manier, & Pizzari, 2017) and through the characteristics of each male's sperm (Cornwallis & Birkhead, 2007).

More typically, though, males compete directly for access to mates or for control of the resources that females need to raise their offspring (e.g., nesting sites). I review the many different ways in which males compete—physically, behaviorally, and cognitively—and the evolutionary result: The traits that aid in male–male competition will become exaggerated over evolutionary time (Andersson, 1994). The exaggeration of these traits and the traits that females often use in their choice of mates create corresponding sex differences. Although female–female competition is less common than male–male competition, it occurs much more frequently than C. Darwin (1871) realized, especially for species in which the males parent. I explore this competition among females. When males invest in parenting or females differ in the quantity or quality of the offspring they will produce, males become choosy and I discuss this as well.

Chapter 4: Sexual Selection and Life History

Some people wonder why evolution has not resulted in humans living forever or at least for a few hundred years, but this is the wrong question. The real question is why does our species live as long as we do, given that the lifespan of most species on this planet is 1 year or less (R. D. Alexander, 1987). Life history scientists study how evolution has shaped the length and pattern of the lifespan and how these patterns unfold in the environments in which individuals are situated (e.g., Stearns, 1992). These scientists study how evolution influences how quickly or slowly individuals grow up, their activities (e.g., play) while they are growing up, and the relation between these activities and their later reproduction, as well as why species differ in how they reproduce. Some species have a few high-quality offspring over the course of a long lifetime, whereas other species have many low-quality offspring over a short lifetime.

I cover all these issues, with a focus on sex differences in developmental patterns (e.g., age of maturation), play, parenting, and the influence of sex hormones on the expression of these behaviors and those described in Chapter 3. Within the context of life history evolution, Chapter 4 provides the background needed to fully appreciate and understand human fatherhood (Chapter 6) as well as the sex differences in human physical development, play patterns, and social behavior that are covered in Chapters 10 and 11. More generally, the life history approach allows us to see how the results of evolution unfold during development as a dynamic interaction between genes and environment.

Chapter 5: Sexual Selection in Primates and During Human Evolution

Chapter 5 brings us one step closer to our own species, with a focus on living primates and the implications of the fossil record for understanding our ancestors. I begin with male–male competition and female choice in our primate cousins. The section on male–male competition illustrates the relationship between the achievement of social dominance and reproductive dynamics among males. The dynamics largely manifest as one-on-one physical threats and fights for access to receptive females. As I show, DNA fingerprinting to determine offspring paternity confirms that dominant males sire more offspring than do other males, but not always as many as their social dominance would suggest (e.g., M. N. Muller, 2017; Setchell, 2016). Male chimpanzees (*Pan troglodytes*) also engage in between-group coalitional competition (Goodall, 1986). They band together, enter the territory of neighboring groups, and search for males. If they isolate one of them, they will attack and kill him. If they manage to eliminate all the males in the rival group, they expand into their territory, to their reproductive benefit and that of the females in their group. It is not all about male–male competition, however, as females can influence reproductive dynamics in many ways, although it is typically subtler than the males' strategies. I review some of the aspects of female choice and then touch on some aspects of female–female competition and male choice; for example, I discuss why male chimpanzees prefer older to younger females as mates.

I then take readers closer to our species with a discussion of our ancestors, going back about 4 million years to the australopithecine fossil record and then to *Homo*. By contrasting the fossils that likely came from males to those of females and comparing these with patterns of those found in living primates, we can learn a surprising amount about our ancestors. In living primates, physical male–male competition, for example, is associated with polygyny and larger males than females. About 4 million years ago, our male ancestors were much larger than our female ancestors, but this has changed considerably since that time (Grabowski, Hatala, Jungers, & Richmond, 2015); differences exist today, of course, but they are not as dramatic as they once were. I take these sex differences and others and combine them with patterns found in living primates to make inferences about the social and reproductive dynamics of our ancestors. Following Geary and Flinn (2001), I propose that our australopithecine ancestors were more like modern day gorillas (*Gorilla gorilla*) than our closer relatives, the chimpanzee or bonobo (*Pan paniscus*). Like modern humans, male gorillas engage with their offspring and form long-term relationships with females, and we argued the australopithecines were the same (see also Duda & Zrzavý, 2013). Among others, this has profound implications for understanding the evolutionary history of long-term reproductive relationships between women and men, including men's parenting.

Chapter 6: Evolution of Fatherhood

In this chapter, I deal with one of the puzzles of human evolution: Why do many men invest in the well-being of their children? Many readers may see this as an expectation and not a puzzle, but it is a puzzle. This is because male parenting is found in less than 10% of mammals and not at all in our two closest relatives, the chimpanzee and the bonobo (Clutton-Brock, 1989). If our ancestors where more like gorillas than chimpanzees or bonobos, then men's parenting is less of a puzzle. In any case, I organize the discussion of this parenting in terms of the cost–benefit trade-offs described in Chapter 4 for male parenting in nonhuman species. These trade-offs involve a balance between offspring well-being, men's lost mating opportunities, and the risk of cuckoldry (i.e., investing in another man's offspring; Geary, 2000).

We then turn to a cross-cultural review of sex differences in investment in parenting. Although men parent more than most other male mammals, throughout the world they invest in parenting less than women do, as predicted from the principles outlined in Chapter 3 (Konner, 2010; Whiting & Edwards, 1988). The critical twist here is not the sex difference in investment in parenting but that men's investment in their children is facultatively expressed, meaning that it is helpful but not always necessary for children's survival. The result is that whether or not men invest in children will depend on a variety of factors, including the quality of his relationship with the children's mother, the availability of other mates, cultural mores, and marriage rules, among other factors (e.g., Henrich, Boyd, & Richerson, 2012; Parke, 1995). I review all these factors and illustrate how they are expressed across cultures and how they can change across historical time within cultures. More generally, men's facultative investment in parenting is one of the key dynamics that drives conflicts between women and men.

Chapter 7: Choosing Mates

Choosing a mate or mates is one of the most important decisions that anyone will make in their lifetime, and it is one of C. Darwin's (1871) core components of sexual selection. When viewed in terms of any resulting children and grandchildren, these are choices that will echo through subsequent generations. Given this, it is not surprising that in most hunter–gatherer societies, these choices are not left to the whims of young adults or older adolescents (Apostolou, 2007, 2010). Of course, these young women and men may have a say in who they marry, but the ultimate choice is typically made by their parents. In many (but not all) cases, the parental choices and the preferences of their children converge. We will consider the actual choices that women, men, and their parents make across many cultural contexts and the preferred choices of women and men that emerge in psychological studies, including their reports of what they desire in a mate (Lippa, 2007). The psychological studies are important because they provide a window into evolved motivations that are not constrained by the competing interests of others or by wider social mores. I discuss the cognitive and emotional processes that bridge these conscious preferences and actual choices in Chapter 9.

When it comes to long-term marriage partners, men's and women's preferences are more similar than different, but there are sex differences in the traits that are prioritized by one sex or the other and differences in the trade-offs (e.g., physical appearance vs. income) women and men are willing to make in these choices (N. P. Li, Bailey, Kenrick, & Linsenmeier, 2002). I cover these preferences and trade-offs in terms of personal and behavioral characteristics (e.g., cultural success, emotional intimacy) and physical and genetic traits (Apicella, 2014; Low, 1990a). The latter tie human mate choices back to those described in Chapter 3 and even in terms of the factors that may have resulted in the evolution of sexual reproduction described in Chapter 2. Along the way, I review women's and men's alternative (to long-term monogamy) mating strategies, changes in women's mate preferences across the ovulatory cycle, and men's sexual fantasies, among other topics.

Chapter 8: Competing for Mates

In this chapter, I focus on the other core component of C. Darwin's (1871) sexual selection: competition for mates. Darwin focused on male–male competition in large part because it is much more common and dramatic than is competition among females. In many species, in fact, females do not have to compete at all for mates (although they may compete over other things; West-Eberhard, 1983), because the males do not provide any parental investment, only a little mating time (G. C. Williams, 1966/2008). The situation is different with our species because many men do invest in their children. The more men have to offer, the more valuable they become to women as a reproductive resource, which sets the stage for female–female competition.

I begin with men's competition for mates and review the different ways this competition can be expressed across traditional societies and early empires, as well as in highly developed modern nations. There are two key concepts here. The first is that competition among men can be based on physical dominance (as in other primates), cultural prestige, or some combination (Henrich & Gil-White, 2001). Prestige is based on culturally important competencies (e.g., hunting skills) that can contribute to the well-being of others who then freely confer status to the individual with these competencies. As I show, human history reflects an important change in the relative balance of dominance- and prestige-based competition; the former drove men's reproductive competition during the rise of humanity's early empires (Betzig, 1986, 2012) and the latter is slowly emerging as the primary form of competition with the rise of modern, highly developed and economically diverse societies.

The second key concept is Irons' (1979) *cultural success*. The point being that men in all cultures are highly motivated to attain social status and control of culturally significant resources, whether they do so using dominance, prestige, or some combination. These are resources needed to support survival and to attract a mate or mates and can vary from land to herds of cows to a large paycheck. Whatever the form of resource, the outcome is the same. Women prefer culturally successful men as mates, and therefore these men have more reproductive options. I consider all these different forms of competition and link them to those found in other species (Chapters 3 and 4), to patterns that were likely during our evolutionary history (Chapter 5), and to research on sex hormones, risk taking, and population genetics.

As with men, women compete for control of important resources (Stockley & Campbell, 2013), including prospective husbands and for preferential access to their husbands' resources in the context of polygynous marriages. One way that women compete is by enhancing the traits that men prefer in a mate (i.e., they "dress to kill"; N. P. Li, 2007). This form of competition is common in societies with socially imposed monogamy (i.e., polygynous marriages are illegal) and when women (not their parents) make their own mate choices. They also derogate these same traits in potential competitors (D. M. Buss, 1988), and manipulate social information and relationships in other ways to drive competitors away from potential romantic partners and to disrupt their friendships with other women (these friendships are social resources as well; T. Reynolds, Baumeister, & Maner, 2018). Women do not resort to violence as often as men do, but they can in some circumstances (Campbell, 1995). In some polygynous societies in which land is inherited by sons, women will sometimes poison the sons of their co-wives (Strassmann, 1997). In this way, the perpetrator's sons inherit more land. In the modern world, many women also directly compete for cultural success just as men do but not as intensely on average (Hakim, 2002).

Chapter 9: Evolution and Development of the Human Mind

In this chapter, I provide a bridge that links sex differences in parenting, competing for mates, and mate choices to sex differences in the pace of development, play, and social relationships (Chapters 10 and 11), as well as to sex differences in brain and cognition (see Chapters 12 and 13). The building of this bridge includes overviews of my motivation to control model, evolved domains of the human mind (i.e., folk psychology, folk biology, and folk physics), and a description of how developmental activities relate to the expression of evolved biases. The core is the evolution of brain and cognitive systems that support self-awareness and enable people to socially strategize (R. D. Alexander, 1989; Geary, 2005; Humphrey, 1976). The latter involves the ability to generate mental models of their perfect world and to generate and rehearse ways to make this happen or at least reduce the gap between where they are now and where they want to be in the future. I discuss how this model can be integrated with various theories of human motivation (Bandura, 2001; Maslow, 1943; R. M. Ryan & Deci, 2017); with sex differences in sexual fantasy, emotional reactivity, and expressiveness; and with the social and political biases of women and men.

To illustrate, when it comes to politics, women are more inclined to advocate policies that result in a more equitable distribution of social resources and a greater investment in children (e.g., public day care), whereas men are more inclined to advocate policies associated with group dominance (e.g., military spending; Pratto, 1996). These sex differences follow directly from the respective differences in investment in parenting (Chapter 6) and in the forms and intensity of intrasexual competition during human evolution (Chapter 8). These differences in reproductive strategy also result in sex differences in certain cognitive abilities, such as language and spatial navigation, and Chapter 9 provides a way to identify and to more fully understand why such differences exist.

Chapter 10: Sex Differences in Infancy and Play

In this chapter and the following one, I cover a wide range of sex differences in children and integrate these with the principles of life history evolution described in Chapter 4 and with sex differences in mate choice and competition for mates described in Chapters 7 and 8, respectively. I begin with sex differences in physical development because these are readily linked to corresponding sex differences in other primates and specifically to physical male–male competition (Leigh, 1996). In keeping with the physical male–male competition that is common in traditional societies, early empires, and almost certainly throughout human evolution, many of the sex differences that emerge during development contribute to men's advantage in physical fitness, upper body strength, and skeletal structures that support the use of blunt force (e.g., club) and projectile weapons.

One of C. Darwin's (1871) many insights was that nonhuman sex differences tend to be small early in life and become more pronounced as individuals approach reproductive maturity. On the basis of these patterns, we would not expect substantial differences between girls and boys during infancy, but there are a few differences nonetheless (Freedman, 1974). I cover these differences and then move to the different forms of play introduced for nonhuman species in Chapter 4 (i.e., social, locomotor, exploratory, and object-oriented play). Readers learn about sex differences in play fighting, parenting, exploration of the environment, and play with objects as related to tool use (e.g., Golombok & Rust, 1993). These differences in turn provide children with the experiences needed to prepare them for the survival and reproductive demands of our adult ancestors, in keeping with the relation between developmental activities and the experiential adaptation of evolved competencies to local conditions described in Chapter 9.

Chapter 11: Sex Differences in Social Development

We continue with our exploration of the lives of girls and boys but change focus to their social development. Beginning by 3 years of age and continuing throughout development, boys and girls segregate into distinct peer cultures (Maccoby, 1988). Within these cultures, boys tend to organize themselves into large and integrated groups (i.e., all of the boys are friends) that compete against other groups of boys, and girls tend to developed intense and emotionally intimate friendships that are an important source of social support (J. A. Hall, 2011; Rose & Asher, 2017). I provide a framework for placing these peer relationships and the associated social activities into a wider evolutionary picture and through this a means to link these early sex differences to differences in the forms of reproductive competition and other social relationships described in earlier chapters.

Among other issues, I place the different ways in which girls and boys form social networks and maintain friendships into the broader context of male–male coalitional competition and in terms of the different types of same-sex relationships that may have been common during our evolutionary history (Chapter 5). Chapter 11 closes with reviews of parental treatment of girls and boys in Western culture, imitation of parents as a potential source of developmental sex differences, and how parental socialization of girls and boys varies from one culture to the next, as related to sex differences in adult reproductive competition in the society (Barry, Josephson, Lauer, & Marshall, 1976; Low, 1989; Lytton & Romney, 1991).

Chapter 12: Sex Differences in Folk Psychology

The next two Chapters are devoted to sex differences in brain and cognition. Rather than discussing these in the traditional way of focusing on language, mathematics, and spatial abilities, I organize the discussion around the taxonomy of the evolved folk domains introduced in Chapter 9—folk psychology, folk biology, and folk physics. In Chapter 12, I cover sex differences in folk psychology which are the brain and cognitive systems that support social competencies such as language and theory of mind (i.e., the ability to make inferences about the thoughts, feelings, and intentions of other people). Before diving into the sex differences in folk psychology, I provide a more general introduction to sex differences in brain size and organization (e.g., L. Cahill, 2006), including hormonal influences on the expression of these differences and sex differences in the pattern of gene expression in the brain (Lotze et al., 2019; Ritchie et al., 2018). My goal with this first section is not to provide an evolutionary analysis, but rather to document the existence of extensive neural sex differences that beg explanation.

As noted, folk psychology encompasses our ability to process social information (e.g., facial expressions) and our implicit understanding of other people. To the extent that our female and male ancestors' social relationships differed (e.g., in terms of intrasexual competition), sex differences in current folk-psychological abilities will be found. As an example, when girls and women compete with same-sex rivals, the competition is much more likely to involve relational aggression (e.g., gossip) than physical aggression (T. Reynolds et al., 2018). The effective use of relational aggression as well as the development and maintenance of the intimate same-sex relationships covered in Chapter 11 requires sophisticated social-cognitive abilities, which are more highly elaborated in girls and women than in boys and men. These advantages are found for language, reading facial expressions and body language, and theory of mind (e.g., J. A. Hall, 1984). I explore all these differences, hormonal influences on their development and expression, and sex differences in the underlying brain systems (Lotze et al., 2019; Vijayakumar, Op de Macks, Shirtcliff, & Pfeifer, 2018). I provide similar analyses for sex differences in self-awareness and self-evaluations and for ingroup and outgroup dynamics.

Chapter 13: Sex Differences in Folk Biology and Folk Physics

Folk biology refers to people's intuitive understanding of plants and animals in their local ecology and is quite extensive for people living in traditional societies (Atran, 1998). The evolutionary analysis of sex differences in folk biological knowledge is largely based on research by ethnobiologists who study the knowledge of people living in traditional cultures and on the division of labor in these societies (i.e., women's foraging and men's hunting; Silverman & Eals, 1992). The number of available studies is small, compared with those for folk psychology and folk physics. The available research, nonetheless, reveals that women tend to know more about local flora (plants) than men, whereas men tend to know more about local fauna (animals; Boster, 1985), although the sex difference in knowledge of medicinal plants varies from one context to another (Torres-Avilez, de Medeiros, & Albuquerque, 2016). Whether these differences result from sex differences in an evolved bias to learn about these different features of the biological world or from engagement in traditional activities remains to be determined.

Folk physics refers to the brain and cognitive systems that allow people to detect and respond to the physical world, to navigate in this world, to mentally represent physical space, and to learn how to use objects as tools. As I show, there are sex differences in all these areas, most favoring boys and men and but a few favoring girls and women. For example, men's use of projectile weapons during between-group raids in traditional societies (Chapter 8) should result in an evolved male advantage in skill at detecting subtle movement in complex visual arrays, estimating the velocity of moving objects, hitting targets with thrown projectiles, and dodging and blocking projectiles thrown at them. Indeed, boys and men have advantages over girls and women in all these areas (e.g., Cashdan, Marlowe, Crittenden, Porter, & Wood, 2012; Peters, 1997; Watson & Kimura, 1991). I cover these and many other sex differences in folk physics, including hormonal influences on their development and expression and sex differences in the underlying brain systems.

Chapter 14: Sex Differences in the Modern World

In the final chapter, I illustrate how evolved sex differences can be expressed in the modern world. I begin with evolutionary-novel abilities that are learned in school, including reading, writing, and mathematics. Unlike folk abilities, these abilities only emerge with formal schooling but are built from folk domains (Geary, 1995a, 2007). For instance, language and theory of mind are the foundation on which reading and writing are built, and it is not surprising that girls and women have advantages over boys and men in these areas (Hedges & Nowell, 1995). The discussion then leaves school and moves to the workplace, specifically focusing on sex differences in occupational interests and achievement, as related to sex differences in cognitive and academic abilities, motivation, and wider social influences (Stoet & Geary, 2018; Su & Rounds, 2015). In highly developed and liberal nations, many of the sex differences in occupational choices and outcomes can be traced to sex differences in interest in people or things (Chapter 10), the greater investment in children by women than men (Chapter 6), and the greater investment in achieving cultural success by men than women (Chapter 8).

Next is the discussion of behavioral and psychological sex differences, including violence, accidents, and psychopathology. The latter includes sex differences in externalizing (e.g., physical aggression) and internalizing (e.g., depression) disorders (e.g., Martel, 2013). For instance, the higher rates of externalizing disorders in boys and men follows from the use of dominance-based strategies to achieve social standing and resource control. In modern contexts, these are considered psychopathologies because prestige-based status striving is the norm in these societies. I then discuss variations in sexual orientation, gender identity, and sexual relationships. Chapter 14 closes with a model that shows how our understanding of sexual selection can be used to better understand sex differences in trait-specific (e.g., language, spatial) vulnerabilities when exposed to chronic stress, parasites, poor nutrition, and human-made toxins (Geary, 2015).

2

Natural Selection and the Evolution of Sex

The discovery of the principles of natural selection is one of the pivotal events in the history of science. Natural selection is the net that captures all the disparate findings in the biological and life sciences and pulls them together into a coherent whole. It is not surprising that much of the general public does not understand natural selection (Sinatra & Danielson, 2016); it is, however, surprising that many nonbiological scientists do not fully appreciate the eloquence and power of these mechanisms for understanding the natural world, including our own species. This chapter begins with a primer on C. Darwin's (1859) principles of natural selection and how these basic mechanisms shape the natural world. From there, the discussion turns to the evolution of sexual reproduction, which is a pivotal event in the evolution of life on this planet. For humans, an understanding of the evolution of sexuality and distinct sexes sheds light on the dynamics of sexual reproduction. The unfolding of these sex differences in nonhuman species is described in Chapter 3 of this volume, and their expression during the lifespan and as related to exposure to sex hormones and to experiences is described in Chapter 4.

These chapters, and subsequent ones, discuss a variety of species, ranging from bacteria (*Escherichia*) and guppies (*Poecilia*) to finches (*Geospiza*) and mandrills (*Mandrillus*) and more. Readers may wonder how discussion of these species informs our understanding of human evolution and human sex differences. These are good questions. On the surface, bacteria seem entirely irrelevant to our evolution, but the study of these species provides important

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insights into why sexual reproduction evolved in the first place and how it is maintained. By better understanding these issues, we can better frame our study of human mate choices and the processes that influence these choices (see Chapter 7). The discussion of a wide range of species also illustrates the power of the mechanisms of natural selection and sexual selection for understanding evolution in general and sex differences in particular. Even if the details differ from one species to the next, as they often do, the basic mechanisms are the same. Human cultural history and social rules, of course, do add many new elements for our species, but these are built on biological foundations that will be detailed in forthcoming chapters.

NATURAL SELECTION

The following sections begin with a brief overview of how natural selection works. Next, examples are provided of how ecological and social factors influence trait evolution (e.g., beak size, height).

How It Works

C. Darwin and Wallace's (1858; see also C. Darwin, 1859) fundamental observations and insights that led to the discovery of natural selection are shown in Table 2.1. One important facet of nature is that population sizes tend to

TABLE 2.1. Darwin's and Wallace's Observations and Inferences

Observations	Inferences
1. All species have such high potential fertility that populations should increase exponentially.	1. More individuals are born than can be supported by available resources.
2. Except for minor annual and rare major fluctuations, population size is typically stable.	
3. Natural resources are limited, and in a stable environment they remain constant.	2. Increased population results in competition for natural resources.
1. No two individuals are the same.	1. Survival is not random and covaries with heritable characteristics of individuals. The resulting differential survival is natural selection.
2. Much of this variability is heritable.	2. Over generations, natural selection leads to change in the population (microevolution) and the production of new species (macroevolution) or speciation.

Note. Observations and inferences are based on C. Darwin and Wallace (1858), C. Darwin (1859), and Mayr (1982). Darwin knew that selective breeding (artificial selection) influenced domestic species. This gave him the insight that traits, or characters, were passed on from parent to offspring. The science of genetics began in earnest after Darwin's death.

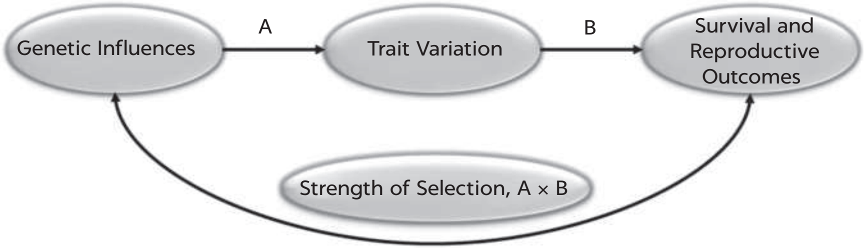
remain stable over the long term, even though these populations should increase rapidly because each set of parents has more than two offspring in their lifetime; this pattern was found in human populations before recent advances in agriculture, medicine, and other fields that reduce mortality risks (Fanta, Šálek, Zouhar, Sklenicka, & Storch, 2018; Malthus, 1798). Darwin and Wallace concluded that more individuals are born than survive to reproduce themselves. This conclusion was fused with a keen awareness of individual variation within each species and that some of this variation was passed from parent to offspring. Genetic inheritance was not understood at that time, but selective breeding in domestic species showed Darwin that some of the variation in one generation was inherited from parents of the previous generation. The critical insight is that individual variation in key traits and individual variation in the chances of survival are linked together. In other words, the relationship between individual differences in some traits (e.g., size) and individual differences in survival prospects is not entirely random. Wallace described this insight in a letter written in 1887:

> it suddenly flashed upon me that all animals are necessarily thus kept down—"the struggle for existence"—while *variations*, on which I was always thinking, must necessarily often be *beneficial*, and would then cause those varieties to increase while the injurious variations diminished. (F. Darwin, 1887/2000, pp. 200–201)

Although most people understand evolution as the cross-generational change in the mean or average of a trait or phenotype (e.g., height; Shtulman, 2006), variation among individuals is equally important, as noted by Wallace (F. Darwin, 1887/2000). This is because natural selection depends on the relation between this variation—resulting in part from genetic mutations (J. F. Crow, 1997) and sexual reproduction (W. D. Hamilton & Zuk, 1982; G. C. Williams, 1975)—and the chances of surviving to adulthood and successfully reproducing (G. R. Price, 1970). Heritability (h^2) refers to the degree to which variation within a group of individuals is due to underlying genetic differences. Most complex traits, such as size, are distributed as a bell-shaped curve, with most individuals being average and some being larger and others smaller. If being larger confers a survival or reproductive advantage, and if size is heritable, then the trait *size* is evolvable (i.e., the genetic variance is distributed around the mean of the trait; Houle, 1992). In other words, when there are many individuals above (e.g., larger) or below (e.g., smaller) average on a particular trait and some proportion of these differences are heritable, there is the potential for the mean of the trait to increase or decrease across generations. This potential is realized only if being above or below average confers survival or reproductive advantage.

The key components of heritable variation and the relationship between this variation and individual differences in survival or reproductive outcomes are illustrated in Figure 2.1. For each generation, the strength of evolutionary selection for a given trait is the product of these two components. If h^2 is .30 then 30% of the individual differences for the trait is due to variation in the

FIGURE 2.1. Strength of Evolutionary Selection



Evolution of a trait occurs when two conditions are present. First, individual differences must be heritable, represented by line A. Second, individual differences in the trait must influence survival or reproductive outcomes, represented by line B. The strength of evolutionary selection is the product (A × B) of these two components.

associated genes, and if the strength of the relation between these individual differences and survival or reproductive outcomes (in terms of standard deviation units) is .30, then the strength of evolutionary selection is .09 (.30 × .30). The strength of selection in this example (.09) does not seem particularly strong, but if the relation is consistent generation after generation (termed *directional selection*), then there will be (making some simplifying assumptions) about one standard deviation change in the trait in every 11 generations. Taking human height as an example, the result would be a 2.5-inch (6.5-centimeter) increase in average height in a little over 200 years (e.g., M. C. Turchin et al., 2012); even if it did not actually occur this quickly, there is clear evidence for natural selection acting on humans over the past millennia or two (Field et al., 2016).

At one time, biologists believed that a trait would evolve until it is highly suited to the conditions that promote survival or reproduction, and at this point genetic variation in the trait would be eliminated (R. A. Fisher, 1930). But this is not the case, as many advantageous traits remain heritable, leading to the question of why beneficial traits do not evolve to their optimal value. There are at least four mechanisms that help to explain this puzzle. First, the elimination of genetic variance requires cross-generational stability in the ecological and social conditions that drove the evolution of the trait. Although this stability may be achieved for some traits and can result in a substantive reduction in the genetic influences on individual differences in the trait (Gustafsson, 1986), the required level of cross-generational stability is not always achievable. Second, genetic variability may also be maintained when the gene or genes that underlie trait expression have multiple effects in terms of cost–benefit trade-offs, called *pleiotropy* (G. C. Williams, 1957). As subsequent chapters show, high concentrations of testosterone promote physical development and behavioral vigor that aid in competing for mates in early adulthood but for some males may compromise immune functions (Mougeot, Redpath, & Piertney, 2006) or increase risk of disease and premature death later in adulthood (Jasienska, Bribiescas, Furberg, Helle, & Núñez-de la Mora, 2017).

In this case, reproductive advantage at a younger age may lead to disadvantage at a later age and vice versa such that neither early nor later reproducers are better over the lifespan. With these types of trade-offs, genetic influences on earlier and later reproduction will be maintained in the population.

A third contributor to the maintenance of genetic variation is called *frequency dependent selection*: The survival or reproductive advantage of one heritable version of a trait or another is dependent on how common each version is in the local population (Gross, 1985). For instance, male guppies (*Poecilia reticulata*) with the more novel or less common coloration pattern are at an advantage because they are less likely to be eaten by predators and because females prefer them as mating partners (Olendorf et al., 2006). Over generations, these males increase in number and their more pedestrian peers decrease in number. As the number of males with novel coloration increases, however, they lose their advantage and the once pedestrian males gain an advantage. The cycle need not continue, as the frequencies may eventually stabilize, but in either case the genetic variation underlying the differences in coloration is maintained. A fourth mechanism might be *sexually antagonistic genes*, which are genes that promote the reproductive fitness of fathers (or mothers) but may reduce the reproductive fitness of their daughters (or sons; Foerster et al., 2007; Pennell, de Haas, Morrow, & van Doorn, 2016). These cross-generational trade-offs will prevent such genes from becoming dominant in the population.

For these reasons, individual differences in many of the traits that influence survival or reproductive outcomes show small to moderate genetic influences and are therefore continually subject to evolutionary change. Mousseau and Roff's (1987) comprehensive review of the genetic (h^2 in this case) variability of life history (e.g., age of maturation), physiological (e.g., cardiovascular capacity), behavioral (e.g., mating displays), and morphological (e.g., body size) traits across 75 species provided an assessment of the first component shown in Figure 2.1 (Line A). Their analysis indicated "significant genetic variance is maintained within most natural populations, even for traits closely affiliated with fitness" (Mousseau & Roff, 1987, p. 188); *fitness* here refers to survival and reproductive prospects. A further twist is that the relative importance of heritable and environment influences on many phenotypes (i.e., traits) can change across the developmental period and from one context to the next and that many heritable influences emerge through gene–environment interactions (West-Eberhard, 2003).

In any case, an analysis of the second component shown in Figure 2.1 (Line B) was provided by Kingsolver and colleagues' review of field studies of variation in survival and reproductive outcomes in wild populations (Hoekstra et al., 2001; Kingsolver et al., 2001; see also Kingsolver & Diamond, 2011; Siepielski et al., 2013). Across species and traits, the median effect size—the correlation between individual differences in the trait and individual differences in the survival or reproductive outcome—indicated that being one standard deviation above (e.g., later maturation) or below (e.g., earlier maturation) the mean was associated with a 16% increase in survival prospects (e.g., probability of surviving to the next breeding season) or reproductive fitness (e.g., number of offspring). If h^2 of any such trait was only .25, "then selection of this magnitude would cause the trait to change by one standard deviation in only 25 generations" (Conner, 2001, p. 216). There was also considerable variation across species and populations in the strength of these relations, indicating that evolutionary change can occur slowly, not at all, or very rapidly. The overall effects were about twice as strong for traits related to mate choices or competition for mates (i.e., sexual selection) than for traits related to survival, indicating the former tend to evolve more quickly than the latter (Hoekstra et al., 2001).

These patterns suggest that evolutionary change can occur much more rapidly than C. Darwin (1859) originally assumed; rapid changes have indeed been empirically documented for a variety of traits and species (e.g., Barluenga, Stölting, Salzburger, Muschick, & Meyer, 2006; P. Grant & Grant, 2002; Hairston, Ellner, Geber, Yoshida, & Fox, 2005; Reznick, Shaw, Rodd, & Shaw, 1997). However, as suggested by Darwin, studies of evolutionary change across a large array of species and time scales, including the fossil record, indicate that rapid change is not the norm (Estes & Arnold, 2007). Rather, rapid changes occur when there is dramatic change in climate, food availability, or social conditions. Natural selection then results in rapid adaptation to these new conditions such that the species quickly reaches stability or a stasis point. This is not actually a point per se but rather a small plateau on which the means of the evolved traits shift around from one generation to the next. The trait means will not stray far from the center of the plateau unless there are dramatic changes in ecological or social conditions.

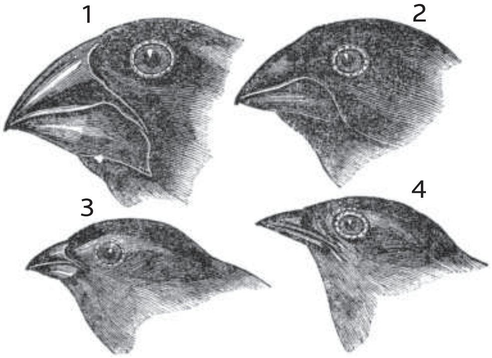
Ecological Selection Pressures

Peter and Rosemary Grant (P. Grant, 1999; P. Grant & Grant, 2014) provided one of the best empirical documentations of a link between trait variation and variation in survival and reproductive outcomes (see Figure 2.1, Line B). For the past 4 decades, the Grants and their colleagues have been studying multiple species of Darwin's finches on the Galápagos islands. They have clearly documented that cross-generational change in the physical traits of these finches is linked to variation in survival and reproductive outcomes that follow dramatic changes in food availability and climate. Their research also provides a useful illustration of two important concepts, natural selection acting on variability to create change within a species (microevolution) and to create new species (macroevolution).

Microevolution

The medium ground finch (*Geospiza fortis*) nicely illustrates how individual differences in a trait can influence survival and reproductive outcomes and therefore evolves; at the top right of Figure 2.2 is an illustration of this species (C. Darwin, 1845). The trait of interest is beak size and its variation across individuals. These differences are moderately to highly heritable for beak length

FIGURE 2.2. Four Species of Finch From the Galápagos Islands



(1) Large ground finch (*Geospiza magnirostris*), (2) medium ground finch (*Geospiza fortis*), (3) small tree finch (*Camarhynchus parvulus*), and (4) warble finch (*Certhidea olivacea*). From *Journal of Researches Into the Natural History and Geology of the Countries Visited During the Voyage of H.M.S. Beagle Round the World, Under the Command of Capt. Fitz Roy, R.N.* (p. 379), by C. Darwin, 1845, London, England: John Murray. In the public domain.

(h^2 = .65), depth (h^2 = .79), and width (h^2 = .90; Boag, 1983; Boag & Grant, 1978), and are highly evolvable in terms of heritable variance around the mean (Boag, 1983); these values mean that between 65% and 90% of the variation in beak size are due to variation in the underlying genes. As might be expected, larger birds have larger beaks.

When food is plentiful, there is little relation between beak size and survival prospects. Under these conditions, the value of the second component in Figure 2.1 (Line B) is close to 0.0, and therefore natural selection does not operate on beak size. When food is scarce, the value of this component becomes larger than 0.0, because the size and shape of an individual's beak determines which foods can be eaten and which foods cannot (B. Grant & Grant, 1993). Individual birds whose beak size and shape allow them to specialize in abundant food sources survive in greater numbers than do individuals whose beak size and shape force them to specialize in a scarce food source.

For example, in 1973, a drought resulted in an 84% decline in the quantity of foods available to Darwin's finches and a sharp increase in mortality. One of the plentiful foods was the seeds of the caltrop plant (*Tribulus cistoides*), which are encased in hard and spiked shells called mericarps. Some medium ground finches were able to exploit this food source, whereas others were not. As described by Weiner (1995),

> *fortis* with bigger beaks can crack the mericarp and gouge out the seeds faster than those with smaller beaks. Tiny variations are everything. A *fortis* with a beak 11 millimeters long can crack caltrop; a *fortis* with a beak only 10.5 millimeters long will not even try. "The smallest grain in the balance" can decide who shall live and who shall die. Between a beak big enough to crack caltrop and a beak that can't, the difference is only half a millimeter. (p. 64)

For medium ground finches and their cousins, life or death depended greatly on beak size. Even when small-beaked males survived, they were at a mating disadvantage. These males were poorly nourished and weaker than their better-fed large-beaked peers, resulting in a difference in the vigor of the courtship displays that females use to make their mate choices. The combination of differential survival rates and female choice (see Chapter 3 of this volume) resulted in a shift in the next generation's average beak size. Individual differences in beak size were still evident, but the average beak size increased, and there were fewer individuals with extremely small beaks and more individuals with extremely large ones. However, having a larger than average beak is beneficial only during droughts. In 1982–1983, an especially strong El Niño event resulted in a 14-fold increase in rainfall (B. Grant & Grant, 1993), a significant decrease in the number of caltrop plants and their mericarps, and a significant increase in the number of plants that produce smaller seeds. Small-beaked individuals can handle small seeds more deftly than their large-beaked peers. The results were that small-beaked individuals survived in greater numbers than did large-beaked individuals and females preferred small-beaked males as mating partners. After several generations of differential survival and mating success, the average beak size of medium ground finches was now smaller than it was just after the drought.

In this seminal study, cross-generational changes in average beak size and shape were found to be linked to cross-generational changes in the distribution of available foods and with mating dynamics. Over the course of 40 years and many generations, the overall evolutionary effects were significant reductions in beak and body size of medium ground finches and a significant change in beak shape, from somewhat blunted to moderately pointed (P. Grant & Grant, 2002). These adaptations resulted in microevolutionary changes in the medium ground finch such that the average individual in the population looked somewhat different than did the average individual just seven generations earlier.

Macroevolution

When microevolutionary changes are sustained and directional (i.e., having the same effect) across many generations but differ for different populations within the species, selection can result in a single species diverging into two or more separate but related ones. Although Darwin did not introduce natural selection until 1858 (C. Darwin & Wallace, 1858), he provided hints in earlier work (C. Darwin, 1845); Wallace (1855) made a similar observation a decade later. With respect to the Galápagos species shown in Figure 2.2 and their cousins, C. Darwin noted the following in 1845:

> Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends. (p. 380)

Darwin's keen insight has been confirmed by genetic studies of the relationships among the 14 species of Galápagos finch. These species arose during the past million years from a single ancestral species that originated from the South American mainland (Lamichhaney et al., 2015). To illustrate one route by which multiple species can evolve from a single species, consider again the medium ground finch. What appears to have happened is that several populations of these birds were separated from the original population such that they were dispersed across different islands. If mericarps were more abundant on one island and smaller seeds more abundant on the other, then the microevolutionary changes described previously would result in the average beak and body sizes of the two populations moving away from each other and from the original population with each successive generation. After many generations of such changes, the evolutionary emergence of distinct species is possible.

In fact, such a process readily explains the relationships between the three ground finch species that currently reside on the Galápagos islands: small, medium, and large ground finches (Petren, Grant, & Grant, 1999). These species specialize in different sources of food and, in addition to body size, differ primarily in beak size and shape, the specializations that allow them to exploit one type of food source or another (see Lamichhaney et al., 2016; Soons et al., 2015). Although there is no overlap in the distribution of beak sizes of small and large ground finches, there is some overlap between the beak size distributions of medium and large, and medium and small ground finches. The beak sizes of the largest medium ground finches, for example, overlap that of the smallest large ground finches. These overlapping distributions are exactly what would be expected for species with a very recent common ancestor. In other words, the distributions of beak size in these three species of ground finch are understandable in terms of a common ancestor that was likely similar in size to the medium ground finch, with the large and small ground finches evolving from the tails, so to speak, of the distribution of medium ground finches (see also Lamichhaney et al., 2018).

Social Selection Pressures

In the same way that ecological changes in food availability influenced the evolution of body size and beak morphology in Darwin's finches, competition among members of the same species (i.e., conspecifics) can result in selection acting on traits that facilitate this competition to the extent these traits are evolvable and influence survival or reproductive prospects (Mayr, 1974; West-Eberhard, 1983). West-Eberhard (1983) referred to these dynamics as *social selection*, which often includes cooperation with others to better help individuals compete for resource control or social influence. An example is provided by the coalitional behavior of females of many species of Old World (Africa and Asia) monkey (Wrangham, 1980).

Cooperative coalitions among female primates are most common in species in which high-quality food sources (e.g., fruit trees) are clustered in one or a few locations (Arseneau-Robar, Taucher, Schnider, van Schaik, & Willems, 2017;

Sterck, Watts, & van Schaik, 1997). In these species, related females cooperate with one another to compete with other female kin groups for control of these high-quality foods, and the larger matrilineal (female kin) coalitions typically succeed. The combination of social dominance—associated with the ability to influence the behavior of conspecifics—and better nutrition results in increased survival rates for individuals of successful coalitions and significant changes in reproductive patterns. Compared with females in less successful coalitions, females in dominant ones mature earlier, have shorter interbirth intervals, and their offspring have higher survival rates (Silk, 1993). The result is a significantly higher lifetime reproductive success for dominant females as opposed to subordinate females. Silk, Alberts, and Altmann (2003) demonstrated that even within matrilineal coalitions, the infants of female baboons (*Papio cynocephalus*) with larger social networks have higher survival rates than the infants of more socially isolated mothers.

Given the strong link between coalitional dominance and size of within-coalition social networks and the wide array of survival and reproductive outcomes, selection will necessarily favor individuals with the social and cognitive competencies needed to develop, maintain, and use social relationships in ways that ultimately benefit them and their kin (e.g., Bergman, Beehner, Cheney, & Seyfarth, 2003). In other words, the survival and reproductive advantages associated with between- and within-coalitional behavior create a social ecology that influences the evolution of behavioral and presumably cognitive social competencies (Dunbar, 1993; Dunbar & Bever, 1998), just as the nonsocial ecology (i.e., available foods) influences the evolution of beak morphology in Darwin's finches. Coalitional control of high-quality food sources, however, is only one example of social selection (see also Geary, 2005; González-Forero & Gardner, 2018; Lukas & Clutton-Brock, 2018).

EVOLUTION OF SEX

From a strictly genetic perspective, asexual reproduction has a distinct advantage over sexual reproduction. Barring mutations, offspring are genetically identical to the parent. With sexual reproduction, in contrast, there is only a 50% overlap between the genes of offspring and those of each parent (Burke & Bonduriansky, 2017; Ridley, 1993; G. C. Williams, 1975; G. C. Williams & Mitton, 1973). On the basis of these genetic and other costs (e.g., finding a mate), we would not expect sexual reproduction to be a viable alternative to asexual reproduction, unless the benefits of the former are more than double the benefits of the latter (G. C. Williams, 1975). To leave the same genetic footprint in the next generation, each parent has to produce two offspring with sexual reproduction for each single offspring produced through asexual reproduction. Despite these costs, sexual reproduction is the norm for most complex, multicellular (and even some single-celled) species.

There must be long-term costs to asexual reproduction and long-term benefits to sexual reproduction. The nature of these costs and benefits is debated, and many nuances remain to be settled (Chastain, Livnat, Papadimitriou, & Vazirani, 2014; de Visser & Elena, 2007; Rice, 2002), but the most likely costs and benefits have been identified. A discussion of these costs and benefits will help us to better understand certain aspects of sexual dynamics, such as mate choices. Various models of the evolution of sex focus on the deleterious effects of accumulating mutations, the creation of variability and the accompanying ability of offspring to adapt to their ecology, and parasite resistance. These models are briefly discussed next. These are not exclusive mechanisms; they may interact, or the importance of one or the other might differ across species (Cooper, Lenski, & Elena, 2005; de Visser & Elena, 2007).

Accumulating Mutations

Genetic mutations can arise in several ways, like mistakes in DNA replication during cell divisions (J. F. Crow, 1997). Although the frequency with which these mutations occur is currently debated and may vary across species—being higher for species with longer developmental periods and more cell divisions before reproduction (Keightley & Eyre-Walker, 2000)—it is clear that a small number of mutations, and sometimes a single mutation, can affect the individual's behavior, physiology, development, and other traits (Ajie, Estes, Lynch, & Phillips, 2005; Kondrashov, 1988). Most mutations that affect the individual are harmful, although each typically results in only small reductions in lifespan and in the number of offspring contributed to the next generation (J. F. Crow, 1997). In most cases, the accumulation of mildly harmful mutations gradually reduces the ability of affected individuals to reproduce, and through this eliminates them from the population (e.g., Poon & Chao, 2004).

Asexual reproduction results in a faster accumulation of harmful mutations over generations than does sexual reproduction (Kondrashov & Crow, 1991; H. J. Muller, 1964). With sexual reproduction, some individuals in the population have only a few mutations and others have many mutations. Those individuals with many mutations are less likely to survive, be chosen as mates, or be successful in competition for mates than are their peers with fewer mutations (Ajie et al., 2005; Cooper et al., 2005; J. F. Crow, 1997; Lumley et al., 2015). The net result is that relatively harmful mutations are eliminated from sexually reproducing populations, without endangering an entire population. Moreover, offspring receive one copy of the same gene from both parents and oftentimes a mutated copy will not compromise offspring because only the nonmutated copy will be expressed and influence trait development.

With asexual reproduction, all harmful mutations that arise in one generation will necessarily be passed on to all members of the next generation, which, in turn, will eventually result in the accumulation of several harmful mutations over successive generations. H. J. Muller (1964) explained the process in terms of a ratchet (*Muller's ratchet*), whereby the number of mutations from one generation to the next necessarily ratchets up or increases. Ridley (1993) likened the process to photocopying:

> Muller's ratchet applies if you use a photocopier to make a copy of a copy of a copy of a document. With each successive copy the quality deteriorates. . . . Once the original is lost [through mutations], the best copy you can make is less good than it was before. (p. 48)

In addition to providing a mechanism that can eliminate harmful mutations from a population, sexual reproduction appears to afford a number of other advantages over asexual reproduction (Cally, Stuart-Fox, & Holman, 2019; J. F. Crow, 1997; Kondrashov, 1988). The genetic recombination associated with sexual reproduction means that at least some offspring will have fewer potentially harmful mutations than their parents; others will, of course, have more. Sexual reproduction also creates the opportunity for beneficial mutations that have arisen in each parent to be combined in their offspring. Direct comparisons of asexual and related sexual species are difficult to conduct, but they generally suggest that the accumulation of harmful mutations places asexual species at an evolutionary disadvantage (Ajie et al., 2005; Poon & Chao, 2004). The more rapid accumulation of mutations in asexual species may not be enough to maintain sexual reproduction, but likely contributed to its original evolution (Cooper et al., 2005; de Visser & Elena, 2007).

More recently, Havird, Hall, and Dowling (2015) proposed that sexual reproduction emerged soon after the evolution of eukaryotic cells to control for the accumulation of mutations. These cells evolved about 1.5 billion years ago and contain a nucleus (nuclear DNA [nDNA]) and mitochondria, small organelles within cells that are critical to energy production (M. W. Gray, 2012). Mitochondria have their own DNA (mtDNA) and these DNA are prone to mutations. These mutations in turn would quickly compromise the amount of energy available to the cell. nDNA can compensate for mutations in mtDNA, and sexual reproduction provides a means to quickly produce nDNA–mtDNA combinations that maintain cellular energy (Lane, 2011). As is discussed in Chapter 4 of this volume, the Havird et al. proposal fits nicely with the proposal that the efficiency of mitochondrial functions is the most fundamental biological process signaled by traits (e.g., the colorful plumage of male birds) that attract mates and deter competitors (G. E. Hill, 2014).

Speed of Adaptation and Advantages of Variation

Sexual reproduction results in greater genetic and phenotypic or trait variation (i.e., individual differences) within a population than does asexual reproduction (G. Bell & Smith, 1987; B. Charlesworth, 1993; G. C. Williams, 1975; G. C. Williams & Mitton, 1973). Large populations are necessarily at greater risk of harmful and beneficial chance mutations (Colegrave, 2002), and the greater variability within these populations allows more rapid adaptation to conditions that change from one generation to the next (C. Darwin, 1859; Reznick et al., 1997; G. C. Williams & Mitton, 1973). One implication is that asexual reproduction will be the most successful when the ecology of the parent and the offspring are the same, although even in this situation accumulating mutations can still compromise asexual species. The parent is adapted to this ecology, and so too are her offspring. But what happens when the ecology changes or individuals migrate to a new ecology? In this situation, the characteristics that enabled the survival and reproduction of the parent might not be well-suited to the new ecological conditions (e.g., Becks & Agrawal, 2010). Sexual reproduction ensures that offspring differ at least to some extent, and this in turn increases the chances that some of them will survive and reproduce under the new ecological conditions.

G. C. Williams (1975) used a lottery analogy to explain the basic point. The ecological conditions that support survival and reproduction represent the winning number. Asexual reproduction is like having 100 lottery tickets, all with the same number. With sexual reproduction, you get fewer tickets—50 in this case—but they all have different numbers. If you do not know the winning number in advance (e.g., if the conditions that support survival and reproduction frequently change or are very harsh), then sexual reproduction, although it costs more (i.e., you cannot buy as many tickets), is more likely to result in a winning number. Experimental studies have confirmed that sexual reproduction results in the more rapid creation and combination of potentially beneficial mutations and that under harsh conditions these mutations result in phenotypes (i.e., measurable traits like beak size) that enhance survival and reproductive prospects (Rice, 2002). Any such beneficial mutations can be passed down by both parents—or each parent provides different beneficial mutations—while at the same time purging mutations that can compromise offspring survival or reproductive prospects (M. J. McDonald, Rice, & Desai, 2016).

The elbow-room model represents another potential advantage to offspring variability (Bulmer, 1994). The basic premise is that offspring that differ to some extent, genetically and phenotypically, do not compete for identical resources. In other words, offspring that differ from one another—those resulting from sexual reproduction—are better able to seek different niches within the same environment and therefore reduce the intensity of competition among them (Dawkins & Krebs, 1979). With asexual reproduction, the primary competitors for survival are often one's identical siblings. Even in relatively stable environments, this competition can be severe if resources are limited (G. C. Williams & Mitton, 1973). Intense competition favors niche seeking (Dawkins & Krebs, 1979), which, in turn, is made possible through the phenotypic variability that results from sexual reproduction. The process is not restricted to siblings or even the same species, as niche construction can also result from intense competition from other species in the same ecology.

Parasite Resistance

W. D. Hamilton and colleagues (1980, 1990; W. D. Hamilton, Axelrod, & Tanese, 1990) and Jaenike (1978) proposed that parasites drove the evolution of sexual reproduction. Parasites such as viruses, bacteria, and worms are ubiquitous and typically negatively affect the fitness of the host (e.g., reduce the number of offspring; Torchin, Lafferty, Dobson, McKenzie, & Kuris, 2003). The key idea is that parasites will specialize on the most abundant hosts in their ecology, and the rapid reproduction of asexual species makes them prime targets (Lively & Morran, 2014). Moreover, with asexual reproduction, the antiparasite defenses of the parent and her offspring are nearly identical, differing only as the result of mutations. Any such mutations are unlikely to result in an effective long-term defense, because parasites have shorter lifespans than their hosts and can evolve around any newly emerging antiparasite defenses (W. D. Hamilton et al., 1990). In such situations, harmful parasites will quickly reduce the viability of, or even eliminate, asexual species.

In this view, the principal function of sexual reproduction is to create highly variable antiparasite defense systems that can respond to a variety of different parasites and can be reshuffled, to some extent, from one generation to the next. And, there is good evidence that this is indeed an important function of sexual reproduction (e.g., Cooper et al., 2005; Lively & Morran, 2014; Vergara, Jokela, & Lively, 2014). Once parasites have adapted to the specific defenses of the parent or parents, then a reshuffling of these defenses will put their offspring one step ahead of the parasites (Penn & Potts, 1999). The parasites will then evolve adaptations to these new defenses (Neu, 1992), which will be reconfigured in the next generation of the host. The process of successive adaptations creates a coevolutionary cycle between parasites and the hosts' defenses (Dawkins & Krebs, 1979). The cycle does not lead to an end point (e.g., permanent immunity) but rather to a potentially never-ending pattern of resistance and susceptibility to parasites (Ridley, 1993). Van Valen (1973) illustrated this concept by means of *Alice in Wonderland*'s (Carroll, 1871) Red Queen. "The Red Queen is a formidable woman who runs like the wind but never seems to get anywhere: . . . [She states to Alice], you see, it takes all the running *you* can do to keep in the same place" (Ridley, 1993, p. 64). Stated otherwise, the coevolution of hosts and parasites ensures constant change and individual variability for the characteristics, such as the immune system, that are the focus of this coevolution, but the mean viability (e.g., average health) of the host does not necessarily change across generations (e.g., Decaestecker et al., 2007).

The immune system provides an excellent illustration of antiparasite defenses; other systems include the chemical defenses of many plant species. The genes that code for aspects of immune responses—the *major histocompatibility complex* (MHC)—are the most variable family of genes ever identified in vertebrates (Apanius, Penn, Slev, Ruff, & Potts, 2017), supporting the prediction that variation is the key to keeping ahead of parasites. There are specific MHC haplotypes (genes that are inherited together) and mechanisms that trigger immunological responses to specific parasites, although the effectiveness of these responses can vary with genetic background (i.e., other genes). The specific evolutionary mechanisms maintaining MHC variation are intensely studied and likely include a combination of natural selection for MHC genes that protect against specific parasites and sexual selection (see Chapter 3, this volume; Jan Ejsmond, Radwan, & Wilson, 2014).

The latter includes disassortative mating; specifically, a preference by the more-choosy sex (typically females) for mates that have MHC genes that differ from their own or at least mates that have diverse MHC genes (Kamiya, O'Dwyer, Westerdahl, Senior, & Nakagawa, 2014; Milinski, 2006). Females of many species can detect MHC genes through prospective mates' olfactory or odor cues. In one related study, W. K. Potts, Manning, and Wakeland (1991) examined the relation between mating patterns in mice (*Mus musculus domesticus*) and MHC disparity between mating partners. Females largely control choice of mating partners in this species and consistently chose males with an MHC different from their own. Moreover, W. K. Potts and colleagues found that "females seek extraterritorial matings with males that are relatively more MHC-disparate than their own territorial mate" (p. 620). Kamiya and colleagues' (2014) meta-analysis indicated this general pattern is found across species of mammal, bird, fish, and reptile. However, females' choice of one mate or another is influenced by multiple MHC genes, not any single gene, and different species differ in the relative importance of natural (e.g., specific MHC genes for specific parasites) and sexual selection (e.g., mate choices) on MHC evolution (Winternitz et al., 2013). There are many issues that remain to be resolved, such as whether mates with highly dissimilar MHC genes produce offspring with increased risk of autoimmune disorders (Milinski, 2006), but the overall results are consistent with the importance of parasites in the evolution of sexual reproduction.

Even so, models of host–parasite coevolution do not preclude the earlier described influence of mutations or facility of adaptation to changing ecologies on the evolution of sexuality (W. D. Hamilton et al., 1990; Kondrashov, 1988). In fact, the models make many of the same predictions: The central feature of the speed of adaptation and host–parasite coevolution models is that the principal function of sexual reproduction is to maintain genetic and phenotypic variability (Lively & Morran, 2014). Moreover, there is some evidence that multiple mechanisms may be involved in the evolution and maintenance of sexual reproduction (de Visser & Elena, 2007). In an experimental study, Cooper and colleagues (2005) manipulated the number of mutations and parasite exposure (exposed or not exposed) for the bacteria *Escherichia coli*. The ability of these bacteria to reproduce decreased as the number of mutations increased, consistent with Muller's ratchet, and decreased with exposure to the parasite, consistent with the Red Queen model. The bacteria strain with the lowest reproductive success had the combination of parasite exposure and a high number of mutations. Sexual reproduction in these bacteria—swapping genes with another individual—reduces mutation load, thereby reducing susceptibility to the parasite, in keeping with the multiple benefits to sexual reproduction.

Anisogamy

Whatever drove the initial evolution and current maintenance of sexual reproduction, once it arose, individuals needed a way to reliably merge their DNA. The result was the evolution of gametes (DNA-containing germ cells) and eventually the evolution of two gamete sizes (i.e., sperm and egg; Bateman, 1948; G. A. Parker, Baker, & Smith, 1972). There are two core selection pressures at work in the evolution of two gamete types. The first is the benefit of producing many gametes, each of which could fertilize the gamete of another individual. The second is the benefit of larger gamete size. Generally, larger zygotes (i.e., fertilized gametes) are more likely to develop and survive than smaller ones, which provides an advantage for larger gametes. The combination of advantages to producing many smaller gametes and of producing fewer but larger gametes results in *disruptive selection*, whereby the best options are at the extremes—produce many smaller gametes and increase the chances of fertilizing the gametes of one or many other individuals or produce larger gametes that are more likely to survive once fertilized (G. A. Parker et al., 1972).

Once two gamete sizes evolve, there are advantages associated with each sex differentially investing resources in the traits that will produce the most surviving offspring. Evolutionary scenarios for how this occurred and the extent to which they produce sex differences vary and are debated (Gowaty & Hubbell, 2009; Lehtonen, Parker, & Schärer, 2016; G. A. Parker, 2014). The most straightforward scenario is for males—the sex producing sperm (the smaller, more plentiful gamete)—to allocate fewer resources to gamete production (sperm are "cheap") and more to traits that allow them to find mates and exclude other males from mating (Lehtonen et al., 2016), and for females to invest fewer resources in competing for mates. The latter is important because it will potentially compromise egg production or investment in the zygote (especially for mammals) and could yield disadvantages to their reproduction. The result is the evolution of distinct sexes that can and often do differ in the strategies used to pursue their best reproductive interests. In fact, the general pattern of females investing more in parenting and males in competing is found throughout the animal kingdom (Janicke, Häderer, Lajeunesse, & Anthes, 2016).

At the same time, the evolution of distinct sexes and different reproductive strategies for males and females in general does not preclude male investment in offspring or competition among females for reproductive resources, as is seen in Chapter 3 of this volume. Ecological and social conditions could favor males that invest heavily in offspring and females that compete for resources (including male parental investment) that benefit their offspring. These apparent exceptions, however, prove the general rule that investment in offspring substantively influences the evolution and expression of many sex differences.

CONCLUSION

The discovery of the principles of natural selection was pivotal in the development and unification of the biological sciences. These principles provide a metatheoretical organization to these sciences and explain three important phenomena: the diversity of life in the natural world, the mechanisms by which this within- and between-species diversity arose, and how and why species continue to change. This is not to say that all aspects of natural selection have been fully resolved (G. C. Williams, 1966/2008). There are multiple ways in which ecological and social selection pressures can influence the dynamics that result in speciation, but these involve nuances in the process of natural selection and not evidence that refutes these principles. Ecological, social, and genetic studies continue to provide support for the theory of evolution and supply an ever finer-grained understanding of how these principles work at multiple levels, from genes to behavior (A. A. Hoffmann & Willi, 2008; Soons et al., 2015), and across a few generations to thousands of generations (Estes & Arnold, 2007).

An intriguing area of evolutionary research concerns the evolution of sex and sexual reproduction. The considerable genetic cost to sexual reproduction—one must give up 50% of one's genes to reproduce—raises the intriguing question of how this form of reproduction evolved. Although there are nuances that remain to be resolved, there is consensus that one of the principal benefits is the generation of genetic and phenotypic variability or individual differences (Kondrashov, 1988). Variation is, of course, the grist on which evolution works and provides several benefits. These benefits include the cross-generational elimination of deleterious mutations, the ability to more rapidly adapt to changing ecologies, niche seeking in socially competitive environments, and an ever-changing system of defense against rapidly evolving parasites (Apanius et al., 2017; Dawkins & Krebs, 1979; W. D. Hamilton & Zuk, 1982). These benefits affect the overall survival of the species, but they do not mean that evolution is for the good of the species (Dawkins, 1989; W. D. Hamilton, 1964; G. C. Williams, 1966/2008). Rather, individual variation largely determines which individuals within the species, or sex, survive and reproduce. The most important point for us moving forward is that the evolution of sexual reproduction resulted in the evolution of two sexes, and a wide range of ways in which each sex can pursue his or her reproductive best interest.

3

Overview of Sexual Selection

With the publication of *On the Origin of Species* in 1859, C. Darwin laid out the argument for natural selection and illustrated the power of these mechanisms for creating evolutionary change. In this treatise, he also introduced another class of evolutionary mechanism, sexual selection, but he only devoted a few pages to it. Twelve years later, Darwin greatly elaborated on these mechanisms in *The Descent of Man, and Selection in Relation to Sex*. In his words, sexual selection

> depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction. When the two sexes differ in structure in relation to different habits of life . . . they have no doubt been modified through natural selection. (C. Darwin, 1871, p. 256)

For Darwin, natural selection (i.e., traits that influence survival prospects) was the principle evolutionary force that shaped the behavior and physiology of the species, including many sex differences (Ghiselin, 1974). Sexual selection was largely restricted to the physical and behavioral traits and accompanying social dynamics that were directly related to and influenced mate choice and competition for mates. Despite a compelling argument for distinguishing sexual selection from natural selection, Darwin's theory languished for a century before being considered seriously as a significant evolutionary process (Cronin, 1991).

The principle components of sexual selection, *intersexual choice* (Which mate do I want?) and *intrasexual competition* (Who do I have to beat to get the mate I want?), have been thoroughly studied and are firmly established as potent

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evolutionary forces (Andersson, 1994). These processes are core influences on social dynamics and contribute to the maintenance of sexual reproduction (Agrawal, 2001), the overall health of the population (Cally et al., 2019), and can contribute to the emergence of new species (Servedio & Boughman, 2017; C. E. Wagner, Harmon, & Seehausen, 2012). They are not the only social dynamics that can influence sex differences, however. Competition for resources other than mates (e.g., high-quality food), called *social selection* (West-Eberhard, 1983), can also influence the evolutionary emergence of sex differences and may be important for understanding competition among females (Lyon & Montgomerie, 2012; Stockley & Bro-Jørgensen, 2011).

This chapter introduces and illustrates the dynamics of intersexual choice and intrasexual competition and focuses on the most common ways in which these are expressed (i.e., female choice and male–male competition). These were C. Darwin's (1871) original foci, but we now know that the processes of competition and choice can operate in both sexes (see also Clutton-Brock, 2009). However, it is important to step back and consider another key aspect of reproduction—parenting. The evolution of parenting, and sex differences in the amount of effort devoted to parenting, sets the stage for the evolution of sex differences in intersexual choice and intrasexual competition.

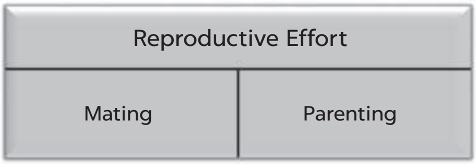
PARENTAL CARE

Although C. Darwin (1871) identified and defined the basic principles of sexual selection, he did not elaborate on their evolutionary origin. G. C. Williams (1966/2008, 1975), and Trivers (1972) proposed that the evolution of intersexual choice and intrasexual competition is related to the degree to which each sex invests in parental care. We now understand that the relationship between parenting and sexual selection is more nuanced than originally proposed (Stiver & Alonzo, 2009); this is discussed further in the following chapter. Nonetheless, the basic insight remains valid. G. C. Williams (1966/2008) noted the following:

> It is commonly observed that males show a greater readiness for reproduction than females. This is understandable as a consequence of the greater physiological sacrifice made by females for the production of each surviving offspring. A male mammal's essential role may end with copulation, which involves a negligible expenditure of energy and materials on his part, and only a momentary lapse of attention from matters of direct concern to his safety and well-being. The situation is markedly different for the female, for which copulation may mean a commitment to a prolonged burden, in both the mechanical and physiological sense, and its many attendant stresses and dangers. (pp. 182–183)

Trivers (1972) formalized these observations and proposed that each individual's overall reproductive effort is largely a combination of mating effort (e.g., time spent searching for mates, the energy spent in vigorous mating displays) and parental investment (e.g., the effort spent on finding food for offspring, defending them from predators), which is shown in Figure 3.1. *Parental investment*

FIGURE 3.1. Distribution of Reproductive Effort



Reproductive effort is distributed between mating effort (e.g., competing for mates) and parental investment (e.g., provisioning and protecting offspring).

includes any cost (e.g., time, energy) associated with raising offspring that reduces the parent's ability to produce or invest in other offspring (see also Trivers, 1974). Both parents must invest something if they are to have any reproductive success, even if it is only the energy to produce gametes (e.g., sperm) and find a mate. But the proportion of reproductive effort that is devoted to parenting can vary significantly between the sexes. According to Trivers (1972), "the sex whose typical parental investment is greater than that of the opposite sex will become a limiting resource for that sex. Individuals of the sex investing less will compete among themselves to breed with members of the sex investing more" (p. 140).

The reproductive success of members of the lower investing sex is more strongly influenced by the number of mates that can be found than by investing in the well-being of individual offspring. The reproductive success of members of the higher investing sex is more strongly influenced, in most cases, by investment in offspring than by competing for mates. The dynamics of sexual selection are influenced by the ways in which each sex distributes their reproductive effort across mating and parenting (Clutton-Brock, 1991). These differences are not directly caused by the anisogamy (i.e., sex differences in sperm and egg size and costs of producing them) discussed in the previous chapter, but anisogamy sets in motion a cascade of evolutionary processes that often results in males investing more in competing for mates and females investing more in parenting (Fromhage & Jennions, 2016).

This is not the whole story, however, as the sex differences in competing and parenting can be influenced by a variety of other factors, including the operational sex ratio (OSR), the potential reproductive rates of males and females, and the mating system of the species. The OSR in particular influences the here-and-now expression of sex differences in competitiveness and choosiness, and this in turn is influenced by the potential reproductive rates of males and females and by the mating system (Clutton-Brock & Parker, 1992; Kvarnemo & Ahnesjö, 1996). For clarity, these factors are discussed in more detail in the following sections.

Potential Reproductive Rate

The potential rate of reproduction is the biological limit on how quickly an individual can produce offspring without constraints; that is, the time between producing one offspring or a clutch of offspring and readiness to produce the next (Clutton-Brock & Vincent, 1991). The limit is determined by the amount of time needed to produce sperm, ova, clutch of eggs, gestation time, and so forth. As an example, a male African elephant (*Loxodonta africana*) can potentially sire many offspring in a single day, but female elephants can only produce a single offspring every 4 to 5 years (Moss, 2001). Across species, sex differences in the potential rate of reproduction are systematically related to sex differences in the relative mix of effort devoted to mating or parenting (Clutton-Brock & Parker, 1992; Clutton-Brock & Vincent, 1991). The sex with the higher potential rate typically invests relatively more in mating than in parenting, whereas the sex with the lower rate typically invests more in parenting than in mating. Once they have mated, members of the sex with the higher potential rate of reproduction can rejoin the mating pool more quickly than can members of the opposite sex. It is often in their reproductive best interest to do so, particularly when biparental care is not necessary for the survival of offspring (Clutton-Brock, 1991; Smith, 1977). In most species, males have a higher potential rate of reproduction than do females because of sex differences in the time and cost associated with the production of sperm and eggs and any cost associated with gestation and postnatal care (Bateman, 1948; G. A. Parker & Simmons, 1996).

For species with internal female gestation and obligatory postnatal female care (e.g., suckling in mammals), the rate with which females can produce offspring is considerably lower than the potential reproductive rate of conspecific males (Clutton-Brock, 1991). The combination of internal gestation and the need for postnatal care necessarily results in more initial maternal than paternal investment and creates a sex difference in the benefits of seeking additional mates. Males in most species can reproductively benefit by seeking and obtaining additional mates, whereas females cannot (Smith, 1977). The sex difference in reproductive rate, combined with offspring that can be effectively raised by the female, create the potential for large sex differences in the mix of effort devoted to mating and parenting. This potential is often realized in nature, if other conditions are also met. In more than 90% of mammalian species, females provide all or most of the parental care; notable exceptions are found among carnivores, primates, and rodents (Lukas & Clutton-Brock, 2013; H. E. West & Capellini, 2016; see also Chapter 4, this volume). Female care of offspring frees males to invest in mating effort. As a consequence, in most mammalian species, the reproductive effort of males is almost exclusively focused on competing with one another for access to mates (Clutton-Brock, 1989).

The exception proves the rule. For species where females have a higher potential reproductive rate than males, they are often the more competitive sex and males are the choosy sex (Clutton-Brock & Parker, 1992). In many of these "sex-role-reversed" species, males incubate, or internally gestate, the fertilized egg or eggs (Andersson, 2004; Berglund, Rosenqvist, & Bernet, 1997; Eens & Pinxten, 2000). Examples of male gestation are found in pipefish (e.g., Broadnosed pipefish, *Syngnathus typhle*), seahorses (e.g., big belly seahorse, *Hippocampus abdominalis*), and seadragons (e.g., leafy seadragon, *Phycodurus eques*). In these related species, females transfer eggs into a front pouch on the male which the male then fertilizes (A. G. Jones, Moore, Kvarnemo, Walker, & Avise, 2003). The male benefits by ensuring he is the sire of all of the offspring and the female benefits by lower parental investment. Female pipefish also have the option of attempting to "impregnate" a second male because they can produce eggs more quickly than the male can incubate them. But now, there are more females with eggs than males that are able to accept them, creating conditions in which females must compete intensely for access to these males. As in species in which males compete intensely for mates, females of pipefish species are often larger, more colorful, and more aggressive than conspecific males (A. B. Wilson, Ahnesjö, Vincent, & Meyer, 2003).

Intense female–female competition is also found in the mating system of many species of shorebird (Clutton-Brock & Parker, 1992), such as the red-necked phalarope (*Phalaropus lobatus*; J. D. Reynolds, 1987). Males of this species provide most or all of the parental care; they build the nest and incubate the eggs. The fledglings are precocial, which means they fend for themselves once hatched. The high level of obligatory paternal care makes it possible for the female to pursue other mates, and she typically does. The crucial factor is that females are ready to produce another clutch about 1 week after laying their first clutch, whereas the incubation time for males is close to 3 weeks. The result is that the potential rate of reproduction is much higher in females than in males. Females can produce about two clutches of eggs for every single clutch incubated by a male. The limiting factor in the number of offspring that can be produced by females is thus the number of unmatched males. As with pipefish, female red-necked phalaropes show many of the characteristics associated with males in species where males are the more competitive sex. They are slightly larger than male red-necked phalaropes, have brighter plumage, fight with other females for access to males, and, once paired, guard their mates against competitors (J. D. Reynolds, 1987). Male red-necked phalaropes, in contrast, rarely threaten or attack one another, although they will guard their mate until the eggs are laid.

There is another important consequence of the sex-role reversal in the red-necked phalarope. The reproductive success of females is more variable than the reproductive success of males; for every female that produces two clutches in a breeding season, one female goes unmated and fails to reproduce. Unmated males, by comparison, are rare. Females that capitalize on the high level of paternal care will produce more offspring than females who assist the male in clutch incubation. As long as the male can effectively incubate the eggs himself, evolution, through differential reproduction, will favor females who are successful in gaining additional mates (i.e., females who invest more in mating effort than in parental effort). Of course, the converse is also true. In species in which females invest more in parenting, males compete for sexual access and maternal investment, and a few males sire many offspring and many males sire no offspring.

Operational Sex Ratio

Operational sex ratio is the ratio of sexually active males to sexually active females in any given breeding area at a given point in time. Sex differences in reproductive rate can have profound effects on the OSR and related behavioral strategies associated with competition and choice (S. T. Emlen & Oring, 1977; Kvarnemo & Ahnesjö, 1996). In a population where there are as many sexually mature females as there are sexually mature males (an adult sex ratio of 1:1), any sex difference in the rate of reproduction will result in an unbalanced OSR. Among the red-necked phalarope, the OSR is unbalanced because there are more unmated females than males in the breeding population at most points in the breeding season (J. D. Reynolds, 1987). The result is there are fewer unmatched males than there are females searching for mates (for other examples see Clutton-Brock & Parker, 1992; Fritzsche, Booksmythe, & Arnqvist, 2016). The higher demand for males results in female–female competition. The OSR is influenced by other factors as well, including sex differences in mortality, time of arrival at breeding sites, the degree of synchrony in female sexual receptivity, and the spatial distribution of resources and mates (S. T. Emlen & Oring, 1977; Shuster & Wade, 2003), among other things. These differences can result in changes in mating dynamics within the species and at different points in the same breeding season (J. W. A. Grant & Foam, 2002; Kvarnemo & Ahnesjö, 1996).

The spotted sandpiper (*Actitis macularia*), another polyandrous (females have many mates) shorebird in which males provide most of the parental care, illustrates the importance of time of arrival at the breeding site (Oring, Lank, & Maxson, 1983). One way in which females compete is to arrive at the breeding site before the males, resulting in many more females than males at the beginning of the breeding season. As individual males arrive, females fight among themselves, sometimes to the point of injury, for access to these males. As with the red-necked phalarope, there are considerable reproductive benefits to successful females, despite the cost of competition (i.e., risk of injury). This is because early breeders are more likely to produce additional clutches than are late breeders.

Even in species in which males intensely compete for access to females, the degree to which female sexual receptivity is synchronized can influence the OSR and through this, the intensity of competition. If all females are sexually receptive at the same time, then males are severely limited in the number of females with whom they can mate (S. T. Emlen & Oring, 1977). Under these conditions, the OSR would mirror the adult sex ratio and if this ratio was close to 1:1, little male–male competition is likely. Asynchronous or prolonged female receptivity, in contrast, creates the potential for polygyny (males have many mates) and results in a shift in the OSR, such that there are more unmated males than females in the mating pool. Males then compete for access to sexually receptive females.

Takahashi's (2004) studies of the Japanese macaque (*Macaca fuscata fascata*) provide a striking example of these dynamics. The social groups of this species include several adult males and a larger number of adult females and their offspring. The females do not go into estrus every mating season, therefore there can be considerable variation across seasons in the number of reproductive females. Across four mating seasons, the ratio of reproductive females to males ranged from 1:5 to 3:1. When there were more males than estrus females, dominant males aggressively monopolized mating access to these females. During these seasons, low-ranking males mated with estrus females less than 20% of the time. In seasons in which there were more estrus females than males, dominant males could not control mating dynamics and low-ranking males mated almost 50% of the time.

Dramatic changes in the OSR can even occur within a single breeding season, as documented for the two-spotted goby (*Gobiusculus flavescens*), a species of fish (Forsgren, Amundsen, Borg, & Bjelvenmark, 2004). At the beginning of the breeding season, there are more reproductive males than females. During this time, males compete intensely for nesting sites, court females, and then fan and protect eggs. These activities are very costly for the male and result in such high male mortality there are many more females than males by the middle of the breeding season. When the OSR reaches about a 4:1 ratio of females to males, females start adopting male-typical behaviors. They begin to court males—"individual males were often surrounded by up to 20 round females courting them at close range" (Forsgren et al., 2004, p. 553)—and they chase other females away from the males to get access to mating opportunities with them.

Ecology of the Mating System

A sex difference in the rate of reproduction or an unbalanced OSR means that one male has the potential to monopolize the reproduction of many females or one female has the potential to monopolize many males. Sex differences in the potential rate of reproduction or OSR are not enough, however, to result in polygamy (either polygyny or polyandry). Polygamy arises when "multiple mates, or resources critical to gaining multiple mates, are economically defendable" (S. T. Emlen & Oring, 1977, p. 215). Sex role differences, particularly parental care, are also crucial; one sex has to provide most or all of this care. For polygamy to be realized, critical resources (e.g., food, nesting sites) need to be clustered in space and, in most cases, members of the higher investing sex need to be sexually receptive at different times and clustered together. If resources or potential mates are sparsely distributed or sexual receptivity is limited to a very short period, then there is little opportunity for members of one sex to monopolize the reproductive efforts of the opposite sex. In these situations, social monogamy and high levels of biparental care may evolve, as is found in many species of bird (J. M. Black, 1996). In many of these species, resources are sparsely distributed and as a result biparental care is often needed to successfully raise nestlings (Clutton-Brock, 1991). If the spatial distribution of resources and the temporal distribution of potential

TABLE 3.1. The Ecology of Mating Systems

Mating system	Core features
Monogamy	Neither sex has the opportunity to monopolize additional members of the opposite sex. Fitness often maximized through shared parental care.
Polygyny	Individual males frequently control or gain access to multiple females. 1. Resource defense polygyny: Males control access to females *indirectly*, by monopolizing critical resources. 2. Female (or harem) defense polygyny: Males control access to females *directly*, usually by virtue of female gregariousness. 3. Male dominance polygyny: Mates or critical resources cannot be economically monopolized. Males aggregate during the breeding season and females select mates from these aggregations.
Polyandry	Individual females frequently control or gain access to multiple males. 1. Resources defense polyandry: Females control access to males *indirectly*, by monopolizing critical resources. 2. Female access polyandry: Females do not defend resources essential to males but, through interactions among themselves, may limit access to males.

Note. From "Ecology, Sexual Selection, and the Evolution of Mating Systems," by S. T. Emlen and L. W. Oring, 1977, *Science*, *197*, p. 217. Copyright 1977 by the American Association for the Advancement of Science. Adapted with permission.

mates coalesce then there is a potential for polygamy, as described in Table 3.1 (Macedo, Podos, Graves, & Manica, 2018; Shuster & Wade, 2003).

Resource defense polygyny occurs when males compete for control of the highest quality territory—one that offers the most food, the best nesting sites, and is defensible—and successful males are able to attract more than one mate. *Female defense polygyny* occurs where females aggregate to lessen the risk of predation or because there are limited birthing sites (Andersson, 1994; Clutton-Brock & McComb, 1993), and a very small number of males can control access to these females. The northern elephant seal (*Mirounga angustirostris*) is an example: A few males exclude other males from mating with females clustered together on relatively confined beaches during the breeding season (Le Boeuf, 1974; Le Boeuf & Peterson, 1969). This behavior is common in many ungulates (i.e., hoofed mammals) and pinnipeds (e.g., seals, sea lions). The elephant seal also provides an excellent example of *male dominance polygyny*, which is discussed in greater detail later in this chapter.

Leks occur when males aggregate in a specific area called an arena, and females visit the arena and assess several males before making a mate choice or choices; males are sometimes more dispersed, called an "exploded" lek (e.g., DuVal, Vanderbilt, & M'Gonigle, 2018). Males engage in some form of competition. The competition can be direct, as in the courtship display shown in Figure 3.2, or indirect, as in ornamentation (e.g., bright plumage; Andersson, 1994). In some lekking species, such as peafowl (*Pavo cristatus*), physical male–male competition is minimal, although some does occur, and female choice largely determines which males reproduce and which do not (Höglund & Alatalo, 1995; Petrie, 1994; Petrie, Halliday, & Sanders, 1991). Peacocks

FIGURE 3.2. Male Display of the Argus Pheasant (*Rheirihardtius ocellata*)

Males spread their wings and erect their tail as part of their courtship display. From *The Descent of Man, and Selection in Relation to Sex* (p. 399), by C. Darwin, 1871, London, England: John Murray. In the public domain.

develop large tail trains with varying numbers and sizes of eye spots. Males display their trains and females choose mates on the basis of multiple cues, including train length, number of eye spots, vocalizations, and potentially infrasonic signals produced by shaking the train (Freeman & Hare, 2015; Petrie et al., 1991). These social signals in turn are correlated with the males' and possibly his offspring's health and his male offspring's future attractiveness to females (Loyau, Saint Jalme, Cagniant, & Sorci, 2005; Petrie, 1994; Petrie, Cotgreave, & Pike, 2009). Following copulation, females leave the lek to nest while the male remains to court other females. In lekking species, the combination of male–male competition and female choice of mates results in a small number of males fathering most of the offspring.

In lekking species in which the male provides most or all of the parental care, as with the Eurasian dotterel (*Charadrius morinellus*), females compete for access to males. Once a dotterel female has chosen a potential mate, she courts the male and attempts to isolate him from the lek. At this point, other females typically interrupt the courtship, and fighting then ensues between the two females, with additional females often joining the fray (Owens, Burke, & Thompson, 1994). This form of female–female competition nicely illustrates *female access polyandry*, whereas the spotted sandpiper is an example of *resource* *defense polyandry* (see also Goymann, Makomba, Urasa, & Schwabl, 2015); female spotted sandpipers arrive at the breeding site before the males arrive and compete for control of nesting territories. Successful females are able to attract one or more males to these territories and unsuccessful females remain unmated.

Although not the focus here, I note that the ecology can also influence the evolution of sex differences in ways unrelated to reproductive competition. This can occur if males and females occupy different feeding niches that in turn require different physical adaptations. An example is shown in Figure 3.3, where the sex difference in beak shape was thought to reflect the different foraging strategies of females and males (K. J. Wilson, 2004). Other examples include sex differences in leg length, with long legs for terrestrial foraging versus short legs for arboreal foraging; examples are provided across species of *Anolis* lizard in the Caribbean (M. A. Butler, Sawyer, & Losos, 2007).

FEMALE CHOICE

It was impossible for early naturalists to deny the existence of male–male competition given it was so visible, whether or not it was important from an evolutionary perspective. C. Darwin's (1871) other proposal—that female choice was also a potent evolutionary force—was met with much more skepticism (Cronin, 1991). These days, the importance of female choice is widely accepted. The debate has shifted to understanding the proximate,

FIGURE 3.3. The Male and Female Huia (*Heteralocha acutirostris*)

The male (front) and female (back) huia. The differences in bill shape were thought to reflect differences in foraging strategy. From *A History of the Birds of New Zealand* (2nd ed., p. Plate II), by W. L. Buller and J. G. Keulemans, 1888, London, England: Author. In the public domain.

here-and-now cues (e.g., plumage color) that drive female choice and the ways in which these choices benefit females (Andersson, 1994). Female choice can operate in many ways, from precopulatory behavioral choice of a mating partner or partners to cryptic choice (i.e., postcopulatory choice of sperm from one male or another; Birkhead & Møller, 1998; G. E. Hill & McGraw, 2006; Neff & Pitcher, 2005; Weaver, Koch, & Hill, 2017; Ziegler, Kentenich, & Uchanska-Ziegler, 2005). The following sections discuss core features of these two forms of choice. The final section provides a brief review of research on females' use of social information to make their mate choices.

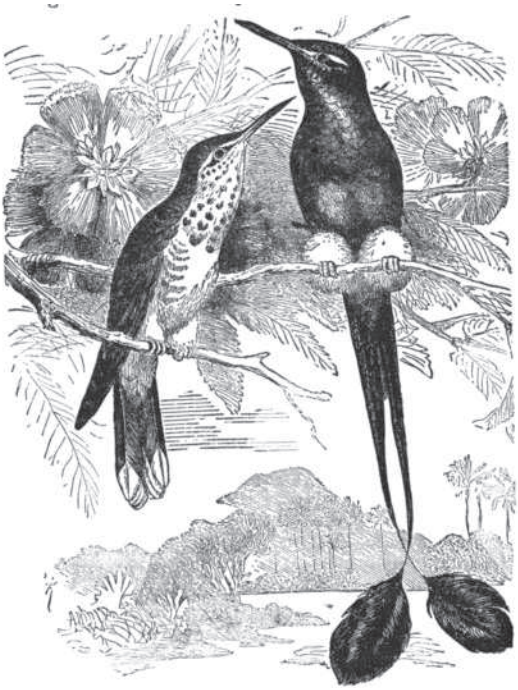
Behavioral Precopulatory Choice

The debates regarding why females are choosy date back to Darwin and Wallace (Cronin, 1991). Although much has been learned since that time, there is still some disagreement regarding whether females choose mating partners for reasons of aesthetics (Darwin's position) or for more practical reasons, like responding to male traits that predict offspring survival (Wallace's position, although his view vacillated; Prum, 2012). These two views are often described as the *good taste* and *good genes* versions of female choice. The predicted evolutionary outcomes of good taste and good genes mate choices, such as bright and colorful males, are often the same and the relative contributions of these mechanisms are sometimes difficult to detect (Endler & Basolo, 1998), and may lie more on a continuum rather than being distinct mechanisms (Kokko, Brooks, McNamara, & Houston, 2002). Nonetheless, separate discussions are warranted, which are followed by a discussion of the trade-offs in female mate choices.

Good Taste

One of C. Darwin's (1871) most important insights detailed in *The Descent of Man, and Selection in Relation to Sex* was that many physical differences or dimorphisms between males and females of the same species cannot be attributed to natural selection. In fact, the bright and oftentimes rather large plumage of the males of many species of bird (see Figure 3.4) likely increase risk of predation (Zuk & Kolluru, 1998). As a result, many of these sex differences would be eliminated by predation and other costs (e.g., energetic costs to building and maintaining the traits), if some other process were not operating. Darwin argued that this other process is sexual selection, in particular female choice of aesthetically pleasing males. For C. Darwin (1871) and later R. A. Fisher (1930), the evolution of good-looking males could occur if females simply preferred more colorful or more elaborate males to their less flamboyant peers. Any such preference might initially result from a female sensory bias for certain color patterns or the brightness of certain colors which "may serve as a charm for the female" (C. Darwin, 1871, p. 92). These charms (e.g., red plumage color) initially evolved for reasons other than enticing females, such as detection of fruit or ease of detecting males in different background environments (see M. J. Ryan & Cummings, 2013).

FIGURE 3.4. Female and Male Hummingbirds (*Spathura underwoodi*)



The large tail feathers of the male are a sexually selected trait and likely to be an honest indicator of the males' health but may compromise escape from predators. From *The Descent of Man, and Selection in Relation to Sex* (p. 77), by C. Darwin, 1871, London, England: John Murray. In the public domain.

Female choice of males that look attractive for reasons other than male quality can lead to the exaggeration of these traits in males, but unlike the good genes models do not predict any particular benefit for females or their offspring (e.g., C. A. Marler & Ryan, 1997); these do not exclude the potential for benefits to later evolve (Prum, 2012). In theory, it is possible for traits that are completely arbitrary (or arbitrarily complex; Gerhardt, Humfeld, & Marshall, 2007) with respect to natural selection or male quality to become exaggerated through *runaway selection*. This can occur if the male trait and the female preference for that trait become genetically linked (R. A. Fisher, 1930). Such a link can evolve if daughters inherit a preference for the sexually selected features of their father and if sons inherit these same features. Any such "sexy son" will, especially in polygynous species, enjoy greater reproductive success than the sons of less elaborate males, as long as the female preference does not change (Andersson, 1994) and as long as this trait does not become so exaggerated that it reduces the viability of the males (R. A. Fisher, 1930). In this way, a relatively arbitrary female preference could, in theory, result in the evolution of many of the secondary sex differences described by C. Darwin (1871). In practice, however, it is often difficult to determine exactly what is driving female choice of mating partners and it is difficult to conduct rigorous tests of the predictions of runaway, sexy son models (M. J. Ryan & Cummings, 2013).

An exception is found in a 24-year study of 8,500 collared flycatchers (*Ficedula albicollis*), a species of bird (Qvarnström, Brommer, & Gustafsson, 2006). Qvarnström and colleagues (2006) were able to assess heritable variation in the primary male ornament in this species (a white forehead patch) and heritable variation in the female preference for males with a large patch. The size of the patch and the female preference for large patches showed heritable variation, but the heritable variation in females' preference for this trait was independent of heritable variation in males' patch size. In other words, there was no genetic link between females' preference for male patches and patch size, inconsistent with the sexy son model. Moreover, because of low levels of paternal provisioning and thus poorer health when they fledged, the sons of sexy fathers did not have a large, sexy forehead patch (Gustafsson & Qvarnström, 2006). Although it is possible that runaway selection occurs in some species (Dale, 2006; Prokop, Michalczyk, Drobniak, Herdegen, & Radwan, 2012), for the collard flycatcher and many other species it is more likely that females choose sexy fathers because these males and their sexy sons are healthier, more resistant to parasites, and generally more vigorous than their duller cohorts.

Findings such as these do not rule out the evolution of female choice based on arbitrary traits (e.g., color preference based on color of prey), as there is ample evidence for these types of mate choices (M. J. Ryan & Cummings, 2013). Any such aesthetically based choices, however, do not rule out the later evolution of these traits into signals that females use to assess the direct (e.g., food provisioning) or indirect (e.g., genes) benefits that will be provided by the male (Chandler, Ofria, & Dworkin, 2013). In other words, female choice of aesthetically pleasing males just makes good sense.

Good Genes

Good genes models of sexual selection, of course, focus on the genetic benefits provided by males to offspring, or rather focus on the traits, such as the elaborate mating display of the Argus pheasant (*Rheirihardtius ocellata*; Figure 3.2), that are thought to be associated with the presence of such genes (Møller & Alatalo, 1999). Although there is a general agreement that females and their offspring often benefit by choosing these males, there is debate over other potential benefits (e.g., better parenting skills) and over the more basic biological processes that are signaled by these traits (e.g., Simons, Maia, Leenknegt, & Verhulst, 2014; Weaver, Santos, Tucker, Wilson, & Hill, 2018). The different biological processes associated with good genes models are discussed in Chapter 4 of this volume. For now, the focus is on the actual traits that influence females' choice of one mate over another, and the associated direct (e.g., parental provisioning) and indirect (i.e., offspring genes) benefits to them or their offspring. In practice, it is hard to tease apart the relative contributions of direct and indirect benefits, because males who provide one benefit often provide other benefits. Whatever the combination of direct and indirect benefits, they are often—but not always (Forstmeier, Nakagawa, Griffith, & Kempenaers, 2014)—associated with better health of the males' offspring (B. C. Sheldon, Merilö, Qvarnström, Gustafsson, & Ellegren, 1997) and sometimes their grandoffspring (J. M. Reid et al., 2005).

The traits that females use to choose mates can be quite varied across species, ranging from degree of coloration, vigor of courtship displays, and quality of male song, among others, and more often than not include some combination of traits (Candolin, 2003). To be useful to females, any such traits have to be reliable indicators of the likelihood the male will in fact provide direct or indirect benefits (W. D. Hamilton & Zuk, 1982; Zahavi, 1975). The traits cannot be easily faked by males who cannot provide the benefits. One way in which any such cheating can be reduced is if the expression of these traits is a "handicap," that is, their development and maintenance incurs some costs to males who are not healthy (Getty, 2006; Zahavi, 1975). If unhealthy males cannot express the trait, such as a prolonged courtship display, without compromising their health, then the trait is an honest signal of the male's condition. The traits are *condition dependent*, their attractiveness varies directly with the condition (including genetic condition) of the male (e.g., Faivre, Grégoire, Préault, Cézilly, & Sorci, 2003; for reviews see Cotton, Fowler, & Pomiankowski, 2004; Geary, 2015; Johnstone, 1995).

Although there are questions that remain to be answered (Simons et al., 2014; Weaver et al., 2017), field and experimental studies show that the quality of sexually selected traits is often a good indicator of the males' general health or specific traits (e.g., parasite resistance) that will affect health. There is evidence too that females benefit, either directly or indirectly, from choosing males with attractive sexually selected traits (Cally et al., 2019; Jennions, Møller, & Petrie, 2001; B. C. Sheldon et al., 1997; von Schantz, Wittzell, Göransson, Grahn, & Persson, 1996; Welch, Semlitsch, & Gerhardt, 1998; Welch, Smith, & Gerhardt, 2014; Zuk, Thornhill, Ligon, & Johnson, 1990). W. D. Hamilton and Zuk (1982) hypothesized that the condition of many sexually selected traits is specifically dependent on parasite load. If one of the selection pressures for the evolution and maintenance of sexual reproduction is resistance to parasites, as described in Chapter 2 of this volume, then indicators of parasite resistance would be a good target for female choice. W. D. Hamilton and Zuk argued that the bright plumage of the males of many bird species varies directly with degree of parasite infestation; infected males often sport duller displays than their healthier counterparts (Delhey, Peters, & Kempenaers, 2007), although the strength of this relationship can vary across species (Weaver et al., 2018).

As one example, Zuk et al. (1990) infected a group of male red jungle fowl chicks (*Gallus gallus*) with a parasitic worm (*Ascaridia galli*) and compared the chicks' growth and later success in attracting mates with a group of uninfected males. Infected males grew more slowly than their healthy peers, and as adults their sexually selected characteristics were more impaired than were other physical characteristics. For instance, the comb of affected males was smaller and duller than that of unaffected males, but many other physical traits did not differ across these groups. A mate choice experiment demonstrated two points. First, uninfected males were preferred 2:1 to their parasitized peers. Second, female choice was related to sexually selected traits (e.g., comb length) but not to other physical traits.

As another example, von Schantz et al. (1996) examined the relations between a sexually selected male characteristic, spur length (a projection on the wing of the male), male health, and major histocompatibility complex (MHC) genes in the ring-necked pheasant (*Phasianus colhicus*). Spur length varied with MHC genotype and both were significantly related to the likelihood of survival to 2 years of age. Equally important, males with longer spurs are preferred as mating partners by females and sire offspring with higher survival rates than their cohorts with shorter spurs (von Schantz et al., 1989). An analysis that included 112 species of mammal, including carnivores, primates, rodents, and ungulates, indicated that MHC diversity was consistently related to female choice (Winternitz et al., 2013; but see Kamiya, O'Dwyer, Westerdahl, Senior, & Nakagawa, 2014). More precisely, MHC diversity was higher in species in which females exert more influence over mate choices (e.g., they mate with multiple males), suggesting a strong preference for males with MHC genes that will confer resistance to parasites in their offspring. It is not simply choosing the most-healthy male, but rather a healthy male that also has MHC genes that are moderately different from their own (Neff & Pitcher, 2005). In this way, her offspring have a more diverse set of MHC genes than either parent and are more resistant to local parasites.

Male quality and female choice are not just a matter of parasite resistance or MHC genes. Female choice can, as noted, also be related to any direct benefits provided by males, such as his ability to provide food for or protect offspring. These direct benefits are often associated with indirect, genetic benefits, but this need not be the case (Borgia, 2006; Chastel et al., 2005; Hadfield et al., 2006; Kirkpatrick & Ryan, 1991). As examples of the direct benefits signaled by sexually selected traits, consider two species of socially monogamous—both parents feed and protect offspring—bird, the house finch (*Carpodacus mexicanus*) and eastern bluebird (*Sialia sialis*). Females of both species prefer brightly colored males, and these dapper males are better providers (G. E. Hill, 1991; Siefferman & Hill, 2005). They provide more food to their mate during clutch incubation and more food to the nestlings than do duller males.

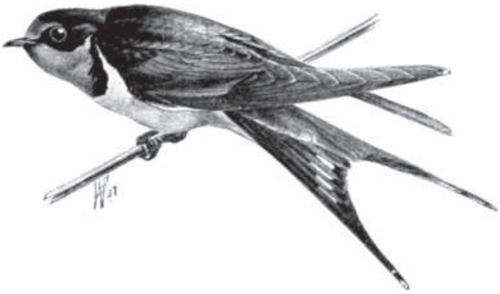
Moreover, different females often prefer different males for reasons other than genetic compatibility (e.g., difference in MHC genes). For species in which males and females form long-term pairs and show biparental care, behavioral compatibility might also influence female choice, as Ihle, Kempenaers, and Forstmeier (2015) found for the zebra finch (*Taeniopygia guttata*). Females that were free to choose their partner showed higher levels of behavioral cooperation with their mate than did females that were not able to choose; in this case, the biologists conducting the study paired the females and males. The behaviorally compatible pairs in turn had higher offspring survival rates. Another example is provided by a study of the brown-headed cowbird (*Molothrus ater*; Ronald, Fernández-Juricic, & Lucas, 2018). In this species, females with good hearing preferred males with a certain type of song and discounted males' visual displays (e.g., spreading their wings), whereas females with better vision preferred males with strong visual displays and discounted song quality.

It is important to note that any males' ability to develop a bright plumage or other sexually selected trait will be influenced by a combination of parental investment (especially his own earlier feeding), current conditions, and genetics (Petrie, 1994). The contributions of genes and environments to the expression of these traits can vary considerably across species, and across breeding seasons of the same species (Hadfield et al., 2006; P. M. Nolan, Hill, & Stoehr, 1998). As a result, a genetically healthy male may at times sport a dull plumage owing to a food shortage early in life, whereas a relatively unhealthy male may sport a brighter plumage during a food glut.

Mate Choice Trade-Offs

There is often a trade-off between the indirect (i.e., genetic) and direct (e.g., food) benefits provided by the male. Sometimes as one goes up, the other goes down (Reed et al., 2006). As an example, female barn swallows (*Hirundo rustica*), at least in northern Europe, choose mates based in part on the length of males' tail streamers, as shown in Figure 3.5 (Hasegawa & Arai, 2015; Romano, Costanzo, Rubolini, Saino, & Møller, 2017); other traits are important as well (e.g., plumage color) depending on the subspecies (Safran et al., 2016). In northern Europe, males with long streamers obtain mates more quickly, are more likely to sire a second brood during any given breeding season, and obtain more extra-pair copulations than their peers (Costanzo et al., 2017;

FIGURE 3.5. Male Barn Swallow (*Hirundo rustica*)



In several subspecies, the length of the tail streamers is attractive to females and is an indicator of male health. From *Birdcraft: A Field Guide of 200 Song, Game, and Water Birds* (p. Plate 24), by M. O. Wright, 1895, New York, NY: Macmillan and Co. In the public domain.

Safran et al., 2016; Vortman, Lotem, Dor, Lovette, & Safran, 2011). These preferred males also mate with higher quality females, as indexed by the quantity of food provided by the female to their offspring. However, unlike the sexually selected traits of the male house finch and bluebird, this sexually selected trait is not a good indicator of later investment in offspring; in fact, it indicates lower than average investment, because attractive males seek extra-pair females instead of investing in offspring. Despite this cost, the parasite resistance and general health indicated by streamer length—and plumage color in other subspecies—is heritable and conveys indirect benefits in terms of healthier offspring (Hasegawa, Arai, Watanabe, & Nakamura, 2014; Møller, 1994; Romano, Saino, & Møller, 2017).

Females also have to balance the benefits of finding high-quality mates against the time and risks (e.g., of predation) associated with searching for better and better males. Gerhardt, Tanner, Corrigan, and Walton (2000) demonstrated this trade-off with the preference functions—How much is enough?—of female gray tree frogs (*Hyla versicolor*). In this species, females choose mates on the basis of the duration of the males' courtship call. Females prefer males with longer calls, and the offspring of these males are healthier than the offspring of males with shorter calls (Welch et al., 1998); males do not provide any direct benefits, and therefore this is a heritable good genes effect. Gerhardt and colleagues presented females with pairs of males with shorter and longer courtship calls. When the duration of both calls was below average, females almost always preferred the longer call. When the duration of both calls was above average, the female preference for the longer call was much weaker. In other words, females consistently reject males with below average courtship calls, but once they find an above average male, they are less likely to reject this male for a marginally better one. Choosing a good enough male makes the search for a suitable mate easier and reduces the chances of predation before having the opportunity to reproduce.

Cryptic Postcopulatory Choice and Sperm Competition

In contrast to the conspicuous traits associated with females' behavioral choice of one mate over another, cryptic choice occurs within the females' reproductive tract and often co-occurs with sperm competition—sperm from different males compete to fertilize the egg or eggs (Andersson & Simmons, 2006; Bernasconi et al., 2004; Birkhead & Møller, 1998; Gil, Graves, Hazon, & Wells, 1999). Cryptic choice and sperm competition are associated with polyandry, where females mate with multiple males, and with an inability of dominant males to monopolize access to females, either through female choice or male–male competition (Simmons, Lüpold, & Fitzpatrick, 2017). In other words, when female choice or male–male competition results in only small number of males mating with most females, there tend to be conspicuous traits associated with competition and choice. If females mate with several males and many males mate with one or more females, then choice and competition can become cryptic.

Cryptic choice can occur in many ways, such as the physical ejection of sperm, changes in the biochemistry (e.g., pH levels) of the reproductive track that influence sperm viability, and storage of sperm from multiple males for later fertilization (Firman, Gasparini, Manier, & Pizzari, 2017; Neff & Pitcher, 2005). Females appear to benefit from polyandry and cryptic choice by higher fertility, reduction of inbreeding, selection of sperm from males with compatible MHC genes, and perhaps more attractive or healthier offspring (Firman et al., 2017; Kvarnemo & Simmons, 2013; Slatyer, Mautz, Backwell, & Jennions, 2012). In some species, cryptic choice and sperm competition work in concert, resulting in the healthiest males siring the most offspring (Bjork & Pitnick, 2006; Simmons & Kotiaho, 2007). In other cases, conflict between the best interests of males and females can result in the evolution of sperm that disable cryptic choice (Bernasconi et al., 2004).

Whatever the dynamics, polyandry and cryptic choice favor the evolution of traits that facilitate sperm competition. These traits can include the evolution of larger testes and the production of more sperm or sperm with other characteristics (e.g., size, speed) that result in a competitive advantage over other males (Lüpold et al., 2016; G. A. Parker & Pizzari, 2010). In some cases, conspicuous traits that influence female choice or male–male competition are an indicator of the males' sperm quantity or quality (e.g., Malo, Roldan, Garde, Soler, & Gomendio, 2005). Malo et al. (2005) found that the size and complexity of the antlers of male red deer (*Cervus elaphus*; see Figure 3.6) predicted sperm quality. More often than not, however, there is a trade-off. Investment (e.g., calories, nutrients) in traits that attract females, such as a vigorous courtship display, can compromise sperm production (Simmons et al., 2017) such that investment in sperm quantity and quality is often associated with less conspicuous traits.

Within the same species, males can sometimes differ in how much they invest in the development of conspicuous traits versus sperm characteristics (J. P. Evans, 2010). J. P. Evans (2010) found that colorful male guppies (*Poecilia reticulata*) that court females and are preferred by them have slower sperm than do duller males. There was a negative genetic correlation between male color and sperm quality, indicating an evolved trade-off. The dull males, in contrast, had higher quality sperm and generally attempt to sneak copulations with females. There is an evolved bias to sneak copulations or court females and this behavioral bias is associated with more or less investment in sperm production. Even individual males can vary in investment in sperm quality and quantity, depending on his health and social context. Cornwallis and Birkhead (2007) demonstrated that dominant male red jungle fowl produce more sperm than subordinate males. Experimentally reversing the status of males changed the amount of sperm produced per copulation; an increase in status resulted in more sperm production and a decrease resulted in less production. Dominant males also produced more sperm and faster sperm when they copulated with attractive females, but the quantity and quality of subordinate males' sperm did not vary across attractive and less attractive females.

FIGURE 3.6. Antlers of the Male Red Deer (*Cervus elaphus*)

The size and complexity of the antlers influence male–male competition but may also be correlated with sperm quality. Photo by Bill Ebbesen. Retrieved from https://commons.wikimedia.org/wiki/File:Red_deer_stag_2009_denmark.jpg. Licensed under Creative Commons Attribution 3.0 Unported. https://creativecommons.org/licenses/by/3.0/deed.en. Reprinted with permission.

Mate Choices and Social Context

For some species, female mate choices appear to be influenced by the mate choice decisions of other females and sometimes through monitoring the results of male–male competition. Sensitivity to this social information could reduce the costs (e.g., reduced foraging time, predation risk) of evaluating and choosing a suitable mate, and may be particularly helpful in ambiguous situations, those that involve discriminating between closely matched males (Pruett-Jones, 1992). Female mate copying has been consistently found in a species of guppy (*Poecilia reticulata*), the sailfin molly (*Poecilia formosa*), and in the Japanese quail (*Coturnix japonica*; Dugatkin, 1996; Dugatkin & Godin, 1993; Galef & Laland, 2005; Heubel et al., 2008). Mate copying has also been found in several species, such as the pipefish, in which males invest more in parenting than females and can occur even in the absence of parental investment (Widemo, 2006; K. Witte, Kniel, & Kureck, 2015). Mate copying is not universal, however, and when it is found, it is more common in species with promiscuous female mating and less common in monogamous species with biparental care of offspring (Vakirtzis, 2011; Vakirtzis & Roberts, 2009).

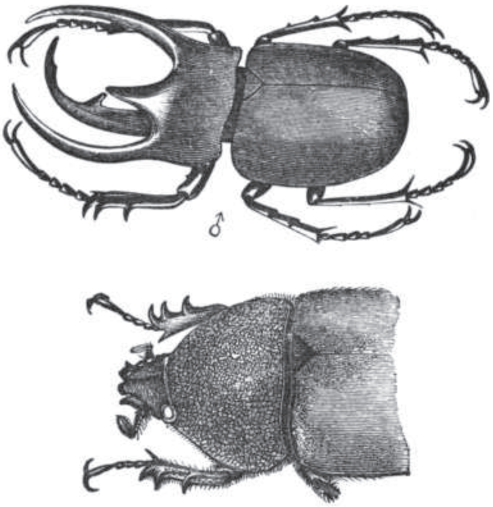
In one illustration of mate copying, the preference of female guppies for orange-colored males was pitted against the choice of another female (Dugatkin, 1996). Imitation was assessed under four conditions: The male courted by the model was paired with another male with equal orange coloring, or with a small (12%), moderate (24%), or large (40%) advantage in the proportion of coloration. When there was no model to imitate, females chose the more colorful male about nine out of 10 times. However, when the model chose the less colorful male, the observer chose the same male about four out of five times, except when the coloration differences between the males was large. These results suggested that females used the mate choices of other females to decide between two similarly attractive males. However, imitation of mate choices has not been found in all populations of guppy (Brooks, 1999) and does not occur in all species (Clutton-Brock & McComb, 1993).

Females sometimes use the outcomes of male–male competition to make their mate choices. Under some conditions and for some species, females prefer dominant males, but this is not always the case, as dominant males might be lacking in other traits (e.g., parenting; see Wong & Candolin, 2005). Still, there are contexts in which females do use this information in their mate choices and may even incite male–male competition to determine the more dominant male. For example, dominance in the black-capped chickadee (*Poecile atricapilla*) is determined by the length and complexity of male–male song contests that function to maintain territorial boundaries. In one experiment, the length and complexity of these contest songs were manipulated such that dominant males lost several of the contests (Mennill, Ratcliffe, & Boag, 2002). Females paired with these once high-status males began engaging in extra-pair copulations such that these males were cuckolded (i.e., raised the offspring of other males) more than 50% of the time for their next brood. Females appear to “eavesdrop” on male–male contests, and if their own mate slips in these dominance encounters, they seek extra-pair mates.

MALE–MALE COMPETITION

The males of many species are not only more ornamented than females, they are also often larger and at times sport some type of armament. Male armament of one type or another is in fact found across a wide variety of species ranging from insects (see Figure 3.7) to mammals (see Figure 3.8). Many of these traits may serve as ornaments that influence female choice and armaments for male–male competition (Borgia, 2006), whereas others are just armaments for male–male competition (i.e., they are not influenced by female choice; McCullough, Miller, & Emlen, 2016). These armaments are almost always used in direct physical competition between males for the establishment of

FIGURE 3.7. Male and Female Beetles (*Chalcosoma atlas*)



Males compete by searching for mates in trees and hook their mandibles under the wings of competitors and attempt to throw them from the tree. From *The Descent of Man, and Selection in Relation to Sex* (p. 368), by C. Darwin, 1871, London, England: John Murray. In the public domain.

social status or for the direct control of mating territories or mates themselves (Andersson, 1994). Female–female competition over mates occurs in some species (e.g., the red-necked phalarope), but it is typically less common or at least less intense than male–male competition (Janicke et al., 2016).

Male–male competition will be particularly intense in species in which males have a higher potential reproductive rate and invest less in parenting than females and have the ability to monopolize sexual access to multiple females (S. T. Emlen & Oring, 1977). One consequence is the evolution of traits—and the underlying pattern of sex-specific gene expression (Poissant, Wilson, & Coltman, 2010)—that provide males with a competitive advantage, but with the cost of a shorter overall lifespan and a shorter reproductive lifespan (i.e., breeding cycles) than females (Clutton-Brock & Isvaran, 2007; Lukas & Clutton-Brock, 2014). Although much of the associated research is focused on observable physical traits, males can also compete behaviorally or in terms of cognitive traits. The following sections illustrate each of these different manifestations of male–male competition.

Physical Competition

This section focuses on how physical male–male competition influences social dominance and how this in turn is related to males' reproductive success. Males that are not successful in these dominance contests do not give up the fight, so to speak, but rather use alternative reproductive strategies to gain access to females.

FIGURE 3.8. The Male Kudu (*Tragelaphus strepsiceros*)

Males compete by locking horns and pulling and pushing each other as a display of physical strength and stamina. Females are hornless. From *The Descent of Man, and Selection in Relation to Sex* (p. 255), by C. Darwin, 1871, London, England: John Murray. In the public domain.

Fighting for Social Dominance

The dynamics and consequences of physical male–male competition are nicely illustrated by studies of the northern (*Mirounga angustirostris*) and southern (*Mirounga leonina*) elephant seal (C. Casey, Charrier, Mathevon, & Reichmuth, 2015; C. R. Cox & Le Boeuf, 1977; Haley, Deutsch, & Le Boeuf, 1994; Hoelzel, Le Boeuf, Reiter, & Campagna, 1999; Le Boeuf, 1974; Le Boeuf & Peterson, 1969). As with many mammalian species, the life histories (e.g., age of first reproduction) and balance of effort devoted to mating and parenting differ markedly for males and females of these species. Male northern elephant seals provide no parental care, become sexually active around 8 years of age (compared with 3 years of age for females), and differ greatly in the number of offspring they sire. The principle factor governing variation in males' reproductive success is one-on-one competition for access to groups of females.

During the breeding season, female elephant seals aggregate on relatively confined beaches and their male conspecifics compete physically with one another for sexual access to these females. One such encounter is illustrated in Figure 3.9 for a pair of northern males. These encounters consist of two males rearing up on their foreflippers

> and trumpeting individually distinct calls . . . at one another. In most cases, one of the males retreats at this stage; if neither male submits, a fight ensues. The two males approach one another and push against each other chest to chest, while delivering open mouth blows and bites at each other's neck, flippers and head. (Haley et al., 1994, p. 1250)

Success in these bouts is related to physical size, age, and duration of residency (i.e., established males as opposed to newcomers) and determines social dominance. Social dominance, in turn, influences reproductive outcomes (Haley et al., 1994; Le Boeuf, 1974). For instance, less than one out of 10 northern males survives to age 8, and less than half of these males mate at all. Among the males that do mate, mating is largely monopolized by socially dominant individuals. On the basis of behavioral observation, Le Boeuf and colleagues (Le Boeuf & Peterson, 1969; Le Boeuf & Reiter, 1988) estimated that the net result of mortality and male–male competition is that fewer than 5% of males sire between 75% and 85% of all pups, although DNA fingerprinting studies suggest that this is an overestimate (Hoelzel et al., 1999).

In any case, one consequence of intense male–male competition is that selection favors the evolution of characteristics that aid males in their quest for social dominance. Size matters for northern and southern elephant seals

FIGURE 3.9. Competition Between Two Male Elephant Seals (*Mirounga angustirostris*)

Photo by Dawn Endio, 2004. Retrieved from https://upload.wikimedia.org/wikipedia/commons/5/5a/Males_Mirounga_angustirostris_fighting_4.jpg. Licensed under Creative Commons Attribution-Share Alike 2.0 Generic license. https://creativecommons.org/licenses/by-sa/2.0/deed.en. Reprinted with permission.

(Lindenfors, Tullberg, & Biuw, 2002). In both species, mature males weigh between 3 and more than 8 times as much as mature females (Le Boeuf & Reiter, 1988; Lindenfors et al., 2002). Although the physical dimorphism of these seals is on the extreme side, it is by no means uncommon. Sex differences in physical size or armament, as well as behavioral aggressiveness, are common for those species in which males physically compete for social status, territory, or direct access to females (Andersson, 1994; Clutton-Brock, Harvey, & Rudder, 1977; C. Darwin, 1871; Schuett, Tregenza, & Dall, 2010).

Sneaky Males and Alternative Mating Strategies

At times, smaller and socially subordinate male elephant seals sire offspring by "sneaking" into harems and mating with females. This happens because these subordinate males resemble females and therefore do not elicit an aggressive response from dominant males (Le Boeuf, 1974). In a study of the relation between mating access and paternity determined by DNA fingerprinting, Hoelzel et al. (1999) confirmed that alpha males in northern and southern elephant seal colonies tended to monopolize mating access. Among the northern elephant seal, there were on average nine males in and around each harem of females. The alpha male achieved 52% of the copulations, or about 5 times the expected rate if access was egalitarian. Paternity tests revealed something else. Alpha males, on average, only sired 40% of the pups. Some of the remaining pups were sired by a recently displaced alpha male or an alpha male from an adjacent harem, but others were sired by subordinate or "sneaker" males.

Moreover, C. R. Cox and Le Boeuf (1977) suggested that female choice may influence reproductive dynamics in elephant seals. Northern females will often "protest" through threat vocalizations the sexual advances of males. These protests, in turn, incite male-on-male aggression, effectively disrupting the mating attempt. Females protest more often when approached by low-ranking than by high-ranking males and their protests are more likely to result in mating disruptions for low-ranking than for high-ranking males. The net effect is an increase in the likelihood that a socially dominant male will sire her offspring, although the DNA paternity results suggest that females may at times prefer to mate with subordinate males.

The northern elephant seal provides just one example of an alternative mating strategy. More examples are presented in the following chapter, as alternative strategies are common (e.g., Magalhaes, Smith, & Joyce, 2017; Wellenreuther, Svensson, & Hansson, 2014) and can reduce the strength of the relationship between the physical and other traits that support social dominance and reproductive outcomes (Isvaran & Sankaran, 2017). In this example, the result is that dominant northern elephant seals are not as large as they might otherwise be, if subordinate males never reproduced.

Behavioral Competition

The bower building of male bowerbirds provides an intriguing example of a complex suite of behaviors that evolved by means of sexual selection

FIGURE 3.10. Bower of the Satin Bowerbird (*Ptilonorhynchus violaceus*)

Males compete by building structures (bowers) that attract potential mates. Photo by Carl Gerhardt. Reprinted with permission.

(Gilliard, 1969); an example of one such bower is shown in Figure 3.10. Bowers are structures that are typically built from twigs and leaves, are decorated with feathers, flowers, shells, bones, and other objects, and serve as a courtship arena, not as nests. The complexity of the bower and the decorations around it influence female choice and are often the focus of male–male competition. The bowers are not the only traits that influence choice and competition—male courtship displays at the bower and male–male fighting are also important—but are an integral part of them (Borgia, 2006; S. W. Coleman, Patricelli, & Borgia, 2004).

In most species, the males' bower provides a good indicator of overall male health (Borgia, 1985a, 1995a, 1995b; Doerr, 2010). Larger, healthier males build bowers that are more attractive to females. Bower quality, as measured by the number of female visitations, is related to overall symmetry of the structure, the types of objects used as decorations, and in some species to bower painting and other species to male displays of colorful objects to females situated within the bower (Bravery, Nicholls, & Goldizen, 2006; Endler, Gaburro, & Kelley, 2014; Hicks, Larned, & Borgia, 2013; L. A. Kelley & Endler, 2012); painting involves males chewing on vegetation and painting the inside of their bower with the plant-saliva mixture. In an extensive series of observational studies of the satin bowerbird (*Ptilonorhynchus violaceus*), Borgia found that 16% of the males fathered most of the offspring and that their success in attracting females was strongly related to the symmetry of their bower, the overall density of construction (i.e., number of sticks), and decoration with relatively rare blue flowers and snail shells (Borgia, 1985a); DNA fingerprinting confirms these males sire the vast majority of offspring (S. M. Reynolds et al., 2007).

Skill at constructing and maintaining high-quality bowers is related to a number of factors, including age, social learning, and social dominance

(Borgia, 1985b; Borgia & Wingfield, 1991; Collis & Borgia, 1992; Pruett-Jones & Pruett-Jones, 1994). Social dominance is determined by the outcomes of male–male threats and other agonistic behaviors at communal feeding sites and influences an important form of male–male competition—the destruction of one another's bowers and the stealing of colorful objects (Borgia, 1985b; Doerr, 2010; Wojcieszek, Nicholls, Marshall, & Goldizen, 2006). Bower destruction and decoration-stealing lower the quality of their competitors' bowers and reduce the likelihood that these competitors will find mates (Pruett-Jones & Pruett-Jones, 1994). In studies of the satin bowerbird, Borgia (1985b) found that socially dominant males were more likely to destroy their neighbor's bowers, and Doerr (2010) found that they were less likely to have objects stolen from their bower. The bowers of socially dominant males were just as likely to be attacked as those of their less dominant peers—attacks almost always occur when the male is not at the bower—but attackers spend less time at the bowers of dominant, relative to subordinate, males. "Threat posed by more aggressive males may cause destroyers to avoid long visits at their bowers, thereby reducing the possibility of the destroyer being caught in the act of destruction" (Borgia, 1985b, p. 97). The net result is that less damage is inflicted on the bowers of socially dominant birds, which, in turn, yields an important advantage in attracting mates.

In all, sexual reproduction in bowerbirds involves a mix of female choice and male–male competition. The most intriguing feature of these behaviors is that male–male competition is not primarily based on physical prowess, but rather on skill at constructing relatively complex structures and on strategic raids of competitors' bowers. These studies clearly indicate that sexual selection can act to create systematic behavioral differences between males and females (see also Schuett et al., 2010).

Brain and Cognitive Competition

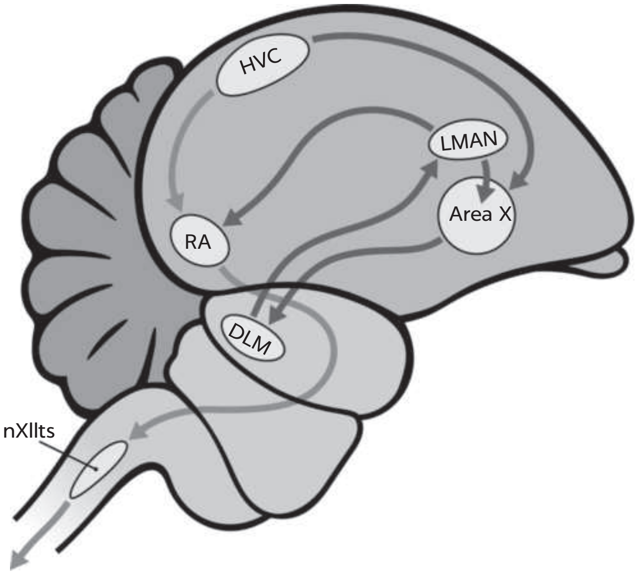
Given the complexity of bower building, it is not surprising that these species have larger brains than do other species that live in the same habitat but do not build bowers (Madden, 2001). For the family of bowerbirds and especially for males, species with more complex bowers have a larger cerebellum than their less sophisticated cousins (L. B. Day, Westcott, & Olster, 2005). The relation between cerebellum size and bower complexity is interesting, because this brain region is important for procedural learning through social observation (Leggio et al., 2000); immature male bowerbirds perfect their bower building prowess through the observation and imitation of older males (Collis & Borgia, 1992). These patterns indicate that sexual selection can shape cognitive traits and the supporting brain systems in the same manner as physical and behavioral traits, if these brain and cognitive competencies influence reproductive outcomes. The next sections illustrate how sexual selection can result in sex differences in brain and cognition using bird song and spatial navigation.

Bird Song

Males' songs have two distinct features, one that influences female choice and another that signals dominance and territorial control to other males (Ball & Hulse, 1998). Song learning and production are ideal for illustrating how sexual selection can influence sex differences in brain and cognition, because the underlying neural systems are well understood (DeVoogd, Krebs, Healy, & Purvis, 1993; Nottebohm, 1970, 2005). A schematic of the basic organization of this brain system is shown in Figure 3.11. Birds learn by generating songs themselves and comparing these against previously heard songs (e.g., from their fathers) stored in memory. Through trial-and-error adjustments, they eventually generate songs that match previously heard ones. Of the areas shown in the schematic, the HVC (sometimes called the higher or high vocal center) is central to the production of these learned songs, acting in concert with the RA (robustus arcopallium). The projections from the LMAN (lateral magnocellular nucleus of the nidopallium) to the RA are important for the trial-and-error learning that leads to the creation of an attractive song (Kao, Doupe, & Brainard, 2005; Ölveczky, Andalman, & Fee, 2005).

In any case, sex differences in the size of the HVC, RA, and Area X (involved in learning routines) are well documented and are quite large (Nottebohm,

FIGURE 3.11. Brain Systems That Support Bird Song



HVC is not an acronym but is sometimes termed higher (or high) vocal center; RA = robust nucleus of the arcopallium; nXIIts = tracheosyringeal half of the hypoglossal nucleus; LMAN = lateral magnocellular nucleus of the nidopallium; DLM = dorsolateral anterior thalamic nucleus; Area X = portion of the basal ganglia. From "The Neural Basis of Birdsong," by F. Nottebohm, 2005, *PLoS Biol 3*(5), e164. Licensed under Creative Commons Attribution-Share Alike 2.0 Generic license. https://creativecommons.org/licenses/by-sa/2.0/deed.en. Reprinted with permission.

2005; Nottebohm & Arnold, 1976). For instance, the size of the HVC can be 3 to 8 times larger in males than in females, depending on the species. For seasonal breeders, the magnitude of these differences becomes most pronounced during the breeding season (Nottebohm, 1981), consistent with hormonal influences on these differences (Alward, Cornil, Balthazart, & Ball, 2018; see Chapter 4, this volume). Nottebohm (1980) demonstrated that testosterone implants greatly increase the size of the HVC and RA in female canaries (*Serinus canarius*) and induce male-like song; male castration reduces the size of these areas and impairs song production. In some species, sex hormones also influence the ways in which these brain areas respond to early environmental cues (e.g., father's song) and song expression in adulthood (Ball & Hulse, 1998). In other words, the learning and later expression of sexually selected songs typically requires early exposure to song (Petrinovich & Baptista, 1987) and exposure to male hormones (DeVoogd, 1991).

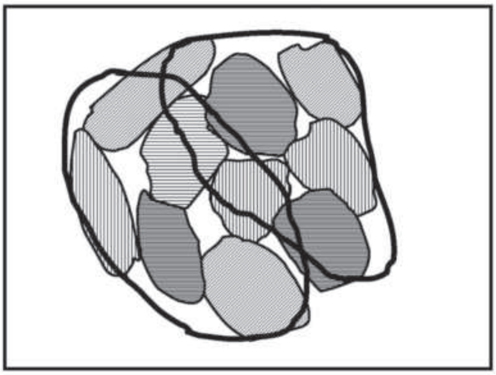
Spatial Navigation

Studies of scramble competition—searching for mates that are dispersed throughout the ecology—provide another example of how sexual selection can shape sex differences in brain and cognition (Gaulin, 1992). With this type of competition, males expand their range during the breeding season to search for potential mates. The dynamics are nicely illustrated by comparing the polygynous meadow vole (*Microtus pennsylvanicus*) with their monogamous cousins, the prairie (*Microtus ochrogaster*) and woodland vole (*Microtus pinetorum*). During the breeding season, male meadow voles expand their range to at least 5 times the area of females' territory, whereas male and female prairie and woodland voles share overlapping ranges of about the same size, as shown in Figure 3.12. Range expansion and the ensuing mate searches favor males with enhanced spatial and navigational abilities. Laboratory and field studies show that male meadow voles have better spatial learning and memory than female meadow voles or male prairie and woodland voles (Gaulin & Fitzgerald, 1986). Follow-up studies have shown that male meadow voles with above average spatial abilities visit more females and generally have higher reproductive success than their lower ability peers (Spritzer, Solomon, & Meikle, 2005). The same pattern of species- and sex-differences in spatial abilities related to scramble competition has now been demonstrated with other mammals (Jašarević, Williams, Roberts, Geary, & Rosenfeld, 2012; Perdue, Snyder, Zhihe, Marr, & Maple, 2011), and the sex difference in at least one species of fish (Lucon-Xiccato & Bisazza, 2017).

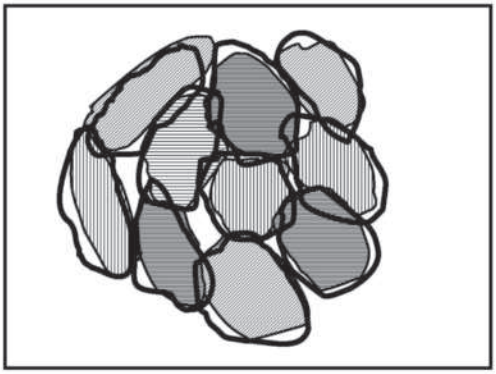
Spatial navigation in turn is highly dependent on an area of the brain called the hippocampus, among other areas (O'Keefe & Nadel, 1978). The entire volume of the hippocampus is not necessarily larger in males that engage in scramble competition (Galea, Perrot-Sinal, Kavaliers, & Ossenkopp, 1999; L. F. Jacobs, Gaulin, Sherry, & Hoffman, 1990). Rather, the function of specific areas that support spatial learning and memory differs for males and females (Galea, 2008; Kee, Teixeira, Wang, & Frankland, 2007; Ormerod, Lee,

FIGURE 3.12. Male Scramble Competition and Male Monogamy

Male Scramble Competition



Male Monogamy



With male scramble competition (top panel), males compete by searching for females whose territories (filled shapes) are dispersed throughout the habitat. Male territories (bold open shapes) will encompass that of many females, and males may physically attack one another in those regions in which their territories overlap. With monogamy and male parental investment (bottom panel), the territories of mates largely overlap.

& Galea, 2004). As is discussed further in Chapter 4 of this volume, the hormone- and season-dependent generation, survival, and incorporation of new cells into the spatial memory networks of the hippocampus are particularly important (Galea & McEwen, 1999; Ormerod & Galea, 2001). Kee et al. (2007) found that male engagement in spatial learning enhanced integration of cells into spatial memory networks, and Ormerod and Galea (2003) found greater cell integration in this region for male meadow voles during the breeding season, although much remains to be learned about these brain mechanisms and spatial abilities (Spritzer et al., 2017).

None of this should be taken to mean that females of all species have less elaborated spatial abilities than males. As noted, there are no sex differences when males do not engage in scramble competition and males and females share an overlapping territory (Gaulin & Fitzgerald, 1986; Jašarević et al., 2012; Perdue et al., 2011). In fact, when females have larger territories than males or use these territories in more complex ways, females should have better developed spatial abilities, which is exactly what has been found for the brown-headed cowbird (*Molothrus ater*), a brood parasite. Females of this species lay their eggs in the nests of host species and need to remember the location of these nests so they can deposit their eggs at times when the unwitting host will accept them. Females of this species have a better spatial memory than males when tested in a large-scale space (Guigueno, Snow, MacDougall-Shackleton, & Sherry, 2014). Females of this species also have a larger hippocampus than males, but there is no sex difference in a related cowbird species (*Molothrus rufoaxillaris*) in which both sexes search for host nests (Reboreda, Clayton, & Kacelnik, 1996).

MALE CHOICE AND FEMALE–FEMALE COMPETITION

C. Darwin (1871) and subsequent naturalists largely focused on female choice and male–male competition, which is understandable given the ubiquity of these two components of sexual selection (Andersson, 1994). But males, too, are sometimes choosy when it comes to mates and females often compete aggressively for mates or other resources. As might be expected, males are choosy when they invest heavily in parenting and, even in the absence of parental investment, when females differ in health or other traits that influence their ability to bear healthy offspring or their ability to later invest in them. West-Eberhard (1983) proposed that competition for resources other than mates is a form of social selection—evolutionary pressures resulting from competition with members of the same species—and that sexual selection is subset of these pressures. From this broader perspective, female–female competition is expected over access to any resources (e.g., high-quality foods) that influence their reproductive prospects, in addition to competition over males. The net result is that sexual selection and social selection more broadly influence the evolution of male and female traits that facilitate competition and attract quality mates. Even so, the overall influence of sexual selection—the rigors of competition and the choosiness of the opposite sex—is stronger in males than females, with the exception of species in which males provide most or all of the parental care and females are the more competitive sex (Janicke et al., 2016).

Male Choice

Choosy males are much more common than once thought and have been found in dozens of species of insect (Bonduriansky, 2001), as well as many species of fish (Berglund & Rosenqvist, 2001; Guevara-Fiore & Endler, 2018; Widemo, 2006), bird (Amundsen & Pärn, 2006; Pizzari, Cornwallis, Løvlie, Jakobsson, & Birkhead, 2003), reptile (Weiss, Kennedy, & Bernhard, 2009), and mammal (Fitzpatrick, Altmann, & Alberts, 2015; M. N. Muller, Thompson, & Wrangham, 2006). Across these species, male preference for one mate or another is influenced by indicators of female sexual receptivity and the likelihood of conception, as well as by female social dominance, health, and indicators of the quality of parental care the female is likely to provide. Male choice is also tied to male–male competition (e.g., the risk of sperm competition, the intensity of female courtship demands; Edward & Chapman, 2011). More demanding courtships necessarily reduce the number of females that can be courted and this in turn means that males must discriminate between those to be courted and those to be ignored.

Mutual mate choices are expected in species in which both parents invest in offspring, as is the case for most bird species. The barn owl (*Tyto alba*) provides one example. Females of this species display a varying number of black spots on their breast plumage, and these in turn are an indicator of female but not male health, as well as an indicator of the health and immunocompetence of her offspring (Roulin, 2004; Roulin, Jungi, Pfister, & Dijkstra, 2000; Roulin, Riols, Dijkstra, & Ducrest, 2001). Critically, males prefer females with these plumage spots and invest more in offspring when paired with these females relative to when they are paired with less attractive ones (Roulin, 1999). Conspicuous traits among female birds are also found when males and females form long-term pairs and predation risks are low (Dale, Dey, Delhey, Kempenaers, & Valcu, 2015); the latter reduces the costs of these signals and favors their evolution even when females invest more in parenting and males compete more intensely.

Male mate choices can also be found in species in which males do not invest in offspring, such as the red jungle fowl (Pizzari et al., 2003). Female jungle fowl sport red combs, although smaller and less colorful than those of males. Females with relatively large combs produce larger eggs with more yoke than their peers, and males prefer to mate with these females. Moreover, when mated with attractive females, males transfer more sperm, indicating cryptic choice in addition to behavioral choice. Males sometimes copy the mate choices of other males, at least in the pipefish (Widemo, 2006), where males provide all of the parental care. As noted earlier, in these sex-role-reversed species, females are often more colorful than males and use behavioral aggression to assert dominance over other females, both of which can influence male choice (Cunha, Berglund, & Monteiro, 2017; Flanagan, Johnson, Rose, & Jones, 2014).

Female–Female Competition

Female–female competition is now well recognized (Lyon & Montgomerie, 2012; Stockley & Bro-Jørgensen, 2011; J. A. Tobias, Montgomerie, & Lyon, 2012; West-Eberhard, 1983). The traits that facilitate this competition are often less conspicuous and less costly to produce than those of males, but they do exist. At one time, these traits were thought to be the result of genetic correlations—females have these traits because of genes inherited from their fathers and not because of female–female competition or male choice

(Lande, 1980). This might be the case for some species, but it is not the case for others (West-Eberhard, 1983). It is now known that many elaborated traits in females (e.g., the red comb of female jungle fowl) are used in status-related competition with other females, in territorial defense against predators or conspecifics of both sexes, or as indicators of fertility or parental behavior in species with male choice (Clutton-Brock, 2009; Kraaijeveld, Kraaijeveld-Smit, & Komdeur, 2007). In many of these species, females form dominance hierarchies that in turn determine priority access to resources that can influence the females' and their offspring's health.

The Soay sheep (*Ovis aries*) provides another example (Clutton-Brock & Pemberton, 2004). Males grow either large horns that are used in male–male competition or smaller horns; males with smaller horns do not compete directly for females but rather attempt to mate opportunistically (i.e., they are sneakers; Clutton-Brock, Wilson, & Stevenson, 1997). Females can grow smaller or larger horns as well, although some are hornless. For males, horn length, body size, and testes size (related to sperm competition) all independently predict male reproductive success (B. T. Preston, Stevenson, Pemberton, Coltman, & Wilson, 2003). M. R. Robinson and Kruuk (2007) demonstrated that females with larger horns had an advantage over their smaller-horned peers during aggressive interactions, but not over access to mates. Instead, female-on-female aggression increases when food becomes scarce and when they have offspring. During these times, horned females are better able to procure food and protect their offspring by intimidating or fending off other females and as a result enjoy higher reproductive success (Clutton-Brock et al., 1997).

These results show that female horns are socially selected weapons that allow females to compete better, not for mates, but for access to limited ecological resources. Female Soay sheep are not alone, as similar results have been found for female red deer (Clutton-Brock, Major, & Guinness, 1985), the cooperatively breeding meerkat (*Suricata suricatta*; Clutton-Brock et al., 2006), and various species of bird (J. D. Reynolds & Székely, 1997), insect (Lorch, 2002), and fish (Berglund et al., 1997; A. B. Wilson et al., 2003). Females also compete directly over access to males, when males provide extensive parental care or other limited resources, such as social protection (Palombit, Cheney, & Seyfarth, 2001), and when females are polyandrous and each male provides some resources (Kvarnemo & Simmons, 2013).

CONCLUSION

Following the evolution of sexual reproduction, the search for a mate or mates became a central issue in the life history of individuals. In fact, sexual reproduction necessarily results in variation in the quality of potential mates and this variation in turn sets the stage for sexual selection and the evolution of sex differences (C. Darwin, 1871). The dynamics of sexual reproduction are typically played out through female choice of mating partners and male–male competition for social dominance, control of the resources that females need to reproduce (e.g., nesting sites), or direct control of mates, each of which can influence which males sire offspring and which do not. The intensity and specifics of female choice and male–male competition varies widely across species and ecologies (S. T. Emlen & Oring, 1977), but they follow from well-understood evolutionary principles (Andersson, 1994).

Across species, female choice tends to focus on those characteristics that are an honest—not easily faked—signal of male quality (Zahavi, 1975), the indirect (i.e., genetic) and direct (e.g., food provisioning) benefits the male can provide. These signals in turn are expressed through males' secondary sexual characteristics, which can range from the brightly colored plumage of the males of many species of bird, to male song, to the complex suite of behaviors necessary to build and maintain bowers (Amundsen & Pärn, 2006; Borgia, 1985b; W. D. Hamilton & Zuk, 1982). The expression of these characteristics is typically costly for the male. In most cases, it appears that only healthy males can develop the quality of secondary sexual characteristic necessary to attract mates and therefore sire offspring. The net result is that a few males sire many offspring and many males never reproduce. Male–male competition typically has the same effect. In some cases, males compete for direct access to sexually receptive females or for control of the resources that females need to reproduce. In other cases, males compete on those traits that females use in their choice of mating partners.

The traditional focus on female choice and male–male competition does not belie their counterparts (i.e., male choice and female–female competition). These aspects of sexual selection have now been observed across a wide variety of species (e.g., Berglund et al., 1997) and in response to many of the same social and ecological factors that influence the evolution and expression of female choice and male–male competition (S. T. Emlen & Oring, 1977; A. B. Wilson et al., 2003). In species in which males parent, they compete less intensely for mates and are more discriminating in their choice of mates than are nonpaternal males in related species. When males parent, they become an important resource over which females compete, in the same way that males compete over mates in species in which females provide most of the parental investment. In some cases, males are choosy even when they do not invest in parenting (Pizzari et al., 2003), and females often compete with one another for resources other than males (West-Eberhard, 1983).

In many species, these aspects of sexual selection are expressed less intensely than female choice and male–male competition, but they are expressed nonetheless. Whether sexual reproduction centers on female choice, male–male competition, male choice, female–female competition, or some combination, the result is the evolution of sex differences for those traits that facilitate choice and competition. Any such differences may be more evident in either females or males, and may involve physical, behavioral, or brain and cognitive traits.

4

Sexual Selection and Life History

Life history is the study of the pace of development, the timing of key milestones (e.g., ages of menarche and first reproduction), and the overall length of the lifespan (Allman, Rosin, Kumar, & Hasenstaub, 1998; Bielby et al., 2007; Brooks & Garratt, 2017; Charnov, 1993; Roff, 1992; Stearns, 1992). A consideration of life history is critical to our understanding of human sex differences because of humans' long development period and because boys and girls develop at different paces and engage in many different types of activities as they grow (see Chapters 10 and 11, this volume). One important function of development is preparation for adulthood, including building up the physical, cognitive, behavioral, and social skills associated with competition, choice, and parenting. Although stretching out development over many years or decades, as is the case for humans, increases the risk of dying before reproducing, there is a substantial payoff when adulthood arrives. Young adults are now physically ready for the rigors of adulthood and have much more sophisticated cognitive, behavioral, and social skills than would otherwise be the case. One way to think about the development of these competencies is in terms of additions to individuals' *reproductive potential*—refining the suite of traits that allows individuals to survive as adults, to compete for and attract mates, and to invest in their offspring (R. D. Alexander, 1987).

The goals for this chapter are to introduce life history theory and research, while weaving core features of sexual selection into this perspective. The weaving allows us to more fully understand why males and females often engage in different types of activities during development, why they often

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mature at different ages, and why they have different lifespans. The discussion focuses on aspects of life history that are of particular importance for understanding topics covered in later chapters. These respective topics include the evolutionary function of play, the evolution of parenting and especially paternal investment, the influence of sex hormones on various sex differences, and the vulnerability of sexually selected traits to stressors.

LIFE HISTORY

Life history includes the suite of traits that defines a species' maturational and reproductive pattern and the factors that govern the evolution of these traits and their expression during the lifespan (Roff, 1992; Stearns, 1992). We must consider a suite of traits because there are often trade-offs in the expression of one trait versus another (G. C. Williams, 1957); there is a cost for every expressed benefit. As shown in Figure 4.1, the most basic trade-offs involve the allocation of limited resources (e.g., calories, nutrients) to somatic or reproductive effort (R. D. Alexander, 1987; G. C. Williams, 1966/2008). *Somatic effort* includes resources devoted to physical growth and to the maintenance of physical systems during development and in adulthood (G. B. West, Brown, & Enquist, 2001); growth can also involve the accumulation of reproductive potential, such as increases in body size needed for male elephant seals (*Mirounga angustirostris*) to successfully compete for mates. *Reproductive effort* is the spending of this potential during adulthood and is largely distributed between mating and parenting.

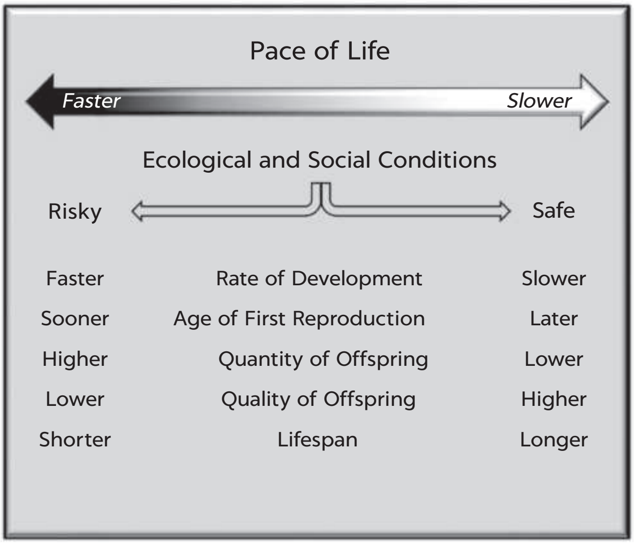
One way to think about life history is in terms of the pace of life, ranging from faster to slower, and the evolutionary and here-and-now proximate factors that place the species or individual somewhere on this continuum, as shown in Figure 4.2 (Mac Arthur & Wilson, 1967; Montiglio, Dammhahn, Dubuc Messier, & Réale, 2018). The following sections explore the most basic of these trade-offs as they are expressed in different aspects of the pace of life, including the pattern of reproduction, growth, and development of offspring;

FIGURE 4.1. Components of Life History

Life History				
Somatic Effort			Reproductive Effort	
Growth	Developmental Activity	Maintenance (Survival)	Mating	Parenting

Development activity refers to social, behavioral, and cognitive activities during juvenility that promote survival and increase the resources that can be later invested in reproductive effort during adulthood.

FIGURE 4.2. Life History and the Pace of Life



Life history is related to the pace of life which in turn is influenced by ecological (e.g., predation) and social (e.g., competition for scarce resources and mates) conditions. Risky conditions typically result in a faster pace of life and a bias toward faster development, earlier reproduction, production of more and lower quality offspring (e.g., smaller size), and a shorter lifespan. Safer conditions typically result in a slower pace of life and a bias toward slower development, later reproduction, production of fewer and higher quality offspring (e.g., larger size), and a longer lifespan.

the function of developmental activities; and phenotypic plasticity (see Charnov, 1993; Roff, 1992; Stearns, 1992; West-Eberhard, 2003).

Life–Time Reproductive Pattern

The pattern of reproductive timing is a key aspect of life history. With *semelparity*, all reproductive potential is spent in one breeding episode, and with *iteroparity*, this potential is spent across multiple episodes. Semelparity is part of a faster pace of life and the more-risky strategy. It is high risk because reproduction during poor ecological conditions (e.g., drought) could result in high offspring mortality with no opportunity to reproduce under better conditions. Despite this risk, evolution will favor semelparity when the probability of surviving to a second breeding season is low. In this situation, individuals that devote minimal resources to somatic effort in adulthood and maximal resources to their one reproductive episode will contribute more offspring to the next generation than will individuals that hold back on reproduction.

Evolution will favor iteroparity when juveniles and adults are likely to survive from one breeding season to the next (Roff, 1992). In this situation, the pace of life will be slower, and lifetime reproductive success will depend on the trade-off between efforts devoted to the current breeding season and how associated costs affect the ability to reproduce in later seasons. Having offspring across different seasons also means that they are less likely to compete with one another and buffers against unpredictable fluctuations in climate, food abundance, and predatory risk. One result is that iteroparous species invest more in maintenance—staying healthy for the next breeding season—and less in reproduction in any single breeding season than their semelparous cousins.

The female Pacific (*Salmo oncorhynchus*) and Atlantic (*Salmo salar*) salmon illustrate the differences between these reproductive strategies. Pacific salmon experience intense competition for suitable nesting sites and must guard these sites after depositing their eggs (De Gaudemar, 1998). Females that do not pay the costs of competition will not obtain a suitable nesting site or will have their site destroyed by other females and will not reproduce at all. As a result, female Pacific salmon must put "everything they have" into competition for nesting sites and producing eggs (e.g., diverting resources away from biological processes that would help them live longer), and most die at the end of the first breeding episode, although a few of them will survive and spawn a second year (M. R. Christie, McNickle, French, & Blouin, 2018). Female Atlantic salmon do not have to compete as intensely for nesting sites and devote more resources to maintenance and less to reproduction during each breeding season, and they survive to reproduce again. Although the female Atlantic salmon produces fewer eggs during any single season than do female Pacific salmon, the number of viable offspring produced during the reproductive lifespan of these two species is comparable.

Predation risks can influence the timing of reproduction within iteroparous species, as illustrated by Reznick and Endler's (1982) research on guppies (*Poecilia reticulata*). On the Caribbean island of Trinidad, three populations of guppy were studied under high (predators feeding on large adults), medium (predators feeding on juveniles), and low (few predators) predation risk. When risk was high, females matured rapidly and were smaller as adults, and this in turn reduced the chances of them being eaten before reproducing. The fast maturation was also associated with less resources devoted to maintaining their health, such as mounting immune responses to parasites (Stephenson, van Oosterhout, & Cable, 2015). When it came time to have offspring, they allocated more resources to their first breeding episode, producing 2 to 3 times as many offspring as females in safer environments. In safer locales where predation was less severe and adult mortality rates were lower, individuals grew more slowly, attained a larger adult size, and females spread their reproduction over several breeding episodes. Follow-up studies revealed this variation in the pace of life was due to a combination of genetic differences that have emerged between these populations and phenotypic plasticity (Reznick & Bryga, 1996; Reznick, Shaw, Rodd, & Shaw, 1997; Rodd, Reznick, & Sokolowski, 1997).

The pattern of life history development is also influenced by more proximal reproductive costs, such as those involved in producing eggs, caring for offspring, and competing for mates. These costs can compromise the physical health and oftentimes the survival prospects of parents (Clutton-Brock, 1991). The underlying physiological processes are not fully understood, but include the energetic demands of reproduction (e.g., parental care) and associated hormonal changes (e.g., an increase in testosterone that can compromise immune functions; Sinervo & Svensson, 1998). Generally, individuals in good health can better withstand the rigors of reproduction than can less healthy individuals, but they still bear the costs of reproduction (Jablonszky et al., 2018). Among red deer (*Cervus elaphus*; see Chapter 3, Figure 3.6, this volume), females that began having offspring early and males that competed intensely for harems in early adulthood showed more rapid physical declines across seasons than did individuals that were just as healthy but delayed first reproduction or competed less intensely early in life (Lemaître et al., 2014, 2015; Nussey, Kruuk, Donald, Fowlie, & Clutton-Brock, 2006). Humans are not exempt from these trade-offs (Bolund, Lummaa, Smith, Hanson, & Maklakov, 2016). In an analysis of multigenerational genealogical records, Bolund and colleagues (2016) found that women who bore many children had a shorter lifespan than did women who bore only a few children.

Offspring Growth and Development

Given the risk of dying before having the opportunity to reproduce, even among iteroparous species living in relatively safe environments, it is easy to think that evolution would always favor a faster pace of life (G. C. Williams, 1966/2008). As shown in Figure 4.2, the risk of dying young is balanced against the benefits that accompany a slower pace of life. A faster life history is associated with producing many, quickly maturing offspring that are smaller, less competitive, and have high mortality relative to offspring associated with a slower life history (Stearns, 1992). Across species of plant, insect, fish, reptile, and mammal, offspring that are larger at time of hatching, birth, or weaning have increased survival rates due to decreased predation risk and decreased risk of starvation (Roff, 1992), and often have reproductive advantages in adulthood (Oosthuizen, Altwegg, Nevoux, Bester, & de Bruyn, 2018). The drawback is that high-quality (i.e., larger and more competitive) offspring come at a cost of having fewer of them during a reproductive lifespan (Rollinson & Rowe, 2015).

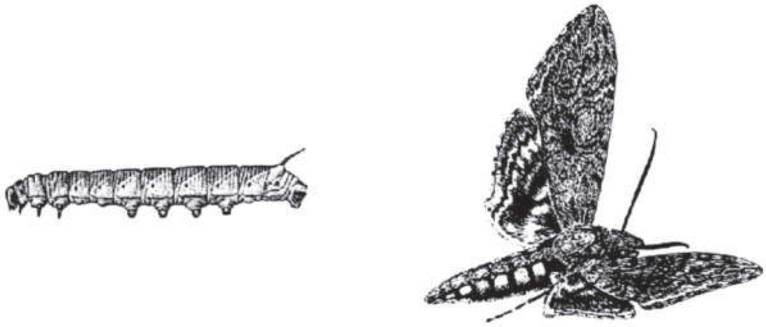
Species that produce fewer and larger offspring also tend to have slower rates of growth during development, higher levels of parental care, and a longer lifespan compared with related species that produce smaller but more offspring (Roff, 1992; Shine, 1978). In addition to size at hatching or weaning, lower juvenile mortality is related to parental protection from predators and provisioning with food (Clutton-Brock, 1991; Shine, 1978). The slower development and delayed maturation that is afforded by parenting and living in less risky environments can have long-term benefits, including a larger body size before competition for mates or investing in parenting. Larger females can give birth to larger and more competitive offspring and larger males often have an advantage in male–male competition (Carranza, 1996; Stearns, 1992). It is not just physical size: In some species, developmental activity, such as play, can improve survival and reproduction-related social, behavioral, and cognitive competencies (Pellis & Pellis, 2007). In short, slow maturation and growth allow for the accumulation of more reproductive potential (e.g., improving social competencies) than is possible in faster maturing species.

Developmental Activity

Developmental activity is included as a feature of somatic effort during infancy and juvenility in Figure 4.1, because these activities can build reproductive potential into the developing organism. The benefits for children are elaborated in Chapters 10 and 11 of this volume, which propose that much of the research in human development up through adulthood can be easily incorporated into life history theory (Geary, 2002a). For now, it is noted that some of these activities promote survival during development (Bjorklund & Pellegrini, 2002), whereas others contribute to the accumulation of reproductive potential that is then spent in adulthood. Accumulation means that some developmental activities result in the refinement of physical, cognitive, behavioral, and social competencies that enhance survival and reproductive prospects in adulthood (Geary, 2002a; Geary & Bjorklund, 2000). These are illustrated in more detail below.

A straightforward example of life history development and the accumulation of reproductive potential is found in many species of *Insecta*, where distinct morphs or body types are associated with different life history stages. In the tomato hornworm moth (*Manduca quinquemaculata*) shown in Figure 4.3 and for related species, the behavior of the larvae (caterpillars) is focused on

FIGURE 4.3. Life History Stages of the Tomato Hornworm Moth (*Manduca quinquemaculata*)



To the left is the larval stage during which the caterpillar's behavior is focused on somatic effort, avoiding predation and growth. To the right is the adult stage during which the moth's behavior is focused on reproductive effort. From *Insects and Mites: Techniques for Collection and Preservation* (p. 75), by the U.S. Department of Agriculture, 1986, Washington, DC: Author. In the public domain.

somatic effort (e.g., to avoid predation, to grow), but the behavior of the adult moth is focused on reproductive effort. In fact, the caterpillar cannot reproduce and in some species of *Insecta* the adult morph does not eat; the sole function of the moth or butterfly is to reproduce (R. D. Alexander, 1987). The more successful the caterpillar is at finding food, the larger it grows before its transformation into the adult moth or butterfly. The increased size during the caterpillar stage results in a larger adult that will typically have a reproductive advantage over smaller adults. Although the development of life history traits will sometimes fall neatly into successive stages, as with the tomato hornworm moth, a more continuous pattern of growth and a gradual emergence into adulthood—sometimes punctuated with a growth spurt and the development of secondary sexual characteristics at puberty—is more typical.

Phenotypic Plasticity

Plasticity is the potential for evolved traits, or phenotypes, to change in response to social and ecological conditions, and conditions within the individual (e.g., exposure to hormones; West-Eberhard, 2003). Phenotypic plasticity enables a more optimal expression of life history traits in response to changing survival and reproductive demands and can be a leading edge of evolutionary change (S. F. Gilbert, Bosch, & Ledón-Rettig, 2015; Levis & Pfennig, 2016). The mechanisms that support this plasticity are not fully understood, but include hormonal responses to social and ecological conditions (Dufty, Clobert, & Møller, 2002; Lessells, 2008), as well as other circumstances (e.g., water availability) that affect the individuals' physical and behavioral condition (McNamara & Houston, 1996; Sinervo & Svensson, 1998). Whatever the mechanisms, plasticity is the norm and is found in species as diverse as plankton, plants, and primates (Alberts & Altmann, 1995; McNamara & Houston, 1996; Roff, 1992; Sultan, 2000). Whatever the species, plasticity is constrained by norms of reaction (Stearns & Koella, 1986). These are limits within which the evolved trait can be expressed; for instance, age of maturation might vary from 10 to 14 months, but not outside of this range. Plasticity can occur over short time intervals, such as a rapid response to a predator (e.g., fleeing), or longer time intervals, such as permanent changes in a trait resulting from prenatal factors, and sometimes across generations.

Plasticity is illustrated by the earlier described differences in the life history of guppies as related to predation risk. As noted, some of the differences are inherited but others are clearly in response to risky experiences (Chouinard-Thuly, Reddon, Leris, Earley, & Reader, 2018; Dzikowski, Hulata, Harpaz, & Karplus, 2004; Gosline & Rodd, 2008; Ruell et al., 2013). Dzikowski et al. (2004) placed some female guppies in an aquarium that exposed them to a predator (that could not get to them) and other females in an aquarium with no predator. When the predator was around, females reproduced sooner and had almost twice as many offspring as females in the safe environment. When the predator was removed, the reproductive differences between these two groups disappeared, providing strong evidence that the original differences were due solely to the predator. Burns, Price, Thomson, Hughes, and Rodd (2016) showed that exploratory behaviors associated with searching for food or mates is restricted by earlier exposure to predators, whether or not the predator is immediately present. In an interesting twist on these types of studies, Ruell et al. (2013) showed that the sexually selected bright colors of male guppies—these attract females and predators alike—were duller and smaller when they grew up with predators in their environment relative to the coloration of their brothers who grew up in a predator-free environment.

There is also evidence for cross-generational plasticity, whereby social or ecological conditions experienced by the mother (e.g., during pregnancy) and patterns of mother-offspring interactions can influence life history development and trade-offs in offspring (Beaman, White, & Seebacher, 2016; Mousseau & Fox, 1998; Pick, Ebneter, Hutter, & Tschirren, 2016; M.-H. Wang & vom Saal, 2000); these are termed *maternal effects*. For example, offspring of nutrient-deprived plants allocate more growth-related resources to root production, whereas offspring of light-deprived plants allocate more resources to leaf production (Sultan, 2000). In mammals, maternal condition during pregnancy and suckling can have lifelong consequences for offspring. Healthy mothers give birth to heavier offspring and they provide more milk, both of which promote early growth that in turn can influence adult size and breeding success (Clutton-Brock, 1991). An example involving social dynamics is provided by one species of baboon (*Papio cynocephalus*), whereby males born to high-ranking females have accelerated testicular maturation and move quickly up the social hierarchy (Alberts & Altmann, 1995).

Nussey, Postma, Gienapp, and Visser (2005) demonstrated that plasticity itself can be heritable, at least in the great tit (*Parus major*). For this species of bird, females time their egg laying so that chicks hatch when their primary food (e.g., caterpillars) is at a peak. The emergence of caterpillars is related to ambient temperature and warming over the last several decades has resulted in caterpillars emerging earlier in the season. As a result, many females lay their eggs too late, resulting in a shortage of food when their offspring hatch. Some females have adjusted their laying dates on the basis of ambient temperature so that their chicks hatch at a more optimal time. In other words, females differ in the plasticity of reproductive timing, such that females that can adjust their laying date on the basis of ambient temperature (as contrasted with only using amount of daylight) have more food available when their chicks hatch. One result is that females that have been able to adjust their reproductive timing have produced more offspring that survive to the next generation. Nussey and colleagues found that about a third of the variation in this reproductive plasticity is heritable, and that there has been a cross-generational increase in the number of females that can alter their egg laying on the basis of temperature.

At the same time, this discussion does not mean that all traits are plastic. Plasticity is expected to evolve when there are cross-generational fluctuations in the conditions that support survival or reproduction or fluctuations within lifespans, and even in these situations much remains to be learned (Beaman et al., 2016). One result is that even related species may show different levels of plasticity in the same or similar traits, depending on the trade-offs of trait expression (e.g., Mukherjee, Heithaus, Trexler, Ray-Mukherjee, & Vaudo, 2014). Even within the same species, some traits may be plastic and others not, and even for plastic traits some individuals will be highly responsive to social and ecological conditions and others much less so. Despite these nuances, the key point is that social and ecological conditions can alter the development and expression of some evolved traits and can do so in the short term or for the entire life of the individual.

LIFE HISTORY AND SEXUAL SELECTION

Now that the basics of life history have been covered, attention is turned to its relation to sexual selection (Andersson, 1994; Badyaev & Qvarnström, 2002). Most generally, as the intensity of competition and the rigor of choice increase, selection should favor fewer and more competitive offspring (Mac Arthur & Wilson, 1967) and the corresponding life history pattern of iteroparity, a long developmental period, high levels of parental investment, and other traits that add to offsprings' quality (Roff, 1992). The first two sections illustrate the relation between life history and competition and choice, respectively, and the final section closes with a discussion of phenotypic plasticity.

Intrasexual Competition

The relation between intrasexual competition and life history is illustrated using physical and behavioral male–male competition. This does not mean that female–female competition does not affect female life history, and indeed, there is some evidence that it does (Swanson et al., 2013). For most species of insect, for instance, females are larger than males—which allows them to produce more or larger eggs (allowing them to out-reproduce other females)—and obtain this size advantage because they have a longer period of development (Teder, 2014). The key points are that competition and choice can influence sex differences in the pace of life, including rate of development, age of first reproduction, and lifespan.

Physical Competition

For many species, males show little or no parental investment and compete intensely for access to multiple females (Andersson, 1994; Clutton-Brock, 1989; C. Darwin, 1871). One result is that many and sometimes most males are prevented from reproducing, creating strong selection pressures for the evolution of traits that support competitive ability (Janicke, Häderer, Lajeunesse, & Anthes, 2016). Among these traits are physical size and aggressiveness such that larger, more pugnacious males are typically more competitive than smaller, less pugnacious ones. Compared with females, a common life history pattern for these species is for males to grow at a slower rate, mature and reproduce at a later age, and experience a shorter lifespan (Stearns, 1992). This does not mean physical male–male competition always results in larger males; the relation between competition and size is mostly found when males fight on land, with faster maturing and smaller males often having an advantage for species with scramble competition (see Chapter 3, Figure 3.12, this volume) or that fight during flight (Andersson, 1994).

Among mammals with intense physical male–male competition, males' developmental period can range from moderately longer (e.g., 2.8 versus 3.5 years in the patas monkey, *Erythrocebus patas*) to more than twice as long as that of females (e.g., 3 versus 8 years in the elephant seal; Harvey & Clutton-Brock, 1985; Le Boeuf & Reiter, 1988). In some of these species, males weigh slightly more than females (e.g., 19% heavier in colobus, *Colobus angolensis*, a monkey) and in others, up to 8 times more (e.g., elephant seals; Le Boeuf & Reiter, 1988). Clutton-Brock and Isvaran (2007) found that males of a typical mammal species with intense male–male completion and polygyny had about a 20% shorter lifespan than that of females, whereas lifespans are similar for monogamous species and sometimes shorter for females (Allman et al., 1998; Tidière et al., 2015). Males' shorter lifespan is related to the nutritional demands needed for growing larger, competition-related injuries in adulthood, and the immunosuppressive effects of testosterone (Clutton-Brock, Major, & Guinness, 1985). Clinton and Le Boeuf (1993), for instance, found that for young adult elephant seals, 50% of males that competed intensely and were successful died before the next breeding season, compared with less than 10% of males who did not compete at that age and died before the next breeding season.

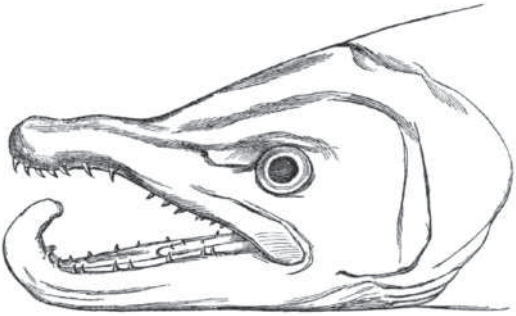
The evolution of larger males is associated with the evolution of larger but fewer offspring, and an accompanying increase in the size of females to accommodate these larger offspring (Carranza, 1996; Roff, 1992). The magnitude of the sex difference in physical size can also vary within a species; groups living at higher latitudes generally show larger sex differences than their peers living closer to the equator (Isaac, 2005). Although uncommon in mammals, female–female competition is sometimes more intense than male–male competition. An example is the fierce fighting over food (social selection) among female spotted hyenas (*Crocuta crocuta*; L. G. Frank, 1986). These females are larger than and dominate males, although their physical advantages are related to faster not slower growth during adolescence (Swanson et al., 2013); in this species, female aggression is related in part to prenatal exposure to high concentrations of androgens (i.e., male hormones; Dloniak, French, & Holekamp, 2006).

Behavioral Competition

Male Pacific salmon have two forms, the smaller jack and the larger hooknose. The alternative reproductive strategies of these two forms illustrate the relation between life history and behavioral competition (M. R. Gross, 1985, 1996). For both sexes, the fry spends the first year of life in the freshwater stream of their hatching and then migrates to the Pacific Ocean. Males that eventually become jacks are larger as fry and spend about 6 months in the ocean before maturing and beginning the journey home to spawn. Hooknose males begin their migration to the Pacific as smaller fry but spend about 18 months in the ocean before maturing and returning to spawn. During this 18-month period, these males grow larger than jacks and develop distinctive secondary sexual characteristics. These include a hooked upper and lower jaw and canine-like teeth, much like that shown in Figure 4.4, as well as red coloration and a humped dorsal area that provides added defense against attacks by other males. Larger and more aggressive hooknose males are almost always dominant at spawning sites and achieve a disproportionate number of fertilizations. In streams that afford hiding spots, jacks furtively spawn while hooknose males are fighting. The jacks are just as reproductively successful, on average, as hooknose males, and early maturity and furtive mating represents a successful life history strategy for males of this species (Gross, 1985). Females mature at about the same time as hooknose males but weigh less and show less exaggerated changes in snouts and body shape (I. A. Fleming & Gross, 1994).

As reviewed in Chapter 3 of this volume, bowerbirds provide an excellent example of the evolution of complex behavioral competition, and illustrate how such competition can result in sex differences in the pace of life. Female satin bowerbirds (*Ptilonorhynchus violaceus*) begin to reproduce at 2 years of age, but males do not produce sperm until 5 years and do not achieve an adult-male plumage until 6 or 7 years (Vellenga, 1980). Even then, bower-holding males do not mate until 10 years of age and most never mate. During development, young males watch older males at their bower and imitate bower building and courtship displays when the older males leave to feed (Collis & Borgia, 1992). It takes 5 to 7 years of practice before males can build an adult-like bower (J. Diamond, 1986). Young males also engage in play

FIGURE 4.4. Male Salmon (*Salmo salar*)



The jaw and teeth of the males of several species morph during the breeding season to support male–male competition. From *The Descent of Man, and Selection in Relation to Sex* (p. 4), by C. Darwin, 1871, London, England: John Murray. In the public domain.

fighting, which may provide the experience needed for dominance-related encounters in adulthood. In short, the delayed maturation of male satin bowerbirds and related species provides an opportunity for them to practice and refine the bower construction and fighting skills—accumulation of reproductive potential—needed for reproductive competition in adulthood.

Intersexual Choice and Mating System

Intersexual choice and the basic mating system of the species (e.g., monogamous or polygynous) is related to life history. Species in which males gather in leks illustrate the basic point (Höglund & Alatalo, 1995). As discussed in Chapter 3 of this volume, leks can be areas in which males gather together to strut, display plumage, or engage in other activities to attract mates, or they can be more dispersed areas in which single males display (e.g., bowerbirds). In both situations, females visit a number of males and then mate with one or a few of them.

Peafowl (*Pavo cristatus*) provide a good example, as males' reproduction is mostly due to female choice, with little male–male competition (Höglund & Alatalo, 1995; Petrie, 1994; Petrie, Halliday, & Sanders, 1991). Peacocks develop large tail trains with varying numbers of eye spots that, among other traits, influence female mate choices (Petrie et al., 1991). Peahens begin to reproduce at 2 years of age, whereas males do not develop their full trains until 3 years of age and do not establish a lekking display site until 4 years (Manning, 1989). Some 4-year-old males successfully mate, but others will not mate until later years, and some will never mate. As with bowerbirds, the traits that females use in mate choice decisions have resulted in an accompanying change in the life history of male peacocks, including a lengthening of the developmental period and an increase in size at maturity (Wiley, 1974).

The monogamous California mouse (*Peromyscus californicus*) provides an example of how the mating system can influence females' life history. Males and females of this species form tight pair bonds and males invest heavily in their offspring and stay loyal to their mate, even when given the opportunity to copulate with another female (Gubernick & Nordby, 1993; Ribble & Salvioni, 1990). Some of their cousin species also tend toward monogamy but others are highly polygynous, where males invest nothing in offspring and attempt to copulate with as many females as they can (Dewsbury, 1981). Generally, high levels of parental care are associated with a slower pace of life, including delayed maturation and fewer but more competitive offspring (Charnov, 1993). Jašarević et al. (2013) reasoned that high levels of male parenting should be associated with a slower pace of life in female California mice relative to females of related but polygynous species. Female California mice and females of a related monogamous species begin reproducing at a later age, produce fewer but larger offspring, and age more slowly than females of polygynous species. For these species, the extent to which males invest in parenting or mating influenced the evolution and expression of females' life history traits.

Plasticity, Ecological and Social Conditions

Plasticity in life history development can take an irreversible form once one trajectory or another is taken, or it can be highly flexible across breeding seasons, age, prospective mates, and social and ecological context (Badyaev & Qvarnström, 2002; Kokko, 1997). The jack and hooknose Pacific salmon are an extreme illustration of the former. More typically, irreversible trajectories involve change in the timing of major developmental milestones (e.g., age of reproductive maturity) that are influenced by a combination of genes and early and concurrent social and ecological conditions (Stearns, 1992; Stearns & Koella, 1986). Current food availability or its availability during the individuals' development are common proximate influences on the timing of reproductive maturation or the readiness to breed in any given season. Oosthuizen et al. (2018), for instance, found that female elephant seals that were larger at weaning had higher survival rates the first 2 years of life, and began reproducing earlier than did other females. Smaller females spent an additional year investing in their physical growth, and the weight gain increased their odds of successfully reproducing the following year.

Although sensitivity to ecological and social conditions allows for adaptive responses to opportunity and risk, this sensitivity can also reveal underlying resilience or vulnerability as related to the development and expression of sexually selected traits (e.g., Hubbard, Jenkins, & Safran, 2015; for review see Geary, 2015). For some species of song bird, for instance, a poor early diet can compromise the developing brain system (see Chapter 3, Figure 3.11, this volume) that supports song learning and production and this can influence the males' later attractiveness to females (K. L. Buchanan, Leitner, Spencer, Goldsmith, & Catchpole, 2004; Nowicki, Peters, & Podos, 1998). Birds are just an example, as early influences on the adult expression of sexually selected traits have now been found for various species of fish (Kodric-Brown, 1989), insect (D. J. Emlen, 1997), and mammal (Jašarević, Hecht, Fritsche, Beversdorf, & Geary, 2014).

The here-and-now dynamics of competition and choice are also important. It is often the case that males are able to reproduce years before they actually have the opportunity to do so (Wiley, 1974). The delay can result from competition from older and more dominant males or a female preference for older males (Kokko, 1997; Selander, 1965). For some species, dominant males can actually delay the physiological maturation or reduce the reproductive potential (e.g., reduce the size of testes) of lower status males through intimidation and behavioral subordination (A. F. Dixson, Bossi, & Wickings, 1993; J. R. Walters & Seyfarth, 1987). Dominant females are often no different, suppressing the reproduction of subordinates in many species, especially cooperative breeders where subordinates invest in the offspring of dominant females (Beehner & Lu, 2013; M. B. V. Bell et al., 2014).

EVOLUTION OF PLAY

Play is an important component of developmental activity (see Figure 4.1) and is reviewed here to provide a foundation for the later discussion of human developmental sex differences. Evolutionary accounts of play date back more than 100 years (Groos, 1898), and its scientific study extends into the 21st century (Bekoff & Byers, 1998; Burghardt, 2005; Pellegrini & Smith, 2005; Power, 2000). Play, in one form or another, is found in many mammalian species and in some species of bird (e.g., many species of parrot, *Psittaciformes*), fish (e.g., great white shark, *Carcharodon carcharias*), reptile (e.g., Komodo dragon, *Varanus komodoensis*), and invertebrate (e.g., octopuses, *Octopus vulgaris, Octopus briareus*; Burghardt, 2005; Fagen, 1981; Kuba, Byrne, Meisel, & Mather, 2006). Across species, play (a) is voluntary; (b) is not immediately functional; (c) involves some components of more functional activities, although they may be muted, exaggerated, or incomplete (e.g., prey capture); (d) is repeated and pleasurable; and (e) occurs only in safe environments (Graham & Burghardt, 2010).

Play is uncommon in species with a fast pace of life but is often found in species with a slow pace, especially those with relatively large brains, a comparatively long developmental period, and parental care (Burghardt, 2005). Across species, the three most common types of play are locomotor, object oriented, and social (Fagen, 1981), and there are ongoing debates about the evolved functions and costs and benefits of play that remain to be fully resolved (Archer, 1992; Graham & Burghardt, 2010; Pellis & Iwaniuk, 2000). Overall, it is likely that play improves various motor skills and social competencies, and these are often precursors to sex differences found in adulthood. The most important of these sex differences are rough and tumble play, which occurs more frequently in the sex that engages in more intense physical competition (typically males), and play parenting (i.e., social play), which occurs more frequently in the sex that invests more in parenting (typically females).

Locomotor and Object Play

Locomotor play involves running, leaping, jumping, and so forth and is nearly ubiquitous in mammals and is found in some species of fish and bird and perhaps some reptiles (Burghardt, 2005). This typically solitary play is found in species that navigate in complex and varied terrains, and in species with elaborate predator evasion or prey capture behaviors (Burghardt, 2005; Fagen, 1981; Power, 2000). Byers and Walker (1995) argued that locomotor play results in long-term changes in the synaptic organization of the cerebellum, which is involved in the coordination of complex motor movements and some forms of learning. In this view, locomotor play results in neural changes that support complex motor skills in adulthood (K. P. Lewis & Barton, 2004; Nunes et al., 2004). There is some evidence for this, but the costs and benefits of this type of play are not fully understood (Graham & Burghardt, 2010).

In one supportive study, Berghänel, Schülke, and Ostner (2015) assessed the locomotor play (e.g., jumping from one tree branch to another) of a group of young wild macaques (*Macaca assamensis*), a species of monkey. Youngsters who engaged in more play showed faster development of motor skills, but at a cost of slower growth (calories spent on physical play were not used for physical growth).

Object play is common in species that feed on a wide variety of foods and that benefit from learning to manipulate different types of objects, including prey and tools, in different ways (Burghardt, 2005; Fagen, 1981; Power, 2000). This form of play is found in many species of bird, carnivore, primate, and a few others (Burghardt, 2005). Object play typically has an exploratory component, especially for novel objects, and includes active object manipulation and for some species combining objects (e.g., placing one object into or on top of another). These activities are more common in juveniles than adults and are similar to prey capture behaviors or behaviors that involve food extraction using a tool. The assumption that object play provides practice and refinement of prey capture skills has not always been supported (Caro, 1980), but it has only been experimentally assessed in a few species (Power, 2000). The assumption that object manipulation allows animals to learn about the different ways in which objects can be used as tools is also in need of further experimental testing, but there is emerging evidence that this is indeed one evolved function of object play (Graham & Burghardt, 2010; Montgomery, 2014).

Sex differences in locomotor and object play have not been as extensively studied as differences in social play. The pattern of cross-species sex differences in locomotor play varies considerably; for some species, no differences are reported, for other species, males engage in more locomotor play, and for still other species, females engage in more locomotor play (e.g., J. M. Pedersen, Glickman, Frank, & Beach, 1990; Power, 2000). The situation is similar for object play (Power, 2000). It may be that no systematic pattern of sex differences in locomotor and object play exists across species, potentially because there are few sex differences in corresponding activities (e.g., predator evasion) in adulthood, although there are some interesting and potentially important differences in primates. Kahlenberg and Wrangham (2010) found that young female chimpanzees (*Pan troglodytes*) were more likely to carry and cradle sticks as if they were infants than were young males, and G. M. Alexander and Hines (2002) found that young female vervet monkeys (*Cercopithecus aethiops sabaeus*) were more interested in dolls than trucks, with males showing the opposite preference (also C. L. Williams & Pleil, 2008).

Social Play

Social play is very common in mammals, in many species of bird, and a few species of fish, reptile, and invertebrate (Burghardt, 2005). Play fighting is the most common form of this type of play and typically involves chasing and rough-and-tumble components; the latter can include wrestling, muted biting, pouncing and jumping on partners, pushing, and so forth (Panksepp, Siviy, & Normansell, 1984; Power, 2000). Play fighting typically involves pairs of evenly matched (e.g., in terms of size) individuals and increases in frequency from infancy to the juvenile years and then slowly declines, often merging into serious fighting by reproductive age. Play fighting includes many of the same behavioral components as intrasexual fighting or territorial defense but differs in enough ways to make a straightforward practice of fighting behaviors unlikely (Pellis & Pellis, 2007). In fact, many of the basic behavioral components of species-specific fighting are evident at birth, but their expression is often better controlled, more nuanced, and more varied for individuals that have engaged in play fighting. By enabling the development of better controlled and more flexible fighting skills, this form of play likely results in improved social competencies and later social-competitive advantage (Graham & Burghardt, 2010; Palagi et al., 2016), as well as establishing dominance relationships before play merges into potentially harmful fighting (Pellis & Pellis, 2007).

Sex differences in play fighting are common and track sex differences in the form and intensity of intrasexual competition and other agonistic behaviors in adulthood (Power, 2000; P. K. Smith, 1982). Power (2000) found that young males of polygynous species with intense physical male–male competition nearly always engaged in more play fighting than females. This pattern is found across species of marsupials (e.g., red kangaroos, *Macropus rufus*), pinnipeds (e.g., northern elephant seal), ungulates (Siberian ibex), rodents (Norway rat, *Rattus norvegicus*), and primates (e.g., chimpanzee), and is not found in their monogamous cousins with less intense intrasexual competition (Aldis, 1975; Chau, Stone, Mendoza, & Bales, 2008; P. K. Smith, 1982). As an illustration, G. R. Brown and Dixson (2000) found that young rhesus macaque (*Macaca mulatta*) males engaged in play fighting 2 to 3 times more often than did females, a pattern that is common among primates (Lonsdorf, 2017). Carnivores are the exception that seems to prove the rule. Intense competition over mates or food is the norm for males and females of most of these species, and both sexes tend to engage in play fighting during development. A notable exception is the spotted hyena in which females compete fiercely with other females over food, are polyandrous (have multiple mates), and dominate males (East, Burke, Wilhelm, Greig, & Hofer, 2003). In this species, females engage in more play fighting than males (J. M. Pedersen et al., 1990).

Females consistently engage in more play parenting than males, although it can occur in both sexes (Nicolson, 1987; Pryce, 1993, 1995). Play parenting in primates and general interest in infants is frequently observed in young females that have not yet had their first offspring. For many of these species, play parenting (e.g., caring for siblings) is associated with higher survival rates of their first-born, and sometimes later-born, offspring (Nicolson, 1987). Across five primate species it was found that first-born survival rates were

2 to more than 4 times higher for mothers with early experience with infant care than mothers with no such experience (Pryce, 1993). Maternal behavior is also influenced by the hormonal changes that occur during pregnancy and the birthing process, such that a combination of play parenting and these hormones contribute to maternal skill in many primates (Pryce, 1995), including a heightened interest in infants (G. M. Alexander & Hines, 2002; Heintz, Murray, Markham, Pusey, & Lonsdorf, 2017). At the same time, in some species young females' interest in infants might simply reflect a bias that evolved to directly support parenting and is "automatically" expressed throughout development, whether or not it refines parenting skills (Meredith, 2015).

PARENTAL INVESTMENT

Unfortunately, life is not always about play, and in fact for many species the transition to adulthood not only brings reproductive competition and choice, it oftentimes brings investment in offspring or parenting. As shown in Figure 4.1, this investment is a key feature of adulthood and one in which sex differences are common. The focus here is on direct investment, which typically involves providing offspring with nutrients during gestation or egg production, and feeding and protecting them from predators postnatally (Clutton-Brock, 1991). For social species, investment can also involve assistance in establishing and navigating social relationships and hierarchies (Alberts & Altmann, 1995; Buchan, Alberts, Silk, & Altmann, 2003). Whatever the form, the most fundamental question is why parents—maternal or paternal—provide direct investment at all, given the costs (e.g., Bolund et al., 2016; Gustafsson & Sutherland, 1988). The answer is simple:

> [in] virtually all species where young are fed by their parents, they do not survive if parents are removed, though where both parents are involved the removal of one is not necessarily fatal. . . . Both across and within species, there is usually a close relationship between feeding rate and the growth rate and survival of young. . . . Early growth may also affect reproductive success in adulthood. (Clutton-Brock, 1991, p. 25)

In short, parents pay the cost of investing in offspring, because these offspring are more likely to survive and reproduce than are offspring that receive reduced or no direct parental investment. As discussed in Chapter 3 of this volume, maternal parenting is much more common than paternal parenting, especially in mammals, which leaves us with the riddle of human fatherhood. The riddle is not why mothers provide more investment in their children than fathers, but why fathers invest anything at all (Geary, 2000). The following provides an assessment of the factors associated with the evolution and expression of paternal investment across species that in turn allows for a richer understanding of men's parenting which is discussed in Chapter 6 of this volume.

Male Parenting

The first section discusses the difference between male parenting that is absolutely necessary for offspring survival and when it is helpful but not always necessary. The distinction strongly influences the extent of males' investment in offspring and the intensity of conflicts of interest between males and females. The second section reviews the cost–benefit trade-offs associated with males' parenting.

Obligate and Facultative Investment

Paternal investment is found in many species of bird and fish, and in some species of insect, reptile, and mammal (J. D. Gilbert & Manica, 2015; Mank, Promislow, & Avise, 2005; J. D. Reynolds, Goodwin, & Freckleton, 2002). The study of the attendant cost–benefit trade-offs is complicated by the evolutionary history of the species and other factors (Bleu, Gamelon, & Sæther, 2016; Westneat & Stewart, 2003), and by whether the investment is *obligately* or *facultatively* expressed (K. E. Arnold & Owens, 2002; Clutton-Brock, 1991). Obligate investment means that male care is necessary for the survival of his offspring and will favor paternal males. One common outcome is that all males show high levels of parenting, independent of proximate conditions. For many species, including humans, paternal investment is facultatively expressed, that is, it is not always necessary for offspring survival and therefore can vary from one condition or male to the next (Westneat & Sherman, 1993). In these species, males sometimes invest considerably in offspring and other times they abandon them. The level of any male's parenting will reflect the trade-offs between the costs and benefits of this investment in the context in which the male is situated.

Whether the investment is obligate or facultative, there are often considerable benefits to offspring. These benefits can be demonstrated by removing fathers in species in which one or both parents protect or provision offspring, as is found in many species of bird. In an analysis across 31 such species, Møller (2000) estimated that 34% of the variability in offspring survival was due to paternal investment. In some species, removal of the male results in the death of all nestlings (obligate investment) and in other species male removal has smaller effects, because females can often compensate for lost provisions (facultative investment; Royle, Hartley, & Parker, 2002).

Trade-Offs

The evolution and facultative expression of male parenting is related to a balancing of the benefits to offspring, the cost of lost mating opportunities, and the risk of cuckoldry or paternity certainty (i.e., whether they are investing in their own or another male's offspring), as shown in Exhibit 4.1 (Birkhead & Møller, 1998; Perrone & Zaret, 1979; Remeš, Freckleton, Tökölyi, Liker, & Székely, 2015). When it occurs in fish, male parenting is almost always found when males fertilize eggs externally and defend nesting sites from competitors (Mank et al., 2005). Under these conditions, paternity certainty is relatively

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EXHIBIT 4.1

Evolution and Facultative Expression of Male Parenting

Offspring quantity and quality

1. If paternal investment has little or no effect on offspring survival rate or quality, then selection will favor male abandonment, if additional mates can be found (Trivers, 1972; Westneat & Sherman, 1993).
2. If paternal investment results in the ability to produce more surviving offspring (e.g., by reducing time between litters), then a polygynous mating strategy, monogamy, and high levels of paternal investment could evolve (H. E. West & Capellini, 2016).
3. 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 focus on mating or parenting, depending on social (e.g., male status, availability of mates, cuckoldry risk) and ecological (e.g., food availability) conditions (Remeš et al., 2015; Westneat & Sherman, 1993).

Mating opportunities

1. If paternal investment is not obligate and mates are available, then selection will favor
    a. male abandonment, if paternal investment does not improve offspring survival prospects or quality (Clutton-Brock, 1991); or
    b. a mixed male reproductive strategy, if paternal investment improves offspring survival rate and quality (e.g., Perrone & Zaret, 1979; L. Wolf, Ketterson, & Nolan, 1988).
2. Social and ecological factors that reduce the mating opportunities of males, such as dispersed females or concealed (or synchronized) 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; Dunbar, 1995; Westneat & Sherman, 1993).

Paternity certainty

1. If the certainty of paternity is low, then selection will favor male abandonment (Clutton-Brock, 1991; Remeš et al., 2015; Westneat & Sherman, 1993).
2. If the certainty of paternity is high, then selection will favor paternal investment, if
    a. investment improves offspring survival prospects 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; Westneat & Sherman, 1993).
3. If paternity certainty is high and the opportunity costs are high, then selection will favor males with a mixed reproductive strategy (i.e., the facultative expression of paternal investment) contingent on social and ecological conditions (Dunbar, 1995; Remeš et al., 2015; Westneat & Sherman, 1993).

Note. 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.

high, and males are able to fertilize the eggs of several females, which means that investment does not reduce mating opportunities. Paternal investment is rare in fish with internal fertilization, because paternity is not certain and because males can abandon females after fertilization and avoid the cost of investment. Nevertheless, paternal investment does occur in some species with internal fertilization, including most species of bird and some mammals, scattered among the carnivores, primates, and rodents (Dunbar, 1995; Mock & Fujioka, 1990). 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 across- and within-species relationship between the level of males' parental investment and the likelihood of paternity (K. E. Arnold & Owens, 2002; Birkhead & Møller, 1998; Harts, Booksmythe, & Jennions, 2016). Cuckoldry rates tend to be very low for species with obligate male parenting. Females do not risk abandonment by their social partner by copulating with other males, although it sometimes does happen (Safari & Goymann, 2018). For species with facultative paternal investment, cuckoldry rates often vary with male quality (e.g., as indicated by tail streamer length); for example, the female barn swallow (*Hirundo rustica*) often risks loss of male investment and copulates with healthier and more attractive males, if they are paired with a low-quality mate (Møller & Tegelström, 1997). In some cases, it is not male quality per se, but the degree of genetic difference (e.g., to avoid inbreeding) between the female and prospective mates (Brouwer et al., 2017; J. I. Hoffman, Forcada, Trathan, & Amos, 2007). Extra-pair copulations can also occur through male coercion or as "insurance" against infertility of their social partner (Forstmeier, Nakagawa, Griffith, & Kempenaers, 2014; Hsu, Schroeder, Winney, Burke, & Nakagawa, 2014; Yasui & Yoshimura, 2018).

Generally, when males detect their partner mating or simply cavorting with another male, they abandon the female or reduce their provisioning of offspring, although this does not always happen (Dixon, Ross, O'Malley, & Burke, 1994; Kempenaers, Lanctot, & Robertson, 1998). Sometimes the male continues to provide for offspring, but this is likely because he did not detect the extra-pair relationship (Neff, 2003). As an example of the general pattern, Ewen and Armstrong (2000) studied the relation between male provisioning and cuckoldry risk in the socially monogamous stitchbird (*Notiomystis cincta*); 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, as the frequency of female extra-pair copulations increased, male provisioning of the brood decreased ($r = -.72$).

The same pattern emerged in a large-scale analysis of 45 species of biparental bird that used DNA fingerprinting to determine the father. Males that mate guarded (e.g., watched the female and monitored for extra-pair males) sired more offspring than their less vigilant peers (Harts et al., 2016), indicating that males behave in ways that reduce risk of investing in the offspring of another male. The analysis also showed that attractive males did not mate guard as much as less attractive ones but were still less likely to be cuckolded. This latter finding is consistent with females mating with extra-pair males only when their social partner is relatively low status or unattractive. However, provisioning and protecting offspring is not always because of paternal investment. Male provisioning is sometimes an attempt to obtain sexual access to the offspring's mother (Rohwer, Herron, & Daly, 1999; Smuts & Gubernick, 1992); male care of unrelated juveniles often increases the likelihood that the mother will choose this male as the sire of her next offspring (Kvarnemo, 2006).

In any case, paternity certainty and increased survival prospects for 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 more than one female, and there are several ways in which this can occur. Paternal investment often reduces maternal investment (e.g., lactation time) that in turn allows females to reproduce more often, and increases the number of offspring these males can sire (Lukas & Clutton-Brock, 2013; H. E. West & Capellini, 2016). Paternal investment in canids (e.g., coyotes, *Canis latrens*) is associated with large litters that result in males siring more offspring with a monogamous, high parental investment strategy than with a polygynous strategy (Asa & Valdespino, 1998). Paternal investment might also evolve if females are ecologically dispersed and males do not have the opportunity to pursue multiple mating partners (S. T. Emlen & Oring, 1977), as with callitrichid monkeys, such as marmosets (*Callithrix*; Dunbar, 1995; Goldizen, 2003). In these species, paternal investment is related to joint male–female territorial defense, which limits the male's ability to expand his territory to include other females; female-on-female aggression that prevents males from forming harems; concealed ovulation, which prolongs the pairs' relationship to ensure conception; and females often having twins, which increases the benefits of paternal care.

Implications

The patterns associated with the facultative expression of paternal investment in nonhuman species, summarized in Exhibit 4.1, provide a critical backdrop for our later review of human fathers (see Chapter 6, this volume). Across species, males' reproductive behavior is especially complicated when paternal investment improves offspring survival rate and offspring quality, and when the reproductive benefits of seeking additional mates do not always outweigh the reproductive benefits of paternal investment; these dynamics parallel those found in humans. Under these conditions, selection will favor a mixed reproductive strategy, with different males varying in their emphasis on mating or parenting, and individual males varying in their emphasis on mating or parenting in their relationships with different females. Individual differences in paternal investment, in turn, are likely to relate to male condition (e.g., social status), ecological factors (e.g., operational sex ratio), female strategies to induce paternal investment, female quality, and genetically based differences in male reproductive strategy (Krebs & Davies, 1993).

SEX HORMONES AND SEXUAL SELECTION

The goals of this section are to highlight the influence of sex hormones, including testosterone and estrogens (e.g., estradiol), on the development and expression of sexually selected traits and on parenting. The first part provides a review of hormonal influences on earlier-discussed behaviors, such as play and parenting, as well as influences on male–male competition (see Chapter 3, this volume). The second part ties testosterone to the expression of male traits associated with female choice. The third part addresses the relation between sex hormones and cognitive and brain systems. Needless to say, the relation between sex hormones and sex differences in life history development and sexually selected behaviors and cognition is more nuanced and complex than can be described here; some of these sex differences are due to direct genetic effects that are independent of hormones (A. P. Arnold, 2017). Nevertheless, it is clear that prenatal and postnatal exposure to sex hormones contribute to the majority of sex differences that have been covered so far and will be covered in later chapters.

Most generally, prenatal exposure to sex hormones results in permanent organizational changes in the brain and other physical systems (e.g., sex organs), whereas postnatal exposure results in activational effects. These latter changes reflect the context-appropriate expression of the traits (e.g., copulation) associated with the early organizational effects, as was discovered many decades ago (Phoenix, Goy, Gerall, & Young, 1959). These days, the distinction between prenatal-organization and postnatal-activation is less rigid than originally proposed and includes some organizational effects during puberty, but the distinction still contributes to our understanding of hormonal influences on sex differences in many traits (Adkins-Regan, 2005; Schulz & Sisk, 2016). Activational effects can bias behavior and cognition in one direction (e.g., competing for mates) or another (e.g., investing in parenting), but these hormonal systems are also very sensitive to social context. As illustrated below, hormones coordinate the expression of other systems in ways that support responses to these contexts.

There is not a single male-typical to female-typical continuum, but rather more or less separate continuums that can be influenced by the same or different hormones. These hormonal effects can be subtle and can result in trait masculinization (expression of male-typical traits), demasculinization (suppression of male-typical traits), feminization (expression of female-typical traits) or defeminization (suppression of female-typical traits) or some combination (Whalen, 1974). For mammals, most sex differences emerge with hormonal influences that result in the masculinization and defeminization of males, at least with respect to prenatal and early postnatal exposure. In the absence of these processes, most traits will be feminized which is the "default" in mammals, although default does not mean passive; feminization is an active biological process (Wallen, 2005). The hormonal changes during puberty however can have additional organizational as well as activational effects on behavior and cognition, including the enhanced feminization or demasculinization of females (Schulz & Sisk, 2016). Moreover, many of the effects often associated with testosterone result from the transformation of this androgen by an enzyme (aromatase) into an estrogen which then acts in specific areas of the brain in ways that result in male-typical behavior (McCarthy, 2008).

Sex Hormones and Life History Development

The sections that follow provide brief overviews of the importance of sex hormones for the expression of sex differences early in development and in adulthood. The latter includes discussion of mating dynamics and trade-offs between mating and parenting.

Early Development

As discussed earlier, rough-and-tumble play tends to be more intense in the sex that engages in more physical competition in adulthood. The relationship between sex hormones and the expression of this form of play has been extensively investigated in the laboratory rat (*Rattus norvegicus*) and the rhesus macaque, both polygynous species with physical male–male competition (B. E. Blake & McCoy, 2015; Panksepp et al., 1984; Pellis & Pellis, 2007; Wallen, 1996). For rats, castration of young males results in a level of rough-and-tumble play similar to that of females, and prenatal or early postnatal testosterone exposure increases females' rough-and-tumble play to a level between that of typical females and males (Pellis, 2002). The combination of early organizational effects and increases in testosterone at puberty contribute to the transition from play fighting to actual fighting in males, but only occurs in females if they are treated with testosterone and their ovaries are removed; ovarian hormones (i.e., estradiol) reduce the tendency to engage in actual fighting. Related studies reveal that the expression of rough-and-tumble play is related, in part, to prenatal and in some species, pubertal organization of areas of the amygdala and other brain regions associated with social and sexual behaviors and emotions (Meaney, Dodge, & Beatty, 1981; Schulz & Sisk, 2016).

At least among primates and for some behaviors (e.g., approaching and touching infants), the sex difference in interest in infants is quite large, with the most engaged males showing less interest in and play with infants than the least engaged females (R. A. Herman, Measday, & Wallen, 2003). Among macaques, there appears to be only minor hormonal influences on young females' interest in infants, suggesting this interest emerges as part of the default system (female-typical trait expression; Wallen, 2005). The sex difference in interest in infants and play parenting would then reflect a hormone-related suppression (defeminization) of males' interest. For adult females, however, the expression of maternal behaviors is influenced by exposure to sex and other hormones (Kohl, Autry, & Dulac, 2017), and by their early rearing environment (Maestripieri, 2005; Wallen, 1996).

Adulthood

Exposure to sex hormones in adulthood is important for the expression of mating competition and mate choices, as well as influencing the trade-offs between investment in mating effort or parental effort in males. The latter is especially important for species in which males' investment in offspring is facultatively expressed.

Mating, competition, and choice. Mating is all about arranging a desirable combination of egg and sperm. The meeting occurs through a coordination of courtship and competition for mates, sexual receptivity, and copulation. Sex hormones are well suited for this match making, because they circulate throughout the body and can coordinate the activation of many diverse systems (Adkins-Regan, 2005). To ensure a successful meeting, there must be a close link between the maturational timing of the ova and the female's expression of the cognitive biases (e.g., for a blight plumage) and behaviors that influence her mate choices. Males, of course, have to be sensitive to behavioral and other changes (e.g., sexual swellings, pheromones) that signal females' receptivity to sex, and must respond in ways that increase the likelihood of being accepted as a mating partner or that facilitate engagement in male–male competition and access to receptive females (M. N. Muller, 2017).

The contributions of sex hormones to the orchestration of very basic reproductive behaviors, especially copulation, have been well documented. For the well-studied Japanese quail (*Coturnix coturnix japonica*), for instance, Beach and Inman (1965) noted that for males "all sexual activity disappeared within 8 days after removal of the testes and returned to normal within 8 days after the implantation of an androgen pellet" (p. 1428). Similarly, the sexual receptivity of female Japanese quails is strongly influenced by circulating estrogens (Adkins & Adler, 1972). The relationship between sex hormones and mating behavior is not always this clear-cut, however, even for the Japanese quail. Male courtship behaviors (i.e., crowing and strutting) are activated by testosterone or a metabolite (dihydrotestosterone), whereas copulatory behaviors are dependent on the transformation of testosterone into estradiol in several brain regions (Balthazart & Ball, 1998). The specific hormonal and brain mechanisms that influence these basic reproductive behaviors can vary across species, the sexes, and even individuals within each sex (Goodson, Saldanha, Hahn, & Soma, 2005; R. F. Oliveira, Ros, & Gonçalves, 2005; J. Wade, 2005), but the result is the same: sperm meets egg.

Sex and other hormones are also important contributors to the expression of intrasexual competition and intersexual choice, albeit with many nuances from one species to the next or across the sexes (J. A. French, Mustoe, Cavanaugh, & Birnie, 2013; Goymann & Wingfield, 2014; M. N. Muller, 2017). For some species of bird, for instance, the males' ability to express the bright plumage that influences female choice is due to the absence of estrogens, and in other species the presence of androgens (Kimball, 2006). There is a more consistent relation between exposure to male hormones, especially testosterone, and the coloration of nonplumage traits in birds, such as the red comb on male jungle fowl (*Gallus gallus*; Zuk, Johnsen, & MacLarty, 1995). Testosterone also influences the expression of the physical and behavioral traits needed for male–male competition or female choice in species ranging from reptiles (Eikenaar, Husak, Escallón, & Moore, 2012) to primates (M. N. Muller, 2017), although these relationships can be modified by ecological factors (e.g., latitude), mating system (e.g., monogamy versus polygyny), and current social context (Adkins-Regan, 2005; Wingfield, Lynn, & Soma, 2001).

The downside is that the testosterone-related development and expression of traits that facilitate competition or choice can be costly in terms of physical health and reduced investment in parenting. These costs can be reduced if testosterone and related hormones are only elevated during the breeding season and even then, only when necessary to gain or retain access to mates or the resources (e.g., nesting sites) that females need to reproduce. The dynamic sensitivity of testosterone and related hormonal responses to reproductive context is captured by Wingfield and colleagues' *social challenge hypothesis* (Wingfield, Hegner, Dufty, & Ball, 1990; Wingfield et al., 2001). The basic idea is that testosterone and related hormones organize males' behavior in ways that will increase social dominance and through this, priority access to females and key resources (e.g., nesting sites). Once dominance is achieved or the males' relative position in the hierarchy is established (for better or worse), testosterone concentrations drop and remain relatively low during periods of social stability. The accompanying reduction in testosterone can result in health benefits and for many species is associated with increased male investment in parenting. When the males' dominance or resource control (e.g., nesting site) is challenged, testosterone and stress hormones (e.g., corticosterone) spike and organize the males' aggressive response to the challenge.

The relationship between sex hormones and reproductive behaviors is also related to whether or not males invest directly (e.g., protect) in offspring (M. N. Muller, 2017). For polygynous species with no paternal investment, male–male competition can be continuous throughout the breeding system and basal testosterone concentrations tend to remain high but still show modest increases when the male is challenged. For socially monogamous species with paternal care, in contrast, testosterone concentrations often drop once the male finds a mate but rise sharply when defending his territory or guarding his mate, consistent with the challenge hypothesis. There is nevertheless considerable nuance and variation in how males' hormonal profiles change across seasons, with challenge, parenting, and other contextual factors (e.g., group size, presence of females) and how the magnitude of these influences differs across species (Demas, Cooper, Albers, & Soma, 2007; Goymann, Landys, & Wingfield, 2007; Hirschenhauser & Oliveira, 2006).

The bottom line is that much remains to be learned about the relationships among social context and hormones, but Wingfield and colleagues' (1990, 2001) model still provides a useful approach to understanding these interactions as related to male–male competition and male parenting. This is the case for bird species, as originally proposed, as well as a wide range of vertebrates (Hirschenhauser & Oliveira, 2006; M. N. Muller, 2017; Wingfield, 2017), and even some insects (Tibbetts & Huang, 2010). Unfortunately, the relationship between sex hormones and female–female competition is not nearly as well understood and, in many species, may be influenced by different hormonal mechanisms than those influencing male–male competition (J. A. French et al., 2013; Goymann & Wingfield, 2014). For instance, females generally have lower testosterone concentrations than males in sex-role reversed species, even though females are more aggressive than and often dominate males. Therefore, the high level of female aggression is not related to absolute concentrations of circulating testosterone but may be related to a heightened sensitivity to testosterone and related hormones in the brain regions associated with aggression (Voigt & Goymann, 2007). The aggressiveness of these females also appears to be influenced by late prenatal or early postnatal exposure to testosterone and other androgens, which tends to masculinize later behavior (J. A. French et al., 2013; Grebe, Fitzpatrick, Sharrock, Starling, & Drea, 2019).

Moreover, aggression is common outside of reproductive competition in both sexes; for instance, competition for food or shelter (West-Eberhard, 1983). For seasonal breeders and outside of the breeding season, for instance, males' testosterone concentrations tend to be low but behavioral aggression still occurs in many species. The hormonal and neural mechanisms that regulate these forms of aggression differ from those associated with reproduction-motivated aggression (Demas et al., 2007; Soma, 2006). The implication is that evolution has resulted in multiple systems associated with behavioral and other forms of aggression, each of which is active under different ecological, social, and reproductive conditions.

Parenting and mating trade-offs. The basic hormonal or social cues that contribute to parental behaviors, such as feeding or protecting offspring, are well known and many of these are common across species, although there is also variation in exactly how these mechanisms (e.g., different hormones) work in different species and in females and males (Adkins-Regan, 2005; Bales & Saltzman, 2016). For mammals, the hormonal changes that occur during pregnancy and the act of giving birth are similar across species and influence maternal behavior, such as sensitivity to offspring cues (Kendrick & Keverne, 1991; Lévy, Keller, & Poindron, 2004). In species with biparental care, some of these same hormones (e.g., prolactin) are elicited in response to offspring cues and can induce parenting in males, although there are more cross-species differences in mammalian males than females in how these different hormones and related factors influence parenting (Bales & Saltzman, 2016; Rilling & Young, 2014; Saltzman & Ziegler, 2014). These hormonal responses are important for understanding sex differences in parenting and the factors that influence the evolution of parental behaviors. They are particularly important for understanding the facultative expression of men's parenting (see Chapter 6, this volume). In other words, it is important to understand how hormonal responses to social contexts can influence males' relative investment in mating or parenting.

As described earlier and in Exhibit 4.1, when males' investment in offspring is helpful but not absolutely necessary and when there are alternative mating opportunities available to males, there is a potential trade-off between the amount of effort they devote to finding mates versus caring for their offspring. The diversion of effort from parenting to attempts to find extra-pair mates can significantly compromise the well-being of offspring (Bales & Saltzman, 2016; Reed et al., 2006), and is often associated with increases in testosterone (Hirschenhauser & Oliveira, 2006; Ketterson & Nolan, 1999; M. N. Muller, 2017). The presence of alternative matting opportunities can result in increases in testosterone concentrations that in turn focus the males' behavior on mating (Hirschenhauser & Oliveira, 2006) and divert it from parenting.

In some species, however, higher concentrations of testosterone are associated with more vigorous provisioning or protection of offspring (Bales & Saltzman, 2016; S. E. Lynn, 2016). In primates, for instance, this is often associated with infanticide risks, whereby new fathers must aggressively defend their vulnerable offspring from being attacked by other males (M. N. Muller, 2017). If these other males are successful in killing the offspring, the mothers will often abandon the father and mate with the perpetrator. In these situations, testosterone-related male aggression is important for males' reproductive success, but this occurs through protection of offspring rather than pursuit of additional mates. Clearly, testosterone responses to mating opportunities can influence males' relative investment in parenting versus mating, as is discussed in Chapter 6 of this volume, but this trade-off is influenced by other biological (e.g., other hormones or neuropeptides) and social factors.

Sex Hormones, Brain and Cognition

Sex hormones not only influence the behaviors and observable traits associated with intrasexual competition and intersexual choice, such as physical aggression and plumage color, but also they can influence the organization and activation of the brain systems that have been sculpted by these same dynamics. Chapter 3 of this volume described some of the hormonal influences on the sex differences in bird song, and this discussion extends to the hormonal influences on sex differences in the other brain and cognitive traits, specifically scramble competition and spatial navigation and spatial abilities. Not surprisingly, the expression of these and other sex differences can also be influenced by ecological and social conditions and by direct genetic influences (A. P. Arnold, 1996, 2017; Gahr, 2003; Opendak, Briones, & Gould, 2016), but these do not belie the importance of sex hormones.

Males that engage in scramble competition or the expansion of range size during the breeding season have better navigational (e.g., finding the way back to one's burrow) and spatial (e.g., maze learning) abilities than same-species females (Gaulin & Fitzgerald, 1986; Jašarević, Williams, Roberts, Geary, & Rosenfeld, 2012; Perdue, Snyder, Zhihe, Marr, & Maple, 2011). These sex differences were illustrated with the comparisons of the polygynous meadow vole (*Microtus pennsylvanicus*) and their monogamous cousins—prairie (*Microtus ochrogaster*) and woodland voles (*Microtus pinetorum*). The range expansion of male meadow voles during the breeding season is correlated with a seasonal increase in testosterone (B. N. Turner, Iverson, & Severson, 1983), and is related to a corresponding improvement in spatial and navigational abilities (Gaulin & Fitzgerald, 1986). In other species with the same sex differences, these experience-dependent improvements in spatial ability are related in part to integration of newly developing hippocampal cells—the hippocampus is important for spatial learning and memory (O'Keefe & Nadel, 1978)—into the existing network of cells that support spatial memory (Kee, Teixeira, Wang, & Frankland, 2007; Ormerod & Galea, 2003).

Prenatal exposure to sex hormones results in changes in the physical structure of the hippocampus that in turn contribute to the male advantage in spatial abilities in adulthood (Isgor & Sengelaub, 1998; C. L. Williams, Barnett, & Meck, 1990). During adulthood, circulating testosterone and its metabolite (i.e., dihydrotestosterone) increase the survival rate of newly developing neurons and contribute to the sex difference in the integration of these cells into the spatial networks of the hippocampus, but the direct relationship between testosterone and spatial learning is more complex and depends on dosage and length of exposure (Choleris, Galea, Sohrabji, & Frick, 2018; Mahmoud, Wainwright, & Galea, 2016; Spritzer et al., 2011). It appears that the male advantage is largely related to the use of spatial strategies, that is, using distant cues to orient themselves in the general direction in which they need to travel to complete the task (e.g., find a home base), but does not enhance memory for the location of objects in specific contexts (Chow, Epp, Lieblich, Barha, & Galea, 2013).

Estrogens are important for the generation of new neurons within the hippocampus and are associated with a female advantage on some types of learning, but are often associated with poor performance on spatial learning tasks (Galea, Lee, Kostaras, Sidhu, & Barr, 2002; Mahmoud et al., 2016). Barha and Galea (2013) found that the presence of estradiol reduced the activation of new neurons in response to spatial experiences, although the strength of these effects varies with the specific spatial task (Duarte-Guterman, Yagi, Chow, & Galea, 2015). Whatever the specific mechanisms, the potential benefit of lower spatial abilities is reduced exploration and reduced predation risks when the female is caring for her offspring.

Condition-Dependent Trait Expression

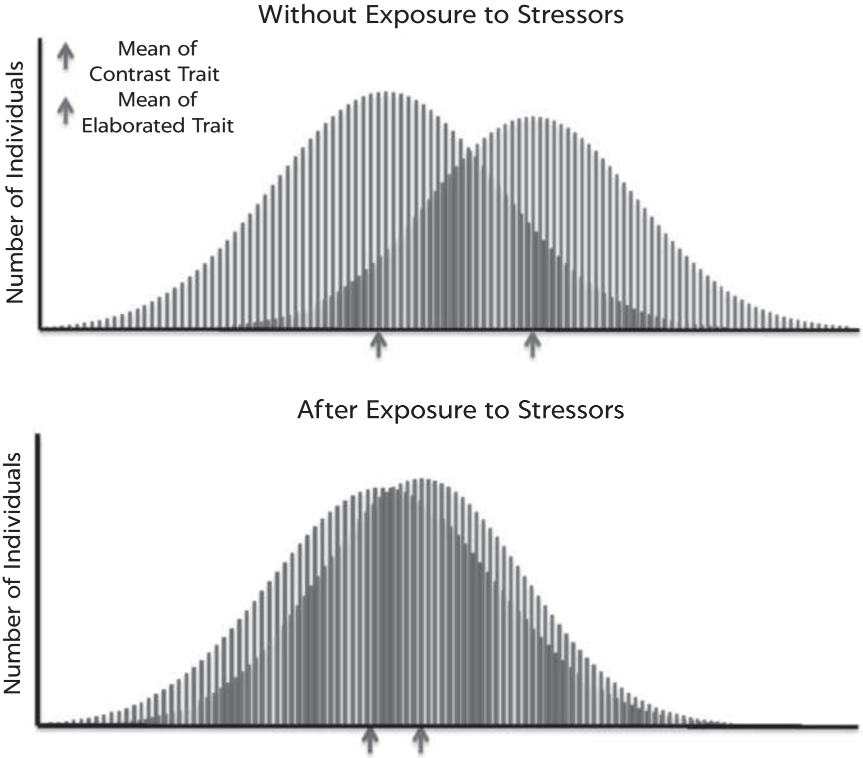
The expression of sexually selected traits (e.g., the peacocks' train) is dependent on the condition of the individual. The development, expression, and maintenance of these traits are thought to impose costs on less healthy individuals and as such, are honest indicators of the individuals' exposure and resilience to natural stressors (Zahavi, 1975). These natural stressors are parasite exposure, poor nutrition, and the rigors of social competition. It is not a coincidence that these same stressors—plague, famine, and war—have captured the imagination of human artists and scientists for millennia, as illustrated by Dürer's 1498 woodcut, "The Four Horsemen, From the Apocalypse" (see Figure 4.5). The evolutionary elaboration of these traits in one sex or the other creates many of the sex differences discussed so far, but at the same time makes these traits more vulnerable to stressors in the sex with the advantage (Cotton, Fowler, & Pomiankowski, 2004; Geary, 2015; Johnstone, 1995; Zahavi, 1975).

The basic idea is shown in Figure 4.6. The top distributions show a sex difference in a sexually selected trait, say plumage color, in males (the right distribution) and the same trait (contrast) in females (the left distribution) when conditions are favorable. However, when exposed to stressors, such as a food shortage, the sexually selected trait is more severely compromised and results in a reduction in the size of the sex difference, and more variability among

FIGURE 4.5. The Four Horsemen of the Apocalypse

The first three horsemen represent plague (infectious disease), famine, and war (social competition), and sex differences in sensitivity to these stressors are common. The fourth horseman is death. From *The Four Horsemen, From the Apocalypse* (Woodcut), by A. Dürer, 1498, New York, NY: The Metropolitan Museum of Art. In the public domain.

FIGURE 4.6. Sexual Selection and the Evolution of Elaborated Traits



Sexual selection will result in the evolution of elaborated traits that signal competitive abilities or influence mate choices. The development, maintenance, and expression of these traits are highly sensitive to stressors and thus reveal the individuals' exposure and resilience to them. The top distributions show larger sexually selected traits (distribution to the right) in one sex versus the other; or larger sexually selected than naturally selected traits in the same individual. Exposure to stressors has stronger effects on the elaborated trait than the contrast trait, such as the same trait in the other sex (distribution to the left).

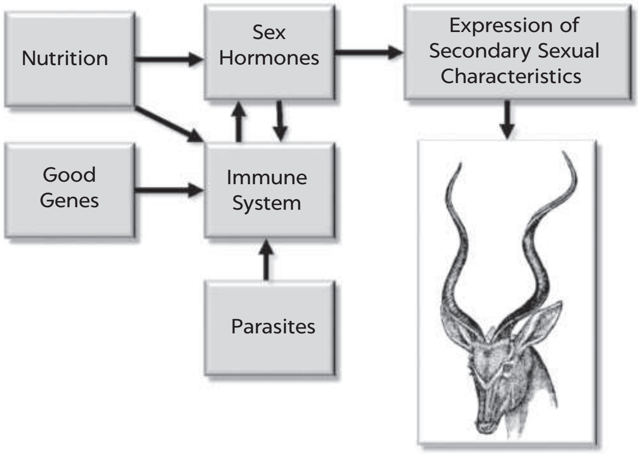
males than females in this example. The increased variability occurs because some individuals are more severely compromised by stressors than are others and this is first and foremost signaled in sexually selected traits. Several examples were provided in Chapter 3 of this volume, and some of the underlying reasons why these traits are vulnerable are discussed next.

Immunocompetence

Much of the early research on condition-dependent traits was conducted with males, largely because of the historical focus on male–male competition and female choice (Johnstone, 1995; Zahavi, 1975), but females' sexually selected traits have also been assessed in recent years (Foo, Nakagawa, Rhodes, & Simmons, 2017). One prominent theory, proposed by Folstad and Karter (1992), focused on the relation between the health effects of parasitic infections and the hormonal concentrations needed to develop and express sexually selected traits, known as the *immunocompetence handicap hypothesis*. A simplified version of the model is shown in Figure 4.7. At the core is the reciprocal relationship between sex hormone concentrations, especially testosterone, and overall competence of the immune system. One prediction is that the increase in testosterone concentrations needed for the development of sexually selected traits will compromise immune functions such that individuals in poor condition cannot express these traits without significant risks to their long-term health (Folstad & Karter, 1992; Saino & Møller, 1994; Zuk et al., 1995). To avoid these risks, individuals in poor health must divert resources from the development of sexually selected traits to the immune system. In this way, they can maintain their health, but they will not be as attractive to the opposite sex and will not be as competitive in contests for reproductive resources. The benefit is an increased chance of surviving to the next breeding season and potentially competing at that time.

The model is appealing because it incorporates Zahavi's (1975) handicap principle and Hamilton and Zuk's (1982) proposal that sexually selected traits signal resistance to parasites; specifically, immunosuppression associated with parasitic infection is predicted to be more evident in the sexually selected traits of unhealthy males. The hypothesis has been the focus of numerous field and experimental studies (Deviche & Cortez, 2005; Mougeot, Redpath, & Piertney, 2006; M. L. Roberts, Buchanan, Hasselquist, & Evans, 2007; Saino, Incagli, Martinelli, & Møller, 2002), and several large meta-analyses that summarize findings across individual studies (Foo, Nakagawa, et al., 2017; Habig & Archie, 2015; M. L. Roberts, Buchanan, & Evans, 2004). The most recent meta-analysis revealed that experimental increases in testosterone reliably

FIGURE 4.7. Relations Among Sex Hormones, Immune Functioning, Parasites, and the Expression of Secondary Sexual Characteristics of the Male Kudu (*Strepsiceros kudu*)



Male kudo from *The Descent of Man, and Selection in Relation to Sex* (p. 255), by C. Darwin, 1871, London, England: John Murray. In the public domain.

suppressed immune functions in males (Foo, Nakagawa, et al., 2017), consistent with immunosuppression. The immunosuppression may occur because the increase in testosterone is associated with higher metabolic activity (e.g., more behavioral aggression) that increases oxidative stress, which in turn compromises several aspects of immune functions (Alonso-Alvarez, Pérez-Rodríguez, Garcia, & Viñuela, 2009; Koch, Josefson, & Hill, 2017).

Deviche and Cortez's (2005) study of house finches (*Carpodacus mexicanus*) illustrates the basic relationship. Here, some males were given testosterone implants and others empty implants, and then they were exposed to two different parasites, across 2 months. In the days following parasite exposure, the males with high testosterone concentrations showed much weaker immune system responses (e.g., 59% fewer antibodies) than the other males. Even longer term trade-offs have been demonstrated in the red grouse (*Lagopus lagopus scoticus*; Mougeot, Redpath, Piertney, & Hudson, 2005). In that study, males were captured in spring and randomly assigned to testosterone-implant or control group. The following month, the testosterone-treated males had a larger comb—this trait signals male dominance and influences female choice—but weighed less, possibly because of increased behavioral aggression during male–male competition for nesting sites. Five months later, during the breeding season, testosterone-treated males were more likely to attract mates than were other males and had more offspring but paid the price in terms of higher mortality (12% higher), compromised immune functions, and higher parasite infestation.

The story is different for studies that examine the relationship between naturally occurring testosterone concentrations and immune functions (Foo, Nakagawa, et al., 2017). In natural contexts, males with higher testosterone concentrations and well-developed sexually selected traits do not have worse immune functions than males with lower testosterone concentrations, despite the fact that high-status males often have higher parasite loads than low-status males (Habig, Doellman, Woods, Olansen, & Archie, 2018); high-status males have priority access to food and mates and greater exposure to parasites. The pattern follows from Folstad and Karter's (1992) model, because males in good health should be able to tolerate high concentrations of testosterone and parasites and maintain a strong immune response (Jennions, Møller, & Petrie, 2001). It is only unhealthy males that pay the price of immunosuppression when testosterone concentrations rise (Getty, 2006), which keeps testosterone concentrations lower and the immune system healthy in these males. The result is that healthy immune responses will be found in males with higher and lower concentrations of testosterone, and that overall there might not be substantial sex differences in immune functions (Kelly, Stoehr, Nunn, Smyth, & Prokop, 2018). The underlying vulnerability of some males will be most evident in experimental studies, where biologists artificially increase testosterone concentrations that will disproportionately compromise the immune systems of less healthy males, those that maintain low testosterone in natural contexts.

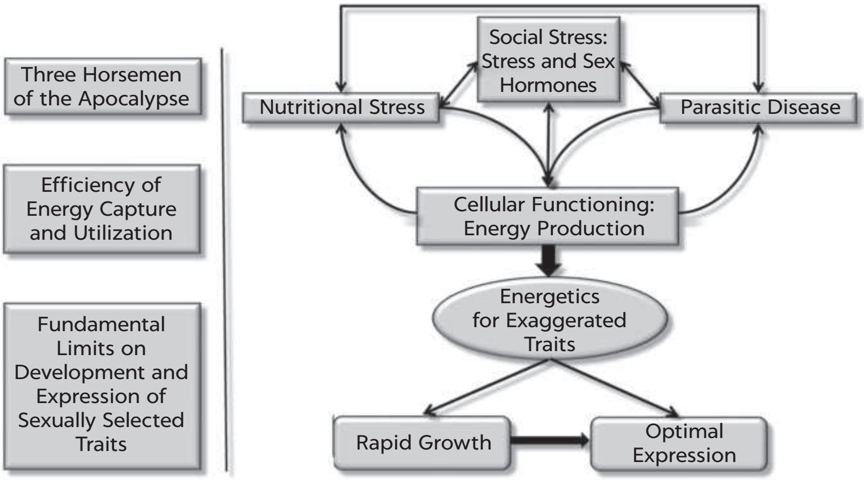
There is now good evidence that male preference for one female over another is much more common than once thought (Bonduriansky, 2001; Fitzpatrick, Altmann, & Alberts, 2015; Weiss, Kennedy, & Bernhard, 2009), and that some of these preferences are related to traits that signal females' reproductive potential and immunocompetence (Roulin, 2004). One possibility is that estrogens have an analogous influence on females' condition-dependent traits as testosterone has for males' traits, but this does not seem to be the case. In fact, if anything, higher estrogen concentrations are associated with better immune functions (Foo, Nakagawa, et al., 2017). Therefore, the factors that influence the condition-dependent expression of traits that influence male choice and female–female competition remain to be determined, but are likely influenced at least in part by priority access to high-quality food.

Cellular Functioning

A more recent proposal is that condition-dependent traits are direct indicators of the efficiency of cellular energy production and other functions that largely occur within the mitochondria (organelles within cells; G. E. Hill, 2014; Koch et al., 2017). The key idea is that the efficiency of mitochondrial functioning limits the development, maintenance, and expression of all energy-demanding traits. Sexually selected traits are generally more exaggerated than are other traits and any disruptions in cellular energy production will be disproportionately reflected in the development and expression of these traits. To illustrate, assume that the relationship between cellular energy and trait development is analogous to the relationship between income and house size. It costs more money to build and maintain a 5,000-square-foot house than a 2,000-square-foot house. Only individuals with sufficient income can build and maintain the larger house, and only individuals with efficient mitochondria and excess energy production can develop and express exaggerated sexually selected traits.

The proposal integrates mitochondrial functioning with the reciprocal relationship between testosterone and immunocompetence described earlier, because mitochondria are critical to the synthesis of sex hormones and contribute to immune responses (Weaver, Santos, Tucker, Wilson, & Hill, 2018; A. West, Shadel, & Ghosh, 2011), and contribute to many other aspects of health and development (Picard et al., 2015; Picard, Wallace, & Burelle, 2016). Oxidative stress is included among the critical, health-related aspects of mitochondrial functioning; this is the generation of cell and DNA damaging molecules during energy production (Morehouse, 2014; von Schantz, Bensch, Grahn, Hasselquist, & Wittzell, 1999). Excessive oxidative stress can contribute to a variety of diseases and will accelerate the aging process (Brooks & Garratt, 2017). As illustrated in Figure 4.8, exposure to three of Dürer's horsemen—parasites, nutritional stress, and social competition—can influence one or several aspects of mitochondrial functioning and related physiological processes (e.g., those that promote trait growth) that will then be reflected in the development or expression of sexually selected traits and signal underlying health (D. J. Emlen, Warren, Johns, Dworkin, & Lavine, 2012; Koch et al., 2017).

FIGURE 4.8. Mitochondrial Energy Production and Sexual Selection



Cellular functioning, including mitochondrial energy production, may be at the nexus of the relation between exposure to natural stressors (i.e., the Horsemen of the Apocalypse)—nutritional stress (famine), parasitic infection (plague), and social competition (war)—and the growth and development of sexually selected traits.

We return to the northern elephant seal to illustrate the potential usefulness of this approach (Sharick, Vazquez-Medina, Ortiz, & Crocker, 2015). Males and females fast during the breeding season, and males engage in energy-demanding physical competition for social dominance and females produce energy-rich milk after they give birth. The combination of fasting and high energy demands (supported by stored fats) greatly increases mitochondrial activity and oxidative stress and in doing so can compromise cellular functioning and overall health (Koch et al., 2017). Sharick et al. (2015) found increased oxidative stress for males and females during the breeding season, consistent with a trade-off between somatic effort (maintenance) and reproductive effort for both sexes. Relative to females, males showed higher levels of cellular and DNA damage and systemic inflammation that is common with chronic diseases, differences that likely contribute to the sex difference in lifespan for this species (Condit et al., 2014). In other words, the energetic demands of reproductive competition, whether this is intersexual choice or intrasexual competition, result in increased cellular energy production and other processes. One by-product of these processes includes an increase in oxidative stress that over time increases susceptibility to a variety of diseases and accelerates normal aging (Lane, 2011).

These processes will occur more intensely in males than females and likely contribute to the shorter lifespan of males than females in species with intense male–male competition. The key point is that whatever the underlying biological processes, chronic exposure to nutritional stress, chronic illness, and vigorous social competition results in wear and tear on the body and this is signaled by the condition (e.g., color) of sexually selected traits. The result is that these traits can be used by the opposite sex to make their mate choices and by the same sex to estimate the competitive abilities of rivals.

CONCLUSION

Ultimately, the function of growth and developmental activity is to accumulate reproductive potential, to build the type of body and acquire the types of behavioral and cognitive competencies needed to survive to reproductive age and then to successfully reproduce (R. D. Alexander, 1987). As illustrated with the semelparous Pacific salmon, once reproduction has occurred, the gene-carrying body or soma is disposable. The same is true for all species: the lifespan and species-typical activities therein are evolved traits and are understandable in terms of the social and ecological selection pressures that resulted in reproductive opportunity and constraint during the species' evolutionary history (Roff, 1992; Stearns, 1992). For species with a relatively long lifespan, the expression of developmental and reproductive activities cannot be too tightly constrained. This is because the corresponding social and ecological conditions can vary across and within lifetimes, and many traits are plastic or flexibly expressed on the basis of these experiences. Individuals of these species still proceed through the species-typical pattern of life history development and adult reproductive activities but can make adjustments (often hormone initiated) in the timing of development or form of these activities.

The core components of sexual selection, intrasexual competition and intersexual choice, as well as the demands of parenting, are key selection pressures in the evolution of life histories, and key influences on the here-and-now expression of life history traits. The male–male competition of northern elephant seals results in conditions that favor a longer developmental period during which males gain the weight and physical size needed to compete for mates (Le Boeuf & Reiter, 1988). Female northern elephant seals do not compete for access to mates and any advantage to delaying reproductive maturation is outweighed by the costs of potentially dying before having the opportunity to reproduce (Condit et al., 2014). The behavioral competition of male bowerbirds reflects the same dynamic. Males have an evolved and hormonally influenced bias to engage in bower building, but it takes years of observation of skilled males and practice before they can build an attractive bower (Collis & Borgia, 1992). For slow maturing species, these developmental activities often include play (Burghardt, 2005), which appears to provide the practice needed to fine-tune a variety of physical, cognitive, and social competencies before adulthood (Graham & Burghardt, 2010; Palagi et al., 2016).

Play and other aspects of development eventually merge into adult activities, including parenting. Male parenting is particularly interesting, because it is much less common than female parenting in mammals and is found in humans. When it occurs, male parenting typically involves trade-offs between benefits to offspring and the corresponding costs of lost mating opportunities and risk of cuckoldry. Sex differences in the proximate expression of parental behaviors and trade-offs in male parenting, among other aspects of reproduction, are moderated by prenatal and postnatal exposure to sex hormones (Adkins-Regan, 2005). These hormones do not deterministically cause sex differences but rather interact with genetic sex, developmental history, and current conditions to bias males and females to behave in ways that often differ (A. P. Arnold, 2017; Choleris et al., 2018; Wingfield et al., 1990). In fact, sex hormones appear to influence the expression of most of the sex differences described in this chapter, including differences in rough-and-tumble play, mating behaviors, parental effort, intrasexual competition, intersexual choice, and health (Mahmoud et al., 2016). A final important point is that the evolution of sex differences in traits related to competition and choice results in an associated sex difference in vulnerability. Paradoxically, the sex with the advantage under favorable conditions shows a heightened vulnerability when conditions become unfavorable, which can reduce and even eliminate many sex differences (Geary, 2015).

5

Sexual Selection in Primates and During Human Evolution

The implication of C. Darwin's (1859) theory of natural selection for understanding humanity's place in nature generated quite an uproar and considerable criticism directed at his theory and Darwin personally (J. Browne, 2001). Even Wallace (1869), who codiscovered natural selection (C. Darwin & Wallace, 1858), joined the fray, arguing that the moral and mental development of humans is not explainable by natural selection alone. The situation only worsened with publication of C. Darwin's (1871) second masterwork, *The Descent of Man, and Selection in Relation to Sex*. Although Huxley (1863) was the first to discuss humans in the context of natural selection, Darwin's work was more thorough and focused on matters that provoked the ire of his contemporaries, as shown in Figure 5.1. One basic sticking point was Darwin's argument that humans shared a common ancestor with other primates, even though Huxley had shown the anatomical similarities between primates and humans several years before, as shown in Figure 5.2.

This chapter takes up these same issues, focusing on how the dynamics of sexual selection unfold in nonhuman primates and how they likely unfolded during human evolution. By examining sexual selection across primate species, we can develop useful constraints on the dynamics, such as the form and intensity of male–male competition, that were likely during the course of human evolution (Foley & Lee, 1989; Rodseth et al., 1991). The consideration of sexual dynamics in primates also brings us one step closer to our own species and demonstrates that many of the reproductive sex differences found in modern humans are evident in many other primates. The first general section

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http://dx.doi.org/10.1037/0000181-005
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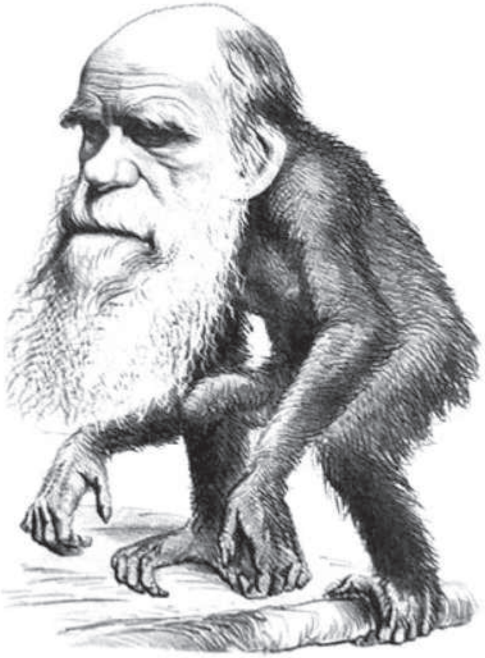
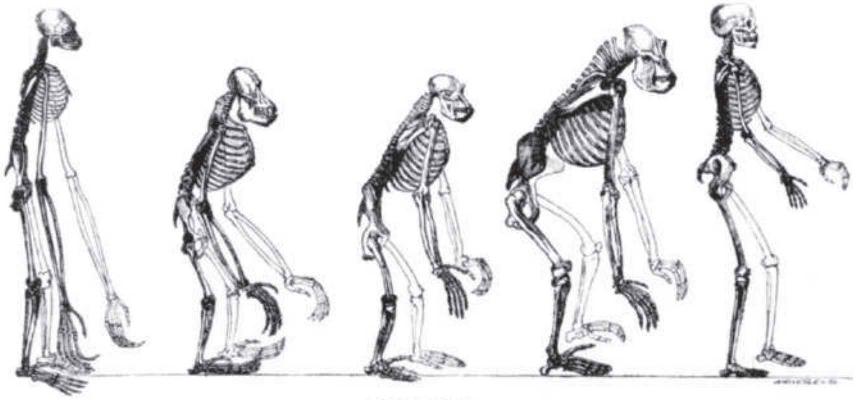
FIGURE 5.1. Satirical Cartoon of Darwin



Following publication of *The Descent of Man, and Selection in Relation to Sex* (C. Darwin, 1871). From "A Venerable Orang-Outang: A Contribution to Unnatural History," March 1871, *The Hornet.* In the public domain.

FIGURE 5.2. Huxley Was the First to Note the Similarities in Evolution Between Humans and Nonhuman Primates



Skeletons of the
Gibbon. Orang. Chimpanzee. Gorilla. Man.

Photographically reduced from Diagrams of the natural size (except that of the Gibbon, which was twice as large as nature), drawn by Mr. Waterhouse Hawkins from specimens in the Museum of the Royal College of Surgeons.

From *Evidence as to Man's Place in Nature* (front piece), by T. H. Huxley, 1863, New York, NY: Appleton and Company. In the public domain.

provides an overview of the dynamics of sexual selection in primates and the second focuses on the implications of these patterns, combined with the fossil record, for drawing inferences about sexual selection during human evolution; for a more general review of primate behavior and evolution see Mitani, Call, Kappeler, Palombit, and Silk (2012).

SEXUAL SELECTION IN PRIMATES

Primate mating systems range from monogamy to polyandry and polygyny to high levels of promiscuous mating by both sexes. Phylogenetic analyses (i.e., analyses based on the evolutionary relatedness among species) suggest that the ancestral state for primates was solitary nocturnal males and females with promiscuous mating. This ancestral state has been retained among some species and largely diverged into polygynous or monogamous systems in others, along with a few polyandrous species (Lukas & Clutton-Brock, 2013; Opie, Atkinson, & Shultz, 2012). Monogamous primates tend to be arboreal (i.e., they live in trees) and show smaller sex differences than humans in physical size and in the pattern of physical development (C. B. Jones, 2003). Polyandrous reproduction occurs in a few primates (e.g., *Callitrichids*; Goldizen, 2003), but with the exception of paternal investment, any corresponding sex differences generally do not fall into the same pattern found in humans.

For these reasons and based on the sex differences in physical size among our ancestors (below), a polygynous mating system provides a better background for understanding human evolution than a monogamous or polyandrous one (R. D. Alexander, Hoogland, Howard, Noonan, & Sherman, 1979; Lukas & Clutton-Brock, 2013). As with other primates with an evolutionary history of male–male competition, men are larger than women and invest less in offspring (see Chapter 6, this volume), mature more slowly (see Chapter 10), compete more intensely for mates (see Chapter 8), and have a shorter lifespan. This chapter focuses on polygynous species and begins with male–male competition and female choice. Following a review of female choice, the discussion moves to the dynamics of female–female competition and male choice. These features of sexual selection are not as well understood in primates as male–male competition and female choice, but merit discussion because they are found in humans.

Male–Male Competition

As with other species in which it occurs, male–male competition in primates is about achieving control of the mating activities of sexually receptive females or of the resources that females need to reproduce (e.g., territory). This section considers how males' relative success at achieving this control is influenced by social rank or social dominance and reviews the relationship between dominance and sex hormones. In most primates, male–male competition is one-on-one, but in some of them males cooperate with each other and form coalitions as a strategy to improve their social status. These dynamics are discussed, and the section closes with a review of the mating strategies of males that have not achieved a high social rank.

Social Dominance

The importance of social dominance for males' reproductive opportunities is confirmed by behavioral observation and by DNA fingerprinting to determine paternity. Core findings in both of these areas are highlighted next.

Behavioral research. The northern (*Mirounga angustirostris*) and southern (*Mirounga leonina*) elephant seal provide prototypical examples of how males establish dominance through physical contests (see Chapter 3, this volume). For polygynous primates, the establishment and maintenance of social dominance is achieved in much the same way, but the overall relation between dominance and reproductive outcomes is not always as straightforward (L. Ellis, 1995; Goodall, 1986). This is because primate social dynamics are more nuanced and complex than those found with elephant seals, including the establishment of coalitions in some primates. A male's rise to or fall from social dominance can also be influenced by the social support of the dominant females within the group, and the relationship between social dominance and reproductive outcomes can vary with the operational sex ratio, degree of inbreeding avoidance, synchrony of females' estrus, the alternative mating strategies of other males, and the preferences of dominant males (Bray, Pusey, & Gilby, 2016; Dunbar, 1984; Gogarten & Koenig, 2013; Newton-Fisher, Thompson, Reynolds, Boesch, & Vigilant, 2010; Perloe, 1992; Setchell, Richards, Abbott, & Knapp, 2016; Smuts, 1987; Takahashi, 2004; Widdig et al., 2016; Wroblewski et al., 2009). Even with these nuances, the establishment and maintenance of social dominance typically has important reproductive consequences for individual males (L. Ellis, 1995).

The mandrill (*Mandrillus sphinx*) provides an excellent example of one-on-one male–male competition in a polygynous primate (see Figure 5.3). C. Darwin (1871) proclaimed that no "other member of the whole class of mammals is coloured in so extraordinary a manner as the adult male mandrill. The face at this age becomes of a fine blue, with the ridge and tip of the nose of the most brilliant red" (p. 292). In addition to this sexually dimorphic color pattern, male mandrills develop more slowly than females and achieve competitive adult status, even becoming alpha males, at about 11 years as compared with about 4 years for females' first offspring. Males are also 3 to 4 times heavier than females and compete by means of behavioral (e.g., threat grunts) and physical (e.g., lunges) threats and frequent physical attacks to establish dominance over other males (A. F. Dixson, Bossi, & Wickings, 1993; Setchell, Lee, Wickings, & Dixson, 2001; Wickings, Bossi, & Dixson, 1993).

The dynamics of male–male competition in mandrills is nicely illustrated by a long-term study of two colonies of free-ranging (i.e., captive but living in

FIGURE 5.3. For Dominant Male Mandrills (*Mandrillus sphinx*), the Outer Portions of the Nose (lighter in the illustration) Turn Blue and the Center Strip Is a Bright Red

From *The Descent of Man, and Selection in Relation to Sex* (p. 292), by C. Darwin, 1871, London, England: John Murray. In the public domain.

a seminatural environment) individuals (A. F. Dixson et al., 1993; Setchell, Charpentier, & Wickings, 2005; Setchell, Wickings, & Knapp, 2006; Wickings et al., 1993). Dominant and subordinate males do not differ in body weight but differ considerably in the degree of facial and sexual organ coloration described by C. Darwin (1871). Red coloration in particular is a sign of social dominance and physical health, with subordinate males sporting a drabber countenance (Setchell, Smith, Wickings, & Knapp, 2008b). The coloration patterns are social signals that cue in other males as well as females to the condition of the male. Males with subordinate coloration avoid confrontations with dominant males and reduce risk of injury. If one male does not immediately withdraw from a potential confrontation, the pair proceeds through a series of displays that frequently escalate into an intense physical confrontation if one of these males does not eventually back down (Setchell, 2016; Setchell & Wickings, 2005). The winners of these confrontations achieve dominance. They then mate guard females (e.g., stay near and drive away other males) during the females' most fertile time (Setchell et al., 2005, 2016), which is signaled by a swelling of females' sexual organs. Many males copulate with females, but only dominant males copulate when females are the most likely to conceive (Wickings et al., 1993). The result is that dominant males sire 7 out of every 10 offspring, and strikingly 2 out of every 3 males never reproduce in their lifetime (Setchell, 2016).

As with the mandrill, males in other polygynous and promiscuous species form dominance hierarchies, and position in these hierarchies influences access to estrus females (de Ruiter & van Hooff, 1993; L. Ellis, 1995; Surbeck, Langergraber, Fruth, Vigilant, & Hohmann, 2017; Weingrill, Lycett, & Henzi, 2000; Wroblewski et al., 2009). However, the relationship between dominance and mating success is not always as strong as that found in the mandrill; some studies have found no relation between rank and mating access (e.g., de Ruiter & Inoue, 1993). The differences are related to whether captive, wild, or free-ranging groups have been studied and to social dynamics within these groups. Studies that find little or no relationship between dominance and reproductive success are often based on captive groups, with studies of wild and free-ranging groups more consistently finding a positive relation (de Ruiter & van Hooff, 1993; Perlman, Borries, & Koenig, 2016).

For some species, the maintenance of social dominance affords the added benefit of protecting offspring from infanticide (Böer & Sommer, 1992; Dunbar, 2018a; Hrdy, 1979). Sometimes when one male or a coalition of males from outside of the group displaces the residing male or males, the new alpha will attempt to kill suckling infants; this is because suckling suppresses ovulation and once suckling ceases the females become fertile. Females often resist these attacks on their infants, but when infanticide does occur, they often become sexually receptive to the male and have his offspring (Hrdy, 1979). In these situations, male infanticide is a reproductive strategy at the expense of the recently deposed male, the female, and, of course, the infant (Borries, Launhardt, Epplen, Epplen, & Winkler, 1999). The threat of infanticide means the maintenance of social dominance can influence the number of offspring sired and, under some conditions, the number surviving to maturity (L. Ellis, 1995). In fact, it has been proposed that the threat of infanticide has contributed to the evolution of monogamy in some primates, and protection from infanticide might be the primary form of male parenting in these species, although this proposal is debated (Dunbar, 2018a; Lukas & Clutton-Brock, 2013; Opie, Atkinson, Dunbar, & Shultz, 2013).

Genetic research. For mandrills, the relationship between social dominance and reproductive success has been confirmed using DNA fingerprinting to determine paternity (Setchell, 2016; Setchell et al., 2005). During one 5-year period, the two dominant males (of six males) sired all 36 offspring, and the number of offspring fathered in any given year was related to the relative dominance of the two males. During the first 3 years, the alpha male sired 17 of the 18 offspring. During the 4th year, the beta male became alpha, but only sired two offspring during this season, whereas the former alpha male sired four offspring. During the fifth year, the new alpha male fathered 9 of the 12 offspring. The same pattern was demonstrated over a 20-year period for this colony and another colony of mandrills (Charpentier et al., 2005). There were two factors that predicted when alpha males did not sire offspring; the first was being genetically related to females (inbreeding avoidance) and to other adult males. Males avoided copulations with their full sisters (or the females resisted copulations), and males were more tolerant of the copulations of closely related males (i.e., brothers). The second factor was having several females in estrus at the same time, which prevented dominant males from mate guarding all of them effectively.

In another long-term study, Altmann et al. (1996) used DNA fingerprinting and behavioral observation to assess the relationship between social dominance and reproductive outcomes in a group of wild savannah baboons (*Papio cynocephalus*). Of 20 adult males, a single individual, Radi, sired 44% of offspring, a disproportionate number. Radi sired 81% of the offspring during a 4-year reign as the alpha male, but only 20% of the offspring during the years before and after his reign. A 40-year study of rhesus macaques (*Macaca mulatta*) revealed that young males in good health and with diverse major histocompatibility complex (see Chapter 3, this volume) genes sired 37% more offspring than the average male across their lifespan, with 17% of males never reproducing (Dubuc, Ruiz-Lambides, & Widdig, 2014; Widdig et al., 2016). This is a common finding. Across 13 species of primate and among wild populations living in multimale–multifemale groups, DNA fingerprinting revealed that alpha males sired between 21% and 100% of the groups' offspring (Ostner, Nunn, & Schülke, 2008). Across species, in a typical group of five males, the alpha sired 2 out of every 3 offspring. Studies that have appeared since Ostner et al.'s (2008) review show the same pattern (Dubuc et al., 2014; Newton-Fisher et al., 2010; Surbeck, Langergraber, et al., 2017; Wroblewski et al., 2009).

Status, Hormones, and Health

Sex and stress hormones influence reactivity to and are responsive to social conditions, coordinating multiple physiological systems to address challenges that arise in these contexts. As discussed in Chapter 4 of this volume, prolonged and excessive exposure to these hormones can compromise physical health, including increases in susceptibility to infections and slower recovery from disease and injury (Glaser & Kiecolt-Glaser, 2005). Any such weaknesses are often exploited by others in the community, especially in the context of male–male competition. Injured or sick males typically experience a drop in social rank and in the number of offspring they sire (Goodall, 1986; Sapolsky, 1993). Cause and effect relations between health and status are difficult to determine, however, because status influences and is influenced by health. One long-term study of wild yellow baboons indicated that healthy males with well-functioning immune systems were more likely to rise to alpha status than their less-robust peers (Lea et al., 2018); in other words, health preceded status.

Even so, the relationship between health, status, and hormones is further complicated by the multiple influences of sex hormones (Adkins-Regan, 2005), the typical social pattern of the species (e.g., solitary monogamous or multimale–multifemale communities; Abbott et al., 2003; Sapolsky, 2005), and fluctuation in social conditions within the same species, especially whether or not the status hierarchy is stable (M. N. Muller, 2017; Whitten & Turner, 2004). Despite these nuances, it is clear that sex and stress hormones are critical to understanding primate social and reproductive behavior. As with other species, testosterone influences status striving among primates and is responsive to challenges to one's status and to the presence of sexually receptive females (Muehlenbein & Bribiescas, 2005; M. N. Muller, 2017).

Sapolsky and colleagues' studies of wild olive baboons (*Papio anubis*) shows how the relationships among hormones, health, and immunocompetence can be influenced by social stability and social rank (Ray & Sapolsky, 1992; Sapolsky, 1993). Dominant males in stable social hierarchies have low levels of stress hormones, are in better physical condition, and appear to have better functioning immune systems than subordinate males. Day-to-day testosterone levels are not higher than those of subordinates, except during challenges to social position. When this occurs, the testosterone and stress hormone levels of the challenged male rise quickly and facilitate defense of his position in the hierarchy. Once the confrontation is over, testosterone and stress hormone levels quickly return to baseline levels in dominant males (assuming they successfully defended their position), but the stress hormone levels of subordinates remain elevated and are associated with the suppression of testosterone.

In some cases, the relationship between male–male competition and testosterone responsivity is related to the presence of sexually receptive and fertile females. For example, M. N. Muller and Wrangham (2004) explicitly tested Wingfield, Hegner, Dufty, and Ball's (1990) challenge hypothesis with a group of wild chimpanzees (*Pan troglodyte*; see Chapter 4, this volume). In the presence of estrus females that had previously given birth—the most attractive females for male chimpanzees—testosterone levels and rates of male–male aggression increased. Alpha males showed the most robust increases in testosterone, which appeared to be directly related to physical fighting for access to the most attractive females and not to sexual behavior per se. A larger-scale study in a different chimpanzee community confirmed this basic finding, although testosterone and aggression increased among males generally—not disproportionately in alpha males—in the presence of attractive and receptive females (Sobolewski, Brown, & Mitani, 2013).

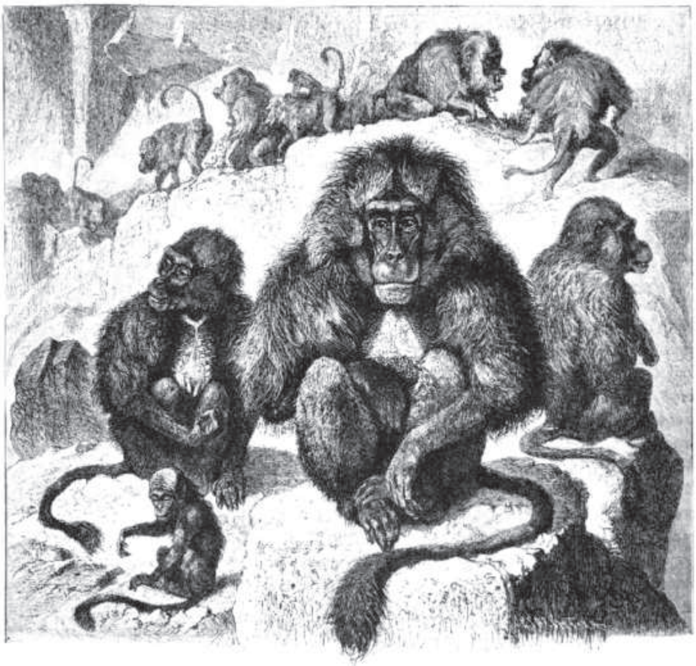
In some species, the testosterone levels of dominant males do not show these types of fluctuations, but rather remain high or even increase once they become dominant. The difference is related to the stability of the dominance hierarchy (M. N. Muller, 2017), and again the mandrill provides a good illustration. Young male mandrills with higher testosterone concentrations are more likely to successfully rise to alpha status, and once they achieve this status their testosterone concentrations rise even further, their facial coloration changes, and their testes become larger (Setchell, 2016; Setchell & Dixson, 2001). The high concentrations of testosterone reflect frequent challenges to their alpha status, and the increase in testes size is likely associated with female cryptic choice and sperm competition. These studies show that testosterone concentrations are associated with the ability to gain and maintain access to reproductive opportunities and are highly sensitive to threats to this opportunity (M. N. Muller, 2017).

For males, a loss of status often results in a decrease in testosterone concentrations, an increase in stress hormone concentrations, and deterioration in health (M. N. Muller, 2017; Setchell, Smith, Wickings, & Knapp, 2010). A striking example is illustrated by the aftereffects of losing a harem in male gelada baboons (*Theropithecus gelada*; see Figure 5.4):

> Defeated harem-holders literally age overnight. Their chest patches fade from the brilliant scarlet of a harem male to the pale flesh-color typical of juveniles and old animals, their capes lose their luster and their gait loses its bounce. The changes are both dramatic and final. (Dunbar, 1984, p. 132)

A similar pattern is found in many species of New World (South American) monkey (i.e., *Callitrichidae*). When dominated by other males, subordinates experience a severe drop in the hormones responsible for testicular development and the maturation of sperm, sometimes resulting in sterility (Abbott, 1993).

FIGURE 5.4. The Breast of the Dominant Male Gelada Baboon (*Theropithecus gelada*) at the Forefront Has a Red Coloration



From *The Natural History of the Mammalia* (p. 56), by C. Vogt and F. Schecht, 1887, London, England: Blackie. In the public domain.

Social dynamics can also have significant effects on females' stress hormone concentrations and their health and ability to reproduce. In many primates, dominant females chronically harass subordinates that are potential competitors for access to mates or food. The chronic harassment and long-term elevation of stress hormones in turn can compromise the health and reproduction of subordinate females. Male–female relationships also influence females' stress levels and health. The most extreme of these dynamics occurs in species in which males commit infanticide. As described earlier, infanticide risks increase sharply if a new male migrates into the group and replaces the current dominant male. The new alpha male will then systematically attack dependent offspring, but mothers resist these attacks, sometimes successfully, and the conflict between the alpha male and females with dependent offspring can extend for weeks or months. During these times, mothers with dependent offspring have much higher stress hormone concentrations (45% higher in one study; Engh et al., 2006) than in the weeks prior to the onset of the attacks. Females with male "friends" (Palombit et al., 2001) that protected their infants showed no increase in stress hormone concentrations. Overall, these hormonal and reproductive effects do not seem to be as consistent as those found in males, and are related to the level of harassment received by subordinates, the level of subordinates' social support, and the stability of the female's dominance hierarchy (Abbott et al., 2003; Setchell, Smith, Wickings, & Knapp, 2008a).

Coalitional Competition

As with the mandrill, male–male competition in primates is typically one-on-one, but in some species and contexts it can involve coalitions. Coalitions occur when two or more individuals act in concert to achieve dominance over a third, and the ability to form these relationships and use them effectively can influence a male's position in the dominance hierarchy and thereby boost reproductive prospects (Gilby et al., 2013). Male chimpanzees provide an excellent example of coalitional behavior and illustrate the potential importance of male philopatry. The *philopatric* sex is the sex that stays in the group of their birth, whereas the other sex emigrates on reaching maturity to avoid inbreeding. Females are typically the philopatric sex among primates and mammals more broadly (Greenwood, 1980; Wrangham, 1980). This is important because coalitional behavior, when it occurs, tends to be among individuals of the philopatric sex (Wrangham, 1980). In addition to chimpanzees, male philopatry is found in other apes, including bonobos (*Pan paniscus*; Eriksson et al., 2006) and sometimes in gorillas (*Gorilla gorilla*), although both sexes tend to disperse (Harcourt & Stewart, 2007). It is also found in a few other primates, such as the hamadryas baboon (*Papio hamadryas*; Sigg, Stolba, Abegglen, & Dasser, 1982). Male coalitions and philopatry among humans are discussed in more detail in Chapter 8 of this volume.

In theory, male philopatry results in greater relatedness among males in the group that, in turn, increases the likelihood that a bias toward coalition formation and competition will evolve, or at the very least result in the potential to form larger and more stable coalitions (Packer, Gilbert, Pusey, & O'Brieni, 1991). Even so, male coalitional behaviors of varying frequency are found in a wide range of primates, including those that leave the group of their birth (Bissonnette, Franz, Schülke, & Ostner, 2014). There are differences in the nature of coalitional behaviors that are not fully understood and are likely to be critical. Coalitions can involve a short-term, mutually beneficial "gang up" on a dominant male, with no long-term relationships between the coalitional partners, or it can involve long-term male relationships and more strategic and "political" social maneuvering (de Waal, 1982). The latter occurs in chimpanzees and in several other primate species, and males that are apt at forming these long-term relationships achieve higher social rank and sire more offspring than their less gregarious peers (Gilby et al., 2013; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Surbeck, Boesch, et al., 2017; Young, Majolo, Schülke, & Ostner, 2014).

Among chimpanzees, these long-term relationships often develop between maternal brothers, but they also form between more distantly related males that are of a similar dominance rank and age (Langergraber, Mitani, & Vigilant, 2007; Mitani, 2009; Mitani & Amsler, 2003; Vigilant, Hofreiter, Siedel, & Boesch, 2001). Regardless of kinship status, males cooperate when it allows them to move up the dominance hierarchy within their group or to mate guard, hunt, and patrol the group's territorial boundaries more effectively (de Waal, 1982; Goodall, 1986; Mitani & Watts, 2005; J. M. Williams, Oehlert, Carlis, & Pusey, 2004). The behavior of coalition partners ranges from the mere physical presence of one male while the other threatens or attacks another male, to joint displays and, occasionally, joint attacks. Goodall (1986) describes such an encounter:

> Goliath arrives in camp alone, late one evening. Every so often he stands upright to stare back in the direction from which he has come. He seems nervous and startles at every sound. Six minutes later three adult males appear on one of the trails leading to camp; one is high-ranking Hugh. They pause, hair on end, then abruptly charge down toward Goliath. But he has vanished silently into the bushes on the far side of the clearing. For the next 5 minutes the three crash about the undergrowth, searching for the runaway. . . .
>
> Early the next morning Hugh returns to camp with his two companions. A few minutes later, Goliath charges down, dragging a huge branch. To our amazement, he runs straight at Hugh and attacks him. The two big males fight, rolling over, grappling and hitting each other. It is not until the battle is already in progress that we realize why Goliath, so fearful the evening before, is suddenly so brave today: we hear the deep pant-hoots of David Graybeard. He appears from the undergrowth and displays his slow, magnificent way around the combatants.
>
> He must have joined Goliath late the evening before, and even though he does not actually join in the fight, his presence provides moral support. Suddenly Goliath leaps right onto Hugh, grabbing the hair of his shoulders, pounding on his back with both feet. Hugh gives up; he manages to pull away and runs off, screaming and defeated. (p. 313)

These coalitions are a common feature of male–male competition within communities, as is the formation of larger coalitions for patrolling the border of their territory and for making incursions into neighboring communities (Mitani & Watts, 2005; Nishida, 1979; Watts & Mitani, 2001; Watts, Muller, Amsler, Mbabazi, & Mitani, 2006):

> A patrol is typified by cautious, silent travel during which the members of the party tend to move in a compact group. There are many pauses as the chimpanzees gaze around and listen. Sometimes they climb tall trees and sit quietly for an hour or more, gazing out over the "unsafe" area of a neighboring community. (Goodall, 1986, p. 490)

When members of such patrols encounter one another, the typical response is pant-hooting (a vocal call) and physical displays on both sides, with the smaller group eventually withdrawing (M. L. Wilson, Hauser, & Wrangham, 2001). At other times, the meetings can be deadly (see M. L. Wilson et al., 2014). Goodall (1986) described a series of such attacks by one community of chimpanzees on their southern neighbor. Over a 4-year period, the southern group was virtually eliminated, one individual at a time, by the northern community who then expanded their territory to include that of the now extinct southern group. As an example of the ferocity of such attacks, consider the fate of Goliath—a member of this southern group—who was attacked 12 years after the incident with Hugh:

> Faben started to attack, leaping at the old male and pushing him to the ground, his functional hand on Goliath's shoulder. Goliath was screaming, the other males giving pant-hoots and waa-barks and displaying. Faben continued to pin Goliath to the ground until Satan arrived. Both aggressors then hit, stamped on, and pulled at the victim who sat hunched forward. Jomeo, screaming, joined in. . . .
>
> The other males continued to beat up their victim without pause, using fists and feet. . . . Faben took one of his arms and dragged him about 8 meters over the ground. Satan dragged him back again. . . . Eighteen minutes after the start of the attack, Jomeo left Goliath, followed by Satan and Faben. . . . In the attack (Goliath) was, inevitably, very badly hurt. He had one severe wound on his back, low on the spine; another behind his left ear, which was bleeding profusely; and another on his head. Like (most other members of the southern group), Goliath, despite intensive searching by all research personnel and field staff, was never seen again. (Goodall, 1986, pp. 508–509)

These types of deadly attacks are found in other chimpanzee groups and occur most often in densely populated communities with a large number of adult males (M. L. Wilson et al., 2014). Depending on community size, patrols occur one to several times each month and successful raids include, on average, five males attacking a single male from another community. Dominant males that have sired many offspring often participate in these patrols and through this, protect their offspring from males from other groups, although many males that have not yet sired offspring also participate (Langergraber, Watts, Vigilant, & Mitani, 2017). The benefits for dominant males and other males include recruitment of females into the group and an increase in territory size, which allows females to expand their individual territories (M. L. Wilson & Wrangham, 2003). The latter results in more food, shorter inter-birth intervals, and thereby a higher reproductive success for the community's females and males.

Alternative Mating Strategies

Recall that mating and reproductive success for male elephant seals is largely determined by the establishment of social dominance and the maintenance of a harem (see Chapter 3, this volume). An alternative mating strategy involves sneaking into harems and attempting to mate with females. This, however, appears to be a strategy that is forced on subordinates because of the monopolization of females by dominant males. In other cases, and as illustrated by jack and hooknose salmon (*Salmo oncorhynchus*; see Chapter 4, this volume), different mating strategies are true alternatives (i.e., each is equally effective in terms of siring offspring). Male primates use a variety of mating strategies if they are not socially dominant, but most of these appear to be forced on subordinate males rather than being true alternatives (Dunbar, 1984; Maggioncalda, Sapolsky, & Czekala, 1999; M. N. Muller, Kahlenberg, Emery Thompson, & Wrangham, 2007; Tutin, 1979; Watts, 2015). Across primate species, nondominant males often reproduce if multiple females are simultaneously in estrus and all of them cannot be effectively guarded by the dominant male (Setchell, 2016; Setchell et al., 2005); if dominant males prefer more attractive females, providing an opportunity for other males to mate with less attractive females (Wroblewski et al., 2009); and, through consortships and intimidation (M. N. Muller et al., 2007; Tutin, 1979).

For chimpanzees, consortships emerge when the pair leaves the group and moves to a more secluded location. These are typically initiated by lower ranking males through preferential grooming of the female, physical intimidation, or some combination (Goodall, 1986; Tutin, 1979; Wroblewski et al., 2009). Consortships require some degree of female cooperation, which may be why they often occur with males that will eventually achieve alpha status (e.g., are attractive to females; Newton-Fisher, 2014). Once the pair is formed, they separate from the community and spend anywhere from several hours to several weeks in isolation at the community's periphery. Despite exclusive mating during these times, less than 10% of offspring are sired during consortships (Newton-Fisher, 2014), indicating that they are not analogous to the jack salmon but rather an alternative mating strategy that is forced on subordinate males. Familiarity between males and females, because of overlapping feeding ranges, also provides subordinate males with reproductive opportunities, whether or not the associated copulations occur in the context of an extended consortship (Langergraber, Mitani, Watts, & Vigilant, 2013).

When females are at the beginning of their estrous cycle, indicating they are nearing their most fertile time, male-on-female aggression increases.

Most subordinate males direct this aggression toward a subset of females, whereas the alpha male directs aggression toward all of these females (M. N. Muller, Thompson, Kahlenberg, & Wrangham, 2011). Whatever the rank of the male, the aggression appears to suppress the females' attempts to mate with other males (M. N. Muller et al., 2007), and the intimidation is often successful. Females mate with their intimidators, regardless of rank, about twice as often as they mate with other males, and this likely contributes to the lower reproductive success of subordinate males. The same pattern has been found in other primates (Baniel, Cowlishaw, & Huchard, 2017).

The two reproductive body types of male orangutans (*Pongo pygmaeus*) illustrate a more dramatic alternative strategy (Banes, Galdikas, & Vigilant, 2015; Maggioncalda et al., 1999; Rodman & Mitani, 1987). Socially dominant males are twice the body weight of females and develop large flanges around their face and a large throat sac which allows them to produce long calls that attract females and signal their dominance to other males. Dominant males control a large territory within which several females and their offspring live, and when sexually receptive these females will seek out the dominant male. Subordinate males, in contrast, retain the juvenile body type; they remain relatively small and do not develop the flanges and other physical features of dominant males. These arrested males are nevertheless fertile and attempt to move unobtrusively through the forest in search of females. If they encounter one, they will often coerce her to copulate.

Dominant and arrested males reproduce in the wild, but these alternative morphs are not the same as those of the hooknose and jack salmon (Gross, 1985). Unlike the smaller jacks, the arrested male orangutan can develop into a flanged dominant male, if the dominant male is removed from the area; the presence of a more dominant male appears to suppress secretion of testosterone and related hormones needed to develop these secondary sexual characteristics (Maggioncalda et al., 1999). These males, in effect, can adopt alternative strategies at different points in their adult lifespan, depending on social context. Genetic analyses of paternity indicate that dominant and subordinate males sire offspring, but when a single flanged male is dominant, he will sire most of them. Unflanged males' reproductive success increases when several flanged males are competing for dominance, suggesting subordinates opportunistically mate during these times (Banes et al., 2015; Utami, Goossens, Bruford, de Ruiter, & van Hooff, 2002).

Female Choice

The importance and bases of female choice are well established in bird species (Andersson, 1994), but these are more difficult to isolate in mammals. This is because male coercion of females and disruption of their mating preferences, as for chimpanzees (M. N. Muller et al., 2007), are more easily achieved in mammals than in birds, and because females' preference for one male or another may actually reflect a preference for the territories occupied by those males or a preference to herd with other females associated with a particular male for predator defense (Clutton-Brock & McAuliffe, 2009). Despite these complications, there is experimental evidence for female choice in a number of mammalian species (e.g., Kavaliers & Colwell, 1995; P. M. West & Packer, 2002), and many indications of female preferences in primates (Setchell, 2005; Tiddi, Heistermann, Fahy, & Wheeler, 2018). An overview of the pattern of female choice in primates is presented next, followed by the bases for these choices.

Pattern of Choice

As discussed in Chapter 3 of this volume, females can express their preference for one mate or another through direct behavioral choices, or they can bias paternity one way or another with cryptic choice and sperm competition. These same patterns are found in many species of primate.

Behavioral choice. Females can directly choose their mating partners by soliciting or refusing copulations from different males and can indirectly choose them by inciting male–male competition or by influencing which males can and cannot enter the group (Wiley & Poston, 1996). For example, unlike chimpanzees, male mandrills do not physically intimidate females but they will attack males that approach attractive females. Therefore, female preferences can be more easily assessed in mandrills than chimpanzees. The mandrill is also interesting because the bright male coloration might be analogous to the colorful male plumage found for many species of bird, as there is some evidence that males' immune system genes influence female choice in mandrills (see Chapter 3, this volume; Setchell, Vaglio, et al., 2010). The key finding is that the bright facial coloration of dominant male mandrills not only impressed Darwin, it also captures the interest of female mandrills. In an observational study, Setchell (2005) found that females near ovulation frequently approached the most brightly colored male in the group, even if he was not the alpha, and were more likely to sexually present themselves to and copulate with this male than with other males.

For chimpanzees, the extent to which male coercion limits female choice is debated and not fully understood (M. N. Muller et al., 2011). Nevertheless, many female chimpanzees show heightened preferences for certain males as they approach ovulation and are often able to express these preferences (e.g., rebuff specific males), despite male coercion (R. M. Stumpf & Boesch, 2005, 2006). In fact, females in many primate species actively rebuff, sometimes quite aggressively, the sexual interests of some males and initiate sex with others (Dunbar, 1984; Kano, 1992; Smuts, 1985). Examples of female-initiated sexual activities are quite clear in a close cousin of the chimpanzee, the bonobo: "A female sat before a male and gazed into his face. When the male responded to this invitation, she fell on her back, elevated her buttocks and presented her genitals. In this case they copulated ventro-ventrally" (i.e., missionary style; Kano, 1980, p. 255).

Smuts (1985) provided other examples from her extensive studies of female–male relationships in the olive baboon. In addition to male–male competition for social dominance and access to estrus females, stable female–male relationships are occasionally found and influence females' mating preferences. Although female baboons prefer such relationships to be with more dominant males, this does not always happen and they will often reject the mating attempts of higher ranking males that have displaced a preferred mate through male–male competition; the same is true for some other species (Perloe, 1992; Smuts, 1987):

> At noon, Delphi, a young adult female, is in consort with Zim, an older, resident male. During an aggressive encounter, Zim loses Delphi to Vulcan, a young natal male about the same age as Delphi. Zim, Alex, and Boz, three older residents, immediately begin to follow the consort pair. Delphi looks back at them and Vulcan nervously herds her away. He tries to groom her, but she pulls away and begins to feed. At 12:56 Vulcan approaches Delphi and begins to mount her. She jumps away, and he watches her as she resumes feeding. At 12:58 he tries to mount her again, placing his hands on her back. Delphi walks away and Vulcan follows, still holding on to her. He maintains this "wheelbarrow" position for several steps, but then Delphi swerves sharply to one side and he falls off. He approaches her again 1 minute later, but she moves behind a large bush before he reaches her. . . . They circle the bush in alternate directions for several minutes, until finally Vulcan catches Delphi. He tries to mount, but Delphi pulls away. . . . During the 3 hours we followed them, Delphi refused 42 copulation attempts. (Smuts, 1985, pp. 170–171)

In some species of baboon, females have been found to influence the outcomes of male–male competition (Bachmann & Kummer, 1980; Smuts, 1985). One of the clearest examples is provided by the dynamics of harem acquisition in the gelada baboon (Dunbar, 1984). These baboons are organized into harems consisting of a single male and between one and 10 females and their offspring. Males have two general strategies for acquiring a harem. In the first, the male follows the group as a peripheral and subordinate member and begins to develop relationships, through grooming, with the juveniles in the group and gradually with individual females. In some cases, the females will desert, usually as a group, the harem-holding male in favor of the follower. The other strategy is a hostile takeover attempt, with the intruder provoking and attacking the harem-holding male. The ensuing fights can last for several days, on and off, and can result in severe injury to one or both of the males. In most cases, "what is crucial to the outcome is the behavior of the females. It is they who decide, by what amounts to a collective decision, whether to desert *en masse* to a new male or to retain their existing harem male" (Dunbar, 1984, p. 132).

Sperm competition and cryptic choice. Promiscuous mating in primates sets the stage for sperm competition among males and female cryptic choice (Harcourt, Harvey, Larson, & Short, 1981; see Chapter 3, this volume). In keeping with sperm competition, males of these species have larger testes and produce more sperm than males of nonpromiscuous species. Moreover, males of species with promiscuous mating have a relatively large penis, which places sperm closer to the uterus, and produce sperm with fast swimming speeds (M. J. Anderson & Dixson, 2002; Claw, George, MacCoss, & Swanson, 2018; Nascimento et al., 2008). All of these are highly consistent with traits that have evolved in response to sperm competition (A. F. Dixson, 2018). The influence of female cryptic choice (e.g., via sperm retention or rejection) is not as well understood, but there is reason to believe it occurs in some primate species (R. M. Stumpf, Martinez-Mota, Milich, Righini, & Shattuck, 2011).

Among mandrills, females' preference for brightly colored males, even those that are not dominant (or not yet dominant), suggests females' interests and those of the alpha male do not always converge. In fact, the increase in testes size after males achieve dominance is consistent with sperm competition and promiscuous mating by females (Setchell, 2016). However, there is not yet clear evidence that cryptic choice is also occurring in mandrills (Setchell, Abbott, Gonzalez, & Knapp, 2013), but it has not been thoroughly assessed and cannot be ruled out. Troisi and Carosi (1998) found that female Japanese macaques (*Macaca fuscata*) were more likely to orgasm when having sex with dominant males, which may aid in the retention and movement of sperm from these males. On the other hand, there is no consistent relationship between female orgasm and primate mating dynamics, and this may simply be a by-product of the evolution of the male orgasm and ejaculation; female primates have the same neural system underlying male ejaculation and this is triggered during an orgasm in both sexes (see A. F. Dixson, 2018). Clearly, much remains to be learned about cryptic choice in female primates.

Bases for Choice

Although it is not as well studied as female choice in birds (see Chapter 3, this volume), much is now known about the mating preferences of female primates. As with birds, their choices are influenced by male traits, such as cues of social dominance and by various genetic indicators that can be signaled through scent (Drea, 2015; Setchell, 2016; Tiddi et al., 2018; Wikberg et al., 2017; Winternitz, Abbate, Huchard, Havlíček, & Garamszegi, 2017). Across species, there is a tendency for females to prefer males with diverse immune system genes (Winternitz et al., 2017), consistent with good genes models of mate choices (see Chapter 3, this volume), and to avoid related males (e.g., Bercovitch, 1997). In many species, females also prefer males that provide direct (nongenetic) benefits in the context of male–female relationships (Baniel, Cowlishaw, & Huchard, 2016; Seyfarth & Cheney, 2012; Smuts, 1985). There are still many unresolved issues. As with some other mammals (Clutton-Brock & McAuliffe, 2009), it is possible that female preferences are influenced by the quality of the territory controlled by males rather than the quality of the males per se (Goodall, 1986; Sigg et al., 1982). Although the male's ability to provide food to the female and her offspring is the basis of female choice in many species, this does not appear to be the case for most primates, with a few minor exceptions related to mating (Goodall, 1986; Kano, 1980).

For the most part, female choice is driven by the dynamics of social and sexual relationships within the group, especially the frequency and intensity of aggressive encounters (Silk, 2007; Smuts, 1987). In these contexts, female choice often involves selecting males that will provide protection for them and their offspring from other group members (Altmann, 1980; Smuts, 1985; Smuts & Gubernick, 1992), including protection from the threat of infanticide by males that have recently immigrated into the group (Baniel et al., 2016; Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2005; Engh et al., 2006; Yao et al., 2016). Infanticide is the most severe threat to females and their offspring, and they have two strategies to reduce this threat. The first was proposed by Hrdy (1979) and involves mating with any male that might be a later threat to her offspring. At an abstract level, the strategy involves confusing paternity—none of the males know who sired the offspring—and works because males are less likely to attack infants if they have copulated with the infant's mother (e.g., Hestermann et al., 2001).

A second strategy is to develop friendships with one or two males that will provide some protection to the female and her offspring (Smuts, 1985), and in fact there is some evidence that protection from infanticide might be a key factor that drove the evolution of male–female relationships in many species of primate (Opie et al., 2012). Male friends tend to be high ranking (e.g., able to protect females and their offspring) but typically not the alpha male; alpha males focus more on mate guarding as many estrus females as possible rather than investing in a few friendships. The friendships are characterized by preferential grooming of and proximity to the friend, as well as by increased sexual activity between the pair. The friendships are not monogamous, vary in length, and have been documented in a variety of primates (Baniel et al., 2016; Goffe, Zinner, & Fischer, 2016; Smuts, 1985; Strum, 2012).

In a study of chacma baboons (*Papio ursinus*), Baniel et al. (2016) found that these friendships formed after the pair began copulating and lasted through the early phase of infant suckling, the time frame in which infants are the most vulnerable to infanticide; the same pattern is found among some chimpanzees (Murray, Stanton, Lonsdorf, Wroblewski, & Pusey, 2016). The friendship dissolves after this time frame, suggesting the relationship serves to protect the infant from other males rather than increasing the males' long-term sexual access to the female (e.g., it was not simply part of the males' mating effort; see Smuts & Gubernick, 1992; Whitten, 1987). The male friend cannot be certain that he is protecting his own offspring, but in many of cases it is his offspring (Buchan, Alberts, Silk, & Altmann, 2003; Cheney, Crockford, Engh, Wittig, & Seyfarth, 2015; Moscovice et al., 2010).

Even in the absence of infanticide risks, day-to-day social activities often involve harassment and attacks from other members of the group, male and female. Male olive baboons, for instance, direct aggressive displays toward females five times a week, on average, and physically attack them once a week (Smuts, 1985). Individual females are, on average, severely attacked (e.g., leaving wounds that require weeks or months to heal) about once a year. Infants are also frequently physically harassed (e.g., pulled out of their mother's grasp) or attacked by other group members, and these attacks are reduced if the female has a male friend or friends (see also Altmann, 1980; Dunbar, 1984; Sigg et al., 1982). For this species, when a female, or her offspring, is attacked and defended, the defender is the female's friend roughly 9 out of 10 times. The principle benefits for a male are his sexual relationships with female friends and their friends' support during conflicts with other group members, as well as protecting his own offspring in many cases.

Female–Female Competition

The section on male–male competition might have created an impression that female primates are not especially aggressive. This is not the case: female-on-female aggression is quite common and indeed there is no consistent cross-species sex difference in the frequency of aggressive encounters (Silk, 1993). In some species, females are relatively more agonistic than males and in other species males are relatively more agonistic (Smuts, 1987). The sex differences primarily emerge in the pattern, severity, and focus of aggressive encounters. Male-on-male aggression results in more severe wounds (e.g., open gashes) than female-on-female aggression in all primate species in which the sexes have been compared. In relation to female–female aggression, male–male aggression also tends to be more ritualized (e.g., it involves more stereotyped social displays) and is more frequently related to mating (Silk, 1993; Smuts, 1987; M. L. Wilson et al., 2014).

As described previously, when male relationships provide a reproductive benefit to females (e.g., a reduction in infanticide risk) and males are limited in the number of females in which they can invest, females compete for males' investment (Palombit et al., 2001). For chacma baboons, Baniel, Cowlishaw, and Huchard (2018a, 2018b) found that pregnant and lactating females aggressively attacked their male friends' other female friends and attempted to disrupt their mating activities. The aggression was the most pronounced among higher ranking females, after a potentially infanticidal male entered the group, and when their competitor was in estrus. The disruption of mating activities and the stress of the harassment reduced the conception rates of harassed females and through this reduced the chances that the male friend would protect her competitors' offspring rather than her own offspring.

Much like the earlier described groups of male chimpanzees, females of many primate species form coalitions to protect access to reproductively important resources, and sometimes to attack other females and their offspring. Females also form dominance hierarchies that can influence access to key resources, although the behaviors involved in the establishment and maintenance of these hierarchies are subtle in comparison with the aggression associated with the establishment of male hierarchies.

Female Coalitions

If female coalitions are found, they typically form among members of the philopatric sex and on the basis of kinship, as in mother–daughter coalitions

(Ghiglieri, 1987; Wrangham, 1980). With the earlier noted exceptions, females are almost always the philopatric sex in Old World (i.e., African, Asian) primates, and these coalitional species are called female-bonded species. Unlike the mating competition associated with male coalitions, female coalitions more typically compete for control of high-quality food sources (e.g., fruit trees; Silk, 1987; Sterck, Watts, & van Schaik, 1997; Wrangham, 1980). Access to these foods has important reproductive consequences for females; specifically, the improved nutritional status results in earlier sexual maturation, a longer reproductive lifespan, shorter intervals between births, and lowered offspring mortality (Silk, 1987; Wrangham, 1980). The result is that females in dominant coalitions have a higher lifetime reproductive success than do females in subordinate ones.

Females also form coalitions as a within-group social strategy to counter male-on-female aggression, for the protection of offspring (e.g., infanticide avoidance), or in response to feeding disputes (Hrdy, 1979). In a study of three captive bonobo populations, Parish (1996) found that coalitions of females were able to dominate individual males and used this domination to control high-quality feeding sites and refuse male-initiated consortships. In these populations, male-on-female aggression was rare, but female-on-male aggression was common. "Most often, the attacks have taken the form of several females holding the male down while biting him in the extremities (fingers, toes, ears, and testicles), although severe attacks by single females have also occurred" (Parish, 1996, p. 77). Female–female affiliations are common in wild populations and a few instances of female coalitions attacking males have been reported, but male-on-male aggression is by far the most common form of agonistic behavior in bonobos (Kano, 1992; Surbeck, Langergraber, et al., 2017).

There have also been a number of reports of female chimpanzees collectively attacking and killing the infants of newly immigrated or low-ranking females (Pusey, Williams, & Goodall, 1997; S. W. Townsend, Slocombe, Emery Thompson, & Zuberbühler, 2007; M. L. Wilson et al., 2014). S. W. Townsend and colleagues (2007) found that the infanticides occurred following an expansion of group size and increased competition for high-quality food. Several newly immigrating females with young infants were attacked by groups of resident females that wrestled the infants from their arms and killed them. Pusey et al. (1997) found that dominant female chimpanzees had more surviving offspring than did lower status females, in part because of frequent harassment of the latter, which suppresses their ability to invest in offspring. There were also several instances in which high-status mother–daughter pairs attacked and killed the offspring of lower status females.

Female Dominance Hierarchies

Female dominance hierarchies—in terms of female kin groups and individuals—are common in female-bonded species, and sometimes for individual females for species in which males are the philopatric sex (Parish, 1996; Pusey et al., 1997;

Silk, 1993; Wrangham, 1980). A female's position within the hierarchy can be determined by agonistic interactions, the rank of her mother, the size and rank of her kin group, or some combination of these (Mori, Watanabe, & Yamaguchi, 1989). However it is achieved, a female's position influences health and reproductive outcomes. The latter is related to differential access to high-quality foods, and oftentimes by the frequent harassment of lower ranking females by their higher ranking peers.

The harassment generally increases when high-quality foods or other critical resources are in short supply, and includes higher status females threatening and chasing lower status ones, as well as disrupting their relationships with males, and sometimes injuring or killing their offspring (Palombit et al., 2001; Pusey et al., 1997). Wasser and Starling (1988) studied this harassment in two wild groups of olive baboons and found that low-status females were most likely to be harassed during estrus and early in their pregnancy. The result was fewer conceptions and more spontaneous abortions. A follow-up study of the yellow baboon confirmed the pattern and found a direct relation between the frequency with which low-status females were victimized and the extent of their reproductive suppression.

Among other things, the resulting stress can disrupt the hormonal systems associated with ovulation and the maintenance of pregnancy (Beehner & Lu, 2013; Smuts & Nicolson, 1989). The most extreme form of this type of reproductive suppression is found in marmoset and tamarin monkeys (*Callitrichidae*), where dominant females can completely suppress the mating behavior of subordinate females and nearly completely inhibit the secretion of the hormones (e.g., luteinizing hormone) that induce ovulation (Abbott, 1993). This socially induced infertility is related to a chemical signal in the dominant female's urine. Should a subordinate female have offspring, the dominant female will kill or eject them from the group (E. C. Price & McGrew, 1991). Again, this is related to competition over reproductive resources, in this case other adults' investment in the rearing of the dominant females' offspring.

Dominant females also have better control of the dynamics of social interactions than do subordinate females, once again to their reproductive benefit. In vervet monkeys (*Cercopithecus aethiops*), high-ranking females allow affiliations between offspring and other females more often than do lower ranking females (Fairbanks & McGuire, 1995). This alloparenting reduces the cost (e.g., reduced foraging) of parental care for high-ranking females, which in turn shortens the interbirth interval. Alloparenting, however, can be risky, as other females will often injure or not protect these infants (Nicolson, 1987). High-ranking vervet females can easily retrieve their infants from allomothers whereas low-ranking females cannot. Therefore, the risks of alloparenting are lower for high-ranking than for low-ranking females and the consequent ability to use allomothers yields reproductive benefits to high-ranking females.

The final issue concerns potential parallels between the hormonal mechanisms and social cues associated with dominance in males and dominance in females. The influence of testosterone and androgens more generally on female primates' dominance striving and the expression of dominance cues is less consistent than that found in males, as is the case for females in many other species (see Chapter 4, this volume). Setchell, Smith, and Knapp (2015), for instance, found that the facial coloration of female mandrills brightened during pregnancy—likely because of increases in testosterone concentrations—but otherwise was not related to androgen levels. Moreover, female androgen concentrations were unrelated to female dominance rank. Rigaill et al. (2017) found the same for female Japanese macaques; females' facial coloration was unrelated to dominance rank. In some other primates, however, females' testosterone concentrations are related to dominance rank and behavioral aggression over access to food (Beehner, Phillips-Conroy, & Whitten, 2005; V. J. Grant, Konečná, Sonnweber, Irwin, & Wallner, 2011). These cross-species differences might be related in part to whether female dominance is established through physical aggression that is facilitated by testosterone or by nonphysical means (e.g., inherited rank) that are unrelated to behavioral aggression. Clearly, much remains to be learned about the hormonal mechanisms that influence female primates' dominance striving and the expression of dominance cues and behaviors.

Male Choice

As discussed in Chapter 3 of this volume for nonprimate species, male primates prefer some females over others as mating partners, even when they do not invest in offspring. These preferences are linked to the males' reproductive best interest and include a general preference for females that are the most likely to conceive or that are the most likely to successfully rear offspring (Altmann et al., 1996; A. F. Dixson et al., 1993; Goodall, 1986; Tutin, 1979). In many primates, the increase in estrogen and progesterone concentrations that results in ovulation also results in pronounced sexual-organ swelling and changes in sexual-organ coloration (reddening). Males find these swellings hard to resist and prefer to mate with females during this time in their ovulatory cycle. These swellings are most often found in species that live in multimale–multifemale groups and where females mate with several males (Nakahashi, 2016). The swellings are honest signals of female fertility and female health and indicate whether males should invest in competing over them (Street, Cross, & Brown, 2016). Males are also sensitive to female scent during ovulation (Drea, 2015) and (at least in mandrills) prefer females with scent cues associated with immune system diversity (Setchell et al., 2016).

In many species, males prefer older females that have given birth over younger ones that have not yet done so (Kobayashi, Koyama, Yasutomi, & Sankai, 2017; M. N. Muller, Thompson, & Wrangham, 2006). The older females are more fertile per ovulatory cycle and tend to be more skilled mothers; their infants are more likely to survive (Nicolson, 1987; Smuts & Nicolson, 1989). In some species, males understandably prefer high-ranking to low-ranking females as mating partners (J. G. Robinson, 1982), given the relationship between female social dominance and reproductive outcomes. Following the relationship between parenting and choosiness (see Chapter 3, this volume), male choice is expected in species where males provide a considerable level of parental investment, although the dynamics of these choices are not well understood (Goldizen, 2003), with the exception of humans (see Chapter 6, this volume).

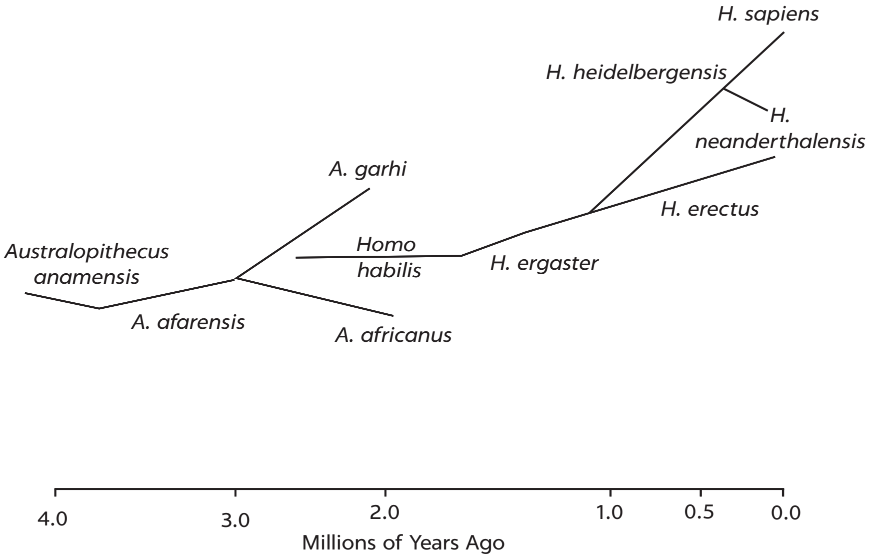
SEXUAL SELECTION AND HUMAN EVOLUTION

The dynamics of sexual selection in primates, as well as the more general principles of sexual selection and life history outlined in Chapters 3 and 4 of this volume, provide pillars on which we can make inferences about the nature of our hominid ancestors (Foley & Lee, 1989). The pillars have deep foundations when it comes to physical sex differences; for instance, the relationship between male–male competition and sex differences in physical size is well established. Inferences can be made about these sexual dimorphisms in our ancestors, and associated inferences about their reproductive behaviors are based on well-established patterns in living primates, within the limits of the existing fossil specimens (Plavcan, 2012a). This section begins with the major species in our evolutionary past and follows with a description of sexual dimorphisms across these species. It then provides an overview of the evolution of brain size and potential evolutionary change in reproductive strategy (e.g., coalition formation). On the basis of these patterns and those described for primates, the section closes with a proposal about sexual selection during human evolution.

Origins

Despite continuing debate over the number of species comprising the genus *Homo* and the predecessor genus *Australopithecus* (Antón, Potts, & Aiello, 2014; McHenry, 1994a, 1994b; McHenry & Coffing, 2000; B. Wood, 2010; B. Wood & Collard, 1999), there is a consensus on the major hominid species and their likely evolutionary relationships; debates, however, continue regarding the number of early hominin species (older than 3.5 million years) and regarding some of the specific phylogenic relations leading to modern humans (*Homo sapiens*; Haile-Selassie, Melillo, & Su, 2016; Haile-Selassie, Melillo, Vazzana, Benazzi, & Ryan, 2019; Pontzer, 2012). A simplified family tree is shown in Figure 5.5. The ancestor common to modern humans, chimpanzees, and gorillas existed before the emergence of these species. Various genetic analyses and the fossil record result in estimates for the most recent common ancestor between chimpanzees and humans to be anywhere from 6 to 12 million years ago (MYA) and from 8 to 15 MYA for gorillas and humans (Langergraber et al., 2012; Moorjani, Amorim, Arndt, & Przeworski, 2016;

FIGURE 5.5. Simplified Hominin Family Tree With Estimated Age of Emergence



A = *Australopithecus*; H = *Homo*.

Steiper & Seiffert, 2012). The exact timing of these more recent common ancestors is not critical to the discussion here, although the earlier the common ancestor the greater the potential for evolved differences between humans and chimpanzees and gorillas.

In any case, the dating of sediments found with australopithecine fossils suggest that *Australopithecus anamensis* existed about 4.0 MYA and its likely descendant, *Australopithecus afarensis* (see Figure 5.6) existed about 3.8 to 3.0 MYA (Haile-Selassie, 2010; Leakey, Feibel, McDougall, Ward, & Walker, 1998; McHenry, 1994a). The most likely (but still debated) link between *Australopithecus afarensis* and the line that eventually led to humans is *Australopithecus africanus*, but *Australopithecus garhi* is also a possibility, as shown in Figure 5.5 (Asfaw et al., 1999); *Australopithecus garhi* is dated at about 2.5 MYA and *Australopithecus africanus* from about 3.0 to 2.3 MYA. *Homo habilis* is a bit of a puzzle, due to many features that are more similar to *Australopithecus* than to *Homo* and because the associated fossils may actually represent two rather than one species (C. Dean et al., 2001; Villmoare et al., 2015; B. Wood & Collard, 1999); either way, they existed from about 2.8 to 1.5 MYA.

There is a general consensus among paleontologists that *Homo erectus* is a direct ancestor of modern humans, with *Homo ergaster* fossils likely representing early specimens of *Homo erectus* (Asfaw et al., 2002; B. Wood, 2010). About 1.8 MYA, *Homo ergaster* migrated out of eastern Africa into Eurasia and eventually deep into Asia and Europe (Carotenuto et al., 2016; Ferring et al., 2011), producing the most recent common ancestor of Neanderthals (*Homo neanderthalensis*) and modern humans. This ancestor appears to have existed about 500,000 to 600,000 years ago, with a touch of interbreeding

FIGURE 5.6. An Artistic Reconstruction of a Female *Australopithecus afarensis*

She was estimated to have been about 105 cm (3 ft 5 in) in height and 29 kg (64 lbs) in weight. Males were estimated to have been about 151 cm (4 ft 11 in) in height and 51 kg (100 lbs) in weight. Illustration by Mieke Roth. Reprinted with permission.

after that time (Pääbo, 1999; Prüfer et al., 2013). Archaeological and genetic analyses suggest that modern humans evolved about 200,000 years ago (perhaps earlier) in Africa and likely made several migrations into Asia, with the most significant one occurring about 60,000 year ago (Bae, Douka, & Petraglia, 2017; Pagani et al., 2016). This latter migration was followed by several waves of expansions deep into Asia and up into Europe and beyond (see Nielsen et al., 2017).

Sexual Dimorphisms

The study of sex differences on the basis of the fossil record is complicated. Central issues involve determining the sex of the fossil, determining whether the pool of fossils under study represents one or multiple species, and determining the most appropriate method for making body size estimates on the basis of partial remains (Plavcan, 2012a). These complications often result in disagreements about the magnitude of sexually dimorphic traits. There is, for example, variability in the estimates of the body weight of male and female *Australopithecus afarensis*, but also agreement that males were moderately to considerably larger than females (Aiello, 1994; Richmond & Jungers, 1995).

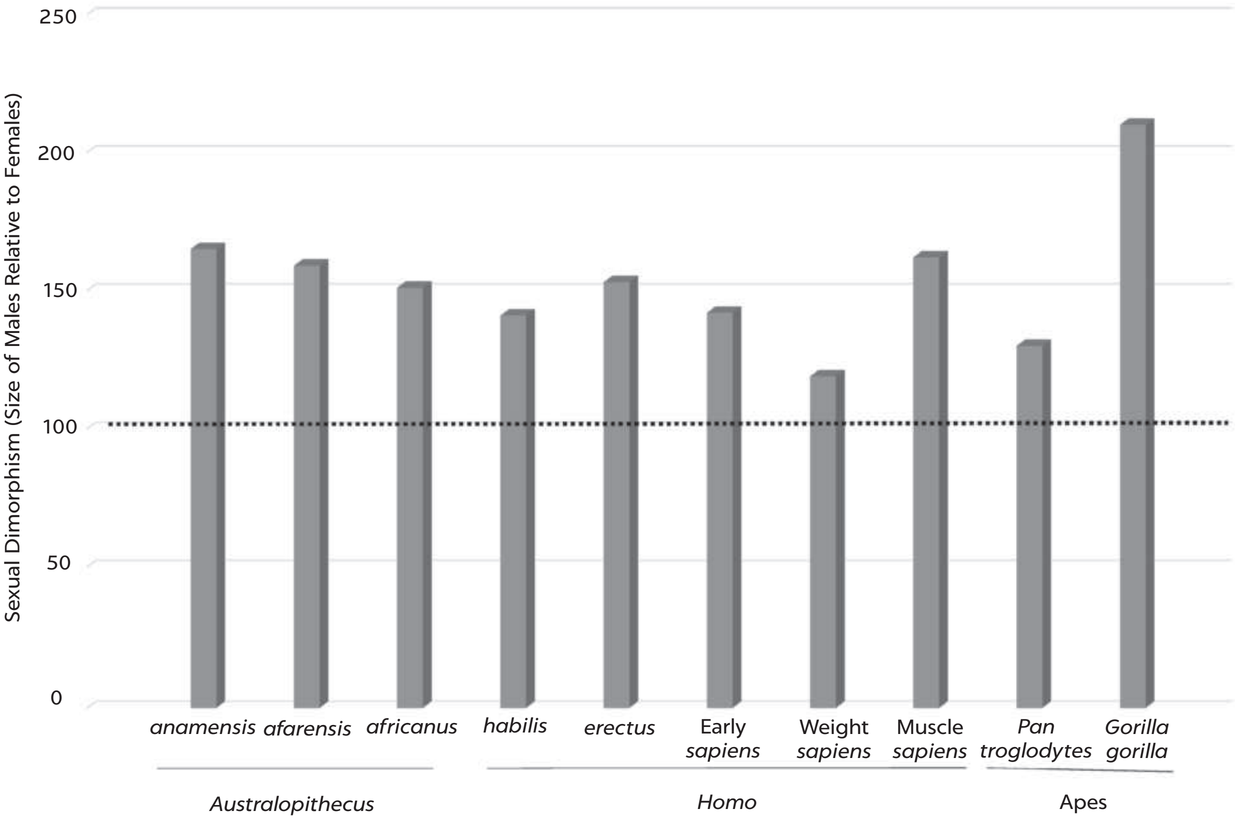
This discussion focuses on sexual dimorphisms in canine and body size for several reasons. First, reliable sex differences in the architecture of teeth and a variety of bones in living primates provides a means for making inferences about the sex of fossilized bones (Plavcan, 2001). Second, the magnitude of the sex differences in body weight and canine size increase as the intensity of physical male–male competition increases (Plavcan, van Schaik, & Kappeler, 1995). Canine size can also be related to diet, with reductions in size associated with some kinds of diets consisting of fruits that cannot be eaten with large canines in the way. Therefore, sex differences in canine size need to be interpreted with some caution (Kikuchi et al., 2018). Still, the combination allows for inferences to be made about the likely intensity of male–male competition during human evolution, and more cautiously inferences about other features of sexual selection (Plavcan, 2012a).

Canine and Body Size

The study of fossilized canines is easier than the study of other bones, because teeth are more likely to be preserved as fossils and are relatively abundant (M. H. Day, 1994). As noted, the determination of sex is based on known sex differences in tooth size and morphology in living primates (Plavcan, 2001), but can still be difficult with fossils, and inferences about sex differences must be made with caution (Wolpoff et al., 1976). In most living primates, males have larger canines than females (Plavcan & van Schaik, 1997), and similar differences are evident in all of the *Australopithecus* and *Homo* species. It has been estimated that male *Australopithecus afarensis* canines were 28% larger than those of females, a degree of dimorphism in between that of living chimpanzees and gorillas. The magnitude of this difference has decreased since the emergence of *Homo*, but a small male advantage is still found (Frayer & Wolpoff, 1985).

The physical size of our ancestors can be estimated based on the relation between the size of certain bones (e.g., the femur) and overall body size and weight in living humans and other primates. Although different methods can yield somewhat different estimates, the pattern of sex differences is the same. Several extensive analyses of these relations indicate larger males than females in all *Australopithecus* and *Homo* species; the sex difference for key species is shown in Figure 5.7 (Grabowski, Hatala, Jungers, & Richmond, 2015; McHenry, 1992; McHenry & Coffing, 2000; Pontzer, 2012). On the basis of these estimates, *Australopithecus anamensis* is the most dimorphic, and in fact the sex difference in physical size might have been as large as that found in modern gorillas (Leakey et al., 1998). A somewhat smaller sex difference is shown in Figure 5.7 for *Australopithecus afarensis*, because there is debate regarding the degree of sexual dimorphism found in this species. The debates result from the different methods used to estimate the dimorphism, with some results suggesting a difference similar to that found

FIGURE 5.7. Sex Differences in Body Weight Among *Australopithecus*, *Homo*, Chimpanzees (*Pan troglodytes*), and Gorillas (*Gorilla gorilla*)



The estimated weight of male *Australopithecus afarensis* is about 150% that of female *Australopithecus afarensis*. The dashed line indicates no sex difference. The weight for *Homo* is the overall weight, and muscle is the amount of lean muscle mass.

in humans (Reno, McCollum, Meindl, & Lovejoy, 2010), but most results suggest a difference closer to that found with gorillas (A. D. Gordon, Green, & Richmond, 2008; Richmond & Jungers, 1995). If so, then the sex differences shown for *Australopithecus anamensis* and *Australopithecus afarensis* in Figure 5.7 are too small.

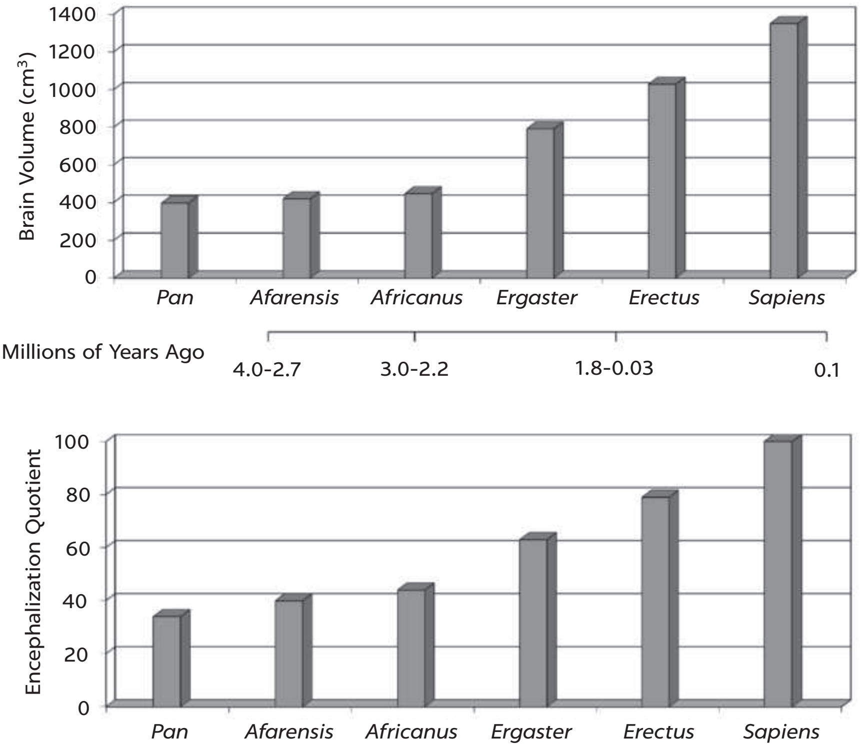
In any event, the most recent and extensive analysis of the fossil record indicates that late australopithecine (*Australopithecus africanus*) males were about 50% heavier than females, with similar differences with the emergence of *Homo* through early humans. I present several estimates for modern humans, because women have about twice as much body fat as men (J. C. Wells, 2007), which makes the sex difference in body weight difficult to interpret (see Chapter 10, this volume). As shown in Figure 5.7, the sex difference in lean muscle mass is in keeping with the sexual dimorphism found in several of our ancestors (Lassek & Gaulin, 2009), but smaller than that found in gorillas and perhaps smaller than that found in *Australopithecus anamensis* and *Australopithecus africanus*, if the latter was as dimorphic as gorillas. Whatever the degree of dimorphism, the fossil record strongly indicates a long history of intense male–male competition in our ancestors, including ancestors that lived well before those shown in Figure 5.7 (Kikuchi et al., 2018).

Brain Size

Men's brains are about 15% larger than women's brains, but this declines to about a 10% difference once body size is considered (Pakkenberg & Gundersen, 1997); the same is true for other primates, suggesting a deep evolutionary history for this sex difference (D. Falk, Froese, Sade, & Dudek, 1999). The reduction of the sex difference in brain size after controlling for body size means that selection pressures that favored an increase in male body size might have resulted in an incidental increase in male brain size without direct selection for improved cognitive competencies (Harvey, Martin, & Clutton-Brock, 1987). This is not the whole story, however, because the dynamics of sexual selection can directly lead to the evolution of sex differences in brain size, organization, and the specific cognitive competencies associated with competition and choice (see Chapter 3, this volume). Indeed, as the intensity of male–male competition increases in primates so does the magnitude of the sex difference in brain size (Pawłowskil, Lowen, & Dunbar, 1998; Sawaguchi, 1997). There are also more specific sex differences related to competition and parenting, including relatively enlarged brain areas associated with the sensory-motor aspects of males' physical fighting and enlarged areas associated with females' enhanced sensitivity to infants (Christov-Moore et al., 2014; Lindenfors, Nunn, & Barton, 2007; Stanyon & Bigoni, 2014). More details on these sex differences in humans are provided in Chapters 12 and 13 of this volume.

The two important issues are evolutionary change in brain size and likely changes in the sex differences in brain size. With respect to the former, there is no question that overall brain size has greatly increased during hominin evolution. As shown in the top portion of Figure 5.8, there has been a threefold

FIGURE 5.8. Brain Volumes and Encephalization Quotients for Chimpanzees (*Pan troglodytes*), *Australopithecus*, and *Homo*



The encephalization quotient is represented as a percentage of that of modern humans.

increase in absolute brain volume since *Australopithecus afarensis* (Antón et al., 2014; R. L. Holloway, 1973; McHenry, 1994b; P. V. Tobias, 1987; B. Wood & Collard, 1999). Even with control of overall body size (*Australopithecus* and early *Homo* were smaller than modern humans), the changes have been substantial, as indexed by the encephalization quotient (EQ); EQ is an index of brain size relative to that of a mammal of the same body weight (Jerison, 1973). The EQ of the typical mammal is 1.0 and that of chimpanzees is 2.0. For modern humans, EQ estimates range between 5.0 and 6.0 (McHenry, 1994b; Ruff, Trinkaus, & Holliday, 1997). The bottom portion of Figure 5.8 presents EQ values for our ancestors as a percentage of that of modern humans. The EQ of *Australopithecus* is greater than that of chimpanzees but less than 50% of that of modern humans. The EQ of *Homo habilis* was slightly more than 50% of that of modern humans, with large increases thereafter.

With regard to the second issue, we cannot directly estimate the brain volumes of our male and female ancestors, but several patterns suggest any differences became smaller during human evolution. First, there was a more substantial increase in the size of females than males since *Australopithecus afarensis* and this will necessarily—because of the allometry (as body size increases, the size of body parts, including the brain, increases)—result in a reduction of the sex difference in absolute brain size. Second, the gap between individuals (regardless of sex) with relatively small and relatively large brain volumes decreased since *Australopithecus afarensis* (R. L. Holloway, Broadfield, & Yuan, 2004). There is twice as much variation in the brain size of *Australopithecus afarensis* than in modern humans and about 1.5 times as much variation in *Homo erectus* as modern humans. In other words, variability in brain volume appears to have decreased since *Australopithecus afarensis*, and one corresponding result will be a reduction in the magnitude of individual differences as well as sex differences in brain volume. The overall pattern indicates substantial changes in the selection pressures that demand sophisticated cognitive competencies, including sex-specific changes associated with sexual selection, as covered in Chapters 12 and 13 of this volume.

Evolutionary Models

Reconstructing the evolution of social behavior on the basis of the fossil record is at best an educated guess, and any such model needs to be treated as such. Nevertheless, when we take patterns in the fossil record and combine them with sex differences in living primates and human universals, the field of possibilities is substantially narrowed (Foley & Lee, 1989). The following sections narrow these possibilities for the main components of sexual selection, and end with discussion of the relation between sexual selection and the sexual division of labor.

Male–Male Competition and Mating System

With respect to sexual selection, the male advantage in physical size is the most important feature of our ancestors. Among living primates and other mammals, this type of sexual dimorphism is consistently related to physical male–male competition and polygyny (e.g., Plavcan et al., 1995; Plavcan & van Schaik, 1997), indicating that these must have been central features of our evolutionary history (R. D. Alexander et al., 1979; Ghiglieri, 1987). The sex difference in physical size does not, however, lead to straightforward implications about the intensity of male–male competition (i.e., the degree to which alpha males dominated mating); whether the competition was largely one-on-one, coalitional, or changed during human evolution; or whether there was paternal investment. Current human sex differences in these and other areas are used to provide an anchor for making inferences about sexual selection in our ancestors and about evolutionary change in reproductive dynamics.

In societies in which monogamy is not socially or ecologically imposed, dominant men are polygynous and may have two, three, or more wives (Murdock, 1981). Polygyny occurs with moderate levels of paternal investment and in a modal social context of male philopatry—at least when there are high levels of between group conflict—and male kin-based coalitional competition (see Chapter 8, this volume). These and other human traits are the endpoints of an evolutionary process that began well before *Australopithecus anamensis* more than 4 MYA. A common approach to anchoring the beginning point in this evolutionary process is to compare human behavior with the behavior of our closest relatives, the chimpanzee and less frequently the bonobo (Kano, 1992; Wrangham, 1999). This is a reasonable starting point in some respects, but even this is sometimes questioned (Sayers & Lovejoy, 2008; T. D. White, Lovejoy, Asfaw, Carlson, & Suwa, 2015). The EQ of chimpanzees, bonobos (not shown in Figure 5.8), *Australopithecus*, and presumably their common ancestor are very similar. Although bonobo males do not engage in coalitional aggression, male-on-male aggression and male dominance hierarchies occur and were presumably features of the ancestor common to chimpanzees and bonobos (Surbeck, Langergraber, et al., 2017). The most common focus of the human–chimpanzee comparison is coalitional male–male competition (e.g., Wrangham, 1999), although Plavcan (2012b) suggested that this evolved independently in chimpanzees and humans and was not found in the common ancestor of these species.

Coalitional competition aside, there are critical differences between chimpanzees and bonobos and between chimpanzees, bonobos, and humans that call into question the sole use of these species as the anchor point for understanding sexual selection during human evolution. In terms of physical size, bonobos are about as sexually dimorphic as chimpanzees but both species are less dimorphic than the estimates for *Australopithecus anamensis* and *Australopithecus afarensis*, perhaps even *Australopithecus africanus* and *Homo erectus* (see Figure 5.7). The magnitude of the sexual dimorphism for the early species of *Australopithecus* suggests intense one-on-one male–male competition, which in turn is most consistent with either single-male harems or solitary males that controlled territories that encompassed the territories of several females (Ghiglieri, 1987; Plavcan & van Schaik, 1997). Unlike men, male chimpanzees and bonobos show little to no paternal investment, and unlike women, female chimpanzees and bonobos show conspicuous estrous swellings and mate promiscuously.

On the basis of these and other differences, Geary and Flinn (2001) proposed that our ancestors might have been more similar to our distant cousin, the gorilla (Geary, Bailey, & Oxford, 2011). This is because moving from a gorilla-like pattern to the current human pattern would require fewer evolutionary changes than needed to move from a chimpanzee- or bonobo-like pattern to the human pattern. Indeed, a recent analysis of the male-specific region of the Y chromosome of great apes, which will provide insights into mating system, is consistent with this proposal:

> Considering the [male-specific region of the Y chromosome] and mtDNA [mitochondrial DNA] phylogenies together, of all the great ape species, the combination that most closely resembles that of humans is in the western lowland gorillas. Taken at face value, this might argue against a long human history of multimale–multifemale mating. (Hallast et al., 2016, p. 433)

Hallast et al. (2106) did not mean that these DNA sequences are identical in humans and gorillas or that they are from a common ancestor. Rather, the results suggest that the evolved mating system of humans is more similar to that of gorillas than that of chimpanzees or bonobos. In a related study, Duda and Zrzavý (2013) applied phylogenetic analyses (on the basis of evolutionary history) to 65 traits (e.g., gestation time, onset of puberty, testes size) found in humans, chimpanzees, bonobos, gorillas, orangutans, and other primates to make inferences about the traits of the ancestor common to these species and subsets of them. They concluded that the common ancestor of humans and great apes had more in common with gorillas than with chimpanzees and bonobos. The most likely traits of this ancestor included either male philopatry or dispersal of both sexes from the group of their birth, single-male harems (which excludes coalitions), male–female relationships that extended beyond mating, male and female mate choices, some form of paternal investment (e.g., protection), simple tool use, and a maximum lifespan of 40 to 50 years. This ancestor was not fully gorilla-like, but nevertheless descriptions of modern gorillas and changes needed to move them closer to modern humans provide useful insights into the potential behavior of our ancestors (see also Geary et al., 2011).

The modal social organization of gorillas is often described as isolated single-male harems, which typically include one reproductive male, two to four females, and their offspring (Fossey, 1984; Harcourt & Stewart, 2007; A. B. Taylor, 1997). At least in mountain gorillas (*Gorilla beringei beringei*), these groups show a facultative expansion (depending on conditions) to two or even three often-related males (M. M. Robbins, 1999; M. M. Robbins & Robbins, 2018), sometimes even more males in recent years (Rosenbaum, Hirwa, Silk, Vigilant, & Stoinski, 2015). The primary benefit that males provide to females and their offspring is protection from infanticide, in keeping with the importance of paternal protection (when male investment is found) in primates more generally (Opie et al., 2013). Encounters between groups of mountain gorillas occur about once every 5 weeks and provide females their only opportunity to transfer from one group to another. During these encounters, physical male–male competition over females and male mate guarding are common (M. M. Robbins & Sawyer, 2007), as is occasional infanticide by extra-group males (A. M. Robbins et al., 2013).

Groups of western lowland gorillas (*Gorilla gorilla gorilla*) more consistently maintain single-male harems, but the groups are less isolated. Several families will occupy the same geographical region and encounters between groups are often friendly, especially among the males (Bradley, Doran-Sheehy, Lukas, Boesch, & Vigilant, 2004; Douadi et al., 2007). DNA fingerprinting indicates that males in neighboring groups are typically related, and females are often related within groups. The kinship organization of male lowland gorillas provides a ready explanation for the lower levels of male–male competition during group encounters in comparison to that found with mountain gorillas.

There are potentially important similarities between families of lowland gorillas and human families. Unlike the unrestricted mating of female chimpanzees or bonobos (during estrous), and a corresponding low level of paternity certainty (Goodall, 1986; Kano, 1992), adult male and female gorillas often form long-term social relationships and females often behaviorally elicit copulations with their mate (Hagemann et al., 2018; Harcourt & Stewart, 2007). DNA fingerprinting indicates that male lowland gorillas show high levels of paternity certainty (>95%; Bradley et al., 2004). For mountain gorillas in multimale groups, dominant males sire 70% to 80% of the offspring (Nsubuga, Robbins, Boesch, & Vigilant, 2008), although most males in these groups affiliate with infants (Rosenbaum, Vigilant, Kuzawa, & Stoinski, 2018). In the absence of intergroup encounters, behavioral observation reveals low levels of male mate guarding, suggesting low risk of cuckoldry, and high levels of affiliation with their offspring. "Associated males hold, cuddle, nuzzle, examine, and groom infants, and infants turn to these males in times of distress" (Whitten, 1987, p. 346). However, if this male dies or is deposed, these infants are at high risk of being killed by the new dominant male.

The genetic findings indicate that the male-kinship structure for lowland gorillas is close to that currently found with humans (Bradley et al., 2004). The primary difference is the degree of cooperation among adult males as related to coalitional competition. Such coalitions could easily evolve from the social structure described by Bradley and colleagues (2004). The formation of more closely knit male kinships would result in greater proximity of males and through this the creation of the types of multimale–multifemale communities found in all human societies (Foley & Lee, 1989; Ghiglieri, 1987; Rodseth et al., 1991). In other words, if gorilla families were placed in closer proximity and if male-kinship bonds were strengthened, the common structure of human families, including polygynous ones, in traditional societies would be formed.

Although humans form large, cooperative groups, throughout the world the day-to-day activities of people in traditional cultures typically occur in groups composed of four families and 15 to 20 individuals (M. J. Hamilton, Buchanan, & Walker, 2018; M. J. Hamilton, Milne, Walker, Burger, & Brown, 2007). More precisely, four often related men (e.g., brothers, cousins) and their families form the core human social group beyond individual families. The number of reproductive males in these human groups is larger than that found in groups of gorillas, but close enough to easily evolve from a gorilla social structure. Indeed, the social structure of western lowland gorilla groups that repeatedly feed in close proximity is very similar to that found in human foraging groups (R. E. Morrison, Groenenberg, Breuer, Manguette, & Walsh, 2019). The merging of these groups and the formation of male coalitions would lessen the importance of physical size and strength during male–male competition (Plavcan et al., 1995) and place a premium on the brain and cognitive systems that support the formation and functioning of long-term coalitions. The predicted result is the observed pattern of an evolutionary reduction in physical sexual dimorphisms and an increase in brain size.

Female Choice

The sexual dimorphisms in *Australopithecus* and *Homo* species do not speak to us as clearly about female choice as they do about male–male competition. We can safely assume that female choice was an important aspect of our ancestors' sexual dynamics. Studies of living primates and traditional societies today (see Chapter 7, this volume) suggest some scenarios for the evolution of female choice are more likely than others. In particular, consideration of female choice in gorillas and in primates that live in multimale–multifemale communities may provide a few useful insights. I am not proposing that female choice in our ancestors was the same as that found in these species, but rather the pattern in these species provides a range of possibilities for understanding our female ancestors.

Female gorillas emigrate from their birth group when they reach reproductive maturity, if the alpha male dies, and sometimes during intergroup encounters. The factors that influence female choice include male protection from infanticide by nonpaternal males and large predators, physical qualities of the male, and the results of male–male fights (Caillaud, Levréro, Gatti, Ménard, & Raymond, 2008; Fossey, 1984; M. M. Robbins et al., 2004; Rosenbaum, Hirwa, Silk, Vigilant, & Stoinski, 2016). A male's failure to protect an infant from the attack of another male can result in the mother abandoning this mate and joining the group of the infanticidal male (M. M. Robbins, Robbins, Gerald-Steklis, & Steklis, 2007). Females are more likely to join males that are larger and more muscular than other males and that have larger head crests. The head crest is composed of adipose and fibrous tissue and appears to be an indicator of male health. It may also be correlated with good genes, as the offspring of these males have higher survival rates than the offspring of other males (Breuer, Robbins, Boesch, & Robbins, 2012). Once females choose a mate, they tend to maintain a long-term relationship with this male as long as he maintains his health and social dominance (Harcourt & Stewart, 2007).

An eventual bias to form patrilocal (centered around male kin) multimale–multifemale communities would have resulted in further complexities in social dynamics, including female choice (Chapais, 2009). For females, one benefit of being part of a multimale group is reduced risk of infanticide by extra-group males, if one of the groups' dominant males dies, as is found in multimale mountain gorilla groups (A. M. Robbins et al., 2013). At the same time, the competitive benefits of a large male coalition create pressures to increase within-group cooperation among males and this likely resulted in less polygyny, although it almost certainly did not eliminate it; a male's cooperation in defending the group will increase when he mates with one or several of the group's females. One corresponding cost is that many females would have been paired with lower quality males. In the context of multimale communities, these pairings heighten the potential for extra-pair relationships and the potential benefits to females if they cuckold lower quality partners. In this situation, paternity certainty would have been lower than that found in lowland gorillas (i.e., <95%), but still much higher than that found in chimpanzees or bonobos (near zero). The maintenance of long-term male–female relationships, a comparatively high level of paternity certainty, and some form of paternal investment would have also required the evolution or strengthening of pair-bonding and continuous female sexual receptivity (Chapais, 2009; K. MacDonald, 1992).

With the formation of multimale–multifemale communities, a corresponding reduction in polygyny, and the maintenance of paternal investment, females would compete more intensely over high-quality mates. The focus of female–female competition and male choice would have almost certainly included female traits that signaled fertility and the likelihood of successfully rearing offspring. These traits likely included the females' age, whether or not they had successfully given birth, and their success at raising offspring.

Sexual Division of Labor

As an alternative to sexual selection, some scientists have proposed that many human sex differences evolved as a result of the sexual division of labor and cooperative child rearing (i.e., male hunting and female gathering and providing childcare; H. E. Fisher, 1982; Lovejoy, 1981). Hunting has clearly been an important feature of human evolution (K. Hill, 1982), but it is not likely to be the evolutionary source of many human sexual dimorphisms. The teeth of *Australopithecus* were primarily adapted for eating fruits and seeds (Teaford & Ungar, 2000). Although they may have eaten some meat, the extreme male advantage in physical size preceded the evolutionary emergence—probably with *Homo*—of consistent hunting and meat eating as a major feature of our ancestors' subsistence (Aiello & Wheeler, 1995). Further, a sexual division of labor is common in many species, including many socially monogamous species, in which there are small or no sex differences in physical size (Clutton-Brock, 1991; Leighton, 1987).

I propose that sexual selection is the primary source of many human sex differences and that the division of labor emerged later—the physical, behavioral, and cognitive sex differences often ascribed to the division of labor are in fact due largely to sexual and sometimes natural selection. There is no reproduction-related sexual division of labor in the chimpanzee but the sex difference in the pattern of hunting and foraging found in many traditional societies is found in this species (Goodall, 1986; McGrew, 1992). Male chimpanzees hunt in a more organized, systematic, and efficient way than do females. Because of their greater size and aggressiveness, male chimpanzees are also able to capture a wider range of prey. As a result of these differences in hunting efficiency, meat represents a relatively larger portion of males' than females' diet. The female diet, in contrast, consists of a much higher proportion of ants and termites. The ants and termites are found in fixed locations that are frequently surveyed, as with human foraging.

The reliance of female chimpanzees on ants and termites as sources of protein and their foraging strategies for obtaining these foods has almost certainly been shaped by natural selection (Goodall, 1986). The physical and behavioral tendencies of male chimpanzees have been shaped by sexual selection and are co-opted—used for a purpose for which they did not originally evolve—for hunting. Hunting then provides a valuable resource that is used for survival and to sometimes enhance mating opportunities. Once meat is systematically used to enhance mating opportunities, it can potentially become a source of male–male competition and female choice (Symons, 1979) and subject to added selection pressures. This is evident across traditional societies today where the ability of men and women to perform roles associated with the traditional division of labor influences mate selection and retention. In an extensive cross-cultural review of marital relationships, Betzig (1989) noted

> inadequate support is reported as cause for divorce in 21 societies and ascribed exclusively to the husband in all but one unspecified case. . . . An interesting thing about these economic factors is that they are so clearly segregated according to sex. Husbands are divorced for failing to provide material means, wives for failing to process them. (p. 664)

These cross-cultural results indicate that skill at performing the tasks associated with the sexual division of labor influences mate choice decisions and is therefore under the influence of sexual selection. Male provisioning is now a component of male–male competition and a feature of female choice in many cultures, but the evolution of the sex differences that enable males to provide certain resources more efficiently (e.g., meat through hunting) or compete more aggressively than females to obtain these resources did not originally evolve for cooperative child rearing, even if it is an aspect of male–male competition and female choice in many contexts today (Crano & Aronoff, 1978).

CONCLUSION

The dynamics of social relationships within primate communities are strongly influenced by the different ways in which males and females pursue their reproductive interests. In most nonmonogamous species, male–male competition is a very conspicuous feature of these dynamics and as such, it is not surprising that this competition is one of the better studied aspects of primate social behavior (Smuts, 1987). Male–male competition is related to the sexual strivings of these individuals and is based on physical contests and in a few species on the ability to form and maintain coalitions with other males. The prototypical result is larger and more aggressive males than females (Plavcan et al., 1995). Whether it involves one-on-one or coalitional competition, male–male contests result in a dominance hierarchy, and the male's position in this hierarchy has important reproductive consequences (M. N. Muller, 2017). Socially dominant males attempt to and are often successful at controlling the social and sexual behavior of other group members, particularly estrus females. DNA fingerprints to establish paternity indicate that this mate guarding consistently, but not always, provides dominant males with a reproductive advantage over subordinate ones (e.g., Setchell, 2016).

Male striving for social dominance is not the whole story. The alternative mating strategies used by less dominant males combined with female choice often undermine the reproductive strivings of dominant males. One such male strategy involves the consortship (one-on-one male–female relationships) and sometimes long-term friendships (Bray et al., 2016; Dunbar, 1984; Smuts, 1985; Tutin, 1979). At times, consortships are controlled by subordinate males; these males aggressively coerce females into the relationship (M. N. Muller et al., 2007). At other times, female choice is involved, especially with long-term friendships. For the female, the development of friendships with one or more males appears to be a strategy designed to elicit male support during times of social conflict and to elicit male investment in her offspring (Hrdy, 1979; Smuts & Gubernick, 1992). For the male, the development of such relationships increases the likelihood of siring offspring and sometimes results in direct investment in their own offspring (Buchan et al., 2003).

Females typically develop these friendships with relatively dominant males, presumably because these males are better able to control social dynamics than are subordinates (Smuts, 1985). In other cases, the mating priorities established through male–male competition and female choice conflict, and in many of these cases, female choice prevails. Male primates also show preferences in their choice of mating partners, although they are not as choosy as females. Males prefer to mate with females that are the most likely to conceive and the most likely to successfully rear offspring (M. N. Muller et al., 2006). For species in which males provide individual benefits to a female and her offspring, some level of female–female competition over affiliations with such males is predicted and found (Baniel et al., 2018a, 2018b).

By combining the reproductive strategies found in living primates with the pattern of physical sex differences in our ancestors, we can draw inferences about the nature of sexual selection during human evolution. The consistent finding of larger males than females indicates that male–male competition was a prominent feature of human evolution and was very likely associated with a polygynous mating system (R. D. Alexander et al., 1979; Ghiglieri, 1987). Following Geary and Flinn (2001; Geary et al., 2011) and using the social structure of gorillas as a model, I suggest that the starting point of this feature of sexual selection was one-on-one male–male competition for control of harems, followed by the evolution of male kin-based coalitions (for a somewhat different sequence see Chapais, 2009). The latter would help to explain the evolutionary reduction in the physical dimorphisms in our ancestors and the corresponding expansion of brain size. The formation of coalitions would reduce the intensity of polygyny, result in the formation of multimale–multifemale communities, and greatly complicate other aspects of sexual selection and male–female relationships. Geary (2005) described how these social complexities might have contributed to the evolutionary expansion in brain size and EQ in both sexes.

The evolution of female choice is more difficult to reconstruct, but patterns in living primates and species that live in multimale–multifemale communities help us to narrow the possibilities. Most likely, female choice was influenced by the social and other resources the male could provide (K. Hill, 1982; Smuts, 1985). Social support would have involved some form of protection of her and her offspring, as well as offspring care. A female preference for material support, such as meat provided through hunting, most likely emerged only after the evolution of a female preference for social support. In either case, it has been argued that human sexuality—concealed ovulation and the more or less continuous sexual receptivity of women—evolved as an adaptation to increase the stability of female–male pair-bonding and facilitate paternal investment in offspring (H. E. Fisher, 1982; K. MacDonald, 1992). If the family structure of *Australopithecus* was similar to that found with gorillas, then paternal care and long-term male–female relationships have been part of our evolutionary history for millions of years. The formation of multimale–multifemale communities would have the resulting benefit of strengthening (not creating) pair-bonding mechanisms that may have already existed. These benefits would include the maintenance and perhaps expansion of male investment in offspring and would reduce the likelihood of females engaging in extra-pair relationships.

6

Evolution of Fatherhood

Men's investment in their children is one of the most remarkable features of the human family. Such investment might not seem unusual to readers with engaged fathers, but it is a riddle in terms of the broader evolutionary picture given that male parenting is uncommon in mammals (Clutton-Brock, 1989). When it is found, it is typically associated with shorter birth intervals between offspring or larger litters (e.g., in carnivores; Asa & Valdespino, 1998) and is associated with reduced infanticide risk among primates (Opie, Atkinson, Dunbar, & Shultz, 2013; H. E. West & Capellini, 2016; but see Lukas & Clutton-Brock, 2013). Under these conditions, both parents benefit from male parenting through an increase in the number of offspring that females can birth and through higher offspring survival rates. These benefits also help to explain why the males of these species do not invest more in finding additional mates instead of parenting (see Chapter 4, this volume). Even so, male parenting in primates is generally found with social monogamy and isolated family groups, such as in *Callithrix* monkeys (Goldizen, 2003; Lukas & Clutton-Brock, 2013). Human paternal investment, in contrast, occurs in large multimale–multifemale communities and often in the context of polygynous relationships (see Chapter 8, this volume). To be sure, there is male investment in offspring in some baboon species that live in multimale–multifemale communities, but this is better explained by short-term protection against infanticide risks (e.g., Baniel, Cowlishaw, & Huchard, 2016) and pales in comparison with the long-term and extensive parenting provided by many men.

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The previous chapter argued that men's parental investment evolved from a gorilla-like family structure, perhaps initially as a defense against infanticide. In this scenario, the formation of multimale–multifemale communities organized around male kin-based coalitions emerged more recently during our evolutionary history but may still date back to *Homo erectus*. Whatever the evolutionary sequence, the combination of men's parenting and families situated in large communities results in many added layers of complexity to human social relationships and results in the potential for humans to form a wide variety of marriage systems and family types (Geary & Flinn, 2001; Pasternak, Ember, & Ember, 1997). The focus here is on the cost–benefit trade-offs that influence when, with whom, and how much (if anything) men invest in their children. The first section is organized around the same basic evolutionary trade-offs that influence male parenting in other species (see Chapter 4, this volume), specifically benefits to offspring and costs to fathers. The second and third sections focus on sex differences in the level of parental investment and on the many factors that influence the expression of men's parenting.

TRADE-OFFS OF MEN'S PARENTING

To fully understand the evolution and maintenance of men's parenting, it is important to consider the cost–benefit trade-offs shown in Exhibit 4.1 (see Chapter 4, this volume). First, men's parenting must have substantively reduced child mortality risks in ancestral environments or otherwise provided children with a socially competitive, and thereby a reproductive, advantage over their father-absent peers. This first part of this section examines the relationship between paternal investment and the physical and social well-being of children in existing populations and throughout history. Second, men's parenting would not have evolved or be maintained without reductions in the costs of lost mating opportunities and the risk of cuckoldry (unwittingly raising the child of another man). These issues are addressed in the second part of this section.

Benefits to Children

Many books have been written about human parenting over the years, but few, if any, have touched on the core function of parenting—to keep offspring alive (Clutton-Brock, 1991). This core purpose is sometimes hard to fathom, given the very low mortality rates among children in developed nations, but this situation is a very recent phenomenon. In a review of child mortality from ancient Greece to modern-day hunter-gatherer societies, T. Volk and Atkinson (2008) estimated that as many as half of all children died before reaching adolescence. These risks were often (but not always) substantially reduced by men's investment. Among the children who did survive, men's investment often contributed to their social competitiveness and thus improved their children's status in adulthood.

Physical Well-Being

Given the low infant and child mortality rates in developed nations today, there is more information on the social and psychological correlates of paternal investment than on fathers' contributions to their children's physical well-being. To estimate the importance of this investment in riskier environments, we can examine the relation between paternal factors (e.g., occupation) and childhood mortality in preindustrial Europe and the United States and in extant developing and traditional (e.g., hunter-gatherer, horticultural) societies. Even when paternal factors correlate with child mortality risks, we cannot be certain that the relation is causal, because men with beneficial qualities are often married to women with beneficial qualities and it may be the joint contributions that lower mortality risks. Moreover, other kin often contribute to the raising of children, especially grandparents (Hrdy, 2009; Sear & Mace, 2008), which further complicates the evaluation of the specific contributions of fathers. Despite this and other potential confounds, paternal investment does appear to lower infant and child mortality risks in some human groups, but the magnitude of this effect likely varies from one context to the next (e.g., whether or not other kin can invest in children).

Mortality in traditional societies. K. Hill and Hurtado's (1996) extensive ethnography and demography of the Ache (a hunter-gatherer society in Paraguay) provides one of the most extensive assessments of the relation between paternal investment and child mortality rates in a traditional society. For forest-dwelling Ache, 1 out of 3 children died before reaching the age of 15 years, with highly significant differences for father-present and father-absent children. Father absence (from death or divorce) tripled the probability of child death because of illness and doubled the risk of being killed by other Ache men or being kidnapped by other groups, presumably to be killed or sold into slavery (Hurtado & Hill, 1992). Overall, father absence at any point prior to the child's 15th birthday resulted in a mortality rate of more than 45%, as compared with a mortality rate of about 20% for children whose father resided with them until their 15th birthday.

Death because of sickness is related, in part, to the adequacy of a 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 fathers do not directly provision their children. Nevertheless, the children of skilled hunters have lower mortality rates than do the children of less skilled hunters (K. Hill & Kaplan, 1988); this is also true in at least some other hunter-gatherer societies (E. A. Smith, 2004). It appears that these children are better treated than the children of less skilled hunters. K. Hill and Kaplan (1988) indicated that better treatment involves a greater tolerance "of food begging by the children of good hunters" (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. The Ache, however, are not generally willing to invest in the well-being of unrelated children and, as noted, often killed children whose father had died or left the group (K. Hill & Hurtado, 1996); they did this because they did not have the resources to raise these children.

Across a variety of other cultures, Sear and Mace (2008) found no consistent relationship between fathers' investment and mortality risks for infants and young children. Sometimes fathers mattered, and sometimes they did not. Across five traditional cultures, Winking and Gurven (2011) found that father desertion resulted in a modest increase in mortality for children under 5 years of age, but here too these risks varied from one group to the next. With the death of the father or following a divorce, other kin (e.g., maternal grandmothers) were often able to compensate for the lost paternal investment (see also Hrdy, 2009; O'Connell, Hawkes, & Blurton Jones, 1999; Perry & Daly, 2017). Even when a father's skill at provisioning his family is related to child mortality risks, a causal link cannot be made (Borgerhoff Mulder, 1990; Irons, 1979). This is because culturally successful men tend to marry women who have qualities that will improve the well-being of their children and it may be these mothers' contributions that have the strongest effects on child mortality. For the Hadza (a hunter-gatherer group in Tanzania), successful hunters have more surviving children than less successful hunters, but "successful hunters tend to have wives who are more efficient foragers than other women" (Blurton Jones, Hawkes, & O'Connell, 1997, p. 301).

Protection from other men may be the one area in which kin might not be able to compensate for the loss of a father. As with the Ache, the presence of a stepfather is associated with increased mortality (although still uncommon) in young children (Sear, Steele, McGregor, & Mace, 2002; see also Daly & Wilson, 1988a) and is associated with ongoing low levels of conflict and poor health, as well as increased risk of sexual abuse, in many other contexts (Flinn, 1992; Lalor, 2004). A unique brain-imaging study revealed that men had distinct patterns of brain activation when viewing a threatened infant whom they imagined was their own as compared with an unknown infant (van 't Veer, Thijssen, Witteman, van IJzendoorn, & Bakermans-Kranenburg, 2019). The corresponding brain regions support threat detection, aggression, and acting on the environment, in keeping with the argument that men have an implicit protective response when their children are threatened.

Mortality in developing societies. In developing and preindustrial societies, fathers often make the difference between whether a child survives to adulthood or not. There is a consistent relationship between marital status, family income, and infant and child mortality rates in developing countries throughout the world (Khadka, Lieberman, Giedraitis, Bhatta, & Pandey, 2015; Sonego, Pellegrin, Becker, & Lazzerini, 2015; United Nations, 1985):

> Both univariate and multivariate results show that 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, although the direction of causation cannot be inferred from the data. (United Nations, 1985, p. 227)

Indonesian children of divorced parents have a 12% higher mortality rate than the children of monogamously married couples. The same relation was found in 11 of the 14 developing nations surveyed, but it is possible that the death of a child increases divorce rates rather than paternal absence increasing mortality risks. Compared with divorce, death of the father is generally associated with higher infant and child mortality rates, suggesting that father absence, independent of maternal characteristics, directly contributes to these risks.

The same pattern was evident in preindustrial Europe, where families living in urban areas were often separated from the kin networks that contribute to children's well-being in traditional contexts. 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 for children born to married couples (Brändström, 1997). The same was true in 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 these "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 relationship between paternal provisioning and infant and child mortality risks has in fact been reported throughout preindustrial and industrializing Europe and the United States (Hed, 1987; Herlihy, 1965; Klindworth & Voland, 1995; A. S. Morrison, Kirshner, & Molho, 1977; Schultz, 1991).

A. Reid's (1997) analysis of mortality risks in early 20th century England and Wales suggested that "a child's chance of survival was strongly conditioned by who its parents were, or more precisely, by what job its father did" (p. 151). The conclusion was based on a strong relationship between socioeconomic status (SES)—defined entirely by the father's occupation—and mortality risks. In comparison with children whose fathers were unskilled laborers, the infants of professional fathers had a 54% lower mortality rate. The children of unemployed fathers, in contrast, had a 38% higher mortality rate than did the children of unskilled laborers. Controlling for SES, environment (e.g., urban vs. agricultural setting), maternal age, and other factors, children (under the age of 3) of working mothers had a 34% higher mortality rate than did children whose mothers did not work outside of the home. If care (from kin) was provided to these children while the mother worked, the children had a 17% higher mortality rate than did children whose mothers were the primary caretakers. These effects appear to have been related to whether the infant was consistently breastfed. In 1900 France, 7% of breastfed infants died as compared with 37% of bottle-fed infants (Rollet, 1997). Paternal employment was important because it often increased breastfeeding by allowing the mother to stay at home with the child rather than work herself (A. Reid, 1997).

In an extensive analysis of birth, death, and demographic records from 18th century Berlin, Schultz (1991) found a strong correlation ($r = .74$) between infant and child mortality rates and SES; the latter was partly defined by paternal occupation. Infant (e.g., birth–1 year) mortality rates were about 10% for aristocrats but more than 40% for laborers and unskilled technicians. "A senior official of the welfare authorities (*Armenbehörde*) observed in 1769 that among the poor weavers of Friedrichstadt 75 out of every 100 children borne died before they reached [the age of 12 years]" (Schultz, 1991, p. 243). During the 1437–1438 and 1449–1450 black plague epidemics in Florence, Italy, child mortality rates increased 5- to 10-fold and varied inversely with SES (A. S. Morrison et al., 1977); a similar relationship is found in some traditional societies today (Kiros & Hogan, 2001). In many contexts, the resources provided by fathers also allowed the family to live in healthier environments, enjoy a more stable food supply, and sometimes hire servants, all of which contributed to the relationship between SES and infant and child mortality rates in industrializing Europe (A. Reid, 1997).

Physical health. Although fathers' contributions to the family do not always lower child mortality rates in traditional cultures (Sear & Mace, 2008), they can have more subtle influences on children's health and development (Lawson et al., 2017; Winking & Koster, 2015). One unambiguous way to assess this is through the relationship between a father's presence in the home, his income, and his children's physical growth. Stunted growth is a common indicator of chronic poor nutrition and poor health and is defined as being in the bottom 2% in height for their age. In a study of 357,340 young children across 31 countries in sub-Saharan Africa, Schrijner and Smits (2018) found that the combination of father presence in the household and his income resulted in about a 10% reduction in the odds of their children being stunted. The same pattern is found in other parts of the world (Bronte-Tinkew & DeJong, 2004; Liu, Rizzo, & Fang, 2015).

There is also a well-established relationship between SES (defined as a composite of income, educational level, and occupational status in developed countries) and health (E. Chen & Miller, 2013). Adler et al. (1994) concluded that

> 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. (p. 22)

The relationship between SES and health holds for all members of the family not just the primary wage earner and is not simply related to access to health care or to differences in health-related behaviors (e.g., smoking). Across developed nations today, paternal income and occupational status are an important, and sometimes the sole, determinant of the family's SES. Given this, paternal investment is correlated with children's physical well-being, even in contexts with low infant and child mortality rates. Whether paternal investment is causally related to child health in these contexts is more difficult to determine because of the shared genes between parents and children and the effects of these genes on health, health-related behaviors, and SES (Deary, Whalley, & Starr, 2009).

One way to draw a stronger conclusion is to determine if decrements in fathers' contributions to the family (e.g., through job loss) are associated with deteriorations in child health. A 10-year study of more than 21 million Swedish parents and their children suggests there is a causal relation between family income and child health, albeit a modest one (Mörk, Sjögren, & Svaleryd, 2014). Controlling prior child health and other factors, there was a 5% increase in the odds of a child being hospitalized, indicating a serious illness, in the first few years after one of their parents lost a job. The effects, however, were more strongly related to maternal than paternal unemployment and do not capture subtle changes in health. These subtle changes, including poor nutrition and slower child growth, were found following the massive layoffs associated with the reorganization of state-owned businesses in China. For these families, the effects on child health were consistently related to paternal and not maternal job loss (Liu & Zhao, 2014). The effects on children were particularly large for lower income (bottom 30%) families and worsened over time if the father remained unemployed. These negative consequences can run even deeper. C. Mitchell et al. (2017) found that the loss of a father (through divorce or death) and his income was associated with a subsequent acceleration of cellular aging in children, with potential long-term health consequences.

Life history. As discussed in Chapter 4 of this volume, life history is the suite of traits that define the species' reproductive development, the factors (e.g., predation risk) that influence the evolution of this pattern (e.g., fast maturation), and the conditions that can influence variation in the here-and-now expression of one or more of these traits (e.g., age of first reproduction). Humans' core life history traits include age of sexual maturation, first sexual experience (e.g., sexual debut), first childbirth, and lifetime number of children. Individual differences in the expression of each of these traits is moderately heritable, and many or all of them may be influenced by a core set of genes that bias individuals toward heavy investment in a few children or lower investment in many children (Figueredo et al., 2006; Kirk et al., 2001; Pettay, Kruuk, Jokela, & Lummaa, 2005; Polderman et al., 2015). As with other species, human life history development is also influenced by early experiences and current circumstances (Belsky, 2019; Gavrus-Ion et al., 2017). The focus here is on the potential relationship between men's parenting and aspects of their children's reproductive behavior (e.g., age of sexual debut) and physical life-history development (e.g., age of menarche).

In an influential proposal, Draper and Harpending (1982) and Belsky, Steinberg, and Draper (1991) argued that paternal absence, marital conflict, and other early stressors within the family can influence children's life history development, including age of sexual maturation and the age of onset of various reproductive behaviors (Belsky et al., 2007; Bereczkei & Csanaky, 2001; Vigil, Geary, & Byrd-Craven, 2005). The basic idea is that the pace of life history development (see Chapter 4, Figure 4.2, this volume) is influenced by the stability of family relationships and the amount of resources available as children are growing up. Exposure to familial conflict and other stressors is thought to trigger stress responses and an early onset of adrenarche (adrenal-gland production of the hormones that will eventually initiate puberty) that in turn accelerates physical maturation (Del Giudice, 2014; B. J. Ellis & Del Giudice, 2019). As was described in Chapter 4 of this volume, reproductive acceleration under risky conditions is found in many species and is an adaptive response to these conditions.

The most controversial prediction is that father absence will hasten reproductive maturation in girls, such that they will experience earlier menarche than will girls who live with their fathers and have good relationships with them. Indeed, father absence is sometimes associated with earlier menarche in girls—at least in contexts with adequate nutrition—and a faster pace of life (e.g., younger age at first birth) more generally. However, several meta-analyses suggest that the strength of the relationship between father absence and age of menarche is modest (Webster, Graber, Gesselman, Crosier, & Schember, 2014) to trivial (Xu, Norton, & Rahman, 2018). The strength of the relationship depends on wider social and health issues. Nearly all of these studies that have found earlier menarche with father absence have been conducted in developed nations. In contrast, most studies conducted in developing nations reveal no relationship between father absence and age of menarche and may in fact result in later menarche, if father absence results in nutritional shortfalls (K. G. Anderson, 2015; Kyweluk, Georgiev, Borja, Gettler, & Kuzawa, 2018; Sheppard, Snopkowski, & Sear, 2014; Sohn, 2017b). Chang and Lu (2018) provided an exception to the latter, with their study of rural China's left-behind children (i.e., children whose parents migrate to urban areas to work). These children are living in low-resource environments and with relatives (e.g., grandparents). A higher proportion of girls who experience extended absence of their father but not mother during childhood experience menarche earlier than their father-present peers.

Whatever the effect on pubertal timing, father absence and exposure to other stressors during childhood and adolescence is consistently associated with behavioral indicators of a faster pace of life for girls and boys, including earlier sexual debut and earlier age of first childbirth (K. G. Anderson, 2015; Belsky, 2019; Gaydosh, Belsky, Domingue, Boardman, & Harris, 2018; Sheppard et al., 2014; Xu et al., 2018). There are many reasons why father absence and familial stress more broadly are related to an earlier onset of sexual behavior, including shared genes and a plastic response to risky conditions (Bogaert, 2005; Chang et al., 2019; B. J. Ellis, 2004; B. J. Ellis & Del Giudice, 2019; B. J. Ellis, McFadyen-Ketchum, Dodge, Pettit, & Bates, 1999). Gaydosh et al. (2018) found that father absence was associated with earlier sexual debut and a younger age of first childbirth for girls, independent of genetic influences on these aspects of life history. These may be related, at least in part, to fathers' monitoring of daughters' early romantic relationships (Flinn, 1988b), which may serve to screen potential mates and delay the onset of sexual activity (Byrd-Craven, Geary, Vigil, & Hoard, 2007). This is not the whole story, as stressors in the local area (e.g., neighborhood violence) are also associated with a faster pace of life for both sexes (M. Wilson & Daly, 1997), as is found in other species (see Chapter 4, this volume).

Despite these consistent relations, there are important individual differences in how children and adolescents react to familial and broader stressors that are not well understood (Belsky, 1997; B. J. Ellis & Del Giudice, 2019). Belsky et al. (2007) found that the relation between family background (e.g., maternal and paternal control) and pubertal timing varied with girls' early emotional and temperamental reactivity. The details of these potential genotype-by-environment interactions remain to be sorted out, but the findings are consistent with Belsky's (1997) prediction of individual differences in children's sensitivity to rearing environment as this potentially influences later reproductive strategy. B. J. Ellis and Essex (2007) found that low investment by both parents and higher levels of marital conflict were associated with earlier adrenarche in boys and girls. These hormones do not result in the expression of secondary sexual characteristics (e.g., facial hair for males), but can result in behavioral changes (e.g., increased aggression) that can bias the dynamics of later reproductive relationships (Del Giudice, 2009).

Social Well-Being

Even when paternal investment can significantly reduce infant and child mortality risks, it is not obligate; many children survive without such investment (Sear & Mace, 2008). Because human paternal investment is facultatively expressed (i.e., depending on conditions), men can and often do shift reproductive effort from parenting to mating (see Chapter 4, Exhibit 4.1, this volume). Even with these trade-offs, some level of paternal investment is found across human societies, and at some point in our evolutionary past our male ancestors benefited by devoting some portion of their reproductive effort to parenting instead of mating. Nonetheless, human paternal investment is puzzling when it occurs in contexts with low infant and child mortality and low risk of infanticide by other males. 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?

If our ancestors evolved in a gorilla-like family structure, as suggested in Chapter 5 of this volume, then some level of male parental investment has a very long evolutionary history and its expression these days might simply reflect evolutionary inertia. It is also possible that paternal investment in low-risk environments provides social-competitive advantages to children (J. N. Davis & Daly, 1997), and long-term reproductive benefits to men (e.g., number of grandchildren). In 18th and 19th century Finland, monogamously married and wealthy men had more children and more surviving children than their less-wealthy peers and 5 times as many grandchildren (Bolund & Lummaa, 2017). In this population, men who had wealth and invested it in their family were reproductively more successful than men without wealth, but there was high child mortality (42% of the children of wealthy men died and 53% of the children of less-wealthy men died), and these findings do not assess the value of fathers' investment in low risk environments. As mortality rates declined through the late 19th and 20th centuries, wealthy monogamously married men still had more children and grandchildren than did their less-wealthy peers, although the gap had narrowed.

These results suggest continued benefits to men's investment in children in low risk environments, but they do not directly address the question of whether men improve the social competitiveness of their children. This is addressed in the first section below, and the second section discusses the importance of social competitiveness from a broader evolutionary context.

Paternal investment and social competitiveness. In developed nations, high levels of paternal investment (e.g., income, playing with children, supporting the mother) are correlated with better social and academic outcomes in children, as well as a higher SES when these children reach adulthood (Kaplan, Lancaster, & Anderson, 1998; Nettle, 2008; Pleck, 2010). Despite the consistency of these findings, a causal relation remains to be firmly established (Amato, 1998; McLanahan, Tach, & Schneider, 2013). Again, the tendency for competent men to marry competent women confounds the interpretation of paternal effects, as do the genetic correlations between parents and children, child-evocative effects (e.g., fathers may invest more in more competent than less competent children), and other factors that influence fathers' investment (e.g., marital conflict, divorce; Cherlin et al., 1991; Rowe, 1994; Scarr & McCartney, 1983). Moreover, nearly all these studies have been conducted in wealthy populations with socially imposed monogamy that promotes men's investment in the family, whether or not it is beneficial to these men.

Despite these confounds, men's parental investment can improve some aspects of children's social competitiveness, although the magnitude of any such effects and whether they vary across contexts are not well understood (McLanahan et al., 2013). In developed nations, a combination of years of education, occupation, and income define SES and is a good proxy of social competitiveness. With control of some or most of the above-mentioned confounds, McLanahan and colleagues (2013) concluded that father absence because of death or divorce did not compromise children's long-term cognitive ability (e.g., mathematics achievement) or their stated educational aspirations but was consistently related to how long they stayed in school; father absence is consistently associated with higher rates of dropping out of secondary school. Paternal influences on educational attainment and age of sexual debut and first reproduction described previously translate into potentially significant long-term economic and social consequences for many of their children (Amato & Keith, 1991; Belsky et al., 1991; Psacharopoulos & Patrinos, 2018).

Steele, Sigle-Rushton, and Kravdal's (2009) study illustrates the relationship between divorce or paternal death and total number of years of schooling from 200,000 Norwegian children. Not only is infant and child mortality low in Norway, government-funded social support programs that mitigate financial hardship make it an especially low-risk environment. Despite the low risks and controlling for multiple other factors, the loss of a father for any reason (there was little difference in child outcomes comparing fathers' death or divorce) was associated with about a 10% reduction in the chances of finishing secondary schooling for boys and girls. In an informative twist on this type of study, Gähler and Palmtag (2015) assessed the relation between divorce and Swedish children's educational outcomes for people born in 1892 through 1991, a time frame with substantial drops in child mortality and increases in government welfare programs. Despite the reduction in risks, divorce (and typically paternal absence) was consistently associated with lower educational attainment for girls and boys throughout the century, even when controlling for other factors (e.g., marital conflict, parental education). The lower educational attainment is correlated with an increased risk of delinquent behavior and more alcohol and substance abuse in adolescence (McLanahan et al., 2013). These patterns are consistent with fathers' monitoring of children's and adolescents' behavior and peer groups, in addition to their economic contributions to the family.

Any more-subtle influences on children are not as well understood (Cabrera, Volling, & Barr, 2018), but it appears that fathers can directly influence children's and adolescents' social and emotional functioning and indirectly influence it through the quality of the marital relationship (B. Barker, Iles, & Ramchandani, 2017; Gutierrez-Galve, Stein, Hanington, Heron, & Ramchandani, 2015; McDowell & Parke, 2009). Paternal involvement in play, especially rough-and-tumble play (see Chapter 4, this volume), is associated with children's skill at regulating their emotional states and their later social competence (R. Fletcher, St. George, & Freeman, 2013). Children whose fathers 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 with their father (Parke, 1995). Several longitudinal studies indicate that this form of play is associated with better social and psychological functioning when these children reach adolescence (Grossmann et al., 2002; Lindsey, Colwell, Frabutt, & MacKinnon-Lewis, 2006). Rough-and-tumble play might also signal paternal dominance in a nonthreatening way to young children (R. Fletcher et al., 2013), which then enables fathers to more effectively monitor and influence adolescent behavior. This in turn may contribute to the reduced adolescent delinquency and higher educational attainment of adolescents with engaged fathers.

In total, these studies are consistent with paternal contributions to children's social and emotional functioning and their social competitiveness in adulthood, but they have all been conducted in relatively wealthy populations in developed nations. Our understanding of fathers' contributions to these aspects of children's functioning in traditional and developing societies is sparse, but there are hints of a similar relation in the ethnographic record (e.g., Turnbull, 1957) and in more recent studies (Scelza, 2010; Shenk & Scelza, 2012). Scelza (2010) found that Martu Aboriginal (western Australia) fathers and other male kin facilitated adolescent boys' and young men's initiation into the adult social network within their community. Critically, biological fathers' presence and engagement results in an earlier age of initiation of their sons into the social network, an earlier age of marriage, and an earlier age of first reproduction. In Bangalore, India, fathers' death during their children's adolescence is associated with less schooling, lower adult income for sons, and marriage to lower status men for daughters (Shenk & Scelza, 2012; see also Shenk, Starkweather, Kress, & Alam, 2013). These benefits, however, have not been found in all traditional contexts (Winking, Gurven, & Kaplan, 2011), indicating that much remains to be learned about the contexts in which fathers' contribution are critical to their children's later social and reproductive success.

Selection and social competitiveness. Even if men contribute to their children's social status in adulthood, the benefits of doing so are unclear in low-risk contexts with low child mortality. These low-risk environments are actually an evolutionary novelty that slowly emerged over the past 200 years in Western nations and more recently in developing ones (Corsini & Viazzo, 1997; T. Volk & Atkinson, 2008) and are associated with lower mortality risks and lower fertility. Before this demographic transition, the Horsemen of the Apocalypse (plague, famine, war, and death; see Chapter 4, this volume) made frequent appearances and resulted in unpredictable population crashes, as documented by Malthus (1798) for developing nations and Hamilton and Walker (2018) for hunter–gatherer societies. It is during these crashes that men's contributions to their children's later social status would be particularly important. This is because an increase in social status would reduce their adult children's and their grandchildren's mortality risks during crashes. Men who maintained paternal investment in contexts with low child mortality risks thus provided their children with an advantage should the Horsemen make one of their unpredictable visits.

The basic idea is that paternal investment could be a viable reproductive strategy if it enabled children to maintain or improve their SES or cultural success in adulthood. Even among relatively equalitarian hunter–gatherer societies, there is cross-generational transfer of various forms of wealth (e.g., material, knowledge, social network) that contribute to social position in succeeding generations (Borgerhoff Mulder et al., 2009). Improved social competitiveness would enhance children's ability to acquire socially and culturally important resources in adulthood (e.g., marrying a competent spouse; generating wealth) that in turn would reduce the mortality risks of their children and their grandchildren, especially during population crashes.

Such a pattern is evident in Song, Campbell, and Lee's (2015) analysis of lineage extinction during China's Qing dynasty (1644–1911). Their analysis of 20,000 patrilineages from this era indicated that higher status men had somewhat higher reproductive success (most men were monogamously married) than lower status men, but more critically, they had a much lower chance of lineage extinction over the next six generations. Extinction risk was independent of the number of children born in each generation, indicating that lineage continuance was not simply due to higher status men having more children. In addition, these children and their descendants were less likely to die than those of lower status men. Song et al. could not determine the cause of the extinctions, but H. F. Lee (2018) documents numerous epidemics, famines, internal wars, and invasions during the Qing dynasty and the preceding Ming dynasty that are typically associated with population crashes that disproportionately increase mortality rates among lower status families. G. Clark (2008) describes an even stronger relation between status and lineage survival in parts of Europe from the 13th to 19th century.

In other words, the achievement and maintenance of status (e.g., through investment in education) and wealth that is transmitted to the next generation helps to keep the Horsemen of the Apocalypse at bay and the lineage viable. However, the payoffs to this strategy might not be strongly evident except during times of high population mortality. In this view, the finding that men's contributions do not influence children's mortality risks in many currently studied traditional societies (Sear & Mace, 2008) may significantly underestimate the evolutionary importance of paternal investment. This is because most of these populations are growing and have not been studied following successive population crashes.

Costs to Fathers

The reduction of infant and child mortality risks and the improvement of children's social competitiveness are not enough to explain the evolution and maintenance of men's parental investment. As shown in Exhibit 4.1 (see Chapter 4, this volume), these benefits have to be balanced against men's lost mating opportunities and the risk of cuckoldry. As covered in Chapter 8 of this volume, successful men who are polygynously married—devoting more to mating effort than to parental effort—have reproductive advantages over their more paternal peers in many contexts. These results indicate that men's parenting often comes at a real reproductive cost, despite the detailed benefits to children (e.g., Blurton Jones, Marlowe, Hawkes, & O'Connell, 2000; Winking & Gurven, 2011). A reduction of the costs of lost mating opportunities and cuckoldry risk are necessary to maintain men's parenting. The factors that reduce these costs are covered in the next two sections.

Women's Strategies and Men's Mating Opportunities

Men's investment in parenting increases when their opportunities for casual sex decrease (Guttentag & Secord, 1983), and there are several aspects of women's preferences and behaviors that reduce these mating opportunities. The first is much less enthusiasm for casual sex relative to that of men

(J. L. Petersen & Hyde, 2010; Symons, 1979; see Chapter 7, this volume); on average, men prefer more sexual partners than do women (D. M. Buss & Schmitt, 1993; R. D. Clark & Hatfield, 1989; B. J. Ellis & Symons, 1990). This is not a conspiracy among women to deny men sexual opportunities, but rather follows from the higher costs that women pay for pregnancy and the sex differences in postpartum investment in children. Recall, the fundamental pattern across species is that the sex that invests more in offspring is the more discerning sex when it comes to mates (see Chapter 3, this volume).

Women's relational aggression is another factor that reduces men's mating opportunities (see Chapter 8, this volume). The dynamic is an aspect of female–female competition and involves gossiping about and attempting to socially manipulate and sully the reputation of other girls and women (Archer & Coyne, 2005; A. Campbell, 1999; A. C. Davis, Dufort, Desrochers, Vaillancourt, & Arnocky, 2018). The goals are to undermine the desirability of potential competitors and, if possible, exclude them entirely from the social group (Geary, 2002b; Geary, Winegard, & Winegard, 2014). When effective, this strategy will reduce the number of women and their desirability in the local group and through this reduce men's mating opportunities.

Concealed ovulation, women's continuous sexual receptivity, and a satisfying sexual relationship also help to maintain the pair bond and thereby promote paternal investment (J. E. French, Altgelt, & Meltzer, 2019). To ensure conception, concealed ovulation requires a longer relationship than is typical among primates, but this is not sufficient to ensure paternal investment. Once the physical signs of pregnancy are evident, men could easily abandon women and avoid the cost of parenting. However, the combination of concealed ovulation and continuous receptivity may reduce the risk of abandonment by fostering the pair bonding that maintains men's investment in their partner and their children (G. J. Fletcher, Simpson, Campbell, & Overall, 2015; K. MacDonald, 1992). Indeed, the hormonal changes—increase in progesterone—that occur after the fertile phase of women's ovulatory cycle appear to promote their sexual interest with their pair-bonded partner (Grebe, Gangestad, Garver-Apgar, & Thornhill, 2013; Grøntvedt, Grebe, Kennair, & Gangestad, 2017). Women initiate sex with their partner during this phase of the cycle, even though they cannot become pregnant, in keeping with an evolved strategy to maintain the relationship.

Pair-bonding and women's satisfaction with the relationship are also likely to increase paternity certainty (i.e., decrease the risk of cuckoldry). However, paternity is not always certain, as discussed in the next section. In the face of cuckoldry risks, men's parenting is influenced, in part, by how closely the children resemble them (Billingsley, Antfolk, Santtila, & Lieberman, 2018; Yu et al., 2019), and women and their kin often manipulate social information in ways that foster perceived resemblance (Daly & Wilson, 1982; McLain, Setters, Moulton, & Pratt, 2000). Daly and Wilson (1982) analyzed videos of new parents in maternity wards from two regions in the United States. In both regions, mothers stated that the newborn resembled the father more than the newborn resembled her, although newborns, in fact, do not resemble their fathers more than their mothers (Alvergne, Faurie, & Raymond, 2007). Follow-up studies confirmed the pattern in Canada and Mexico and suggested it extends to maternal kin; maternal grandmothers often comment on the resemblance as well (Daly & Wilson, 1982; McLain et al., 2000; Regalski & Gaulin, 1993).

Cuckoldry

As discussed in Chapter 4 of this volume, females rarely cuckold their partner when male parenting is obligate; it is necessary to keep offspring alive. Men's parenting however is facultatively expressed, and in this situation, females sometimes engage in extra-pair relationships and cuckold their partner. The latter generally occurs when the females are paired with relatively low-status males. The question here is whether the same pattern occurs for humans and if so, how often (see also Chapter 8, this volume)?

Extramarital affairs are found across cultures and are a common reason for divorce (Betzig, 1989). In developed nations, between 2% and 4% of married people report engaging in some form of extramarital relationship during the previous year (although not necessarily sexual intercourse), and one spouse or the other will engage in this type of relationship during the course of as many as 1 out of every 4 marriages (Fincham & May, 2017). Overall, men report more extramarital affairs than do women during the course of a relationship, but the proportion is similar for men (14%–15%) and women (11%–14%) before the age of 40, at least in the United States (Whisman & Snyder, 2007; Wiederman, 1997). The frequency with which men and women engage in extramarital affairs in traditional cultures is not as well understood, but it clearly happens and is an important risk to the relationship (Neel & Weiss, 1975; Scelza, 2011; Winking, Kaplan, Gurven, & Rucas, 2007). In these societies, men and women reduce the risks of partner infidelity through a variety of informal (e.g., gossip) and formal (e.g., formal sanctions) means, as well as through cultural prohibitions (e.g., religious; Jankowiak, Nell, & Buckmaster, 2002; Strassmann et al., 2012).

The most remarkable aspect of these studies is the relatively low rates of nonpaternity (cuckoldry) found in many populations. In developed, Western nations a variety of methods, including DNA fingerprinting, have revealed nonpaternity rates of 1% to 3% (K. G. Anderson, 2006; M. Wolf, Musch, Enczmann, & Fischer, 2012). The nonpaternity rates have declined since the advent of modern birth control (Voracek, Haubner, & Fisher, 2008), but this is not the whole story. Matches between DNA on the Y-chromosome (inherited from father) and long-term patrilineal genealogies reveal similarly low nonpaternity rates extending back 300 to 500 years in various Western populations (Greeff & Erasmus, 2015; Larmuseau et al., 2013; Solé-Morata, Bertranpetit, Comas, & Calafell, 2015). Strassmann et al. (2012) estimated nonpaternity rates of between 1% and 5% for the natural fertility (i.e., no birth control) Dogon in the Republic of Mali, in west Africa. Neel and Weiss (1975), in contrast, found nonpaternity rates of close to 10% among the Yanomamö (Brazil, Venezuela).

There is also variation within populations. In modern contexts, very high cuckoldry risks (nonpaternity >20%) are found in some lower SES populations (Cerda-Flores, Barton, Marty-Gonzalez, Rivas, & Chakraborty, 1999; McBurney, Simon, Gaulin, & Geliebter, 2002; Potthoff & Whittinghill, 1965), consistent with more extra-pair or unstable relationships for women paired with less successful men. In a traditional context, Scelza (2011) found substantial differences for arranged marriages compared with "love marriages" among the Himba (Namibia); the latter are often arranged but with consent of the bride. She estimated that 23% of children produced in the context of an arranged marriage were sired by an extra-pair man, as compared with none of the children produced in the context of love marriages. Scelza's findings reflect the importance of female choice in humans and nicely confirm the influence of pair-bonding and relationship quality on women's fidelity to their partner which, as discussed later, promotes men's engagement with their children.

It remains to be resolved whether women's extra-pair relationships are explicitly to cuckold their partners or if cuckoldry results from failed attempts to use the extra-pair relationship as a strategy to switch mates. I suspect that cuckoldry often results from a failed attempt to mate switch, rather than simply an attempt to secure better genes without the expectation of a long-term relationship (D. M. Buss, Goetz, Duntley, Asao, & Conroy-Beam, 2017). Support for the mate switching hypothesis 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 extra-pair man, suggesting they have formed the pair-bond associated with long-term relationships (see also Glass & Wright, 1992). The issue is further complicated in contexts with high male mortality. As described in the following chapter, 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; K. Hill & Hurtado, 1996). These relationships are not attempts to cuckold their primary partner but rather are a form of social insurance in case that partner dies.

Overall, human paternity certainty is substantially higher than the near-zero levels found with chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), but in the range (>95%) found in gorillas (*Gorilla gorilla*; Bradley, Doran-Sheehy, Lukas, Boesch, & Vigilant, 2004). These findings are consistent with the argument in Chapter 5 of this volume that human family relationships have many similarities to those found in gorilla families (Geary, Bailey, & Oxford, 2011; Geary & Flinn, 2001). It was argued that the formation of male coalitions and the emergence of multimale–multifemale communities would have resulted in an increase in the number of lower quality males entering the reproductive pool. The combination creates greater opportunity for and greater benefits of cuckoldry, especially when women are paired with low-quality or low-investing men. In this situation, paternity rates are predicted to be lower than the 95% found in gorillas, and this seems to be the case for women married to lower status men in modern contexts (Potthoff & Whittinghill, 1965) and in at least some arranged marriages that circumvent female choice (Scelza, 2011).

SEX DIFFERENCES IN HUMAN PARENTING

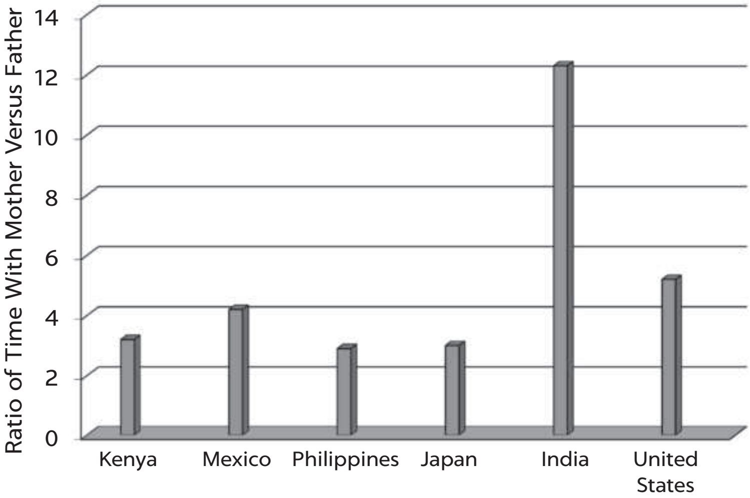
In theory, the facultative expression of men's parenting will create ample opportunity for conflict and compromise between parents. Conflict results as women attempt to get more paternal investment than men prefer to give and men attempt to reduce investment and focus more on mating effort or on achieving status in culturally important domains. Compromise is predicted to result in a level of paternal investment that is higher than men prefer but lower than women prefer. In keeping with this expectation, the sex difference in parental investment described in the following sections is a common source of marital conflict (Dillon et al., 2015; Scarr, Phillips, & McCartney, 1989).

Direct Care of Children

As is common in mammals generally, more maternal than paternal availability for and engagement with children is found in all human cultures (Eibl-Eibesfeldt, 1989; Konner, 2005, 2010; M. M. West & Konner, 1976; Whiting & Edwards, 1988). Whiting and Edwards's (1988) extensive cross-cultural studies of children's social behavior and development provide numerous examples. In one study, 3- to 6-year-olds in Kenya, India, Mexico, the Philippines, Japan, and the United States were in the proximity of or in contact with their mother 32% to 47% of the time in 5 of the 6 cultures and 9% of the time in the 6th (a rural village in Japan); the estimate for the latter is biased because observations were not taken in the household (Whiting & Whiting, 1975). In these same communities, children were in the proximity of or in contact with their father between 3% and 14% of the time. As shown in Figure 6.1, young children were in the presence of their mother 3 to 12 times more frequently than in the presence of their father.

A similar pattern was found for 4- to 10-year-olds in communities in Africa, South Asia, South America, Central America, and North America (Whiting & Edwards, 1988). Here, children were found to be in the presence of their mother 2 to 4 times more frequently than in the presence of their father. Observation of 5- to 7-year-olds in Kenya, Guatemala, Peru, and the United States indicated that children were much more likely to be directly engaged in activities with women (e.g., mothers, grandmothers, aunts) than with men. The smallest difference was found in the United States, where children of this age were found to be directly engaged with women 2.5 times more frequently

FIGURE 6.1. Ratio of Maternal to Paternal Care Across Human Societies



In Kenya, children were in the presence of or engaged in activities with their mother more than 3 times as often as with their father.

than they were engaged with men. A recent national survey found the same 2 to 1 ratio of maternal to paternal engagement with children among highly educated U.S. parents (physicians, lawyers; Ly & Jena, 2018). The overall pattern differed somewhat for boys and girls; girls spent relatively more time interacting with women and boys spent relatively more time interacting with men. The extent of these sex differences varies across cultures and is not as pronounced as the overall difference in the frequency with which mothers and fathers interact with their children (Eibl-Eibesfeldt, 1989; M. M. West & Konner, 1976).

The sex difference in parental care is even more pronounced for infants and toddlers (i.e., the first 3 years of life; Crano & Aronoff, 1978). Breastfeeding is, of course, the domain of mothers and in many preindustrial, developing, and traditional societies continues until the child is 2 to 4 years old (Eibl-Eibesfeldt, 1989; Konner, 2005). Mothers not only breastfeed infants and young children, they provide most of the child's daily care. Observational studies revealed fathers were rarely or never engaged in the care of infants younger than 1 year in Liberia, Kenya, India, Guatemala, or Peru (Whiting & Edwards, 1988). Fathers in the United States provided more care than did fathers in these other settings, but U.S. fathers still provided considerably less care than the infant's mother.

Observation of parental care in the Ache, Yanomamö, !Kung San (Botswana), Hadza (Tanzania), Efe (Congo), Aka (Central African Republic), Agta (Philippines), and other societies reveals the same pattern (Flinn, 1992; Hames, 1992; Konner, 2005, 2010). Studies of the !Kung San are particularly interesting because their social customs center on equality among group members. Despite the social norm of equality, observation of caregiving for children younger than 2 years of age indicated that !Kung San fathers provided less than 7% of this care; the majority of the care is provided by the mother (M. M. West & Konner, 1976). The Aka are a hunter–gatherer society in which fathers provide more direct care to their infants and children than do fathers in any other society that has been studied (Hewlett, 1992). One observational study indicated that when in camp, Aka fathers held their 1- to 4-month-old infants 22% of the time, on average. During the course of the day, "the father would on average hold his infant for a total of 57 minutes while the mother would hold the infant 490 minutes" (Hewlett, 1988, p. 268).

The sex difference in parental engagement is not because men cannot care for children. When fathers do interact with infants and young children, they show many of the same characteristics as mothers and can provide competent routine care (Belsky, Rovine, & Fish, 1989; Eibl-Eibesfeldt, 1989; Parke, 1995). Nor can the sex difference be attributed to father absence, because he is away hunting or working outside of the home. Belsky, Gilstrap, and Rovine (1984) found that when both parents were present, U.S. mothers spontaneously engaged their infant 1.5 to 2 times more frequently and provided routine care 3 to 4 times more frequently than did their husbands. The same pattern is found in Australia, Belgium, Canada, France, Germany, Great Britain, Israel, and Sweden (T. Buchanan, McFarlane, & Das, 2016; Cooke, 2004, 2007; Lamb, Frodi, Hwang, & Frodi, 1982; Lampert & Friedman, 1992; Parke & Buriel, 1998). More recently, Swedish men with strong beliefs about gender equality reported engaging in more childcare than did men with more traditional beliefs (Evertsson, 2014), but as a group they are also less likely to have children (E. Bernhardt, Goldscheider, & Turunen, 2016). Overall, however, there does not appear to be a consistent relation between explicit beliefs about gender roles and patterns of paternal care (Pleck, 2010).

Abandonment

Mothers and fathers also differ in how often they abandon or significantly disengage with their children, such as following a divorce. Although divorced fathers might not be representative of fathers in general, these studies reveal a great deal about the level of paternal investment in a significant portion of men. Studies conducted in developed nations indicate that the majority of noncustodial fathers are not actively involved in the day-to-day raising of their children, typically because most children live with their mother (Amato & Booth, 1996; Furstenberg & Nord, 1985). The general trend in the United States is for fathers to initially see their children about twice per month, but this gradually declines to less than once per month in the years following the divorce (Cheadle, Amato, & King, 2010). This typical trend, however, obscures considerable variation in the extent to which men remain engaged with their children. Cheadle and colleagues (2010) found that about 4 in 10 men stay engaged (visiting once to several times per week) with their children over time, and 2 in 10 are engaged during the first year following the divorce, but this declines to infrequent visits over time. The remaining men have little or sporadic (once or a few times a year) contact with their children. The trends, however, have changed over time, with 37% of fathers having no contact with their children in 1976 as compared with 29% in 2002 (Amato, Meyers, & Emery, 2009). Among engaged fathers, the amount of time they spend with their children increased as well, especially if they were paying child support.

A similar secular increase in father engagement with their children is found in Europe (Westphal, Poortman, & Van Der Lippe, 2014), although there is still considerable variability in the nature of this engagement. The latter is nicely illustrated by Kalmijn's (2015) large-scale ($n = 4{,}524$) and nationally representative study of adolescents from divorced families from England, Germany, the Netherlands, and Sweden. Mothers were the primary caretaker of the majority of adolescents in all of these nations, but about 1 in 3 adolescents were coparented (splitting living arrangements between parents) in Sweden, relative to less than 1 in 5 in the other nations. Among adolescents who were not coparented, about half had face-to-face contact with their father at least once per month. At the same time, more than 1 in 4 children from Sweden and the Netherlands infrequently or never had face-to-face contact with their father, and the same was found for more than 1 in 3 children from England and Germany. The results suggest that the equalitarian ethos in Sweden and broader secular changes across Western nations may promote or enable more paternal engagement than in other contexts, but a substantial number of men still disengage from their children following divorce.

These findings cannot be attributed to the fact that fathers are much more likely to be the noncustodial parent (Furstenberg, Peterson, Nord, & Zill, 1983). Furstenberg and Nord (1985) noted that in comparison with noncustodial fathers, noncustodial mothers "tend to maintain a much more active role in childrearing . . . are distinctively more likely to visit with their child on a regular basis, have overnight visits, and have more indirect contact by phone and letter" (p. 896). Amato and Booth (1996) concluded that "divorce does not appear to weaken mothers' affection for their children" (p. 364) but leads to a deterioration in the relationship between fathers and their children. The pattern of relatively less paternal than maternal investment in children is often more evident for children who are born to unmarried couples (Cheadle et al., 2010), although many of these fathers do maintain intermittent contact with their children (Parke, 1995), especially if the man maintains a good relationship with the children's mother (J. Fagan & Palkovitz, 2007). In addition to relatively little direct involvement with their children, as many as half of the biological fathers who do not live with the mother did not monetarily support their children, and those who do provide support invest less in their children relative to fathers in intact families (Garasky, Stewart, Gundersen, & Lohman, 2010; Maccoby, Buchanan, Mnookin, & Dornbusch, 1993).

The pattern of fathers reducing investment in their children following separation from the children's mother is not confined to developed, Western nations. In other contexts, fathers generally invest more in their children when they are residing with them and the children's mother (K. G. Anderson, Kaplan, Lam, & Lancaster, 1999; Draper, 1989; Hewlett, 1992; K. Hill & Hurtado, 1996). The importance of residence, and presumably sex with their children's mother, suggests some component of men's parenting is mating effort. In an observational study of parent–child social interactions in a Caribbean village, Flinn (1992) found that resident fathers were much more likely to provide some level of care to their children than were nonresident fathers, especially after the nonresident father or the mother remarried (see also Draper, 1989). A similar pattern of fathers' disengagement with their children following their remarriage or the mother's remarriage is found in developed nations (Juby, Billette, Laplante, & Le Bourdais, 2007), although this trend may have lessened in recent decades (e.g., Amato et al., 2009).

Despite the earlier described costs to children, many men initiate divorce or reduce their level of investment in the marriage and their children and contribute to the likelihood their wives will initiate a divorce. From the man's perspective, divorce or activities that prompt a spouse to initiate divorce (e.g., an affair) can be viewed as an implicit reproductive decision; a reflection of the potential benefits associated with pursuing a new mate balanced against the costs to the current family. Support for this hypothesis is found in studies of divorce, remarriage, and reproduction in traditional cultures and developed nations, as well as in the historical record of Western nations (Blurton Jones et al., 2000; Forsberg & Tullberg, 1995; Hopcroft, 2006; Käär, Jokela, Merilä, Helle, & Kojola, 1998; Winking & Gurven, 2011). Following divorce, men—especially higher status men—are more likely to remarry than are women, and when both remarry men do so more quickly. When men remarry, they typically marry women younger than their just-divorced wife and are more likely to have children with the new spouse than are women (Buckle, Gallup, & Rodd, 1996). Moreover, twice (or thrice) married men, but not women, sire more children, on average, than their monogamous peers (Forsberg & Tullberg, 1995; Käär et al., 1998). In short, a reduction in parental investment in favor of mating effort is a more viable reproductive strategy for men than women and reflects, at least in part, the inherent cost–benefit trade-offs of men's investment in parenting or mating.

PROXIMATE EXPRESSION OF MEN'S PARENTING

The facultative expression of men's parenting means that there will be considerable variation in how much different men invest in their children as well as variation for the same man across different relationships and children. The following sections review the biological, social, developmental, and cultural influences on when and how much men invest in parenting. The core influences on the quantity and quality of men's parenting are shown in Figure 6.2.

FIGURE 6.2. There Are Multiple Levels of Influence on Men's Parenting

These include reciprocal relations among hormone levels, especially testosterone, and marriage quality, as well as broader influences. The latter includes formal or informal social rules that enforce monogamy and the operational sex ratio (i.e., the ratio of available women to men).

Biological Correlates

The first focus is on the hormonal influences on men's investment in seeking mates versus committing to a monogamous relationship and investing in children. The discussion then turns to genetic influences on individual differences in men's investment in parenting.

Hormones and Men's Parenting

As covered in Chapter 4, developmental exposure to testosterone and circulating testosterone concentrations orchestrate males' reproductive strategies, including their relative focus on mating or on parenting. In nonhuman species with facultative male parenting, higher concentrations of testosterone are associated with a focus on mating over parenting and lower concentrations—combined with high concentrations of prolactin (among other hormones)—are associated with a focus on parenting. Men's focus on mating or on parenting is influenced by many of the same biological and contextual factors that influence male parenting in these nonhuman species (S. E. Lynn, 2016; M. N. Muller, 2017; Storey & Ziegler, 2016). The bottom line is that men's investment in parenting is reciprocally related to basal (typical every day) concentrations of testosterone and changes in testosterone and prolactin concentrations, among other factors, associated with many social dynamics, including marriage, marriage quality, and interactions with infants and children (Delahunty, McKay, Noseworthy, & Storey, 2007; A. S. Fleming, Corter, Stallings, & Steiner, 2002; Gettler, McKenna, McDade, Agustin, & Kuzawa, 2012; P. B. Gray, McHale, & Carré, 2017; Mazur & Booth, 1998; Roney & Gettler, 2015).

Monogamously married men in long-term committed relationships have lower testosterone concentrations than do other men (P. B. Gray et al., 2017; Mazur & Michalek, 1998), consistent with the allocation of less effort to competing for mates (Gettler, McDade, Feranil, & Kuzawa, 2011; P. B. Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002). The dynamic is illustrated by Gettler et al.'s (2011) longitudinal study of testosterone concentrations in 22-year-old men and changes in these concentrations 4 years later, after many of them married and had children. As would be expected if testosterone concentrations contribute to a focus on mate seeking, the 22-year-olds with higher testosterone concentrations were more likely than other men to be married and have children 4 years later. The important twist is that these fathers had a substantially larger drop in testosterone concentrations over these 4 years than did men who remained single or were married without children. Men who reported significant engagement with their children had the lowest testosterone concentrations among the married men with children. In other words, nurturing interactions with children and the quality of the marital relationship are reciprocally related to men's testosterone concentrations and can result in decreases in these concentrations that in turn focus them on parenting (Edelstein, van Anders, Chopik, Goldey, & Wardecker, 2014; van Anders, Tolman, & Volling, 2012).

The influence of testosterone on men's reproductive strategies is confirmed by the finding that married men who are open to an extramarital affair have higher testosterone concentrations than their more-committed peers (McIntyre et al., 2006). In a 10-year longitudinal study, Mazur and Michalek (1998) found that men's testosterone concentrations varied with their marital status and the quality of the marital relationship. In comparison with the early years of the marriage, testosterone concentrations were higher in the several years preceding a divorce and during the mate-search years immediately following a divorce. Once men remarried, their testosterone concentrations dropped. Follow-up studies, however, have revealed a more nuanced relationship between marriage and testosterone concentrations. For men who are satisfied with their marriage, higher concentrations of testosterone are often associated with greater engagement in the marital relationship (perhaps reflecting more sexual activity), whereas higher testosterone concentrations in the context of unsatisfying relationships are associated with greater marital conflict (Booth, Granger, Mazur, & Kivlighan, 2006).

The relationship between marriage and testosterone is also influenced by whether or not men can marry polygynously but with some nuance. The pattern is illustrated by P. B. Gray's (2003; P. B. Gray, Ellison, & Campbell, 2007) studies of the relationship between testosterone and marriage in two polygynous societies in Kenya: the Swahili and the Ariaal. Swahili men with two wives had higher testosterone concentrations than did monogamously married men or single men (see also Alvergne, Faurie, & Raymond, 2009); the two latter groups did not differ from one another. The higher testosterone concentrations of the polygynously married men were likely related to their multiple simultaneous sexual relationships, as van Anders, Hamilton, and Watson (2007) found for Canadian men who maintained multiple relationships. The failure to find a difference in the testosterone concentrations of married and single men is likely due to the polygynous culture. In these contexts, a first or second marriage does not mean an end to reproductive competition, as it typically does in monogamous cultures—when polygyny is allowed, most men maintain mate-search testosterone concentrations even after marriage. In contrast, in traditional cultures where most men marry monogamously, the pattern is similar to that found in more developed contexts where polygyny is illegal. Men's testosterone concentrations are lower once they marry and become lower still if they frequently engage with their children (M. N. Muller, Marlowe, Bugumba, & Ellison, 2009).

There is also variation in men's testosterone concentrations within the context of marital relationships. Men in a committed and monogamous relationship and who wish to become a father may have a different hormone profile than do other men, including married men who do not wish to become a father (S. J. Berg & Wynne-Edwards, 2001; Hirschenhauser, Frigerio, Grammer, & Magnusson, 2002). The testosterone of prospective fathers fluctuates with the ovulatory cycle of their mate (Hirschenhauser et al., 2002), presumably in response to their wife's heightened interest in sex around the time of ovulation and their mutual interest in becoming parents (see Chapter 7, this volume). Expectant fathers who respond to infant distress cues (e.g., crying) with concern and a desire to comfort the infant have higher prolactin concentrations and lower testosterone concentrations than do 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 concentrations and greater posttest reduction in testosterone" (Storey et al., 2000, p. 79). Higher paternal (and maternal) cortisol concentrations are also correlated with more attentive and sensitive parenting of newborns (Corter & Fleming, 1995).

The basic dynamic between men's testosterone concentrations and their relative focus on mating or on parenting is established, although variation among individual men in basal levels of these concentrations and other influences on their reproductive strategies are not fully understood (Gettler et al., 2019; P. B. Gray et al., 2017). Lower testosterone concentrations are sometimes associated with greater sensitivity to infant cries among men who are not fathers, suggesting that basal hormone concentrations may influence men's bias toward mating or parenting (A. S. Fleming et al., 2002). Men who respond to infant cues in a nurturing manner show declines in testosterone concentrations, but nonnurturing men show increases, indicating that other factors that are not well understood (e.g., personality, interest in marriage) influence how men's testosterone concentrations change in parenting contexts (van Anders et al., 2012). Men with lower testosterone concentrations are also more committed to their relationships and these relationships are less conflicted over time (van Anders et al., 2012).

The relationship between men's parenting and prolactin is also complex (P. B. Gray et al., 2017; Storey, Noseworthy, Delahunty, Halfyard, & McKay, 2011). For many men, separation from their children is associated with increasing prolactin concentrations that then decline once they engage with them. The pattern suggests that prolactin concentrations may motivate men to engage with their children (Storey & Ziegler, 2016). On average, men's prolactin concentrations appear to be more sensitive to developmental experiences (e.g., having younger siblings) and social context than do women's concentrations (Delahunty et al., 2007), perhaps reflecting the facultative nature of men's parenting.

Finally, infanticide risks may have contributed to the evolution and maintenance of male parenting in primates (Dunbar, 2018a; Opie et al., 2013). Although the relationships between men and their stepchildren are more conflicted than the relationships with their biological children (Daly & Wilson, 1988a; Flinn, 1988b), there is no systematic bias for stepfathers to commit infanticide (Nobes, Panagiotaki, & Russell Jonsson, 2019). The reason may be related to the earlier weaning from breastfeeding for humans (about 2 years old) than for gorillas or chimpanzees (about 4–5 years old), which reduces the benefits of infanticide (e.g., hastening females' ability to conceive). No doubt the social consequences, such as retaliation by the infants' kin and cooperation of the mother in the raising of the would-be perpetrators' children, also contributed to the evolutionary elimination of this bias. In any case, men should still be sensitive to threats to the well-being of their children and their testosterone concentrations should rise in these contexts to better enable them to address these threats (M. N. Muller, 2017). In the absence of these threats, testosterone concentrations are responsive to social context (e.g., mating opportunities, presence of children) and generally bias men toward seeking mates or investing in children, as is the case in other species (see Chapter 4, this volume).

Heritability of Men's Parenting

Much of the complexity of parental behavior can be captured by three core components: warmth toward children, negativity in the parent–child relationship (e.g., criticism, conflict), and degree of parental control (e.g., monitoring children's activities and friendships; Plomin, Reiss, Hetherington, & Howe, 1994). The parent–child relationship is influenced by the genes of the child and the parents. Children's genes contribute to behavioral differences (e.g., compliance) that can evoke differences in how parents treat them and are called *child-evocative effects* (Scarr & McCartney, 1983). Child-evocative effects on parents are moderately heritable—explaining between 23% and 40% of the variation in parents' behavior—and are larger for mothers than for fathers (Klahr & Burt, 2014). In other words, mothers' parenting is more sensitive to the individual characteristics of the child, whereas fathers' parenting is more sensitive to the general family environment (e.g., marital quality), consistent with the facultative expression of men's parenting.

Klahr and Burt's (2014) meta-analysis revealed moderate influences from parents' genes on parental warmth and negativity (explaining 27% to 38% of the variation in parents' behavior) and limited influences for parental control. Unlike child-evocative effects, the influence of parental genes on the parent–child relationship was similar for mothers and fathers, although this does not mean that the underlying influences (e.g., hormonal) are necessarily the same. In other words, variation among men and women in their investment in children, above and beyond child-evocative effects, is moderately heritable, but the underlying neurobiological systems differ in important ways.

These systems have been extensively studied in maternal mammals (Rosenblatt, 1994), and human mothers' parenting is influenced by some of the same, evolutionarily conserved systems, as well as by human-specific aspects of parenting (R. Feldman, 2016; Mileva-Seitz, Bakermans-Kranenburg, & van IJzendoorn, 2016). To be sure, there are similarities in the hormonal and brain systems underlying mothers' and fathers' engagement with children, but there are also some important differences (R. Feldman, Braun, & Champagne, 2019; Proverbio, 2017). For instance, there are heritable differences in how much parents' oxytocin (a neuropeptide that influences parental behavior and bonding with children) increases after a child is born. Both parents show these increases, but high oxytocin concentrations in mothers are associated with more affectionate care of their infant, whereas similar concentrations in fathers are associated with stimulating and arousing play with infants (I. Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010). In short, oxytocin increases engagement in sex-specific parenting behaviors. In reviewing a series of brain imaging studies of parents while they viewed images or film clips of their children, R. Feldman (2016) noted that there is

> greater amygdala activation [associated with emotions] in mothers and greater cortical activation in fathers, suggesting that the hormones of pregnancy may chart a unique limbic path to parenting in mothers, which in fathers is constructed via cortical networks and active caregiving behavior. (p. 12)

In other words, mothers' engagement with children is, at least initially, more strongly influenced by the same brain systems that promote parenting in other mammals. The brain systems influencing men's parenting is, in part, constructed during their engagement with their infants and children and eventually incorporates some of the same systems that contribute to mothers' parenting.

Heritable influences on personality may also affect marital quality and men's parenting (Belsky, 1984), independent of any evolved biases to engage in parenting. Mothers and fathers who are agreeable (e.g., cooperative) and open minded generally have warmer relationships with their children than do other parents, whereas emotionally negative and unstable parents tend not to have warm relationships with their children (Prinzie, Stams, Deković, Reijntjes, & Belsky, 2009). Although much remains to be determined, it appears that many of the heritable influences on parental behavior are largely independent of heritable influences on personality traits, with one exception

(Spinath & O'Connor, 2003): The relation between emotional negativity and lack of parental warmth appears to be influenced by some of the same genes. In any event, factors other than those that have directly evolved to promote parenting, maternal and paternal, can influence parent–child relationships.

Social Correlates

The quality of the marital relationship and men's social status are important social influences on the quantity and quality of men's investment in parenting and in the types of resources they invest.

Marital Relationship

Although the quality of the marital relationship can influence how both parents interact with their children (Belsky et al., 1984; S. Feldman, Nash, & Aschenbrenner, 1983; Lamb, Pleck, & Levine, 1986; J. P. McHale, Kuersten-Hogan, Lauretti, & Rasmussen, 2000), conflict undermines men's engagement with children more significantly than it does women's engagement (Krishnakumar & Buehler, 2000). A good marital relationship promotes men's engagement with children more significantly than it does women's engagement (Amato & Keith, 1991; M. J. Cox, Owen, Lewis, & Henderson, 1989). In short, "paternal parenting is more dependent on a supportive marital relationship than maternal parenting" (Parke, 1995, p. 37). Observational studies, for instance, reveal a significant sex difference in the relation between marital satisfaction and parental engagement with children (Belsky et al., 1984; S. Feldman et al., 1983). S. Feldman and colleagues concluded that "the quality of the marital dyad, whether reported by the husband or wife, is the one most consistently powerful predictor of paternal involvement [with his infant] and satisfaction [with the parenting role]" (p. 1634).

The same pattern is found for infants, children, and adolescents, across ethnicities, and for stepfathers and biological fathers (Planalp & Braungart-Rieker, 2016; Stevenson et al., 2014). The pattern is also found for unmarried, nonresident fathers (J. Fagan & Palkovitz, 2007, 2011). The latter are more engaged with their infants and children (e.g., visited more frequently) if they have a good relationship with the child's mother. The factors that contribute to men's disengagement with their children when in a conflicted marital relationship are not fully understood but include aspects of the marital dynamic and men's hormonal responses to conflict (Makhanova, McNulty, Eckel, Nikonova, & Maner, 2018; Stevenson et al., 2014). In the context of a conflicted relationship, women often become more critical and controlling of men's behavior, including how they engage with their children (e.g., caregiving, play). Maternal "gatekeeping" in turn is associated with reductions in men's engagement with children. Marital conflict also appears to increase men's (but not women's) testosterone concentrations (Makhanova et al., 2018). As discussed earlier, higher testosterone concentrations will reduce men's engagement in parenting and shift their focus to searching for a new mate.

Whatever is driving men's investment in parenting, the gist is that they invest more when in a satisfying relationship with their children's mother and disengage when this relationship is fraught with conflict. These relationships suggest that women's efforts to maintain an intimate and cooperative 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 less likely to incite conflict with their wives or seek extra-pair relationships than are other men, and that the relationship between marital satisfaction and paternal investment reflects genetic as well as social effects (K. MacDonald, 1997). Even so, the marital dynamic is important and predicts aspects of the facultative expression of men's parenting (e.g., Planalp & Braungart-Rieker, 2016; Stevenson et al., 2014).

Social Status

The extent to which fathers are directly engaged in parenting is also related to the nature of their work and their 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 and older children than are fathers in lower status occupations (S. Feldman et al., 1983; Strazdins, Baxter, & Li, 2017). Lamb et al. (1986) suggested there is a trade-off between family involvement and commitment to work. In comparison with 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 relationship between a man's success in culturally important endeavors and caretaking of children has been found for the Aka and the Ache (Hewlett, 1988; K. Hill & Hurtado, 1996; K. Hill & Kaplan, 1988). High-status Aka men are those with large kin networks and therefore high hunting success. These men hold their infants less than half as much as men with few kin. The latter men must therefore hunt either alone or with their wife and are generally less successful hunters as a result. The less direct care provided by 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). As fathers' efforts to obtain income through a job or meat through hunting increase, direct caretaking of children often decreases. It is not clear, however, whether efforts to obtain more income or other indicators of cultural success are components of paternal investment (e.g., gaining resources that will be invested in children) or if they are components of mating effort. It is probably more strongly related to parenting in monogamous societies and mating effort in polygynous ones.

Developmental Correlates

There is a modest, yet reliable cross-generational continuity in parenting behaviors and levels of parental investment. Children who experience generally supportive or harsh parenting while growing up tend to show the same parenting style with their own children (Conger, Belsky, & Capaldi, 2009). Given the heritability of parenting behaviors, some of this continuity is likely related to the genes shared between parents and children (Klahr & Burt, 2014), but this does not seem to be the whole story. Harsh or supportive parenting can influence children's developing social competencies that in turn influence the quality of their later relationships (e.g., Neppl, Conger, Scaramella, & Ontai, 2009). In evolutionary context, these early social experiences are thought to influence men's developmental trajectory toward a later focus on mating or on parenting, although they are certainly not the only influence on their reproductive strategy (Belsky et al., 1991; Chisholm et al., 1993; Draper & Harpending, 1982; B. J. Ellis, 2013; B J. Ellis & Del Giudice, 2019).

The basic idea is that parents who are exposed to harsh social and ecological stressors (e.g., high conflict, high mortality risks) are less responsive to their children and generally develop a more conflicted parent–child relationship, whereas parents with abundant resources and low social stress are more engaged with their children and develop a more supportive parent–child relationship. These relationship patterns are thought to bias the nature of children's relationships outside of the family. The mechanisms that might link the form of parent–child relationship to later reproductive strategy have been elaborated on by Del Giudice and Belsky (2010; see also Del Giudice, 2009, 2014, 2015). By middle childhood, low-attentive and conflicted parent–child relationships are associated with heightened risk of ambivalent (e.g., emotionally insecure, dependent) attachment styles in girls and avoidant (e.g., emotionally distant) styles in boys; these styles continue into adolescence and adulthood. Del Giudice (2009) proposed that the emergence of these sex differences is triggered by earlier adrenarche, which in turn is associated with heightened parent–parent and parent–child conflict (B. J. Ellis & Essex, 2007). An ambivalent style is hypothesized to result in behaviors that facilitate gaining resources from others, including the women's spouses. An avoidant style may facilitate later male–male competition—often related to polygyny and higher mortality (see Chapter 8, this volume)—and result in an emotionally distant, exploitative view of social and sexual relationships.

Most of the tests of these predictions have focused on the correlates of an early conflicted home life and stressors and risks in the wider community (Bereczkei & Csanaky, 2001; B. J. Ellis, 2004; Quinlan, 2007). As reviewed by Del Giudice (2009), the avoidant attachment style is associated with 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. M. Wilson and Daly (1997) found age of first reproduction, number of children born per woman, mortality risks, and local resource availability were all interrelated in modern-day 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 (54 years vs. 77 years) comparing the least and most affluent neighborhoods. A shorter lifespan, in turn, was associated with earlier age of first reproduction for men and women and nearly twice as many children born 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—shifting to a faster pace of life (see Chapter 4, Figure 4.2, this volume)—to early and continuing stressors (e.g., high mortality rates), or at least a response to the perception that the future is uncertain and not likely to bring a better life (J. N. Davis & Werre, 2008).

In samples of Ache and Mayan (Central America) men, Waynforth, Hurtado, and Hill (1998) 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" (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. Other critiques have focused on the tendency for other species, and at times humans, to delay reproduction and reduce parental investment when resources are particularly scarce (Davies, Krebs, & West, 2012; K. MacDonald, 1997). But, with intermediate levels of mortality risk and fluctuating resource availability, investment in more rather than fewer offspring is assumed to ensure that at least some of these offspring will survive to adulthood (Chisholm et al., 1993). Investing limited resources in a few offspring might improve their social competitiveness, but if mortality risks are high such an investment is very risky.

The final word on these issues remains to be heard. The relationships between early family stressors, an increased risk of insecure attachment, and an early onset of adrenarche in both sexes represent plausible mechanisms linking parent–child relationships to later reproductive strategy, including the quality of their marriage and associated influences on parenting. For men, an insecure relationship with one or both parents appears to result in increased risk of detached, exploitative social relationships in adulthood, including sexual relationships, and lower investment in parenting (Del Giudice, 2009). Long-term studies that control for heritable influences and that measure all hypothesized mechanisms (e.g., parent–child attachment), as well as mortality risks and the sources of these risks during development, are needed to firmly establish causal relations between early developmental experiences and later reproductive activities (see Nettle, 2010; R. Walker et al., 2006).

Cultural and Ecological Correlates

The quantity and nature (e.g., direct care or provisioning) of men's investment in parenting or mating are also influenced by wider cultural and ecological factors. These factors include whether or not monogamy is socially imposed (i.e., it is illegal to have more than one spouse at a time); subsistence activities (e.g., foraging, agriculture); and the operational sex ratio (OSR; Draper & Harpending, 1988; Henrich, Boyd, & Richerson, 2012; Konner, 2010; Marlowe, 2000; Ross et al., 2018; Schacht, Davis, & Kramer, 2018). Draper and Harpending (1988) proposed a very useful way of organizing some of these influences under the umbrellas of father-absent societies and father-present societies, described next. The second part of this section describes how fluctuations in the OSR can influence men's focus on mating or on parenting.

Father-Absent and Father-Present Societies

Father-absent and father-present societies in this context do not refer to the absence or presence of paternal investment per se, but rather the nature of the marital and father–child relationships and the contextual factors that influence them.

Father-absent. These societies are characterized by aloof husband–wife relationships, a polygynous marriage system, local raiding and warfare, male social displays (verbal and with ornamentation), and little or inconsistent direct paternal investment in children (Draper & Harpending, 1988; Konner, 2010; Marlowe, 2000; M. M. West & Konner, 1976). These conditions "are particularly prevalent in so-called middle-range societies, i.e., those where agriculture is practiced at a very low level" (Draper & Harpending, 1988, p. 349) and in resource-rich ecologies. In the latter, women and their kin (e.g., through access to land provided by their husband) can often provide adequate care to their children (e.g., through small-scale agriculture) without substantial direct contributions from the father (Draper, 1989; Sellen, Borgerhoff Mulder, & Sieff, 2000). If men are able to accumulate resources beyond what is needed to attract and support a single wife and her children and they live in a society that allows polygyny, they have the option of investing these additional resources in their existing children or in finding a second or third wife. Most men opt for the latter.

In these societies, men compete with each other for the establishment of social dominance or for the control of the material resources (e.g., land, animal herds) that women need to raise their children (Borgerhoff Mulder, 1990; Marlowe, 2000). The achievement of social or economic dominance, in turn, influences the number of women the man can marry (Chagnon, 1988; Irons, 1993). Given this, the investment of "excess wealth" in mating effort is often a successful reproductive strategy for men, sometimes at a cost to their existing wives (see Chapter 8, this volume). An example is provided by Borgerhoff Mulder's (2000) analysis of the reproductive strategies of Kipsigis (Kenya) men and women. In this pastoral society, men are allowed to marry as many women as they can support. The resource they need to support one or more wives is the land controlled by their male-dominated kin-group. When men marry, they provide their wife (or wives) and their children a specific amount of land, which is then used for small-scale agricultural production. The land will be inherited by their sons, who, in turn, will use it in their attempts to marry. Social custom dictates that the land is to be divided evenly among sons. If a woman has too many sons, then none of these men will have enough land to marry and reproduce.

Borgerhoff Mulder (2000) confirmed that the optimal reproductive strategy for women, as indexed by the number of surviving grandchildren, is to invest in a smaller number of sons (i.e., to have fewer children than their biological potential). Women who had fewer children than their land could support had more surviving grandchildren than did women who had as many children as their land could support. By having fewer children, each of their sons inherited proportionately more land and was better able to attract wives. Men in this society are also faced with complex reproductive decisions. If they marry as many women as they can support and maximize the quantity of children, then each of their sons will inherit less land than if they married fewer women. Despite this potential cost, most men married as many women as they could support at the time. Strassmann (2000) reported a similar strategy among Dogon men (Mali). In other words, these men invested their wealth in mating effort rather than parental effort.

Father-present. Father-present societies tend to be found in harsh or unstable ecologies and in developed, or other relatively large, stratified societies (Draper & Harpending, 1988; Ross et al., 2018). These are societies that are sometimes characterized by ecologically or socially imposed monogamy (Flinn & Low, 1986). Under harsh ecological conditions, the vast majority of men are unable to acquire the resources (e.g., meat obtained through hunting) needed to support more than one wife and family. The reproductive aspirations of most men are thus ecologically restricted to monogamy. This is because high levels of paternal investment are often necessary to ensure the survival of his children and because these ecologies limit the ability to accumulate excess wealth and limit mating opportunities.

In most developed nations, monogamy is socially imposed with formal laws that prohibit polygynous marriages. The historical dynamics that led to the cultural evolution of socially imposed monogamy are not fully understood but likely included a social strategy to increase cooperation among men that in turn increased community cohesion and stability and provided a competitive advantage by increasing the size of male coalitions (e.g., R. D. Alexander, Hoogland, Howard, Noonan, & Sherman, 1979; Eibl-Eibesfeldt, 1989; Henrich et al., 2012; Ross et al., 2018). Scheidel's (2017) sweeping overview of world economic history as related to wealth inequality supports this view. Large-scale wars and other external threats (among other things) are associated with wealth redistribution, whereby wealthy men transfer resources to other men to secure their cooperation in dealing with the threat. Although Scheidel focused on material wealth, the same dynamics—external threat and reduced inequality to increase ingroup cooperation—almost certainly extend to reproductive inequality, a reduction in polygyny and eventually legally imposed monogamy (Herlihy, 1995). In addition to increasing community cohesion and reducing violence and crime within communities, socially imposed monogamy suppresses men's mating effort and frees resources to invest in parenting.

Individual differences. The descriptions of father-absent and father-present societies do not capture variation within these societies. Even though direct paternal investment tends to be lower in cultures that allow polygynous marriages, most of the men (>80%) in most of these societies are monogamously married (Murdock, 1981; Ross et al., 2018). It is nevertheless common for these monogamously married men to divert social and material resources from the family in attempts to attract a second wife (Hames, 1992, 1996). Many men engage in polygynous relationships in monogamous societies through serial marriages or affairs, often to their reproductive benefit. In an extensive study of more than 900 Swedish women and men over the age of 40 years, Forsberg and Tullberg (1995) found that men, but not women, who engaged in serial monogamy had more children than their peers who stayed monogamously married.

Under some conditions, high-status polygynously married men are able to invest more material and social resources in their many children than are lower status and monogamously married men. On the Ifaluk islands in the Western Pacific, chiefs tend to have more wives (serial monogamy in this case) and children than lower status men but spend twice as much time with their children as these lower status men (Betzig & Turke, 1992). This is possible because high-ranking men receive tributes from other families and receive relatively more food from communal fishing than do low-ranking men. The net result is that chiefs spend less time working and have more material resources and time to invest in their children.

Operational Sex Ratio

As with the males of other species (see Chapter 3, this volume), the OSR influences men's relative investment in mating or in parenting (Grosjean & Brooks, 2017; Guttentag & Secord, 1983; Pollet & Nettle, 2008; Uggla & Andersson, 2018). The OSR is determined by sex differences in birth rates, death rates, and migration patterns, and essentially influences the supply-and-demand dynamics of romantic and sexual relationships. When there are fewer men than women looking for partners, men are better able to express their preferences, and vice versa when there are fewer women than men looking for partners:

> Sex ratios by themselves do not bring about societal effects, but rather that they combine with a variety of other social, economic, and political conditions to produce the consequent effects on the roles of men and women and the relationship between them. (Guttentag & Secord, 1983, p. 137)

In developed nations, for instance, expanding populations result in more women than men looking for partners, 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. Similarly, with a contracting population (e.g., because of lower birth rates), women will be competing for marriage partners from a larger cohort of older men.

The resulting imbalance in the numbers of men and women is correlated with changes in divorce rates, sexual mores, and levels of paternal investment (Guttentag & Secord, 1983). During periods when there are more women than men looking for partners (e.g., from 1965 through the 1970s in the United States), men's mating opportunities increase and their investment in marriage and parenting decrease. These historical periods are generally characterized by liberal sexual mores (i.e., many sexual partners for men and women), 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 women's participation in the workforce, and generally lower levels of paternal investment (Guttentag & Secord, 1983). The bottom line is that during these periods men are better able to express their preference for a variety of sexual partners and relatively low levels of parental investment (F. A. Pedersen, 1991), although Uggla and Mace (2017) found that highly educated men who are married to desirable women invest in parenting independent of the OSR.

In any case, a different pattern emerges when there are too many men (Guttentag & Secord, 1983). Here, women are better able to enforce their preference for a monogamous, high-investment spouse. As a result, these periods are generally characterized by an increase in the level of men's commitment to marriage, as indexed by declining divorce rates and greater levels of paternal investment (F. A. Pedersen, 1991). Pollet and Nettle (2008) illustrated this relation with demographic and marriage data from the 1910 U.S. population. During this historical period, more men than women migrated to the western United States, resulting in large across-state differences in the OSR. In all states, wealthier men were more likely to marry than were other men, but the strength of this relation increased dramatically as the sex ratio became unbalanced. When there were too many men, women demanded more, in terms of wealth, before they would marry. In states with a balanced OSR, a man with a somewhat below average amount of wealth had a 56% chance of marrying by age 30, and a man with a somewhat above average amount of wealth had a 60% chance. For states in which there were 110 men to every 100 women, the chance of marrying by age 30 declined for men in both of these wealth categories, but much more dramatically for below average men. These men had a 24% chance of marrying by age 30, as compared with 46% for their wealthier peers. With an excess number of men, women demanded more resources from men and got them.

Hurtado and Hill (1992) found that the OSR influences men's focus on mating or parenting in the Ache and the Hiwi (Venezuela). Ache men live in a social environment that provides many mating opportunities (because of high male mortality and thus fewer men), whereas having more men than women greatly restricts Hiwi men's mating opportunities:

> Differences in levels of mating opportunities between the Ache and the Hiwi occur alongside marked contrasts in marital stability. Whereas serial monogamy and extramarital promiscuity are very common among the Ache, stable lifetime monogamous unions with almost no extramarital copulation is the normative mating pattern among the Hiwi. (Hurtado & Hill, 1992, p. 40)

These patterns are found despite high infant and child mortality risks associated with paternal abandonment with the Ache, and low risks with the Hiwi. These same patterns have been documented among the !Kung and Hadza (Blurton Jones et al., 2000), and the Makushi (Guyana; Schacht & Borgerhoff Mulder, 2015). The overall pattern indicates that the reproductive strategy of some men is more strongly influenced by mating opportunities than by child mortality risks.

CONCLUSION

In the broader context of mammalian reproduction, it is unremarkable that mothers throughout the world show a much greater availability for and engagement with their children than do fathers (Whiting & Edwards, 1988). As reviewed in Chapter 3 of this volume, this is because the biology of mammalian reproduction results in higher levels of maternal than paternal investment and creates a faster potential rate of reproduction for males than for females. For the vast majority of species with this reproductive biology, females are focused on parental effort and males on mating effort (Trivers, 1972). Given this pattern, the most remarkable feature of human reproduction is that many fathers show some degree of direct (e.g., childcare) and indirect (e.g., monetary) 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 with the little paternal care found in the two species most closely related to humans and in terms of the more general pattern found with mammals (Clutton-Brock, 1989; Whitten, 1987). Men's investment is nevertheless consistent with paternal protection of and engagement with infants in gorilla families and may have a long evolutionary history if the family relationships of our ancestors were similar to those found in gorillas (Geary & Flinn, 2001).

Whatever the evolutionary backdrop, men's investment in their children reflects the same cost–benefit trade-offs found with facultative paternal investment in other species (see Chapter 4, Exhibit 4.1, this volume). The benefits of paternal investment include reductions in infant and child mortality rates, at least in some contexts, and improvements in children's later ability to compete for essential social and material resources (A. Reid, 1997; Scelza, 2010). As found with other species with high levels of paternal investment, men's parenting is associated with high (>95%) levels of paternity certainty, especially for higher status men.

The facultative expression of men's parenting is correlated with many factors, including hormonal profile, heritable individual differences, the quality of the spousal relationship, and child characteristics (A. S. Fleming et al., 2002; P. B. Gray et al., 2017; Klahr & Burt, 2014). The nature of the parent–child attachment and the level of parent–parent conflict in the family of origin may also influence later investment in parenting or mating by biasing the nature of the child's later relationships outside of the family (Belsky et al., 1991). Conflict at home and harsh parenting are associated with aggressive and emotionally distant relationships in boys and men and a focus on short-term sexual relationships rather than parenting (Del Giudice, 2009). 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 rather than focusing on mating (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.

7

Choosing Mates

The benefits of men's investment in parenting come with the cost of greatly complicating the dynamics of sexual and romantic relationships. When men invest in children and especially in societies with socially imposed monogamy, they become choosier when it comes to mates, and in these situations, women have to compete more intensely to develop and maintain relationships with the men who have the most to offer. On top of the standard male–male competition and female choice components of sexual selection, male choice and female–female competition are central features of human reproductive dynamics. Chapter 8 of this volume reviews the dynamics of male–male and female–female competition, and focus of this chapter is on how and why women and men are selective in their mate choices. Female and male choice follow from the relation between parenting and choosiness described in Chapter 3. At the same time, the sex differences in the quantity and forms (e.g., pregnancy) of investment in children result in different cost–benefit trade-offs for women and men when it comes to mates. The trade-offs shown in Table 7.1 provide a framework for thinking about the costs and benefits of short-term and long-term sexual relationships for women and men.

The most fundamental sex difference is that the cost of reproduction is higher for women than it is for men because of pregnancy and the sex differences in postnatal parental investment. It is not surprising that women are more careful than men in their mate choices for short-term and long-term relationships. Women, in fact, generally avoid short-term relationships, because the potential costs will typically outweigh the potential benefits, although

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TABLE 7.1. Potential Costs and Benefits of Short-Term and Long-Term Mate Choices

Mate choices	Costs	Benefits
Women's short-term mating	Risk of STI Risk of pregnancy Reduced value as a long-term mate	Some resources from mate Good genes from mate
Women's long-term mating	Restricted sexual opportunity Sexual obligation to mate	Significant resources from mate Paternal investment
Men's short-term mating	Risk of STI Some resource investment	Potential to reproduce No parental investment
Men's long-term mating	Restricted sexual opportunity Heavy parental investment Heavy relationship investment	Increased paternity certainty Improved social competitiveness of children Sexual and social companionship

Note. STI = sexually transmitted infection. From "Evolution of Human Mate Choice," by D. C. Geary, J. Vigil, and J. Byrd-Craven, 2004, *Journal of Sex Research*, *41*, p. 29. Copyright 2004 by Taylor and Francis. Adapted with permission.

these types of relationships do occur. Men's preferences are different because the potential benefits of short-term relationships will often outweigh the potential costs. When men do commit to a long-term relationship, their level of choosiness increases because of the costs of parental care and lost mating opportunities. Before the details of women's and men's mate preferences and choices are discussed, this chapter first provides a primer on marriage systems. A consideration of a culture's marriage system is essential, because this influences who people can and cannot marry and often places constraints on the realization of men's and women's preferences for one spouse or another.

MARRIAGE SYSTEMS

Chapter 5 of this volume argued that a gorilla-like family structure emerged during hominin evolution; specifically, a male and one or several females and their offspring embedded in a larger male-biased kin-group. Although this is indeed a common form of family constellation across cultures (D. E. Brown, 1991; Pasternak, Ember, & Ember, 1997), the unpredictable nature of social dynamics and variation in the ecologies and cultures in which families are situated result in a mix of marriage systems and family types (Murdock, 1981). Recall, for other species the most common forms of mating system (see Chapter 3, Table 3.1, this volume) include polygyny, polyandry, and monogamy (R. D. Alexander, Hoogland, Howard, Noonan, & Sherman, 1979). Each of these forms of marriage is found in humans, although to varying degrees, as described in Table 7.2.

The social and ecological conditions that account for this variation are not fully understood, but there are some general patterns (Flinn & Low, 1986;

TABLE 7.2. Marriage Patterns and Family Formation

Marriage	System variations
Polygyny	1. Resource-based polygyny: In resource-rich environments and cultures in which polygyny is not legally prohibited, male kin-based coalitions compete for control of these resources (e.g., land, cows) and dominant men in successful coalitions marry polygynously. A common family structure is a husband who lives separately (e.g., in a different hut) from his wives and their children (e.g., Draper, 1989; Borgerhoff Mulder, 1990). 2. Social-power polygyny: In ecologies in which resources are abundant but not easily controlled by coalitions and in which polygyny is not prohibited, male kin-based coalitions compete for social dominance and power (e.g., through warfare). Dominant men in successful coalitions marry polygynously. A common family structure is a husband, two or three wives and their children (e.g., Chagnon, 1988). Family units consisting of a husband, wife, and their children are common as well (e.g., Hames, 1996).
Polyandry	1. Fraternal polyandry: Although rare, in societies in which land is of low fertility and yields poor crops, families tend not to divide inherited land (E. A. Smith, 1998). In these societies, brothers share the land, which can only support a small number of children, and marry polyandrously. In these cases, the family consists of two husbands, one wife, and their children. If one brother acquires additional wealth, he will often marry another woman, who does not become the wife of his brother.
Monogamy	1. Ecologically imposed monogamy: In environments with sparse and widely distributed food sources, high levels of maternal and paternal investment are needed to successfully raise offspring, and polygyny is rare. Monogamy and family units that consist of a husband, wife, and their children are common (Flinn & Low, 1986). 2. Socially imposed monogamy: Legal prohibition of polygamy in Western culture suppresses the male tendency to form polygynous marriages in resource-rich ecologies. Monogamy and family units consisting of a husband, wife, and their children are more common than would otherwise be the case. Serial monogamy and single-parent (typically mother) families are also common in these societies. 3. Serial monogamy: In resource-rich ecologies with socially imposed monogamy, men and women often have a series of legal marriages, although this pattern is sometimes found in other cultures as well (e.g., K. Hill & Hurtado, 1996). Men, but not women, who marry serially have, on average, more children than do men who stay monogamously married to one person (Buckle et al., 1996; Forsberg & Tullberg, 1995).

Note. From "Evolution of Human Parental Behavior and the Human Family," by D. C. Geary and M. V. Flinn, 2001, *Parenting: Science and Practice*, *1*, p. 33. Copyright 2001 by Taylor and Francis. Adapted with permission.

Marlowe, 2003). The key ecological variables include the number of pathogens (e.g., parasitic worms) and disease risk and the quantity, type, and distribution of food and other material resources, as well as whether these resources (e.g., cows) can be monopolized by male kin-based coalitions (e.g., sparse hunted game). The key social variables include the rules for marriage, the extent of intragroup competition and warfare (e.g., raiding nearby villages), paternity certainty, and the extent to which individual males provision their families (vs. sharing hunting gains; Marlowe, 2003; D. R. White et al., 1988; D. R. White & Burton, 1988). The vast majority (about 85%) of traditional societies have marriage rules that allow polygynous or polyandrous unions, although the former is many times more common than the latter (Murdock, 1981). In these societies, coalitions of related men often cooperate to gain access to and maintain control of the resources women need to rear their children or to control reproduction-related social dynamics. Control of material resources (e.g., land, cattle) results in resource-based polygyny (Borgerhoff Mulder, 1990), whereas control of social dynamics results in social-power polygyny (Chagnon, 1988).

The material and social resources that are controlled by kin-based coalitions are not simply related to these men's mating efforts; they are oftentimes used to influence the social and reproductive relationships of their children (Chagnon, Lynch, Shenk, Hames, & Flinn, 2017). With resource-based polygyny, younger men in the coalitions are often dependent on the wealth of their father, uncles, and other relatives to pay the brideprice needed to marry (e.g., cattle paid to the prospective bride's parents; e.g., Borgerhoff Mulder, 2000). At the same time, a young woman's parents and other relatives will often use their wealth and social power to facilitate her marriage to a wealthy or socially powerful man and kin-group, and to influence her treatment by the man and his kin after she has married. A similar pattern is found with social-power polygyny, whereby men's coalitions engage in negotiations to influence the reproductive prospects of their sons and daughters. In both forms of marriage system, women almost always marry, either into monogamous or polygynous unions (Hartung et al., 1982). High status men (10%–20% of men) typically have several wives, other men marry monogamously, and some men never marry (Marlowe, 2003; Murdock, 1981). Polyandry is a common form of marriage in less than 1% of human societies and is also related to resource control (E. A. Smith, 1998).

Monogamous marriages and families consisting of a husband, wife, and their children who reside in the same household are common in societies in which monogamy is ecologically or socially imposed, as reviewed in Chapter 6 of this volume. The result is the suppression of polygynous marriages in higher status men, although serial monogamy is common in these societies, as are single-parent families (typically headed by mothers and aided by maternal kin). These societies are also unusual in that nuclear families are often physically isolated from the wider kin network, although kin are still a source of social and economic support; this isolation is more common in the professional classes, where jobs often require moving away from kin (Argyle, 1994). In many societies with socially imposed monogamy, kin-based negotiations for marriage partners are uncommon, but intergenerational transfer of wealth from parents to children, as related to children's later marriage prospects or the well-being of the donor's grandchildren, is common (Gaulin & Boster, 1990).

Men and women are involved in family formation and parental investment, but the dynamics of these vary across different physical and social ecologies (see Chapter 6, this volume). When it is not prohibited, men attempt to acquire the resources needed to marry polygynously but must do so through cooperation with their male kin and often through the cooperation of prospective brides (e.g., Chagnon, 2013). The combination of male coalitions, their status within the coalition, and the distribution of resources in the wider ecology influences men's reproductive strategies and patterns of family formation, spousal warmth, paternal investment, and men's and women's mate choices. In some cultures, women are able to influence these patterns, from attempting to bias men's negotiations for marriage of their daughters (e.g., Borgerhoff Mulder, 1990) to negotiating the nature of the spousal relationship. In other cultures, the mate choices of men but especially women are constrained because their spouses are often chosen by their parents or other kin (Apostolou, 2007). As described elsewhere (Geary, 2005) and reviewed in Chapter 9 of this volume, all of these dynamics are variations on the same theme—humans form complex kinship and friendship networks that cooperate to control social dynamics and to gain access to resources in the wider community.

WOMEN'S MATE CHOICES

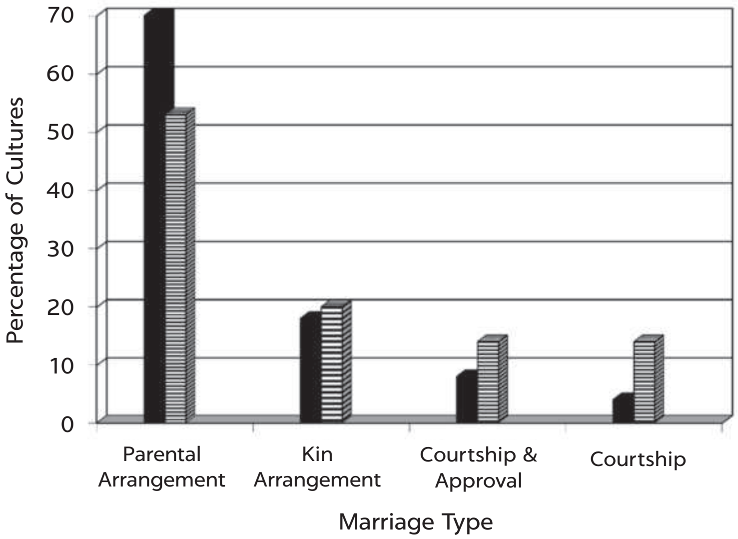
In terms of evolutionary logic (i.e., the best reproductive interests of women), an ideal situation for women is to be monogamously married to a long-term partner who has good genes (e.g., looks healthy, handsome), social influence, and material resources (B. S. Low, 2000). Importantly, any such prospective husband has to be willing to invest in her and her children. Indeed, women prefer marriage to men who are culturally successful, who have social influence and control of material resources that are important in the current context (Irons, 1979), and who will invest the rewards of this success in her and her children. Putting one's preferences into practice, however, is more easily said than done. The above described cultural and ecological influences on marriage systems place constraints on women's and men's mate choices, as do the competing interests of kin (e.g., parents). The section will first describe the ubiquity of kin influences on marriage and the importance of men's cultural success when women and their kin choose the woman's marriage partner. This section will then review research on the behavioral and physical traits that women prefer in prospective partners and closes with a discussion of women's alternative mating strategies.

Who Chooses Whom?

Unlike other primates who typically go their own way when choosing mates, humans' mate choices are embedded in an often-complex network of kin and wider social relationships that can place significant constraints on these choices (Chagnon et al., 2017; Chapais, 2009). The complexity of these choices is illustrated by Apostolou's (2007) study of marriage types across 190 hunter–gatherer societies. The marriages were classified into four categories based on who made the decision: parental arrangement, kin arrangement (e.g., brother, uncle), courtship with parental approval, and free-choice courtship. Each society was classified in terms of its most common or primary marriage type and whether or not any of the other marriage types occurred; these were classified as secondary. Figure 7.1 shows that parents arranged most of the marriages in 70% of these societies and free-choice courtship was the primary marriage type in only 4% of them. Courtship with parental approval was a secondary marriage type in 14% of the societies. Unconstrained mate choices (primary or secondary) were not reported for 4 out of 5 of the hunter–gatherer societies. Even stronger parental or wider kin influence on mate choices is found for agricultural and pastoral communities (Apostolou, 2010). Across societies, men (usually the father) typically exert more influence on mate choices than women, and daughters typically have less choice than sons. The latter occurs in part because daughters are married or parents agree on a marriage partner when daughters are younger (often 12 to 15 years of age) and are more dependent on parents than are sons.

Apostolou's (2012) analysis of the historical record dating back 5,000 years reveals essentially the same pattern of parental influence, especially that of fathers, on their children's marriage choices. Again, there was a stronger influence on daughters' than sons' marriage partners. Among the more consistent criteria for a prospective spouse was his (or her) family's social background and status, consistent with marital relationships being used as a way to form alliances with other families or groups (Chagnon et al., 2017; Chapais, 2009). A phylogenetic analysis (estimating evolutionary and historical relatedness) on the basis of mitochondrial DNA (inherited exclusively from

FIGURE 7.1. Primary and Secondary Marriage Types in Hunter–Gatherer Societies



Primary (solid line) refers to the most common way in which marriage partners are chosen and secondary (striped line) refers to whether or not an alternative type occurs. Data from Apostolou (2007).

the mother) and the ethnographic record of relations among traditional groups suggested that the practice of kin influences on marriage choices may date back as far as 50,000 years (R. S. Walker, Hill, Flinn, & Ellsworth, 2011). The pattern is consistent with a parental influence on the evolution of mate choices, such that individuals, especially prospective grooms, from socially influential or wealthy families have had a mating advantage (e.g., more choice of brides), independent of their personal traits (e.g., healthy immune system; Apostolou, 2016).

Conflicts of interest between parents and their children over a prospective spouse are common, because the costs and benefits of these marriages can differ for parents and children (Chagnon et al., 2017). Conflicts between women and their parents or other kin over marriage partners are especially evident in societies where young women are an economic asset to their families. These are societies in which brideprice (i.e., material resources) or brideservice (i.e., labor) are required of prospective suitors. In an analysis of the dynamics of marriage across 860 societies, Daly and Wilson (1983) found that the bride's kin required a substantial brideprice or brideservice in 500 (58%) of them and a less substantial brideprice in 53 others. In another 27 societies, men from different kin-groups often acquire wives through a direct exchange of daughters, circumventing female choice. In keeping with Apostolou's (2007, 2010) analyses, woman's marriage preferences were relatively unencumbered by the priorities of her kin in less than 1 in 4 societies, and these were typically in modern, developed nations.

Even in societies in which women and men are relatively free to choose their own spouses, kin monitor the romantic relationships of their children and often attempt to influence their marriage choices (Faulkner & Schaller, 2007; Flinn, 1988b). Despite the influence of parents and other kin on mate choices, there are ways in which women and men can express their own preferences. These include extramarital affairs, running away from a marriage partner and refusing to cooperate with the arrangement, and divorce and remarriage (Apostolou, 2010; Scelza, 2011). For the latter, parents' influence wanes as adolescents grow into adulthood and, as a result, they have less influence on their children's second marriages.

Culturally Successful Men

All else being equal, female primates prefer sexual and oftentimes longer term relationships with dominant males and males that can provide them with some type of direct benefit (e.g., social protection; see Chapter 5, this volume). The same is true for humans, although the consistency of these advantages is not always obvious when examined across cultures. This is because men's dominance and status can be achieved in different ways from one culture to the next (Irons, 1979). Whatever the context, culturally successful men are preferred as marriage partners by women and their kin. These men wield social influence and often have control over more reproductively useful resources than do other men. Women's marriage and mating preferences indicate they are motivated to capture and use these resources for their own reproductive ends.

Few women (or men) always get what they want, because of the competing interests of kin, competition with other women over desirable mates, and men's mate preferences. This does not mean that preferences, as are often measured in psychological studies, do not provide useful information about the evolution of human mate choices. As described in Chapter 9 of this volume, these preferences are components of mental representations of the "perfect world." This is a world in which one has social influence and control of culturally important resources. The fantasized world provides a goal to be achieved and the associated components of these fantasies provide a window through which we can see the types of resources that improved social and reproductive prospects during human evolution. In short, preferences and fantasies provide a glimpse into evolutionarily salient motivations and desires that are not constrained by the competing interests of others, but first let us consider actual mate choices.

Actual Choices

The marriage patterns of the Kipsigis (Kenya) provide an example of how kin can influence women's actual mate choices and the benefits of marrying a culturally successful man (Borgerhoff Mulder, 1990, 2000). As is common in many traditional societies, choice of marriage partners is made by the young woman's parents. In most cases, however, the parents' decision is influenced by their daughters' preferences. These joint decisions are strongly influenced by the amount of land made available to her and her future children. Land and cattle are controlled by men and gaining access to them has important reproductive consequences for women:

> Land access is correlated with women's reproductive success, and may be an important causal factor contributing to reproductive differentials, given the greater availability of food in the homes of "richer" women and the lower incidence of illness among them and their offspring. (Borgerhoff Mulder, 1990, p. 256)

The benefits continue to the next generation. Land is divided among her sons who eventually use it to attract wives (see Chapter 6, this volume). As a result, women who gain access to large land plots (through marriage) have more surviving grandchildren than do women with small plots (Borgerhoff Mulder, 2000). Given these relationships, it is not surprising that across an 18-year period, Borgerhoff Mulder (1990) found that the two men offering the most land were chosen as husbands by 13 of 29 brides and their families, and either one or both of these men were married in 11 of the 15 years in which one or more marriages occurred. The two lowest ranking men were chosen as husbands in only 1 of these 15 years. The pattern clearly follows the evolutionary prediction that women and their parents prefer culturally successful men as marriage partners, because these men provide the resources women need to keep their children alive and healthy.

Among hunter–gatherers, good hunters are higher status, more physically fit, and their children have lower mortality risks compared with those of less-skilled hunters (Apicella, 2014; Hawkes, O'Connell, & Blurton Jones, 2001; K. Hill & Hurtado, 1996; E. A. Smith, 2004; Wiessner, 2002). These men are desirable mates despite sharing the proceeds of successful hunts with other families in their group. Even with sharing, the families of successful hunters often receive more meat or higher quality meat than do other families (B. M. Wood & Marlowe, 2013). In addition to providing meat, Marlowe (2003) found that good Hadza (Tanzania) hunters were also more successful than were other men at locating and securing honey and other resources and are better able to compensate for their wife's reduced foraging while she is pregnant or nursing. In contexts with intense male–male competition, successful warriors are desirable mates and provide social resources (e.g., protection) to their wives and children (Chagnon, 2013; Escasa, Gray, & Patton, 2010).

More generally, a woman's decision to stay married or not is influenced by the quantity and quality of resources provided by her husband (Betzig, 1989; Buckle, Gallup, & Rodd, 1996). In the most extensive cross-cultural study of the pattern of marital dissolution, Betzig (1989) found that "inadequate support is reported as cause for divorce in 21 societies and ascribed exclusively to the husband in all but one unspecified case" (p. 664). The overall pattern clearly shows that women and their parents who are arranging marriages prefer men who are able to provide the forms of social and material resources needed to support reproduction in the local context.

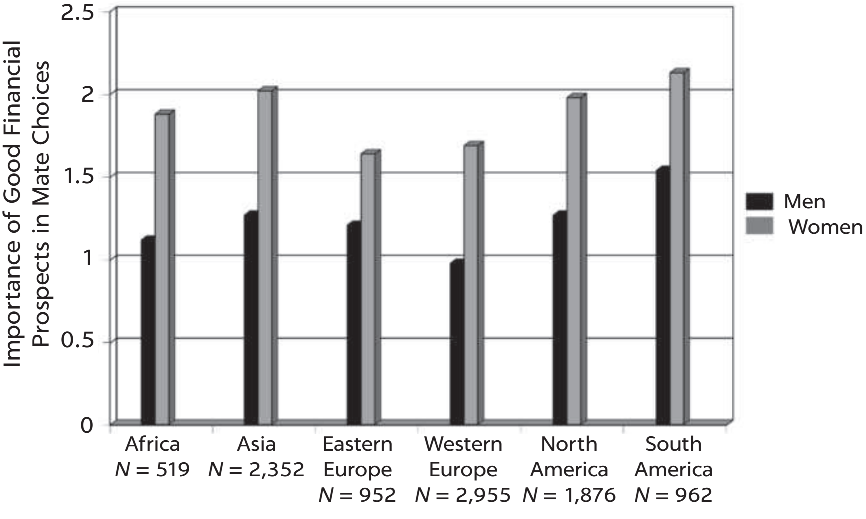
Preferred Choices

A woman's preferred marriage partner and her actual marriage partner are not typically the same, because preferences cannot always be put into practice. The gap between reality and fantasy makes social psychological studies of explicit and implicit preferences useful. For instance, a preference for an attractive face without conscious awareness of why it is attractive provides a very useful addition to research on actual marriage choices. The explicit and implicit preferences that are assessed in these studies are less constrained by the competing interests of other people and capture the processes associated with the social and psychological mechanisms that can influence reproductive decisions and behaviors (D. M. Buss & Schmitt, 2019; Kenrick, Sadalla, Groth, & Trost, 1990). Preferences can nevertheless be influenced by social and sexual dynamics in the local community (Kenrick, Li, & Butner, 2003), by wider economic and social conditions, and by the individual woman's attractiveness as a mate (because attractive women demand more from their mates). To complicate matters further, some traits in a would-be mate are necessities and others are luxuries (N. P. Li, Bailey, Kenrick, & Linsenmeier, 2002).

At the most general level, the preferences of women and men are based on a combination of the would-be partners' cultural success, personal attributes (e.g., kindness, intelligence), and physical attractiveness. The sex difference for any one of these traits is small to moderate but the overall mix of traits that are most preferred by women and men are quite different (Conroy-Beam, Buss, Pham, & Shackelford, 2015). The difference emerges because women and men prioritize different traits and are willing to compromise on different traits. The result is that the mix of traits preferred by the average woman (statistical average) is so different than the mix of traits preferred by the average man that there is little overlap in this combination of traits. The sex difference in the preference for a culturally successful mate is discussed first and then turns to mate choice trade-offs and wider influences.

Culturally successful men. Women throughout the world prefer spouses who have achieved cultural success or have the attributes that are likely to lead to success (e.g., ambition, good financial prospect; D. M. Buss, 1989b; Fales et al., 2016; N. P. Li et al., 2002). One of the first large-scale studies of women's and men's mate-choice preferences included more than 10,000 people in 37 cultures across six continents and five islands (D. M. Buss, 1989b). As shown in Figure 7.2, women rated *good financial prospect* higher than men in all cultures, although the magnitude of this sex difference was lower in cultures in which women had more political and economic freedom (Conroy-Beam et al., 2015). The latter indicates that women's economic dependency on men makes this a more salient trait than it would otherwise be, but the sex difference is found even in wealthy nations in which women have political and economic independence. Overall, Conroy-Beam et al. (2015) found that the sex difference for *good financial prospect* was about twice as large as the cross-cultural differences on this trait.

FIGURE 7.2. The Importance of "Good Financial Prospects" of a Prospective Marriage Partner



The scale is from 0 (*unimportant*) to 3 (*indispensable*). Data from D. M. Buss (1989a).

Hatfield and Sprecher's (1995) study of college students in the United States, Japan, and Russia illustrates the importance of cultural success in highly developed nations. In each of these nations, women valued a prospective spouses' potential for success, earnings, status, and social position more highly than did men. A meta-analysis of research published from 1965 to 1986 revealed that 3 out of 4 women rated socioeconomic status (SES) as more important in a prospective marriage partner than did the average man (Feingold, 1992a). Studies conducted prior to 1965 showed the same pattern (e.g., R. Hill, 1945), as do more recent studies (Souza, Conroy-Beam, & Buss, 2016; Sprecher, Sullivan, & Hatfield, 1994; G. Wang et al., 2018). Across age, ethnic status, and SES, women prefer husbands who are better educated than themselves and who earn more money than they do. The same preference for a high-status husband is found for women ranging in age from their 20s to 60s (Buunk, Dijkstra, Fetchenhauer, & Kenrick, 2002), although the sex difference declines after women reach menopause and converges by the time people are in their 70s and 80s (Whyte, Chan, & Torgler, 2018).

Women's preference for culturally successful men is also found in studies of singles ads (Greenlees & McGrew, 1994; Strassberg & English, 2015), popular fiction novels (Whissell, 1996), online dating (Whyte et al., 2018), speed dating (Asendorpf, Penke, & Back, 2011), and for selection of sperm donors (Whyte, Torgler, & Harrison, 2016). In a study of 1,000 "lonely hearts" ads, Greenlees and McGrew (1994) found that British women were 3 times more likely than British men to seek financial security in a prospective partner, whereas Oda (2001) found that Japanese women were 31 times more likely than Japanese men to seek financial security and social status. Whissell (1996) found the same themes across 25 contemporary romance novels and 6 classic novels that have traditionally appealed to women more than men, including two stories from the Old Testament written about 3,000 years ago. In these stories, the male protagonist is almost always an older, socially dominant, and wealthy man who ultimately marries the woman. The importance of a man's cultural success is also reflected in studies of "deal breakers" in a relationship. These are traits that will lead to the rejection of the man, even if all of his other traits are positive (Jonason, Garcia, Webster, Li, & Fisher, 2015). Among deal breakers for women are a man's laziness and lack of confidence, both of which will compromise his status striving.

Consistent with the description of developing nations and many traditional societies (see Chapter 6, this volume), marriage to a culturally successful man can have reproductive consequences for a woman in modern societies. Bereczkei and Csanaky (1996) studied more than 1,800 Hungarian men and women who were 35 years of age or older and not likely to have more children. They found that women who had married men who were older and better educated than themselves had more children, were less likely to get divorced, and reported higher levels of marital satisfaction than did women who married younger and/or less educated men. Fieder and Huber (2007b) found the same for Swedish women who were married to men who were about 4 years older (and presumably more established) than they were. In general, however, in developed nations the benefits of marrying a wealthier and higher status man are not reflected in number of children, but rather in the man's ability to contribute to the long-term social competitiveness of their children (see Chapter 6, this volume).

Trade-offs. Mate choices always involve a type of balancing act whereby potential partners are evaluated across multiple traits, and the best choice is the one who comes closest across all of these traits (Conroy-Beam & Buss, 2017). This balancing act also highlights the traits that are the most important for one sex or the other, including women's preference for a culturally successful partner. The importance of success is highlighted when women must make cost–benefit trade-offs between a partner's cultural success or traits that predict cultural success against other important traits, such as his physical attractiveness (N. P. Li, 2007; N. P. Li et al., 2002; N. P. Li, Valentine, & Patel, 2011; Souza et al., 2016).

When their "mate dollars" are limited, women spend more of them on the social status and resources of a long-term partner than on other traits. When they have additional mate dollars, they spend proportionally less on status and resources—but still more than men spend—and more on the personal traits of a prospective spouse (e.g., his friendliness). In yet another study, college women reported the minimally acceptable earning potential of a prospective husband was the 70th percentile—on the basis of earning potential alone, 70% of men were eliminated from the pool of potential marriage partners. The corresponding figure for college men was the 40th percentile (Kenrick et al., 1990). G. Wang et al. (2018) found that women rated the physical attractiveness of men higher when those men were reported to have a high annual salary, but salary had little effect on how men rated women's physical attractiveness.

Once a prospective husband has achieved the minimal social standing, additional resources and status yield diminishing results. Kenrick, Sundie, Nicastle, and Stone (2001) found that the desirability of a man as a marriage partner increased sharply as his income rose from a low- to an upper-middle-class level (about $100,000/year) and then leveled off. An increase in a man's income from $25,000/year to $75,000/year resulted in a substantial increase in his desirability but increasing his income from $100,000/year to $300,000/year had little effect. As noted, women who have their own resources (e.g., well-paying job) do not value men's income as much as women with fewer resources, but even women with prestigious and well-paying jobs prefer men who are higher status and make more money than they do (Conroy-Beam et al., 2015; Lu, Zhu, & Chang, 2015).

Wider cultural wealth and mores. Even when women's mate choices are unconstrained by kin, there are wider economic or cultural factors that can influence stated preferences and the magnitude of some but not all of the sex differences in these preferences (D. M. Buss, 1989b; Conroy-Beam et al., 2015; Eagly & Wood, 1999; Lippa, 2007). D. M. Buss' (1989b) study showed that women and men rated the financial prospects of a prospective mate as less important in Europe than in other regions of the world (see Figure 7.2). At the time of the study, central governments in Eastern Europe provided many basic necessities (e.g., housing, health care), and there were constraints on earned income. To a lesser degree, the central governments in Western Europe provided similar economic supports and high taxes constrained income differences. The same pattern is found when responses in China are compared with those of the rest of Asia (not shown in Figure 7.2).

Eagly and Wood (1999) found that the magnitude of the sex difference in the value of a prospective mates' financial prospects, from D. M. Buss' (1989b) study, was smaller in nations in which women had political and social influence and when they had some financial independence. The gist is that when economic supports are provided by sources outside of the marital relationship, women and men downgrade the importance of a prospective mate's financial prospects and presumably focus more on luxuries. Despite this cultural variation, the sex difference in the importance of a would-be partner's cultural success remains, even in highly egalitarian nations. This is true in terms of what women state they prefer in a marriage partner (Conroy-Beam et al., 2015; Zentner & Mitura, 2012) and in terms of whom they actually marry (Fieder & Huber, 2007a)

Personal and Behavioral Attributes

A preference for a culturally successful marriage partner is not enough, in and of itself, to constitute the best reproductive strategy for women. Culturally successful men are often arrogant, self-serving, and are better able to pursue casual sex or polygynous marriages in some cultures than are other men. When situated in a wealthy country with large numbers of men who make a sufficient income, women do not have to tolerate the competing interests of the most culturally successful men, but rather can focus on traits that will make for a satisfying long-term relationship. These traits are interpersonal luxuries that provide information on the willingness of the man to cooperate in a long-term relationship and to invest in children. This does not mean that a man's cultural success is no longer important, only that many women are willing to trade some of this success for other traits, especially in Western, educated, industrialized, rich, and democratic (WEIRD) contexts (Henrich, Heine, & Norenzayan, 2010). These are evolutionarily novel contexts in which peoples' behavior and preferences are not always representative of peoples' behavior and preferences in traditional contexts.

Interpersonal Luxuries

In addition to traits that signal cultural success, women in WEIRD cultures often rate the emotional stability and the family orientation of prospective marriage partners more highly than do men (e.g., Oda, 2001). D. M. Buss (1989b) found that women rated a prospective husband who was kind, understanding, and intelligent more highly than a prospective husband who was none of these, but had the potential to become culturally successful. In his Internet survey of more than 200,000 people, Lippa (2007) found that women value men's sense of humor, honesty, kindness, dependability, and communication skills more highly than do men. These are traits that enable women (and men) to form stable long-term marital relationships. Preferences for these traits are a luxury that can be expressed in wealthy, individualistic and monogamous WEIRD nations and especially in the middle and upper middle classes of these societies (Argyle, 1994).

In less wealthy, more collectivistic societies (e.g., Latin America) women weigh a prospective mate's social respectability, competence, and responsibility more heavily than their interpersonal traits (e.g., humor, kindness) and more heavily than do women in WEIRD societies (Lippa, 2007):

> Emotional satisfaction is central to White middle-class Euroamerican marriages because the Euroamerican family is so mobile, nucleated, isolated, and far away from relatives so that emotionally close relationships are hard to come by. . . . Husband–wife emotional satisfaction is not as critical for the Aka as it is for Euroamericans. (Hewlett, 1992, p. 170)

Hadza women report wanting "nice" husbands but in this society, nice means these men do not hit them (Marlowe, 2004). In the Hadza, Ache (Paraguay), Yanomamö (Venezuela, Brazil) and many other traditional societies, wives and husbands spend much of their time in sex-segregated groups, with sometimes emotionally distant and tense spousal relationships (Chagnon, 1997; Hawkes et al., 2001; K. Hill & Hurtado, 1996; Pasternak et al., 1997).

This is not to say that emotional satisfaction is not preferred by women in these societies, but rather it is a luxury that cannot be as easily realized as it can in WEIRD societies. When women must focus on keeping their children alive and healthy, luxuries like her mate's attentiveness to her emotional needs, cannot be substituted for the resources controlled by culturally successful men and the potentially less desirable characteristics of these men. Even if they cannot indulge in these luxuries, they would still like to have them in a husband, as illustrated in this interview. K. Hill and Hurtado (1996) asked an Ache woman, Achipura, but Achipuragi responded:

K. HILL: Achipura, what kind of man could get many women, what kind did women love, the kind who could easily find a wife?

ACHIPURAGI: He had to be a good hunter.

K. HILL: So, if a man was a good hunter, he could easily find a wife?

ACHIPURAGI: No, not just a good hunter. A good hunter could find a wife, but a man needed to be strong.

K. HILL: When you say strong, do you mean a man who could beat up others in a club fight?

ACHIPURAGI: No, women don't like those men. Women don't like men who love to hit others. I mean a strong man. One who would walk far to hunt, one who would carry heavy loads. I mean a man who would work hard when everyone was tired or build a hut when it was cold and rainy. I mean a man who was strong. A man who could endure and not get tired.

K. HILL: Did women love big men then [i.e., men of large body size]?

ACHIPURAGI: No, they would love a small man or a large man, but he had to be strong.

K. HILL: What other men would be able to acquire a wife easily?

ACHIPURAGI: A man who was "a good man."

K. HILL: What does it mean, "a good man"?

ACHIPURAGI: A good man is one who is handsome [attractive face]. One whom women love. One who is nice and smiles and tells jokes. He is a man who is handsome. A "good man" is a man whom women love. (p. 228)

Emotional Commitment and Jealousy

As mentioned previously, many women find emotional intimacy with a partner to be an attractive part of their relationship, which follows from the pair-bonding mechanism that promotes male paternal investment as described in Chapter 6 of this volume. Although female–female competition over male investment is not common among mammals, it does occur in primates when males invest a limited resource, such as social protection, in one or a few females (Baniel, Cowlishaw, & Huchard, 2016; Smuts, 1985). Recall that among chacma baboons (*Papio ursinus*) females with offspring at risk of infanticide or lower levels of harassment are protected by a male friend, and these females will attack any other female that attempts to develop a relationship with their male friend (Baniel, Cowlishaw, & Huchard, 2018a, 2018b). To the extent that men's protection and provisioning has benefited women and their children throughout human evolution, women should show similar responses and experience relationship jealousy. In other words, jealousy is an emotion triggered by a threat to the relationship and motivates a protective response, and it only would have evolved if these relationships provide an important reproductive benefit to women and their children.

Women and men experience jealousy and are broadly distressed by threats to their reproductive relationships, although men are particularly sensitive to sexual infidelity, as described later in this chapter (Daly, Wilson, & Weghorst, 1982). Women are also sensitive to a partners' potential sexual infidelity and may be even more sensitive to their partner developing an intimate relationship with another woman, even without (or before) sex (D. M. Buss, Larsen, Westen, & Semmelroth, 1992). The corresponding proposal is that men experience relatively more jealously when their partner has a sexual affair and women more jealousy when their partner develops an emotional affair (i.e., an intimate relationship with another woman). The proposed sex difference in jealousy sparked a vigorous and drawn-out debate (e.g., whether men are more sexually jealous than women) that, for some, detracts from the importance of the basic phenomenon (DeSteno & Salovey, 1996; Edlund & Sagarin, 2017; C. R. Harris, 2003; Sagarin et al., 2012). The core point is that women are especially sensitive to their partners' investment in them and their children and any threats to this investment, whether due to a sexual or emotional affair, will trigger jealousy.

Women's sensitivity to their partners' emotional connections to other women is nevertheless an interesting and important point. The development of emotional intimacy often precedes sexual affairs or mate switching and is an early signal of risk of abandonment and risk of losing access to the man's resources (Whisman & Snyder, 2007). Intimacy is a cue to relationship stability and continued investment in the context of monogamous relationships (Haselton & Buss, 2000). In the context of polygynous marriages, a husband's development of greater intimacy with one wife over others typically instigates jealousy and conflict among the cowives because this may bias his relative investment in them (Jankowiak, Sudakov, & Wilreker, 2005; Meekers & Franklin, 1995). In these contexts, jealousy can be over the husbands' sexual attention but more often it is related to the distribution of material resources, especially those that will affect the health and well-being of children (Ware, 1979).

The key point is that women are sensitive to men's emotional investment in them and their children and they would not experience intense jealousy, whether triggered by emotional or sexual affairs, and the conflict it often incites if the maintenance of these relationships did not provide women with substantial benefits. The benefits of men's investment were outlined in Chapter 6 of this volume. Geary and Flinn (2001) proposed that family relationships in our australopithecine ancestors were similar to those found in modern gorillas (see Chapter 5, this volume). Female–female competition over food or proximity to the alpha male sometimes occurs in gorillas but is not frequent (Watts, 1994), and it is nothing like the often antagonistic and hierarchical relationships among women in polygynous marriages. This difference is important, because it indicates an evolutionary shift in the quantity and quality of resources that males provided to females. For gorillas, males can simultaneously protect all females and their offspring from infanticidal outgroup males but, at some point during human evolution, the quantity or quality of males' investment became more restricted and limited to one or a few females and promoted female–female competition.

Physical Attractiveness and Good Genes

In classical literature and romance novels, the male protagonist is almost always socially dominant, wealthy, and handsome (Whissell, 1996). Women's preference for a handsome husband (or short-term partner) makes biological sense (Gangestad & Buss, 1993), as many of the physical traits that women find attractive in men are likely to be indicators of the man's physical and genetic health and will be especially so in traditional contexts with extensive physical demands and health risks (Apicella, 2014; Low, 1990a). The pattern is essentially the same as described in the section on female choice in Chapter 3 of this volume, whereby females' mate choices are often influenced by several of the males' physical traits. Using the same logic, physically attractive men should not only sire children who are attractive and sought out as mating and marriage partners in adulthood, but they and their children are also likely to be physically healthier than are other men and their children.

Body and Facial Attractiveness

If good genes models of mate choices are correct (see Chapter 3, this volume), then women should be sensitive to the facial and body features of men that are correlated with health and physical fitness and they should find these traits particularly attractive (Thornhill & Gangestad, 2008). Physically healthy men generally have a relatively low percentage of body fat and a high percentage of lean muscle mass which lowers one's risk of cardiovascular and other diseases (Salonen et al., 2015; Segal et al., 1987). Importantly, these correlates of physical health are identifiable by the man's body shape (Malara, Kęska, Tkaczyk, & Lutosławska, 2015) and are heritable (Maes et al., 1996). Women can quickly (in several seconds) identify and rate men's body shapes as masculine and attractive and focus on the same features that are correlated with physical fitness and overall health (Brierley, Brooks, Mond, Stevenson, & Stephen, 2016; Hönekopp, Rudolph, Beier, Liebert, & Müller, 2007).

Men who are rated attractive by women are above average in height (but not too tall), and have an athletic body shape with a 0.8 to 0.9 waist-to-hip ratio (WHR) and 0.7 waist-to-chest ratio (i.e., no "beer bellies"); these men have a muscular V shape (Beck, Ward-Hull, & McLear, 1976; Fan, Dai, Liu, & Wu, 2005; Hatfield & Sprecher, 1995; Singh, 1995; Sorjonen, Enquist, & Melin, 2017; Stulp, Barrett, Tropf, & Mills, 2015). These physical features are a good indicator of upper body strength that in turn is important in the context of male–male competition (Kordsmeyer, Hunt, Puts, Ostner, & Penke, 2018; Sell et al., 2009) and is predictive of hunting success in traditional contexts (Apicella, 2014). The attractiveness of these men is confirmed by women's preference for them as short-term and long-term partners and by these men's higher reproductive success in many contexts (Hönekopp et al., 2007; Kordsmeyer et al., 2018; Nettle, 2002; Pawłowski, Dunbar, & Lipowicz, 2000; Sear, 2006; M. D. Taylor et al., 2005).

The facial features that women generally rate as attractive include somewhat larger than average eyes, a large smile area, prominent cheek bones and chin and overall facial symmetry (Barber, 1995; Cunningham, Barbee, & Pike, 1990). More recent studies have focused on diet-related carotenoid levels that are expressed as slight changes in facial color and are correlated with some aspects of immune functioning and on facial adiposity (i.e., fat percentage). Facial color and adiposity can influence facial attractiveness (de Jager, Coetzee, & Coetzee, 2018; Stephen, Coetzee, & Perrett, 2011). At the same time, the strength of the relation between these various facial features and men's actual health, including immune-system functioning, is unclear; sometimes relationships are found for some aspects of health and immunity and sometimes they are not found (e.g., Coetzee, Perrett, & Stephen, 2009; Foo, Simmons, & Rhodes, 2017; S. C. Roberts et al., 2005). Of these various traits, facial adiposity appears to be the most reliable cue to men's health because it is related to overall body shape that in turn is correlated with various health-related risk factors (de Jager et al., 2018).

The relation between body shape and physical health is due in part to the health effects of excess weight and is more of an issue in WEIRD nations than in traditional contexts. In fact, many of the previously mentioned studies should be taken with a grain of salt, because most of them have been conducted with young and educated adults in wealthy countries with minimal nutritional stress and well-developed health care systems. For these populations, any relations between physical traits (e.g., facial features, body muscularity) and health outcomes are likely to be weak (Weeden & Sabini, 2005). A more realistic assessment of the relationship between physical attractiveness and health can be found in studies conducted in developing countries and in more traditional cultures. Here, men are much more variable in their overall health than are men in WEIRD nations, and women's mate preferences are more strongly related to men's physical attractiveness and masculinity than they are in less risky contexts (DeBruine, Jones, Crawford, Welling, & Little, 2010; Gangestad & Buss, 1993; Low, 1990a).

These results are more consistent with what is found in nonhuman species. Recall, the expression of sexually selected traits is dependent on the condition of the individual (see Chapter 4, this volume), and many of the traits that women find attractive in males would be expected to be especially vulnerable in boys and men for populations living in more difficult circumstances (Geary, 2015, 2016). Consistent with this expectation, in more natural contexts chronic poor nutrition and disease are associated with shorter stature, less muscle mass, and poor physical fitness in adolescent boys and men (e.g., Halsted et al., 1972; McGarvey et al., 1992; Prista et al., 2003; for review see Geary, 2015). It is not a coincidence that these are many of the same traits that women in developed nations find attractive in men, even when these traits are only weakly related to the health of young men in these nations.

Immune System Genes

Genes of the major histocompatibility complex (MHC) are involved in immune system responses to parasites and to other pathogens (see Chapter 2, this volume) and are tied to male health (see Chapter 4, this volume). Recall that mates with highly similar MHC genes may produce offspring with resistance to fewer parasites, whereas mates with highly dissimilar MHC genes may produce offspring with increased risk of autoimmune disorders (Milinski, 2006). Women's choice of mates with MHC genes moderately different from their own might then result in the best immune system for their children. Women are not aware of these genetic differences, but they detect them on the basis of odor and other cues (e.g., voice; Arnocky, Hodges-Simeon, Ouellette, & Albert, 2018). Among mammals, odor cues are often correlated with immune system genes and infections (e.g., Kavaliers & Colwell, 1995), and humans are also sensitive and respond to these scents. Nevertheless, the actual relation between MHC genes and women's mate choices are complex and not fully understood.

There is a difference between the odor cues associated with illness and those associated with detection of MHC genes in healthy individuals. Olsson et al. (2014) showed that triggering the innate immune response—a response triggered by many different types of parasites—results in the development of a detectable and unpleasant body odor within a few hours. Moshkin et al. (2012) found a similar pattern when women were asked to evaluate the odor (collected in underarm cotton pads embedded in t-shirts) of men currently infected with gonorrhea (*Neisseria gonorrhoeae*), successfully treated men, and never-infected men. Women reported the odors of infected men, but not never-infected or cured men, to be unpleasant ("putrid"), and the degree of unpleasantness was related to the intensity of the men's immune responses. These types of findings are consistent with odor cues providing reliable information about some disease conditions and that the unpleasantness of these odors creates a behavioral defense against infectious disease. Men's body odors and immune functions are also influenced by diet quality, whereby those with a healthy diet produce odors that are attractive to women (Zuniga, Stevenson, Mahmut, & Stephen, 2017).

The detection of odors associated with MHC genes in healthy individuals and whether this influences mate choices is another matter, however. Natural scents can influence the attractiveness of potential mates and may provide clues about the diversity of the donor's immune system genes (Penn et al., 2007; Wedekind, Seebeck, Bettens, & Paepke, 1995), but the sensitivity of women to subtle differences in men's MHC genes is uncertain (Thornhill et al., 2003). Whatever is influencing women's mate choices, Winternitz, Abbate, Huchard, Havlíček, and Garamszegi's (2017) meta-analysis and more recent studies indicate that spouses are not any more dissimilar on MHC genes than are two randomly paired men and women (e.g., Qiao, Powell, & Evans, 2018). Spouses are more dissimilar on MHC genes than they are on non-immune system genes, but this is due to the variability of the MHC and not necessarily to women's choice of men with dissimilar genes. The degree of dissimilarity that occurs without active mate choices may be enough, nevertheless, because MHC genes from mother and father only need to be modestly different to confer a strong immune system benefit in their children (Pierini & Lenz, 2018). When there is evidence of an explicit preference for one man or another, women prefer men with highly variable MHC genes, which would confer immunity to a wide-range of parasites, independent of how similar these are to their own MHC genes (Winternitz et al., 2017).

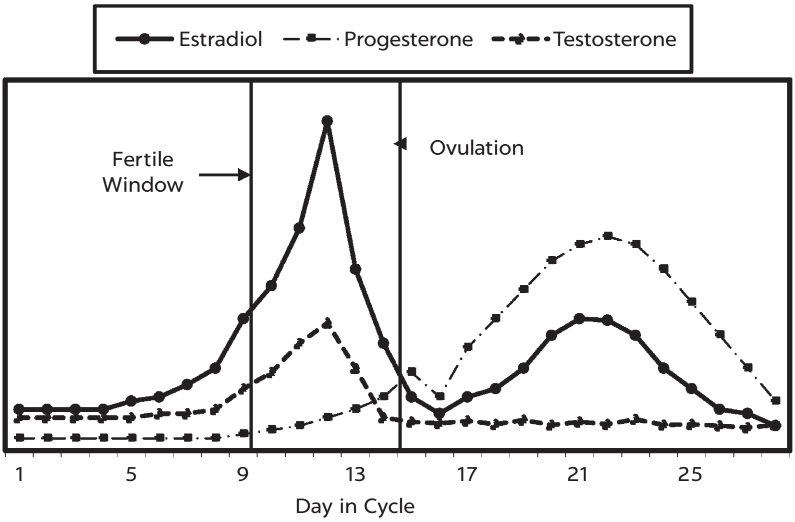
Even so, there may be subtle advantages for couples with more diverse MHC genes, although the issues are not fully resolved (Garver-Apgar, Gangestad, Thornhill, Miller, & Olp, 2006; Kromer et al., 2016; Saphire-Bernstein et al., 2017). Kromer and colleagues (2016) provided a very thorough assessment of MHC gene similarity for 254 couples. They found that couples with more dissimilar immune system genes reported higher sexual and overall satisfaction with the relationship. This was true of husbands and wives (or unmarried men and women in long-term relationships) but the effect was strongest in women. Women who had husbands or partners with dissimilar MHC genes also reported a stronger desire to have children with this partner than did women who had partners with MHC genes similar to their own. There is also some evidence that couples with differences in immune system genes may conceive more quickly and have fewer spontaneous abortions than couples with highly similar immune system genes (F. L. Black & Hedrick, 1997; Ober, Elias, Kostyu, & Hauck, 1992; Ober et al., 1997). These latter studies, however, were conducted in small populations with limited mate choices that would result in a level of spousal MHC similarity that would not typically occur in larger populations with more varied choices.

In all, the studies confirm that the diversity of men's immune system genes influences women's sexual interest and likely the health of their children (see also Field et al., 2016), but it also indicates that cues associated with men's MHC genes (e.g., odor) do not influence women's mate choices as strongly as other factors (e.g., his status; Wu et al., 2018). In large populations with many potential mates, most couples will have sufficiently different MHC genes without a strong explicit preference for mates based on cues associated with these genes. In smaller populations with limited mate choices, including those in which parents choose women's spouses, MHC-based preferences may be more important and may motivate women to seek extramarital relationships if their immune system genes are too similar (e.g., indicated by unattractive odors) to those of their husbands (Garver-Apgar et al., 2006).

Ovulatory Cycle

For female mammals, some sequence and combination of estrogens (especially estradiol) and progesterone contribute to ovulation and sexual receptivity and proceptivity (courtship) to males, although the sequencing and relative influence of these hormones differs somewhat across species (Adkins-Regan, 2005; Brenner & West, 1975). The ovulatory cycle in women follows (on average) the 28-day cycle as shown in Figure 7.3. The surge in estradiol concentrations begins about Day 8 or 9 in a typical cycle and in combination with the increase in progesterone and other hormones (especially luteinizing hormone, not shown) contributes to ovulation. There is a corresponding window of fertility that represents the highest probability of conception and runs from about

FIGURE 7.3. The Hormonal Changes Across Women's Ovulatory Cycle



Estradiol (top line in the Fertile Window) begins to increase at about Day 8 or 9 in a typical cycle and contributes to ovulation (about Day 14) and women's sexual motivation. The corresponding increase in testosterone (middle line in the Fertile Window) may also contribute to women's sexual motivation. The progesterone (bottom line in the Fertile Window) increase contributes to ovulation and the preparation of the uterus for implantation of a fertilized egg. Illustration by Melanie Sheldon. Reprinted with permission.

5 days before to a few days after the day of ovulation (A. J. Wilcox, Weinberg, & Baird, 1995), although there is still a modest (about 10%) likelihood of conception the following week (A. J. Wilcox, Dunson, & Baird, 2000). Roney and Simmons (2013) found that young and single women's sexual motivation and sexual behavior increased with the increases in estradiol shown in Figure 7.3. The influence of the peak in testosterone concentrations was less consistent but in combination with estradiol may increase women's sexual motivation and desire, depending on social context (Shirazi et al., 2019; van Anders et al., 2007; Wallen, 2001). The postovulation increase in progesterone concentrations contributes to the preparation of the uterus for implantation of a fertilized egg, should fertilization occur, and was associated with a decrease in sexual motivation and behavior (Roney & Simmons, 2013).

The pattern is broadly consistent with that found in other mammals, but with some important differences. For most mammals, females' sexual receptivity and their attraction to male traits that are indicators of physical and genetic health are tightly linked to their ovulatory cycle (Adkins-Regan, 2005), but this link is moderated by women's relationships. The importance of relationships and the corresponding weakening of the link between hormones and women's sexual behavior is likely related to the evolution of continuous sexual receptivity and its importance for the maintenance of long-term relationships with their partners. Women's continuous sexual receptivity and concealed ovulation also make it much more difficult for men to mate-guard their partners and provide women with more opportunity to form extra-pair relationships, should they be in an unsatisfactory one and/or paired with a less attractive man.

In species with facultative male parenting—as is seen in humans—females will sometimes engage in extra-pair sex if their partner is not especially attractive or healthy (see Chapter 4, this volume). These extra-pair partners typically have traits (e.g., plumage color) that indicate good genes (e.g., immune system genes) that will benefit the females' offspring (see Chapter 3, this volume). The corresponding dynamic for humans is called the *ovulatory shift hypothesis*, whereby women who are paired with unattractive men are predicted to show more interest in other men and may cheat with these men during the fertile window of their cycle (Gangestad & Thornhill, 2008; Gangestad, Thornhill, & Garver, 2002; Pillsworth & Haselton, 2006; Thornhill & Gangestad, 2008). These women are thought to focus their attention on their partner during the nonfertile phase of their cycle and, in this way, they can maintain his investment in them and any children. The short-term focus on attractive men reduces the chances of detection, should an affair occur, and helps to maintain the investment of their long-term partner.

If the hypothesis is correct, then women should show a stronger preference for masculine and attractive men during the fertile phase of their cycle. This is not to say that women will be prone to cheating on their partners during this time, but rather those women who are in unsatisfactory relationships will be more likely to consider other men during this time. These issues have been extensively studied, are vigorously debated, and remain to be fully resolved (Gangestad, Dinh, Grebe, Del Giudice, & Thompson, 2019; Gildersleeve, Haselton, & Fales, 2014; Stern, Arslan, Gerlach, & Penke, 2019; W. Wood, Kressel, Joshi, & Louie, 2014). There is agreement, nevertheless, that women are attracted to men with the body and facial features described previously, but there is not yet a consensus on whether this attraction is even stronger when women are in the fertile phase of their cycle. Although it is reasonable to expect that women's hormonal status will influence how much they attend to men's traits, the critical issue is whether they shift their focus to extra-pair men during this time. In a meta-analysis, Gildersleeve et al. (2014) found that women were more attracted to men's masculine traits (e.g., muscularity) during the fertile phase of their cycle and particularly in the context of a potential short-term rather than long-term mate, but the shift was modest; W. Wood et al. (2014), however, disputed these findings.

A large-scale study that included more the 26,000 daily reports of sexual desire and behaviors (e.g., flirting) confirmed that naturally cycling women (i.e., those not using hormonal contraceptives) have more sexual interest in, fantasies about, and flirt more with extra-pair men during the fertile phase of their cycle, but they were not more likely to be sexually intimate with them (Arslan, Schilling, Gerlach, & Penke, 2019). During this time, women also reported feeling sexier and were more sexually interested in their long-term partner, consistent with a general increase in sexual motivation and sensitivity to men's attractiveness during the fertile phase of the cycle

(Roney & Simmons, 2016). The latter findings were confirmed in another large-scale study, but this was especially true in the early phases of relationships, where their stability is not yet certain, and for women with a fast pace of life (i.e., women who grew up in difficult circumstances and might be at risk for relationship instability; see Chapter 6, this volume; Dinh, Pinsof, Gangestad, & Haselton, 2017). For women in satisfactory relationships, in contrast, there was no increase in extra-pair interest or flirtations during the fertile phase of the cycle.

So, the influence of women's hormonal status and their sexual motivations and potential interest in a short-term mate is influenced by the quality of their long-term relationship. Gangestad and his colleagues (Grebe, Emery Thompson, & Gangestad, 2016; Grøntvedt, Grebe, Kennair, & Gangestad, 2017) have proposed that the increase in progesterone concentrations toward the end of the cycle may contribute to women's sexual interest in their long-term partner, although it is generally associated with a decline in single women's sexual interest (Roney & Simmons, 2013). The combination of high progesterone concentrations and loyalty and faithfulness in a long-term relationship was associated with women's interest and engagement in sex with their partner. The sexual behavior of women who are less committed in their relationship, in contrast, was more strongly influenced by estradiol concentrations, as found by Roney and Simmons (2013). These findings are preliminary (see Roney & Simmons, 2016), but if correct suggest that women's continuous sexuality in the context of pair-bonding and men's investment in the family is maintained, in part, by an evolved change in the influence of sex hormones on women's sexual interest in their long-term partner.

My overall interpretation of these studies is that the hormonal changes around the time of ovulation result in a general increase in attention to men and sexual motivation (Jünger, Kordsmeyer, Gerlach, & Penke, 2018; Roney & Simmons, 2013) and not necessarily a shift in mating strategy (i.e., a search for a short-term mate). Women in an unsatisfactory long-term relationship are in search of a new mate, or at least willing to consider one, and as such are influenced by the same hormonal mechanisms as single women; increases in estradiol concentrations result in increases in attentiveness to attractive men (Roney & Simmons, 2013). What appears to be a strategy to cuckold their partners by having sex with a more attractive man during the fertile window may, in many cases, simply be a failed attempt to switch mates rather than an evolved strategy to obtain good genes from a fit man and long-term investment from another man. This type of dynamic is consistent with the low cuckoldry rates (less than 3% in many contexts) described in Chapter 6 of this volume and the finding that women rarely act on their attraction to handsome men (e.g., Arslan et al., 2019), and they typically only engage in affairs after they have developed an emotional relationship with the extra-pair man (Whisman & Snyder, 2007). In some cases, a failed attempt to mate switch will effectively result in cuckoldry, even if this was not the original intent.

One final issue is whether women's sensitivity to the risk of a sexual assault varies with their risk of becoming pregnant should an assault occur. J. S. Brown's (1952) survey of traditional societies found that the abduction and rape of women is documented in the ethnologies of the vast majority of societies, and that men are severely punished for raping women in their ingroup. These patterns indicate that rape and sometimes abduction are common risks in these contexts (see also Thornhill & Palmer, 2000). As covered in Chapter 8 of this volume, women are generally more risk averse than men. The question here is whether vigilance for sexually predatory men increases with the increase in estradiol concentrations that precedes ovulation, as heightened vigilance during this time would reduce the risk of pregnancy should an assault occur.

There is some evidence that women's sensitivity to men's potential to be sexually coercive (Garver-Apgar, Gangestad, & Simpson, 2007) and their general cautiousness (Bröder & Hohmann, 2003; Chavanne & Gallup, 1998) is higher when the risk of conception is high. Younger women and women who rate themselves as attractive appear to be particularly cautious during this time frame (M. M. McDonald, Coleman, & Brindley, 2019; McKibbin, Shackelford, Miner, Bates, & Liddle, 2011). These results have been interpreted as being consistent with an evolved adaptation to avoid the risk of sexual assault when the risk of conception is at its highest (e.g., McKibbin et al., 2011). On the other hand, young and attractive women generally have more unwanted attention from men than do other women and may be more cautious on the basis of these experiences. The vigilance of these women could result from these prior experiences combined with the heightened attentiveness to men during the fertile window (Snyder & Fessler, 2013). Either way, the result would be a reduction in the risk of an unwanted pregnancy associated with an assault, but the matter remains to be fully settled (Fessler, 2003).

Alternative Mating Strategies

There are many places in the world and many reasons why women are unable to obtain the type of relationship described in romance novels: a long-term monogamous relationship with a handsome, socially dominant, and high-investing man. In the absence of this option, and sometimes even when it is an option (e.g., high male mortality), it is sometimes in women's best interest to maintain long-term polyandrous relationships (Starkweather & Hames, 2012) or to engage in short-term sexual relationships (D. M. Buss & Schmitt, 2019). The latter can occur for a variety of reasons, including an attempt to attract the attention of and develop a longer term relationship with a desired man (D. M. Buss & Schmitt, 1993; Regan & Dreyer, 1999). In these relationships, the traits women find attractive in a long-term partner are the same as those used to select a short-term partner (Vigil, Geary, & Byrd-Craven, 2006).

In other situations, the traits preferred in long-term and short-term partners differ. In a study of 460 women, the majority of whom were living in economically challenging circumstances, Vigil et al. (2006) found variability in the trade-offs that women make when choosing short-term and long-term mates. There was little difference for the majority of women, consistent with using short-term relationships to find a long-term partner (D. M. Buss & Schmitt, 1993), but almost 2 out of 5 of these women differed in the traits they desired in a long-term and short-term mate. The women who reported differences clustered into two groups. The first focused on the physical attractiveness of a short-term mate, as predicted by good genes models (Gangestad & Simpson, 2000). The other group focused on the potential financial gains of such a relationship. These women were more likely to be dependent on government assistance, had more children, and were less conscientious. In other words, some women use their sexuality and men's desire for short-term mates and sexual variety for financial or other material gains (Brewer et al., 2000). This may not be their preference, but rather circumstances may have pressed them to use this strategy.

In many parts of the world, there are large numbers of men who do not have the material or social resources to support a family. To adapt to this circumstance, some women develop a successive series of relationships with a number of these men (serial polyandry) or several simultaneously (informal polyandry), each of whom provides some investment during the course of the relationship (Borgerhoff Mulder & Ross, 2019; Campbell, 2002; Lancaster, 1989). In recounting a study conducted in the Dominican Republic, Lancaster (1989) noted that, compared with women monogamously married to men with low incomes,

> women who excluded males from the domestic unit and maintained multiple liaisons were more fecund, had healthier children with fewer pre- and postnatal mishaps, were able to raise more children over the age of 5, had better nourished children (as measured by protein per capita), and had better psychological adjustment (as measured by self-report and lower maternal blood pressure). (pp. 68–69)

These types of polyandrous relationships are found in many parts of the world and occur more frequently than suggested by the low percentage (about 1%) of societies in which polyandry is a common family type (see Table 7.2). These types of polyandrous families are common in Himalayan societies and occur when two brothers marry the same women to avoid splitting their farmland into plots that would not be large enough to support a family. Starkweather and Hames' (2012) review indicated that polyandrous relationships and sometimes marriages can also occur in societies that are typically classified as polygynous or monogamous. In these contexts, some lower status men choose a polyandrous marriage to no marriage at all. Sometimes women prefer polyandrous relationships if they are dependent on men's provisioning of resources and male mortality is high. In this way, they can maintain a resource stream for themselves and their children, should one of the men die.

Outside of formal polyandrous marriages, the most extensively studied form of polyandry occurs in the lowlands of South America. In these regions, about

2 out of 3 Amerindian societies practice partible paternity (R. S. Walker, Flinn, & Hill, 2010), such as the Ache and Barí (Columbia, Venezuela). Here, women maintain sexual relationships with two (sometimes more) men, one of whom will be considered the primary father of any resulting children and the other a secondary father (Beckerman et al., 1998; K. Hill & Hurtado, 1996). By tradition, secondary fathers are socially obligated to provide material resources and social protection to the woman's child, although not all of them do so. The main benefit for women is that they receive more resources than do women who maintain only a single relationship (Ellsworth, Bailey, Hill, Hurtado, & Walker, 2014); the same benefit has been found for traditional cultures outside of South America (Scelza & Prall, 2018; Starkweather & Hames, 2012). The result is lower mortality of children with one secondary father. Children with more than one secondary father, however, often have higher mortality rates, presumably because none of the men invest much in them if paternity is too uncertain.

Sexual jealousy between the primary and secondary fathers is common, although mitigated if they are related (e.g., cousins) and members of the same foraging group or camp (Ellsworth et al., 2014; R. S. Walker et al., 2010). Although many primary and secondary fathers are unrelated, a substantial number of them are more closely related to one another than would be expected by chance (Ellsworth et al., 2014; R. S. Walker, Yvinec, Ellsworth, & Bailey, 2015). In these cases, even if the investing man is not the biological father of the child, he is at least investing in a relative. In many of these contexts, male-on-male aggression is common (see Chapter 8, this volume) and men are therefore highly dependent on one another for support during conflicts. Cofathers who reside in the same group are often important allies in the context of this aggression (Ellsworth et al., 2014). Men can also benefit from having a cofather when male mortality is high (often because of male–male competition), whereby the surviving father provides protection and resources to the children of the deceased man.

MEN'S MATE CHOICES

Men's and women's preferences for long-term partners are largely captured by a mix of that partners' cultural success, personal attributes (e.g., kindness, intelligence), and physical attractiveness. The sex differences are not so much in terms of whether or not these traits are important, but rather in how much each of them is prioritized by one sex or the other (Conroy-Beam et al., 2015). Important exceptions are that, relative to women, men are more enthusiastic about casual sex and more interested in sexual variety. At a very basic level, the sex difference in interest in casual sex follows from the sex difference in parental investment and the sex difference in the cost–benefit trade-offs of pregnancy (see Chapter 3, this volume). Men's interest in sexual variety is consistent with an evolutionary history of polygyny and the reproductive benefits that polygynously married men enjoy, as is discussed in Chapter 8 of this volume.

After describing the sex differences in preference for casual sex and sexual variety, this section moves to the personal and behavioral attributes that men prefer in marriage partners, followed by a discussion of women's physical attributes that men find attractive. Individual differences in men's mate preferences and choices, such as the importance they place on a mate's attractiveness, vary with the man's desirability as a mate, as it does with women. Desirable men devote more time and effort on obtaining short-term sexual relationships and have a stronger preference for physically attractive short-term and long-term mates than do other men (Pérusse, 1993; Pratto & Hegarty, 2000; Surbey & Brice, 2007).

Casual Sex

As described previously, women will sometimes pursue short-term sex as a means to initiate a long-term relationship, secure material or other resources for themselves or their children, and more rarely to cuckold their partner. Many men, in contrast, pursue short-term sex as an end in and of itself, not as means to some other end (D. M. Buss & Schmitt, 2019; Symons, 1979). The sex difference here is not surprising, as it is likely to be true for any species in which females invest more in parenting than males. To be sure, there are species in which females mate promiscuously (e.g., chimpanzees, *Pan troglodyte*), but this serves some other purpose such as confusing paternity or inciting competition among males. It is not to say that all men are actively searching for casual sex partners, or that there are not any women who enjoy casual sex, but rather that there are significant sex differences (on average) in the willingness to engage in casual sex, in the evaluations of these sexual relationships (e.g., postcoital sexual regret), and in the desire for sexual variety.

There are many ways in which these sex differences can express themselves, including the time and energy devoted to seeking short-term partners, cheating on a long-term partner, sexual fantasies, willingness to accept propositions, and use of prostitutes, among many others (D. M. Buss & Schmitt, 2011). As an example of the magnitude of some of these sex differences, consider that D. M. Buss and Schmitt's (1993) review and studies indicated that young men reported, on average, a desire for 18 sexual partners over their lifetime compared with four or five partners for women (see also McBurney, Zapp, & Streeter, 2005). Schmitt et al. (2003) found the same sex difference for samples of 6,822 men and 9,466 women from nearly all regions of the world, and confirmed that many more men than women in all of these regions—married or not—were actively seeking short-term mates and sexual variety. Lippa's (2009) study of more than 250,000 people across 53 nations indicated that men, regardless of where they are in the world, have a stronger sex drive than women; close to 3 out of 4 men have a stronger sex drive than the average woman. Lippa along with Schmitt (2005) also found corresponding sex differences in attitudes toward and willingness to engage in casual sex. Both studies indicated that 3 out of 4 men have more liberal attitudes toward casual sex than does the average woman (see also Oliver & Hyde, 1993; J. L. Petersen & Hyde, 2010).

However, women's attitudes about and willingness to engage in casual sex differed from one country to the next, whereas those of men were consistent across countries. Women were more open about casual sex in WEIRD nations with liberal mores, and expressed particularly negative attitudes about casual sex in countries in which Islam was the majority religion (Lippa, 2009; Schmitt, 2005). In highly developed nations, there was much more variation among women as a group than among men, with some women being open to casual relationships and others were not interested in them at all. The cross-cultural variation in women's attitudes about and willingness to engage in casual sex is consistent with Baumeister's (2000) argument that women's sexuality is more variable across relationships and contexts than is men's sexuality. Even so, in these liberal nations and across the 20th century, 7 out of 10 men were more enthusiastic about casual sex than was the average woman (Lippa, 2009; B. E. Wells & Twenge, 2005). Overall, the sex differences in attitudes and willingness to engage in casual sex was 3 to 4 times larger than the cultural variation in these aspects of sexuality.

These are not simply reported attitudes. There are corresponding sex differences in the pattern of regret associated with actual casual sexual relationships (Galperin et al., 2013; Kennair, Bendixen, & Buss, 2016). Women report more regrets for engaging in short-term sexual relationships (e.g., "I lost my virginity to the wrong partner"), whereas men report more regrets about not acting on opportunities for such relationships (e.g., "I wish I was more sexually active when I was young"). Galperin et al.'s (2013) study of more than 24,000 people from various backgrounds indicated that nearly 3 out of 4 women had more regrets about their most recent casual relationships than did the average man, whereas nearly 4 out of 5 men had more regrets about the most recent missed opportunities (at least in their minds) for casual relationships than did the average woman. The same sex differences are even found in Norway, one of the most sexually liberal and gender-equal countries in the world (Bendixen, Asao, Wyckoff, Buss, & Kennair, 2017). These sex differences in sexual regret are related, in part, to women's more intense feeling of moral disgust than men in these situations, especially if they did not initiate the encounter (Kennair, Wyckoff, Asao, Buss, & Bendixen, 2018).

Sexual Receptivity, Fantasy, and Use of Prostitutes

Men's preference for short-term mates and the correlated preference for sexual variety are not typically realized, because of women's desire for more committed relationships, but they are nevertheless real. The best window on the strength of these preferences comes from studies on sex differences in receptivity to sexual propositions, sexual fantasies, and in the use of prostitutes.

Men's reported attitudes about casual sex are not simply talk to impress peers. When given the opportunity, most men will put this desire into practice. R. D. Clark and Hatfield (1989) demonstrated as much in a set of studies in which undergraduates approached attractive but unfamiliar members of the opposite sex and asked them for a date, to go to their apartment, or to engage in casual sex. When asked for a date, 1 out of 2 men and 1 out of 2 women accepted. When asked to engage in casual sex, 3 out of 4 men agreed, but not a single woman agreed. In his classic work on the evolution of human sexuality, Symons (1979) further illustrates this sex difference with a contrast of the sexual and intimate lives of male and female homosexuals. This contrast is telling, because these individuals do not have to deal with the oftentimes competing interests and motivations of the opposite sex:

> Fundamental male–female differences also are apparent in variety-seeking. The search for new sexual partners is a striking feature of the male homosexual world: The most frequent form of sexual activity is the one-night stand in which sex occurs, without obligation or commitment, between strangers. . . . In one-night stands and in longer liaisons the basis of the male homosexual relationship usually is sexual activity and orgasm. . . . But lesbians form lasting, intimate, paired relationships far more frequently and easily than male homosexuals do; stable relationships are overwhelmingly preferred to any other, and monogamy is the ideal. (Symons, 1979, pp. 293–298)

There are also extensive differences in the quantity and nature of men's and women's sexual fantasies. G. D. Wilson (1997) found that men were 2.5 times more likely to fantasize about group sex than were women, and Trudel (2002) found an even larger difference (40% of men, 13% of women) in a random sample of nearly 1,000 married adults. B. J. Ellis and Symons (1990) found that men were twice as likely as women to report having sexual fantasies at least once a day and were 4 times as likely to report having fantasized about sex with more than 1,000 different people (32% of men, 8% of women). Although there were no sex differences in feelings of guilt over sexual fantasies, men and women differed considerably in the content of their fantasies. Women were 2.5 times as likely to report thinking about the personal and emotional relationship with their partner and that they were the object of sexual desire (Bogaert, Visser, & Pozzebon, 2015), whereas men were nearly 4 times as likely to report focusing on their partner's physical characteristics. Moreover, women were twice as likely to report fantasizing about someone with whom they are currently romantically involved with or had been involved with, whereas men were 3 times as likely to fantasize about having sex with someone with whom they were not involved and with whom they had no intention of becoming involved.

Some men put these fantasies into practice with their use of prostitutes. The demand for prostitutes is almost entirely driven by men, and it can focus on other men (i.e., male prostitutes) but is predominantly focused on women (Brewer et al., 2000; C. F. Turner et al., 1998), especially women in their early 20s (Sohn, 2016). Across two national (United States) surveys of 9,066 adults between the ages of 18 and 59 years, Brewer et al. (2000) found that men, on average, reported between 1.5 and 2.5 times as many sexual partners during the past 1 year and 5 years, respectively, than did the average woman. On the basis of prostitution arrest and rearrest records, surveys, interviews, and other techniques, they further estimated that a typical female prostitute in the United States will have 700 male sexual partners per year. This number was then combined with the estimated prevalence rate of 22 prostitutes per 100,000 adults and used to determine if the sex difference in the reported number of sexual partners might be because of the use of prostitutes. It was. Once the estimated use of prostitutes was controlled, there was no sex difference in the reported number of sexual partners.

It is difficult to estimate the number of men who have visited a prostitute, because men are reluctant to admit to this behavior (Brewer et al., 2000). C. F. Turner et al. (1998) found that 1 in 40 adolescent boys reported having had sex at least once with a prostitute. Given the age range in this sample, the percentage of men who visit a prostitute at some point in their lifetime must be considerably higher than this. Indeed, a random sample of 852 Danish and Swedish adults between the ages of 23 and 87, revealed that 1 out of 6 men, but none of the women, reported having visited a prostitute at least once (Jæger et al., 2000). Monto and McRee (2005) compared the sexual attitudes and behavior of 1,672 men arrested for soliciting a prostitute with those of more than 3,800 men across two nationally (United States) representative samples. The would-be "Johns" were less likely to be married (40% vs. 50%) and those who were married were more likely to be unhappy in this relationship (22% vs. 3%). The men in the representative samples were more conservative in their sexual attitudes and were less likely to have bought sexually explicit material during the past year. But, "[most] differences were small, indicating customers as a category differ from other men in degree rather than quality" (Monto & McRee, 2005, p. 505).

Personal and Behavioral Attributes

Whether or not they pursue casual sex, nearly all men want a marriage partner. These are long-term reproductive relationships in which men have committed to investing in children. Given the attendant costs of investment, it is not surprising that most men are careful in their choice of marriage partners. When it comes to the personal and behavioral attributes of a prospective bride, men are particularly choosy when they are culturally successful and living in societies with socially imposed monogamy. These are societies in which men's marriage opportunities are legally restricted and the opportunity cost of marriage is higher for these men than it is for similarly successful men in societies in which polygyny is legal. As described in Table 7.2, families in societies with socially imposed monogamy tend to be more independent of kin-group influences, and as a result, the husband–wife relationship is more central to men's social life than it is in many other societies (Pasternak et al., 1997).

For wealthy, Western cultures with socially imposed monogamy (e.g., United States, Canada, Western Europe, other WEIRD nations), Lippa (2007) found few differences in the personal attributes men and women preferred in a long-term mate, although there are significant differences in the relative importance of one trait versus another (Conroy-Beam et al., 2015). For instance, when making trade-offs between one potential spouse or another, one person might weigh financial success, emotional stability, and good looks as highly important, similar political views as moderately important, and housekeeping skills as unimportant. Another individual might weigh these same traits very differently. Although men and women in these societies prefer a marriage partner with traits (e.g., agreeable, sense of humor) that will facilitate a long, cooperative interpersonal relationship (Kenrick et al., 1990; N. P. Li et al., 2002), they put different weightings on the importance of this combination of traits. The result is that only about 12% of men and 12% of women overlap in the combination of traits they rate highly (Conroy-Beam et al., 2015). There are also sex differences in the traits that are relationship deal breakers (i.e., they lead to the termination of the relationship). Women have more deal breakers than do men, but a partners' low sex drive is a deal breaker for more men than women (Jonason et al., 2015).

Across a wider range of cultures, there is even more variation in the personal attributes that men and women want in marriage partners. Men in Latin America, Malaysia, India, Singapore, and Japan rated interpersonal traits (e.g., agreeableness) as less important than did women in these nations and, with the exception of Japan, rated them as less important than did men in WEIRD nations generally. Even in these nations, men place a higher priority on a prospective marriage partner's physical appearance than on these personal and behavioral attributes (N. P. Li et al., 2002; Lippa, 2007).

Sexual Fidelity and Jealousy

As addressed previously, men and women experience jealousy when their romantic relationships are threatened. Independent of the controversies over the magnitude of the sex differences in emotional and sexual jealousy (Edlund & Sagarin, 2017), men's behaviors indicate that they are especially sensitive to the risk of their partners' sexual infidelities. Men's concern about sexual infidelity is an evolutionarily coupled feature of the cuckoldry risks described in Chapter 6 of this volume and the costs of investing in the child of another man. It is not simply about sex; it is sex that can lead to pregnancy. Sagarin, Becker, Guadagno, Nicastle, and Millevoi (2003) found that men were distressed by the prospect of their partner having an affair with another man and therefore risking pregnancy, but were not distressed by the prospect of their partner having an affair with a woman. The social and psychological manifestation is sexual jealousy, which has a near universal influence on the dynamics of men's and women's relationships, including male-on-female aggression and men's attempts to control the social and sexual behavior of their partners (Daly & Wilson, 1988a, 1988b; Daly et al., 1982; Flinn, 1988a; Stöckl et al., 2013).

The dynamics of men's sexual jealousy are nicely illustrated by Flinn's (1988a) observational study of mate guarding in a rural Trinidadian village. In this village, "13 of 79 (16.4%) offspring born . . . during the period 1970–1980 were putatively fathered by males other than the mother's coresident mate. Clearly, mate guarding could have significant effects on fitness" (Flinn, 1988a, p. 10). Mate guarding by men but not women was found to be a common feature of long-term relationships but varied with the woman's risk of pregnancy. Men monitored the activities less diligently and had fewer conflicts with pregnant and older wives than they did with younger and nonpregnant wives. Sexual jealously is also implicated in the dissolution of many relationships. After sterility, adultery is the most common cause of marital dissolution across cultures. "In 25 societies, divorce follows from adultery by either partner; in 54 it follows only from adultery on the wife's part and in 2 only from adultery on the husband's [part]. If marriage qualifies as near universal, so must the double standard" (Betzig, 1989, p. 658).

More seriously, Daly and Wilson's (1988b) seminal study of homicide revealed that a common motive for a man killing his wife was her committing a sexual infidelity, his suspicion that she has been or is being unfaithful, or her desertion of him. In an analysis of the circumstances surrounding a man's attempt to kill his partner, 22 of 30 attempts occurred when she attempted to end the relationship (Nicolaidis et al., 2003). "Twenty-five of the 30 women (83%) described examples of their partners using stalking, extreme jealousy, social isolation, physical limitations, or threats of violence" (Nicolaidis et al., 2003, p. 790), a pattern that is common among women who are at risk of male-on-female homicide (C. M. Spencer & Stith, 2020). In an analysis of 844 Federal Bureau of Investigation cases in which a man killed his wife, 345 (41%) involved a lover's triangle (Shackelford, Buss, & Weekes-Shackelford, 2003). In keeping with Flinn's (1988a) findings, younger wives were much more likely to be murdered as a result of infidelity than were older wives, independent of the husbands' age. Takahashi et al.'s (2006) imaging study revealed that the brain areas associated with sexuality and aggression (i.e., amygdala, hypothalamus) showed heightened activity when men, but not women, imagined their partner engaging in a sexual infidelity.

These are serious examples of male-on-female aggression and attempts by men to control the sexual behavior of their partners. In the United States, physical aggression that is directed toward a romantic partner does not typically escalate to this level, due in part to legal consequences. Women are just as likely to hit men as men are to hit women for more minor physical disputes, but women are more likely to be seriously injured during these fights (Archer, 2000). The pattern is different in societies in which women's social, political, and economic opportunities are limited and families live among male kin. In these societies, men are more likely than women to physically assault their spouse or partner (Archer, 2009). Some men even abuse their wife if she objects to their infidelities and their diversions of family resources to other women, as a way to suppress their wife's objections (Stieglitz, Gurven, Kaplan, & Winking, 2012).

Physical Attributes and Fertility

People of both sexes prefer physically attractive to less attractive partners, but this preference is consistently found to be more important—a necessity and not a luxury—for men than for women (D. M. Buss, 1989b; Feingold, 1990; Hatfield & Sprecher, 1995; N. P. Li et al., 2002; Lippa, 2007). Indeed, the largest sex difference in Lippa's (2007) study was for the importance of good looks in a prospective spouse. In each of the 53 nations, men valued a good-looking spouse more highly than did women, confirming D. M. Buss' (1989b) earlier results from another multinational study. The overall magnitude of the sex difference in Lippa's study indicated that 7 out of 10 men rated a partner's good looks as more important than did the average woman. But what makes a woman good looking? Are these traits related to her reproductive fitness, especially to her fertility?

Young, Attractive Women

Men are most attracted to women in their late-teens to early 20s and with the following physical features: WHR of about 0.7 (sometimes higher), facial features that signal a combination of sexual maturity but relative youth, proportionally longer legs, firm breasts, and small abdomen and waist (Cunningham, 1986; B. J. Dixson, Sagata, Linklater, & Dixson, 2010; Fan, Liu, Wu, & Dai, 2004; Havlíček et al., 2017; D. Jones et al., 1995; Rilling, Kaufman, Smith, Patel, & Worthman, 2009; Singh, 1993a, 1993b; Sohn, 2016). The key facial features seem to be large eyes, prominent cheek bones, and a large smile area, along with smooth and unblemished skin (Stephen et al., 2011). Among individuals from Europe, Africa, and Indonesia there was modest agreement about which women have the most attractive faces and strong agreement regarding the least attractive faces, suggesting the most desirable facial features are influenced in part by local ideals of beauty (Kleisner et al., 2017; Sorokowski, Kościński, & Sorokowska, 2013). Nevertheless, consistent with some inherent contributions to these preferences, when men view attractive female faces there is heightened activation of the brain's built-in reward center (i.e., nucleus accumbens), as well as concurrent activation of other brain areas that are associated with reward-driven social behaviors and motivations (e.g., orbital frontal cortex; Cloutier, Heatherton, Whalen, & Kelley, 2008).

Many men are also fascinated by women's breasts. Women's breasts are actually an interesting topic because they are larger than they need to be outside of suckling, and they may be an indicator of maturity and fertility (B. J. Dixson et al., 2011). Indeed, Havlíček et al. (2017) found that some men from Europe, South America, and Africa preferred average-size breasts and others preferred larger breasts but they all preferred women with firm breasts. The latter is correlated with age and the number of children the woman has had and would be a reliable indicator of the number of children she is likely to have in the future (i.e., her residual fertility; Lassek & Gaulin, 2019; Symons, 1979).

Women's WHR, waist size, and body mass index (BMI)—a measure of leanness to obesity independent of height—are all highly correlated and associated with rated attractiveness (Brooks, Shelly, Jordan, & Dixson, 2015). In many of the associated mate-choice studies, men have a consistent preference for relatively slender women. For a sample of young Canadian adults, Hume and Montgomerie (2001) found that for women, but not men, higher BMI values were associated with lower rated attractiveness. K. L. Smith, Cornelissen, and Tovée (2007) found the same relationship for young adults in the United Kingdom using a more direct measure of body fat. In both studies, leaner women (BMI < 22; 22 is average) were rated as more attractive than heavier ones. All of these studies, however, have been conducted in WEIRD nations that are composed of well-nourished populations and are not likely be representative of ancestral conditions. In fact, women with below average BMIs (< 20) and WHRs (< 0.7) have more difficulties conceiving and are more likely to have low birth-weight children than are women with more body fat (Lassek & Gaulin, 2018a, 2018b; Rich-Edwards et al., 2002).

These relationships are almost certainly why a preference for relatively slender women is not universal. Across 62 cultures, J. L. Anderson, Crawford, Nadeau, and Lindberg (1992) found that relatively slender women were preferred in 12 of them, whereas moderately heavy or "plump" women were preferred in 23 and 27 cultures, respectively. In subsistence populations, many women are slender because of poor nutrition and those with higher body weight and BMIs are considered to be more attractive and have more children during their lifetime (Hochberg, Gawlik, & Walker, 2011; Sorokowski, Kościński, Sorokowska, & Huanca, 2014; Tovée, Swami, Furnham, & Mangalparsad, 2006; Wetsman & Marlowe, 1999); in these contexts, WHRs between 0.7 and 0.9 are considered equally attractive. There is also consistent evidence that men's preference for slender or heavier women is influenced by context, with heavier women preferred in subsistence contexts and more slender women in WEIRD contexts (Sorokowski et al., 2014; Tovée et al., 2006). Basically, heavier women are preferred and considered beautiful in contexts in which the food supply is unreliable, and average weight to slender women are preferred in contexts in which food is readily available and where lower status women are heavier, on average, than higher status ones.

Women's age is a different matter, as men's preference for relatively young women is found in WEIRD nations and in traditional contexts. Why is age so important in men's ratings of women's attractiveness? It is simple: men's mate preferences evolved to be sensitive to indications of a woman's age, because age and fertility are tightly linked in women. Women's fertility is low in the teen years, peaks at about age 25, and then gradually declines to near zero by age 45 (Menken, Trussell, & Larsen, 1986). Teenagers are less likely to become pregnant than women in their 20s for any given sexual episode (Lassek & Gaulin, 2018b), and if they do become pregnant they experience more complications (e.g., ectopic pregnancy, stillbirth) than do women in their 20s (Nybo Andersen, Wohlfahrt, Christens, Olsen, & Melbye, 2000).

Risks begin to increase as women move into their 30s and increase sharply after age 35. Spontaneous abortion is the most common cause of fetal loss, with the risk of loss at 1 in 11 for a 22-year-old woman, 1 in 5 for a 35-year-old woman, 2 in 5 for a 40-year-old woman, and 1 in 2 for a 48-year-old woman.

D. M. Buss' (1989b) 37-culture study and many others confirm that men prefer and marry women younger than themselves—younger brides have more reproductive years ahead of them than do older ones—and marry women in the age range of high fertility (e.g., Buckle et al., 1996; D. M. Buss & Shackelford, 1997; Kenrick & Keefe, 1992; Kenrick, Keefe, Gabrielidis, & Cornelius, 1996). Across cultures, D. M. Buss found that brides were, on average, 3 years younger than their grooms in early adulthood. Kenrick and Keefe (1992) demonstrated this same pattern across samples from the United States, Germany, Holland, and India, and Grøntvedt and Kennair (2013) found the same in gender-equal Norway. Marriage patterns across the 20th century in the United States and Poro, a small Philippine island, also revealed that men marry younger women. As men get older, they tend to marry relatively younger and younger women (Buckle et al., 1996; Kenrick & Keefe, 1992).

For instance, in 1923 the typical American man in his 20s married a woman who was about 3 years younger than himself, as did the typical Filipino man between 1913 and 1939. The typical man in his 60s married a woman who was about 15 years younger than himself in the United States and 20 years younger in Poro (Kenrick & Keefe, 1992). Korean men who "purchase" brides from poorer nations (e.g., from Southeast Asia) overwhelmingly prefer women in their 20s (Sohn, 2017a). The typical 50-year-old Korean man who makes such a purchase will marry a woman who is about 28-years-old. These patterns cannot be attributed to a social norm that "men should marry younger women, and women should marry older men." Kenrick et al. (1996) found that the most attractive dating partner for teenage boys was a woman about 5 years older than they were—a woman with higher fertility than teenage girls of the same age or younger than these adolescent boys.

Attractiveness, Health, and Nubility

The assessment of the relation between the traits that men find attractive in women and women's actual health and fertility is plagued by the same confound described for men. Most of the studies have been conducted with well-nourished and vaccinated populations with access to modern health care (i.e., WEIRD populations; Foo, Simmons, & Rhodes, 2017; Weeden & Sabini, 2005). As noted previously, in these circumstances the relationship between attractiveness and health is likely to be much weaker (or nonexistent) than any such relationship during our evolutionary history (e.g., Cai et al., 2019). As described in the section above, men's preference for slender women with relatively low BMIs, WHRs, and body fat has actually drifted away from the biological optimum (Lassek & Gaulin, 2018b; Rich-Edwards et al., 2002). The drift is likely due to media (e.g., in magazines) that link status-related cues with thin women, combined with women's competition with one another on the basis of the physical traits that they believe men prefer (Rozin & Fallon, 1988).

The broader question here is whether men's preference for these and related traits (e.g., breast shape, facial features) evolved because they are indicators of women's health and the ability to conceive (W. J. Brown, Mishra, Kenardy, & Dobson, 2000; Rich-Edwards et al., 2002; Singh, 1993a), or an indicator of their remaining reproductive years. Following Symons (1979), Lassek and Gaulin (2019) argued that these attractive traits are a better indicator of sexual maturity and parity (i.e., the number of children the woman has birthed) than health and the ability to conceive per se. These traits are at their most attractive, from the perspective of men, 3 to 5 years after menarche and in young women who have not yet given birth. These nubile women are at their peak in terms of the number of children they can have in the coming decades, and compared with older women, they have higher stores of the fatty acids that will contribute to their children's prenatal and early postnatal (through breastfeeding) brain development. Of course, most 30-year-old women can conceive but they cannot have as many children from that point on as an 18-year-old. If a man were to marry the latter, the pair could potentially have more children together than if they married when she was 30.

A focus on traits that indicate the number of children a bride could have in the future makes sense in many traditional contexts, where child mortality can be quite high and delaying marriage and the starting of a family is much riskier relative to WEIRD contexts. The relationship between women's attractiveness and nubility provides a straightforward explanation of what men find attractive and why, but health issues can still influence attractiveness. Outside of WEIRD populations, billions of people, including many of the poor in developing nations are chronically exposed to a variety of parasitic and other diseases (Hotez, 2015). The challenges faced by these people provide a much better view of the potential relationship between women's attractiveness and their health than is apparent in WEIRD contexts (see also Geary, 2015, 2016), although much remains to be learned.

To illustrate, facial attractiveness is influenced by the features described earlier and by skin color and texture (Fink, Grammer, & Matts, 2006; Stephen et al., 2011). In traditional populations, common parasitic infections often cause noticeable skin lesions on the face or other body areas. For instance, Dreyfuss et al. (2000) found that women infected with hookworms (e.g., *Ancylostoma duodenale*; *Necator americanus*) were iron deficient and at elevated risk of anemia (see also Brooker, Hotez, & Bundy, 2008). Iron-based anemia increases the odds of premature birth, low birth weight, and poor infant health (L. H. Allen, 2000), and results in a pale, unhealthy looking skin tone. These parasitic infections can in turn lower women's marriage prospects (Amazigo, 1994; Brieger, Oshiname, & Ososanya, 1998). In a review of the consequences of chronic infection in traditional societies, Litt, Baker, and Molyneux (2012) concluded that generally, men "become concerned about sexual performance and economic prospects, whereas women express worries about life chances and marriage" (p. 197). Holm, Esmann, and Jemec (2004) found that adolescent girls and women with skin diseases reported a lower quality of life than did similarly affected boys and men, especially if the disease was in a visible area of the body, specifically, face, neck, or hands.

In traditional contexts, some types of parasitic infections and other diseases can also affect women's WHRs and body shape. Schistosomiasis, for instance, is an infection with a common parasitic worm (e.g., *Schistosoma mansoni*) and often results in liver disease and abdominal enlargement that in turn will increase the WHR and lower women's attractiveness (e.g., Olveda et al., 1996). Kjetland et al. (2010) found that women with schistosomiasis were 3.5 times more likely to be infertile than uninfected women, but treatment improves the chances of becoming pregnant (El-Mahgoub, 1982). Women's WHR can also be affected by vitamin D deficiencies early in life that in turn affect pelvic development and predict their children's later health (D. J. Barker, Osmond, Kajantie, & Eriksson, 2009).

CONCLUSION

There is no question that women's and men's mate preferences have been influenced by our evolutionary history and are a reflection of the same processes—sexual selection—that influenced the evolution and the proximate expression of mate choices in nonhuman species (C. Darwin, 1871). To be sure, human mate choices are complicated by men's investment in children and by variation in customs from one culture to the next. All of this variation, however, is wrapped around a core of invariants that are only understandable in terms of sexual selection. The bottom line is that the preferred mates and attendant cognition and behaviors of both sexes evolved to focus on and exploit the reproductive potential and reproductive investment of the opposite sex. Reproductive potential is the genetic or other resources (e.g., ability to have children) that an individual can potentially invest in children, whereas investment is the actual use of resources to promote the well-being of children. When it comes to choosing mates, women and men prefer traits that signal reproductive potential and a bias to invest this potential in children.

Although the details vary from one setting to the next, culturally successful men have more to offer women and their children (i.e., they have higher reproductive potential) than do less successful men (Irons, 1979; Low, 2000). These are men who wield social influence and control the resources (e.g., money, land, cattle) that women would prefer to have invested in themselves and their children. When men invest resources in parenting, the mortality rates of their children often drop and these children are better prepared for the rigors of adult life (see Chapter 6, this volume). It is not surprising that women and their kin throughout the world prefer these men as marriage partners. This preference is expressed in social-psychological studies, reading materials, lonely heart ads, and other measures (Lippa, 2007, 2009; Oda, 2001; Whyte et al., 2016), and in their actual mate choices (e.g., Borgerhoff Mulder, 1990, 2000; Hopcroft, 2006). In short, most women prefer monogamous marriages to wealthy, socially dominant, and physically attractive men (i.e., healthy men with good genes) and want these men to be devoted to them and their children. For most women, this preference is not achieved and they have to make trade-offs (Conroy-Beam & Buss, 2017). These typically involve trading his physical attractiveness for his cultural success. In some circumstances, women develop multiple relationships and secure social and material resources from each of these men (Scelza & Prall, 2018; Starkweather & Hames, 2012), but the underlying dynamic is the same: Women use men to increase the quantity and quality of resources available to them and their children.

The reproductive effort of most mammalian males (see Chapter 3, this volume) is largely or exclusively focused on mating (Andersson, 1994). Men's investment in children changes this dynamic and results in a more mixed reproductive strategy (D. M. Buss & Schmitt, 2019; Gangestad & Simpson, 2000). As with other mammals, men can reproduce with little investment in parenting or the relationship. More unique to humans and in keeping with the gorilla-like model described in Chapter 5 of this volume, men can also reproduce with an exclusive, long-term monogamous or polygynous relationship with heavy parental investment. Or, men can reproduce with a mixture of these strategies. The approach men take is influenced by their ability to attract (or not) short-term mates, by social mores, and by partner characteristics. When men invest in long-term relationships, the types of traits they prefer (e.g., kindness) are similar to those of women (Lippa, 2007), especially in WEIRD nations, although they often differ on the value they place on one trait versus another (Conroy-Beam et al., 2015). Men consistently differ from women, regardless of where they are in the world, in terms of their enthusiasm for casual sex and sexual variety and in terms of the importance of the physical attractiveness of a potential mate. The desire for casual sex and sexual variety is likely related to the sex difference in the costs of reproduction and an evolutionary history of polygyny. The physical traits (e.g., age) men find attractive are generally reliable indicators of the women's health and fertility, at least outside of WEIRD nations (Litt et al., 2012); even in WEIRD nations, these traits are good indicators of the woman's remaining reproductive years (Lassek & Gaulin, 2019).

8

Competing for Mates

As discussed in Chapter 3 of this volume, males' faster reproductive rate and lower parental investment result in more intense male–male than female–female competition in most mammals. Humans are no different, despite men's relatively high level of investment in their children. To be sure, men differ from other mammals in the many creative ways in which they compete (Barkow, 1989; Griskevicius, Cialdini, & Kenrick, 2006; G. F. Miller, 2000; Winegard, Winegard, & Geary, 2018), but underneath this variation is a very real and often times deadly struggle for social influence and control of culturally important resources (Betzig, 1986; Daly, 2016; Scheidel, 2017). The combination of social influence and resource control determines men's cultural success, which in turn influences their ability to attract and support mates. Irons' (1979) concept of cultural success allows us to understand how ecology, cultural history, and current conditions influence how men express an evolved desire for social status. Pastoral raiders who steal another tribe's cattle to pay a brideprice and Wall Street "raiders" (mostly men) who seek hostile takeovers of companies are not that different. Both of these activities are an expression of men's desire for control of the resources that affect their social status, reproductive prospects, and general well-being. A Wall Street raider does not, of course, need an extra $10 million to attract a bride or live well, but as long as there are other raiders who make more than him, the Wall Street raider will continue the struggle for status and cultural success.

For many men it is not simply the absolute level of resource control vis-à-vis what it takes to raise a family, it is the level of influence, control, and status

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relative to that of other men in the communities and niches in which they compete. Even in modern highly developed societies (Western, educated, industrialized, rich, & democratic [WEIRD]; Henrich, Heine, & Norenzayan, 2010), high status confers better health and a longer lifespan on men, women, and their children (Marmot, 2004). Before the emergence of modern health care and sanitation, parental status in these societies had a significant influence on which children survived to adulthood and which did not. Relative status matters for women as well as for men, but more so for men. As detailed in Chapter 5 of this volume, the relationship between social dominance and reproductive success is stronger for male than for female primates, and is typically stronger for males than females across species more broadly, from fruit flies (*Drosophila melanogaster*) to mandrills (*Mandrillus sphinx*; Janicke, Häderer, Lajeunesse, & Anthes, 2016). The same has been the case throughout our evolution.

The first section of this chapter describes how the corresponding motivation for social dominance, status, and resource control are expressed as male–male competition in traditional societies and early empires, as well as in developing and developed nations. When men differ from one another in status and resource control and in what they can potentially invest in children, women view high-status men as potentially useful resources (see Chapter 7, this volume). The second section describes the associated female–female competition and how women compete with one another for these desirable men and for other resources in developed nations and in polygynous societies. Both sections provide overviews on related issues, including hormonal influences on men's and women's competitiveness and on the relationship between cultural success and reproductive success.

MALE–MALE COMPETITION

Male–male competition and female choice are, in some respects, different sides of the same coin. As with many other species (see Chapter 3, this volume), men often compete on those dimensions that women desire in marriage partners (e.g., social status) or in short-term mates (e.g., physical attractiveness; N. P. Li, 2007). Women's mate choice preferences were covered in the previous chapter, and there is no need to repeat them here as they relate to male–male competition. In cultures in which there are relatively few restrictions on women's choice of partners, men will attempt to enhance those traits (e.g., income) that women prefer, but there is much more to men's mating effort.

More broadly, men are focused on their status relative to other men, as determined by their social influence and control of culturally important resources (e.g., money, cows, land). As noted, the extra $10 million earned by the Wall Street raider does not enhance his survival prospects. His drive to continue to earn money is an expression of the relation between relative status and health and longevity at all levels of the social hierarchy (Marmot, 2004), and more deeply the relation between relative status and reproductive outcomes. The result is an evolved disposition to engage in social-comparative processes (Festinger, 1954) that result in a focus on relative status and control, not simply the acquisition of sufficient resources for survival and reproduction (R. D. Alexander, 1989; Flinn, Geary, & Ward, 2005; Geary, 2005). Women's preference for high-status partners has contributed to the evolution of the social-comparative processes that focus men on their relative status, but the desire for status and control often takes on a life of its own. Many men are focused on the attainment of sociopolitical power and, where possible, resource control. When successful, many of these men will use this power to control the sexual behavior of women and other men, independent of female choice, although their ability to achieve this end will depend on cultural context and their competitors' ability to keep these would-be despots in check (Betzig, 1986; Boehm, 2009).

The discussion begins with a description of how male–male competition is expressed in traditional societies and in early human empires, and then moves to its expression in developing and developed (largely WEIRD) societies. Again, Irons' (1979) concept of cultural success pulls together all of these different ways of competing and ties them to the underlying motive to achieve social status and resource control vis-à-vis that of other men in their communities (Betzig, 1986; Hopcroft, 2006; Irons, 1979; Scheidel, 2017). There is a critical distinction between the blatant use of dominance-based strategies to get what one wants and prestige-based strategies (Henrich & Gil-White, 2001). *Prestige* is based on the acquisition of culturally important competencies (e.g., hunting skills and hunting returns) that can contribute to the well-being of others who then freely confer status to the individual with these competencies (C. Anderson, Hildreth, & Howland, 2015). *Dominance* is simply the use of force or threat of force to coerce others into relinquishing their property or doing as one wishes, whether or not it is in these others' best interest. This is typically instrumental or proactive aggression that is focused on achieving a particular goal, and not impulsive or reactive aggression. (Wrangham, 2018). As argued by Hobbs (1651), the suppression of dominance-related strategies for enhancing status or resolving conflicts changed the nature of social dynamics and for that matter altered the course of human evolution.

Once male–male competition in these different contexts is covered, the discussion moves to male–male competition and testosterone, risk taking, and sperm competition. The section closes with a discussion of genetic studies as these relate to the issues of male philopatry (i.e., whether males tend to stay in their kin-groups or migrate to the group of their wives) and male–male competition during human evolution.

Competition in Traditional Societies and Early Empires

There is a consistent relationship between dominance rank and reproductive success in male primates (see Chapter 5, this volume), and the same is true for men. von Rueden and Jaeggi (2016) assessed the relationship between men's status and their reproductive success across 33 traditional cultures with various subsistence strategies (e.g., foraging, low-level agriculture). In all of these cultures, high-status men, regardless of how status was achieved, had more wives in polygynous societies, were more likely to marry in monogamous ones, and had more surviving children in all societies relative to their low-status peers. However, the strength of these relationships varied from one culture to the next and is lower than that described for many primates in Chapter 5 of this volume. In these traditional contexts, there are social and material constraints on status striving that keep dominant men from monopolizing relationships with women (Boehm, 2009; Flinn & Low, 1986). These constraints include coalitions of other men that keep would-be despots in check and a limited ability to accumulate excess material wealth. The lifting of these constraints opened the door for the emergence of early human empires, and here the relationship between men's status and their reproductive success is at least as strong as, if not stronger than, that found with many nonhuman primates (Betzig, 1986, 2012).

Across traditional contexts, the achievement of status results from a mix of physical dominance and prestige (e.g., hunting skills). The importance of hunting success and men's reproductive prospects was discussed in Chapter 7 of this volume. In addition to helping to attract a mate and provision children, some portion of the proceeds from successful hunts are shared with other group members and results in significant prestige for successful men.

The focus here, however, is on dominance-related status seeking. The associated issue of whether people are inherently aggressive or cooperative has occupied philosophers for many centuries and remains a point of contention among anthropologists (Culotta, 2013; Fry & Söderberg, 2013; Gat, 2019; Hames, 2019). The debate is largely over whether or not hunter–gatherers engaged in coalitional between-group competition or warfare, as was described for chimpanzees (*Pan troglodytes*; see Chapter 5, this volume). The twist is that warfare will favor the evolution of cooperative behavior among members of the ingroup (Bowles, 2009), such that humans might not be such extraordinary cooperators without an evolutionary history of warfare. When combined with the argument presented in Chapter 5 of this volume, the anthropological and archaeological records are consistent with an evolutionary history of physical male–male competition, including lethal violence and warfare—if this was not the case, then men and women would be about the same size and muscularity. Phylogenetic analyses (i.e., cross-species analysis to infer evolutionary history) also reveal that the killing of members of ones' own species (conspecifics) is common in mammals and especially in primates, and humans in hunter–gatherer groups fit right in with the general pattern found among primates (Gómez, Verdú, González-Megías, & Méndez, 2016; Wrangham, Wilson, & Muller, 2006).

As described in the following sections, per capita violence occurs much more frequently in traditional societies and in the historical record than it does in highly developed nations today. The result is much higher rates of male-on-male physical aggression and homicide in these traditional contexts (Daly & Wilson, 1988b), as well as an ongoing potential for the eruption of violence in modern nations. These dynamics were captured by Hobbs' (1651) conclusions about the nature of man:

> So that in the nature of man, we find three principal causes of quarrel. First, competition; secondly, diffidence [anxiety regarding one's security]; thirdly, glory [prestige]. The first maketh men invade for gain; the second, for safety; and the third, for reputation. . . . Whatsoever therefore is consequent to a time of war, where every man is enemy to every man . . . and which is worst of all, continual fear, and danger of violent death; and the life of man, solitary, poor, nasty, brutish, and short. (pp. 96–97)

Hobbs' argument does not mean that men will impulsively attack one another with the slightest offense, but rather that social structures (e.g., third-party policing) are necessary to reduce the frequency with which conflicts of interest escalate to lethal violence and to prevent the predatory violence (e.g., raiding) of other groups (Eisner, 2003). The modern world is a testament to the importance of these structures (e.g., treaties, trade; Pinker, 2011), but the ability to live cooperatively with other groups and sustain the peace has more shallow evolutionary roots than does the potential for violence (Gómez et al., 2016; Hames, 2019). This is all the more reason to acknowledge our evolutionary history and the corollary that peaceful coexistence requires continual effort.

Traditional Societies

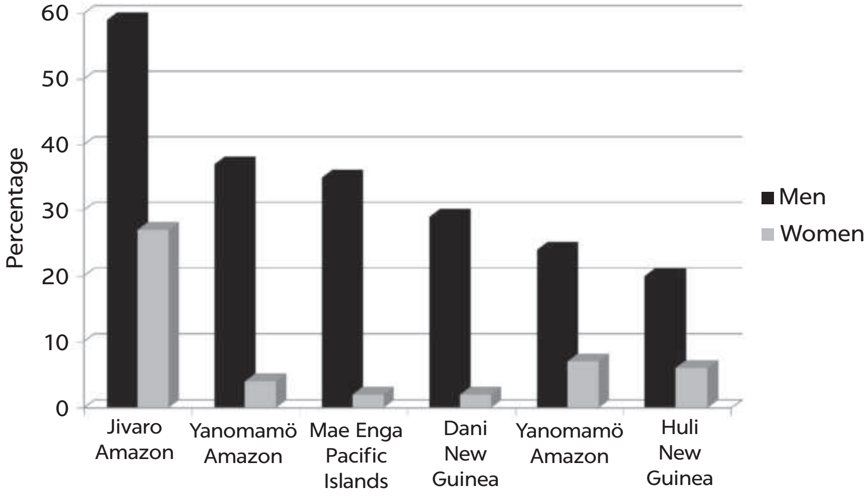
Across species, sex differences in the physical size and strength of males and females is consistently associated with an evolutionary history of intense male–male competition and polygyny, and there is clear evidence for this during human evolution (see Chapter 5, this volume). It is not surprising that polygynous unions are common in 6 out of every 7 traditional societies, whereby 10% to 20% of men will have several wives (Murdock, 1981). As was shown in Table 7.2 (see Chapter 7, this volume), polygyny can be achieved through social power, resource control, or some combination.

Social power polygyny is the most similar to male–male competition in nonhuman primates and is common in societies in which material resources are not easily controlled. The Yanomamö (Venezuela, Brazil) provide a well-studied illustration of these dynamics (Chagnon, 1997, 2013). Social relationships among Yanomamö men include within-group one-on-one social displays and physical aggression to resolve disputes and to establish social dominance, a pattern still found among certain subgroups in developed nations (R. King & O'Riordan, 2019). Wherever they occur, within-group aggression often results from conflicts over sexual relationships (e.g., infidelity) and ranges from chest pounding to club fights to machete fights (using the flat part of the blade). The goal is not to kill the opponent but to cause sufficient injury to make him withdraw from the duel. The clubs are 8 ft to 10 ft long and are used to deliver blows to the top of the opponents' head. The welts that accumulate over many years of such fights become a status badge, as they indicate courage and the ability to survive these fights. The fights do not typically result in death, but they can; K. Hill and Hurtado (1996) found that 8% of Ache (Paraguay) men died as a result of similar club fights.

As was described for chimpanzees, men also cooperate and form coalitions as a means to gain advantage over or in defense of the competing interests of other communities. These between-group dynamics can be quite varied, ranging from cooperation and low levels of conflict to the political intimidation of smaller groups by larger ones and the raiding of neighboring villages. When they occur, the raids are often for blood revenge (i.e., avenging harm inflicted on kin) and, when opportunity permits, the capture of brides (Chagnon, 1988, 1997). In this social climate, men who are skilled at political negotiations or are fierce warriors enjoy a higher social status than do other men, but they do not have more material wealth (Hames, 1996). Fierce warriors are men who have participated in the killing of a man from a rival village. In the Yanomamö villages studied by Chagnon (1997), 2 out of 5 men have participated in at least one such killing. These men marry sooner and more often. They have 2.5 times as many wives as men who have not participated in a killing and 3 times as many children. Overall, among the Yanomamö and across South American tribes before contact with the outside world, about 1 out of 4 men died violently, and largely during the course of between village raids (R. S. Walker & Bailey, 2013). Chagnon concluded male-on-male violence is ultimately about reproductive competition.

These patterns of male-on-male violence are not restricted to South American groups, and in fact are common features of hunter–gatherer, horticultural, pastoral, and agricultural societies generally. In a review of violence before the rise of "civilization," Keeley (1996) found that ambushes and raids occur near continuously or frequently in about 70% of hunter–gatherer societies and even more frequently in agricultural and pastoral societies (see also Ember, 1978; Ember & Ember, 1994; D. R. White & Burton, 1988). Many of the more peaceful societies are relatively isolated or politically subjugated to larger groups, which often suppresses between-group conflict (Keeley, 1996). Across societies, Keeley estimated that about 1 out of 3 men died as a result of some form of raid, ambush, or larger-scale conflict. Examples of mortality rates resulting from these forms of male–male competition are shown in Figure 8.1. As can be seen, women were not immune to this violence, but still had consistently lower rates of violent death than did men. The motives reported in ethnographies of North American Indian tribes for initiating between-group conflicts are shown in Figure 8.2 (Keeley, 1996). These are similar to those reported in other regions of the world and include blood revenge, economic gain (e.g., land, booty, slaves), the capture of women, and personal prestige. The latter involves the accumulation of culturally important trophies (e.g., the heads of competitors) that influence the man's reputation and social status within the community, which in turn will influence his desirability as a marriage partner.

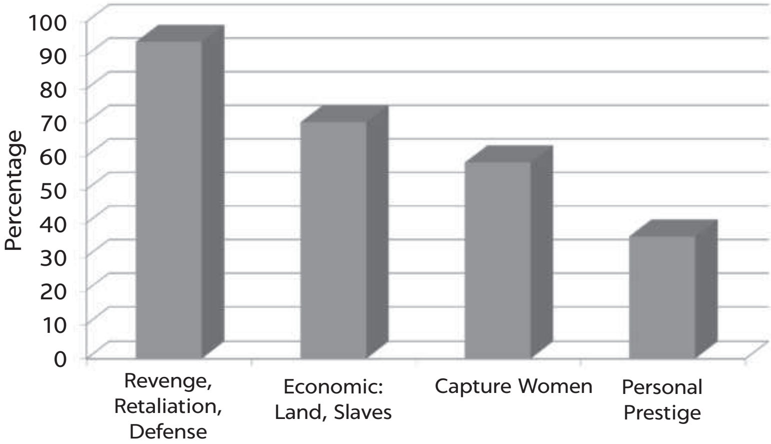
FIGURE 8.1. Mortality Rates From Ambushes, Raids, or Large-Scale Warfare for Six Traditional Societies



The values for the Yanomamö are from two different groups, the Shamatari (left) and the Namowei (right). Data from Keeley (1996).

Deadly male-on-male violence is found in other regions of the world, as shown in Figure 8.3 for Australian aborigines, including societies without explicitly designated status differences among men. The Gebusi of New Guinea, for instance, are described as being primarily a gatherer society (with some hunting) with men's social life "markedly devoid of male status rivalry. Instead, there is a pronounced aura of diffuse male friendship and camaraderie" (Knauft et al., 1987, p. 460). Yet, the Gebusi had one of the highest per capita

FIGURE 8.2. Reported Motives for Warfare for North American Indian Tribes



Data from Keeley (1996).

FIGURE 8.3. Australian Aborigine Band Under Attack From Another Band

From "Ancestral Hierarchy and Conflict," by C. Boehm, 2012, *Science*, *336*, p. 844. Copyright 2012 by the American Association for the Advancement of Science. Reprinted with permission.

murder rates in the world, including a precontact homicide rate that was estimated to be more than ten times that found in most major cities in the United States. Although Knauft and colleagues (1987) argued that the proximate cause of Gebusi murders are superstition (e.g., sorcery, casting of a magic curse) and other psychological factors and not reproduction, they nonetheless concludes that "sorcery homicide is ultimately about male control of marriageable women" (Knauft et al., 1987, pp. 465–466). Similar patterns are found in other so-called peaceful societies (Daly & Wilson, 1988b; Ember, 1978; Keeley, 1996; Knauft et al., 1987). Male-on-male violence extends deep into human history and is reflected in archaeological evidence dating back up to 20 to 30 thousand years:

For example, at Crow Creek in South Dakota, archaeologists found

> [a mass] grave containing the remains of more than 500 men, women, and children who had been slaughtered, scalped, and mutilated during an attack on their village a century and a half before Columbus's arrival (ca. A.D. 1325). The attack seems to have occurred just when the village's fortifications were being rebuilt. All the houses were burned, and most of the inhabitants were murdered. This death toll represented more than 60 percent of the village's population, estimated from the number of houses to have been about 800. The survivors appear to have been primarily young women, as their skeletons are underrepresented among the bones; if so, they were probably taken as captives. (Keeley, 1996, p. 68)

The capture of women and the murder of competitors has nothing to do with female choice—it is men pursuing their reproductive interests at the expense of other human beings (D. R. White & Burton, 1988). The potential for coalitional violence can be heightened in populations with a high proportion of young men (15 to 30 years of age) who do not have sufficient resources to attract a wife (Mesquida & Wiener, 1996). In these circumstances, the reproductive prospects of many young men drop and, as a result, the costs of risky aggression decrease and the potential benefits increase (M. Wilson & Daly, 1985). In traditional societies, expansion into neighboring territories—to acquire resources or to capture women—is one potential and apparently common response to these conditions (Mesquida & Wiener, 1996). This is not to say that having too many men will necessarily lead to violence, and in fact when this violence is kept in check (e.g., third-party arbitration of disputes), men often compete by becoming better husbands and providers (see Chapter 6, this volume; Schacht, Rauch, & Borgerhoff Mulder, 2014), but this does not belie the importance of physical male-on-male violence as a component of sexual selection in many traditional contexts and throughout human evolution (T. L. Carter & Kushnick, 2018).

Early Empires

The development of large-scale agriculture supported larger populations and helped to keep at least one Horseman of the Apocalypse, Famine, at bay or at least reduced the frequency of its visits (G. Clark, 2008). At the same time, the additional calories produced by these initially small agricultural communities and the ability to store them (e.g., grains, livestock) created a temping source of wealth for the taking (Hirschfeld, 2015; P. Turchin, 2009). The details are not critical here, but the theft of these communities' resources by nomadic raiders created benefits for the formation of larger agricultural communities. To counter the defensive advantage of these larger communities, smaller nomadic groups had to unite to continue their raiding. This type of cycle appears to have occurred in many parts of the world, aided by advances in military technology (e.g., chariot), and eventually led to the formation of empires (P. Turchin, 2009; P. Turchin, Currie, Turner, & Gavrilets, 2013) and the out-sized influence of one of the other Horsemen, War.

The formation of larger states, and ultimately empires, was achieved and maintained by an increase in the level of male-on-male violence and resulted in a substantial increase in the level of polygyny and reproductive and material inequality among men and their families (Betzig, 1986, 2012; Gómez et al., 2016; Raffield, Price, & Collard, 2017; Scheidel, 2017). As noted, in hunter–gatherer societies would-be despots are kept in check by coalitions of other men, but this is no longer effective in larger groups (Boehm, 2009, 2012). The result is the potential for despots and their allies to emerge and to exert control over other people with force or threat of force. In these societies, coalitions of men practiced a combination of social power and resource-based polygyny.

Betzig (1986, 1993) argued that in each of humanity's early civilizations (ancient Mesopotamia, Egypt, Aztec [Mexico], Inca [Peru], and imperial India and China), "powerful men mate with hundreds of women, pass their power on to a son by one legitimate wife, and take the lives of men who get in their way" (Betzig, 1993, p. 37). The population genetic studies described below confirm that these social dynamics have occurred many times during recent human history, in many parts of the world, and must have altered the path of human evolution. The overall historical pattern is consistent with Boehm's (2012) argument that in the absence of social controls and moral constraints, a subset of men will more fully express the ancestral dominance-related reproductive strategies seen in nonhuman primates (see Chapter 5, this volume).

Reproductive Skew

As described in Chapter 5 of this volume, dominant males sire more offspring than their less-competitive peers, resulting in reproductive skew. The same is true for men in traditional societies. Among the Yanomamö studied by Chagnon (1979, 2013), the most successful man, nicknamed Shinbone, had 11 wives and 43 children, as compared with 14 children for the single most successful woman. Shinbone's father "had 14 children, 143 grandchildren, 335 great grandchildren and . . . 401 great-great grandchildren" (Chagnon, 1979, p. 380): the two latter estimates are low because many of the descendants of Shinbone's father are still in their reproductive years. At the same time, many low-status Yanomamö men never marry or reproduce (Jaffe et al., 1993).

More typically, the reproductive differences across men in societies with social power polygyny are not this extreme but can still be substantial and evolutionarily significant. There are, of course, individual differences in the number of children that women successfully raise to adulthood, but the differences are larger among men than among women (Archer, 2009; Betzig, 2012). For example, in the traditional society of the Xavante (Brazil), women had on average 3.6 surviving children and variation among women (i.e., standard deviation) was 3.9 children (Salzano, Neel, & Maybury-Lewis, 1967). The average number of children for men was also 3.6, but the variation among men was 12.1. In other words, the differences in the number of children among men was about 3 times larger than the differences among women. Betzig (2012) reports similar ratios for hunter–gatherer, horticultural, and pastoral societies. In all cases, there was more variation in the reproductive success of men than women, but this ranged from a slight difference among the Yomat (Iran; male:female ratio of *SD*s = 1.14) to a large difference among the Kipsigis (Kenya; male:female ratio of *SD*s = 14.5). The !Kung San (Botswana) were right in the middle, with the reproductive variation among men being almost twice that of women. In other words, there were more men than women at the extremes of having many children or no children.

These patterns are consistent with the cross-species findings that sexual selection is a potent evolutionary pressure (Janicke et al., 2016), and specifically indicate that competition for control of the social and material resources that contributed to the ability to have children was stronger in men than in women in traditional contexts. The sex difference in reproductive outcomes only became larger with the advent of larger-scale societies and empires. Compared with the !Kung San, reproductive variation among men was 8 to

40 times larger in humanity's early empires (Betzig, 2012), indicating a substantial increase in the importance of male–male competition and the use of dominance-related strategies during this phase of human history. Betzig recounts many examples from the historical record, including the following:

> In the Ancient Near East, where civilization began, the emperor Shulgi, the law giver and ziggurat builder, left behind the names of at least 54 dumu lugal (or princes, or "sons of the king") and dumu-SAL lugal (or princesses, or "daughters of the king")—"because I am a strong man, rejoicing in my loins," as he bragged in stone. (Betzig, 2012, p. 312)

Competition in Developing and Developed Nations

Hobbs' (1651) solution to the short and brutish life of man was the biblical Leviathan or in the flesh an all-powerful sovereign (monarch) who had the ability to suppress the violent resolution of disputes and act as a third-party arbiter (see Figure 8.4). Despite the increase in male-on-male violence in early empires, the emergence of larger states often had the paradoxical effect of suppressing violence among members of the ingroup (Hirschfeld, 2015), although rapacious wars against outgroups often continued (Scheidel, 2017). The suppression of ingroup violence was not out of any particular concern for the well-being of these citizens, but rather the more pragmatic goal of allowing them to produce more that might then be taxed or expropriated by elites in other ways. Even so, one result was long stretches of history in which ingroup social stability was achieved in many parts of the world, with some basic individual rights (e.g., property; G. Clark, 2008). In the Western world, for instance, there was a steady decline in violence and a steady increase in individual rights throughout the middle ages that continues to this day (Daly & Wilson, 1988b; Eisner, 2003; Gómez et al., 2016; Pinker, 2011, 2018), and this once again altered the pattern of evolutionary selection (Corbett, Courtiol, Lummaa, Moorad, & Stearns, 2018).

An important aspect of these historical changes was the gradual emergence of socially imposed monogamy that reduced the reproductive skew among men and thereby reduced the benefits of extreme violence (Henrich, Boyd, & Richerson, 2012). Moreover, fewer restrictions on women's reproductive behavior and mate choices in these societies almost certainly contributed to the change in the flavor of men's competition, shifting it toward traits that reflect women's preferences. Overall, these historical changes reduced the benefits of dominance-based competitive strategies and enhanced the benefits of prestige-based strategies. Even if expressed in different ways, the achievement of cultural success remained important for men, for developing nations and for developed nations today.

Developing Nations

The relationship between men's social status and their children's mortality risks in industrializing Europe and the United States was discussed in Chapter 6 of this volume. The children of high-status men were healthier and more

FIGURE 8.4. Hobbs and the Leviathan

Hobbs argued that an all-powerful sovereign was needed to keep people in awe and suppress the violent resolution of disputes. The resulting commonwealth would create a more peaceful society. From *Leviathan, or the Matter, Forme, & Power of a Common-Wealth Ecclesiastical and Civill* (frontispiece), by T. Hobbs, 1651, London, England: Andrew Crooke. In the public domain.

likely to survive to adulthood than the children of low-status men (Hed, 1987; Schultz, 1991). However, if low-status men had many children their reproductive success could have been equal to or better than that of their high-status peers, even if many of these children did not survive to adulthood. At times this was the case, but it was not the norm (Korpelainen, 2000). Despite socially imposed monogamy, high-status men had more children survive to adulthood for a combination of reasons. They were more likely to marry, and relative to low-status men who did marry, high-status men often married earlier, married younger brides, were more likely to remarry following divorce or death of a spouse, and were more likely to sire illegitimate children (Käär et al., 1998; Low & Clarke, 1992; Nettle & Pollet, 2008). High-status men were also less likely to die prematurely and therefore had a longer reproductive lifespan than did low-status men (J. L. Boone, 1986; Low, 1990b).

The pattern is illustrated by extensive parish and government birth, marriage, and death records between 1720 and 1874 for Krummhörn men in Northwest Germany (Klindworth & Voland, 1995; Willführ & Störmer, 2015). Information from tax records indicated large differences in the wealth (e.g., land, cattle) held by different families. Relative to other men, the wealthiest men sired more children, largely because they married younger wives who had a longer reproductive lifespan and shorter inter-birth intervals. Across generations, low-status men were 4 times more likely than wealthy men to experience an extinction of their lineage (i.e., leaving no direct descendants); the same pattern emerged during China's Qing dynasty (Song, Campbell, & Lee, 2015). In developing societies, men's relative status influenced their reproductive success even among the privileged classes. The majority of these men had a single legal wife with whom they sired legitimate heirs, but those of the highest status (e.g., king) were more like to have concubines (e.g., J. L. Boone, 1986). For some groups within Western culture (e.g., early Mormons), polygynous marriages remained common and resulted in reproductive advantages for high-status men (Mealey, 1985).

Overall, status in these societies still influenced men's reproductive prospects, although socially imposed monogamy reduced the strength of the relation between status and reproductive outcomes relative to that found in traditional societies (Nettle & Pollet, 2008; Ross et al., 2018). At the same time, high-status women did not always have more surviving children than their low-status peers (J. L. Boone, 1986; Low, 1990b). High-status women were less likely to "marry down" than were high-status men, and the pool of available mates was smaller for high- than for low-status women. J. L. Boone (1986), for instance, found that about 40% of Portuguese noblewomen in the 15th and 16th century lived their adult years in convents and never reproduced, compared with about 28% of low-status women. The decline in family size that followed reductions in child mortality in Western Europe began earlier with nobility than with other women. Despite great wealth and access to servants, the typical British noblewoman had an average of 2.3 children during her lifetime in 1500, declining to an average of 1.5 children by 1850 (Westendorp & Kirkwood, 1998): the smaller number of children may have resulted in the benefit of a longer lifespan for these women. At the same time, bourgeoisie women often had more children than did low-status women, typically because they were married to wealthier men, even if most of these men were not nobility (G. Clark, 2008).

Developed Nations

The relationship between men's cultural success and their reproductive success continues today in developed nations, although the strength of this relation is smaller than is found in developing nations or traditional societies (Hopcroft, 2019; Nettle & Pollet, 2008; Ross et al., 2018; Weeden, Abrams, Green, & Sabini, 2006). The cross-context differences in the strength of this relation are due in part to socially imposed monogamy and contraceptive use in developed nations (Moorad, Promislow, Smith, & Wade, 2011; Pérusse, 1993).

These factors may reduce reproductive skew among men, but they do not decouple the relationship between men's status and their ability to attract sexual partners. Pérusse (1993) studied the relation between socioeconomic status (SES; a composite of income, occupational status, and education) and the sexual behavior of more than 400 men from Québec, including the number of reported sexual partners and the overall frequency of intercourse. The two latter factors were used to derive an estimate of the likelihood of paternity, in the absence of birth control. For unmarried men 30 years of age and older, higher SES was associated with more sexual partners and more overall sexual activity. The combination explained as much as 63% of the individual differences in the likelihood of paternity in the absence of birth control. This relationship was somewhat lower, but still positive, in younger unmarried men. The basic relationship between status and mating success remains intact but is not as strongly related to the number of children men sire in developed nations relative to other contexts.

Hopcroft (2006) confirmed this pattern using a series of large, nationally (United States) representative surveys of adults. Men with higher incomes reported more sexual activity than did men with lower incomes and women at any income level. Hopcroft also found that men with higher intelligence had less sex than their more average peers. Her findings suggest that composite measures of SES may obscure the relationship between men's status and sexual opportunity, because income and intelligence work against each other when it comes to finding partners. The same result emerged for the number of biological children. The highest income men, on average, had about 2.5 children compared with an average of 1.4 children for the lowest income men. These results are likely to underestimate the actual relationship, because institutionalized men were not included in these surveys and the highest income group collapsed across a very wide range of incomes. Again, men's intelligence worked against their reproductive success, except to the extent that it influenced their income. Nettle and Pollet (2008) found the same in Great Britain and Goodman and Koupil (2010) found the same in Sweden: Men who earned more had more children, but men with advanced educational credentials did not.

The importance of income and status has also been underestimated in some studies, because they have excluded men who were childless. This is a critical oversight because from an evolutionary perspective being childless terminates the man's direct lineage. Fieder and Huber (2007a) addressed this confound using a sample of 7,000 45- to 55-year-old Swedish men. When childless men were excluded, men in the lowest 25% of income had the most children, followed by men in the highest 25% of income. When childless men were included, however, men who were higher in the income hierarchy had more children than did men lower in the hierarchy, as found by Hopcroft (2006, 2015) for the United States and von Stumm, Batty, and Deary (2011) for Scotland. The different patterns emerged because about 1 out of 3 men in the lowest income category were childless by age 55 and were likely to remain so, whereas about 1 out of 9 men in the highest income category were childless. Using a national sample of 45- to 55-year-old men in the United States, Weeden et al. (2006) also found that men with higher incomes had more children and were less likely to be childless than men with lower incomes. The same was found among Harvard graduates. Independent of their wives' incomes, the most successful graduates had more children than their less successful peers, although they were all successful overall. A similar relationship between status and number of children was found for 2,693 university employees (Fieder et al., 2005).

Men's cultural success contributes to their reproductive success in developed nations, but the strength of this relationship is weaker than in other contexts. The relation emerges largely because fewer lower status and lower income men marry relative to men with average or better incomes. When it comes to defining cultural success in these contexts, at least in terms of marriage prospects, it's the money that matters, independent of intelligence or educational background. A man's diploma from a fancy university will not pay the rent, but his paycheck will. This is effectively the same pattern found in other contexts. It is the resources that can be directly transferred from men to women that matter. In developed nations, it is cash instead of cows.

Testosterone

Testosterone and related hormones (e.g., dihydrotestosterone) are critical for the emergence of primary sex differences (e.g., sex organs) and the secondary physical, behavioral, and cognitive sex differences related to sexual selection in males (see Chapter 4, this volume). Individual males will differ in terms of the amount and timing of prenatal and early postnatal testosterone exposure, basal (everyday) levels, and in the extent to which testosterone concentrations change in response to social conditions (Adkins-Regan, 2005). In adulthood, testosterone organizes males' reproductive behaviors, including status striving, responses to status-related challenges, and sexual behavior (M. N. Muller, 2017). For species with facultative male parenting, circulating testosterone concentrations can influence whether they invest relatively more in parenting or in seeking mates (Wingfield, Hegner, Dufty, & Ball, 1990).

The same basic hormonal mechanisms operate in people. The production of testosterone increases about 20-fold as boys move from childhood into adolescence, resulting in a 15-fold difference in the plasma (blood) concentrations of testosterone in healthy young men and women (Handelsman, Hirschberg, & Bermon, 2018). Although the behavioral sex differences found in other primates are also found in people, fully understanding them is complicated by the different ways in which men can achieve status; by the dynamics of marital relationships (see Chapter 6, this volume); and by sexual experience, social context, and other factors. Despite these complications, much is known about the influence of testosterone on adolescent boys' and men's motivations and behavior. The following sections review the relationship between testosterone and changes in adolescents' behavior, men's status striving and response to challenges, and their sexual motivations, respectively.

Puberty and Aggression

Adolescent boys and girls show the same basic hormone-dependent changes in brain, cognition, and behavior that prepare other mammals for competition for mates and parenting in adulthood (Schulz & Sisk, 2016). In male mammals that engage in intense male–male competition, there are testosterone-dependent increases in areas of the brain (e.g., amygdala) that are important for reacting to and learning from social experiences, including the establishment of dominant–submissive relationships among males and sexual behavior with females (Sisk, 2016). These social-affective systems (e.g., related to emotions) also become more fully integrated with the brain systems that support physical competencies and acting on the environment. The sex difference in these latter systems tends to be particularly pronounced in species with intense male–male competition (Stanyon & Bigoni, 2014), and it is not surprising that testosterone-dependent sex differences in these same brain systems have now been documented in adolescent boys and girls (Goddings et al., 2014; Neufang et al., 2009). Many of these pubertal changes are also dependent on prenatal exposure to testosterone and can be weaker or stronger depending on current testosterone concentrations (Ernst et al., 2007; Stanton, Wirth, Waugh, & Schultheiss, 2009).

Play fighting among juvenile males is common in species with intense physical male–male competition over mates (see Chapter 4, this volume), and the associated sex differences for children are discussed in Chapter 10 of this volume. It is noted here that this type of rough-and-tumble play begins to merge into more serious physical aggression and bullying as boys enter adolescence (Konner, 2010; Olweus, Mattsson, Schalling, & Löw, 1980; Pellegrini & Bartini, 2001; A. A. Volk, Camilleri, Dane, & Marini, 2012) and is associated with an uptick in the potential for much more serious aggression and risk taking as boys move through adolescence and into early adulthood (M. Wilson & Daly, 1985). However, studies of developing adolescents indicate that the increases in testosterone concentrations during puberty do not, in and of themselves, result in a reflexive increase in male-on-male physical aggression for most boys (Archer, 2006; C. T. Halpern, Udry, Campbell, & Suchindran, 1993) as it does in some other species, such as the mandrill (*Mandrillus sphinx*). The very intense one-on-one male–male competition in mandrills is associated with a rapid pubertal increase in body size and in physical aggressiveness (Leigh, 1995).

Unlike rapidly maturing adolescent mandrills, adolescent boys are not prepared for the rigors of male–male competition found in traditional contexts, and the relationship between testosterone and competition should be weaker for them than for mandrills or for adult men. The drawn-out period of boys' adolescence is more about beginning to test, learn about, and form one-on-one dominant–submissive relationships among peers and the forming of more cohesive competition-related groups (see Chapter 11, this volume). All of these changes in the nature of peer relationships are preceded by changes in adrenal hormones during childhood and facilitated further by the pubertal increase in testosterone concentrations, for instance by improving learning from competition-related experiences (P. B. Gray, McHale, & Carré, 2017; Sisk, 2016).

These adolescents also need to begin to integrate into men's social networks and to intensify engagement in culture-specific forms of competing for status. For instance, in societies in which warfare is frequent and deadly, men assess boys' ability to cope with extreme stressors through painful initiation rites or a series of rites (Sosis, Kress, & Boster, 2007). The pubertal increase in testosterone concentrations will facilitate the suppression of fear and the ability to tolerate these types of rituals (Stanton et al., 2009). The initiates' composure during the ritual is an assessment of their readiness for adulthood and very likely is an assessment of their ability to engage in potentially deadly male–male competition, especially warfare (Straight et al., 2019). Sosis et al. (2007) provided an example of this for the Eastern Toraja (Eastern Indonesia):

> In this society, boys are subincised (a cut along the bottom of the penis) yearly beginning at 6 years old and ending at 15. Around age 12, boys are circumcised in a public ritual. . . . There is a public initiation rite into manhood where boys are cut on their arms, hands, and legs, as well as, burned on the torso and arms. Boys cannot show any pain during the public ceremonies. (p. 238)

The albeit toned-down expression of the same types of social rituals is also found in developed societies, with the hazing common in adolescent boys' and young men's groups (K. R. Browne, 2002). These rites of passage test the developing males' ability to regulate their emotions under stress and are important components of building trust and bonding among the group of men and of course for initiating new members into the group. These types of social behaviors and processes are consistent with men's coalitional competition and an evolutionary history of warfare. The overall pattern suggests that boys' drawn-out adolescence is a life-history period in which they are learning about their place in the dominance hierarchy among peers, refining strategies for achieving status in their culture, and integrating into the wider social network of men. The hormonal changes that occur during this time appear to motivate boys to engage in these social behaviors (e.g., status seeking) and contribute to their ability to cope with the increased intensity of competition.

Competition and Social Challenge

The relationship between men's testosterone concentrations and their relative focus on mating or on parenting was described in Chapter 6 of this volume. The questions addressed here are whether circulating testosterone concentrations influence men's status striving and the intensity with which they react to challenges to their status (P. B. Gray et al., 2017; Mazur & Booth, 1998), as it does with nonhuman primates (M. N. Muller, 2017). Despite similar hormonal influences on status striving, men compete using a combination of dominance- and prestige-based strategies (Henrich & Gil-White, 2001; Maner, 2017), as contrasted with the dominance-based status striving in nonhuman primates. As noted previously, prestige-based status is the norm in developed nations and results in many different ways in which men can achieve cultural success that do not include physical aggression. Of course, dominance-based relationships do still occur, but their frequency and their influence on social status decline across traditional cultures, developing nations, and developed nations.

Putting aside differences between dominance- and prestige-based strategies, the overall relation between circulating testosterone concentrations and status striving, aggression, and related behaviors is reciprocal, but the strength of these relations is modest and not yet fully understood (Archer, Graham-Kevan, & Davies, 2005; Dekkers et al., 2019; Mazur & Booth, 1998). As with other primates, men's status-related competitiveness is associated with multiple hormone systems. Status striving may be suppressed when the concentrations of the stress hormone cortisol increase (Mehta & Prasad, 2015), but this is not certain (Grebe, Del Giudice, et al., 2019). For men, higher testosterone concentrations are generally related to stronger status striving but not necessarily to more overt aggression and might even prompt generosity if this improves status (Dreher et al., 2016). Moreover, the reactivity of men's testosterone concentrations to status-based competition and challenges will be influenced by their current status (Maner, Miller, Schmidt, & Eckel, 2008), and by how relevant the current challenge is to their status in the culture-specific niches they occupy (Carré & Archer, 2018). A status-related challenge to one man may not be important to another, depending on how closely the activity matches the man's interpretation of how the event influences his position in the niches that are important to him (D. Cohen, Nisbett, Bowdle, & Schwarz, 1996; Gonzalez-Bono, Salvador, Serrano, & Ricarte, 1999; Salvador, 2005).

Despite these nuances, most men will show the same basic challenge response found in nonhuman primates (M. N. Muller, 2017) and in other species during status-related confrontations (Wingfield et al., 1990). As in nonhuman primates, men's basal testosterone concentrations and the extent to which these concentrations change in confrontational and competitive situations can influence the vigor of their responses to these challenges (Carré & Olmstead, 2015; Goetz et al., 2014; Josephs, Sellers, Newman, & Mehta, 2006; Kaldewaij et al., 2019; Mehta, DesJardins, van Vugt, & Josephs, 2017), especially if they have a high need for social dominance and are biologically sensitive (e.g., many cell receptors) to testosterone (Geniole et al., 2019). Testosterone concentrations generally increase prior to competitions that are meaningful to men and increase further if the man wins the competition, but will often decline if he loses (Geniole, Bird, Ruddick, & Carré, 2017). This pattern is called a winner–loser effect, and it contributes to men's adaptive responses to current circumstances (see Geniole & Carré, 2018). Rapid increases in testosterone concentrations when challenged organizes the man's physiological, including sensitivity to social threats, and behavioral responses to the challenge, and facilitates his learning from these experiences (Schultheiss et al., 2005). Repeated success at achieving status-related goals or competitions and associated increases in testosterone concentrations are rewarding and will motivate further attempts to increase status that in turn can result in further increases in testosterone. Repeated failures can result in long-term depression of testosterone concentrations that prompts disengagement from the competition and if possible, the seeking of status within an alternative cultural niche.

These hormonal patterns and associated behavioral responses appear to be exaggerated among men with strong dominance-related social motives or would-be alpha males (Carré et al., 2017; Schultheiss, Wirth, & Stanton, 2004; Schultheiss et al., 2005). Relative to their less ambitious peers, men with strong status-related motivations show larger increases in testosterone concentrations after winning a competition and larger declines after losing one. They also have stronger stress responses after losing a competition, as indicated by a spike in cortisol concentrations (Archer, 2006; Wirth, Welsh, & Schultheiss, 2006). There is some evidence that low-status men who are status strivers have higher than average testosterone concentrations and engage in more dominance related behaviors that would facilitate attempts to move up the hierarchy (Josephs et al., 2006; van der Meij, Schaveling, & van Vugt, 2016). However, striving to become the alpha male and actually achieving this status are two different things. Many men who are strong status strivers will not achieve the level of acclaim and dominance they desire, which will weaken the relationship between testosterone concentrations and actual status.

In any case, most of these studies have examined short-term changes in circulating testosterone concentrations, and oftentimes cortisol concentrations, and with respect to some type of direct one-on-one competition. Men's testosterone concentrations can also influence and be influenced by prestige-based status and coalitional competition. In a unique study, J. T. Cheng, Kornienko, and Granger (2018) examined the relation between testosterone concentrations and musical talent among members of a large college band. Men but not women with recognized and appreciated musical talent or prestige-based status showed substantial increases in circulating testosterone concentrations over time. Among the Tsimané (Bolivia), men who were successful on a hunt or part of a successful hunting party showed the standard winner-effect increase in testosterone concentrations, whereas men who were not successful showed no change or a slight drop in testosterone concentrations (Trumble, Smith, O'Connor, Kaplan, & Gurven, 2014). Most of the hunting proceeds were used to provision their family and were not part of a public display of prestige, but still revealed a hormonal response to success at a culturally important activity that contributes to men's social reputation.

In keeping with an evolutionary history of coalitional competition, hormonal responses can influence the formation and social dynamics among members of an ingroup and competitive and aggressive responses directed toward outgroups (Diekhof, Wittmer, & Reimers, 2014; Flinn, Ponzi, & Muehlenbein, 2012;

Oxford, Ponzi, & Geary, 2010). In the context of group-level competition, higher testosterone concentrations appear to facilitate ingroup cooperation and cohesion while simultaneously enhancing hostility toward the outgroup. Where the group-level competition occurs and individual men's contributions to the outcome can also influence their circulating testosterone concentrations (P. B. Gray et al., 2017). Neave and Wolfson (2003), for instance, found larger pregame increases in testosterone concentrations when soccer teams played in their "territory" (home field) than when they played in another team's territory. The increase in testosterone concentrations may provide home-team players with a modest physiological advantage and contribute to the home-field advantage effect (i.e., playing on the home field improves the chances of winning).

Postgame changes in testosterone concentrations are influenced by each competitor's contribution to their team's victory or loss and their attributions about whether the outcome was due to factors under their control (e.g., poor relative skills) or not (e.g., poor referee calls). Gonzalez-Bono et al. (1999) assessed testosterone concentrations in professional basketball players before and after a National Basketball Association (Spain) game. Compared with pregame concentrations, the testosterone concentrations of the players on the winning team increased and those of the losing team decreased, but these changes were small. Players on the winning team who thought the result was due to luck or to mistakes made by the referees did not show an increase in testosterone concentrations, but players who contributed the most points to their team's win had the highest pre- to postgame increases in testosterone concentrations. Trumble et al. (2012) found the same for Tsimané men who played well during a soccer match. Men's sensitivity to coalitional dynamics is even evident when they are simply viewing a competitive interaction. P. C. Bernhardt, Dabbs, Fielden, and Lutter (1998) found that the circulating testosterone concentrations of basketball and soccer fans increased if their team won and decreased if it lost.

Sexual Motivation

There is a tight relationship between prior hormone exposure, circulating sex hormone concentrations, and sexual behavior in most mammals, but this relationship is loosened in primates (Wallen, 2001; see Chapter 4, this volume). For primates, sex hormones motivate sexual activity, but its expression is also related to prior experience and to social and relationship context. It is not surprising that the same nuance is found in humans (P. B. Gray et al., 2017). Men in monogamous relationships, and especially men who have children, have lower testosterone concentrations than their peers (see Chapter 6, this volume). Men in monogamous relationships but who are open to an extra-pair affair or married men in polygynous societies do not show this reduction in testosterone concentrations (P. B. Gray, 2003; P. B. Gray, Ellison, & Campbell, 2007). These men are still primed to compete for mates and to quickly respond to novel mating opportunities should they arise.

Men on average have a consistently higher sexual desire than do women, but circulating testosterone concentrations are not consistently related to their sexual desire (e.g., frequency of thoughts about sex), in part because desire is also related to current mood, stress levels, and other factors (van Anders, 2012). Other factors aside, higher testosterone concentrations appear to be related to more positive attitudes about casual sex in men but not women (Puts et al., 2015). In keeping with this, for younger and older men higher testosterone concentrations are associated with higher numbers of sexual partners and, relative to other men, presumably more time and effort devoted to finding mates, although the magnitude of these relations is modest (Bogaert & Fisher, 1995; Peters, Simmons, & Rhodes, 2008; Pollet, van der Meij, Cobey, & Buunk, 2011; van Anders, Hamilton, & Watson, 2007). Actively maintaining several sexual relationships can increase testosterone concentrations, but these concentrations are also contributing to mating effort. Young men with relatively high circulating testosterone concentrations are more likely to be married 4 years later than are other men (Gettler, McDade, Feranil, & Kuzawa, 2011). Pollet et al. (2011) found this relationship even among men who were (on average) about 70-years-old and not likely to be engaged in multiple sexual relationships. Older men with higher basal testosterone concentrations reported a higher number of lifetime sexual partners, suggesting that basal levels are associated with effort devoted to finding mates, consistent with a relation between circulating testosterone and sexual motivations (Booth & Dabbs, 1993; Mazur & Booth, 1998).

Men's testosterone concentrations generally increase in contexts that provide or at least are perceived to provide sexual opportunity, with smaller increases when just viewing sexual activity (Escasa, Casey, & Gray, 2011; Roney, Lukaszewski, & Simmons, 2007). Roney, Mahler, and Maestripieri (2003), for instance, found increases in young men's testosterone concentrations after they interacted with a young woman, but only for men with prior sexual experience and primarily for men whom the woman rated as *displaying* (e.g., showing off, trying to impress). Flinn et al. (2012) found the same relationship for men interacting with potential mates on the Caribbean island of Dominica but suppressed testosterone concentrations when these same men were interacting with the partner of a friend and coalition partner. The latter would reduce mate poaching and thereby help to maintain the cohesion of the ingroup.

Experimental manipulations of testosterone concentrations in normal men also reveal nuanced effects that can vary from man to man. In a well-designed study, O'Connor, Archer, and Wu (2004) administered testosterone to normal men such that their concentrations reached that of the 98th percentile of all men. Following the increase in testosterone, these men reported less fatigue and more anger-hostility (in the normal range) but no increase in aggressive or sexual behavior. It remains unclear, however, whether these men would have showed an increase in sexual behavior with a novel partner. R. A. Anderson, Bancroft, and Wu (1992) found little change in men's sexual behavior following administration of testosterone but there was an increase in sensitivity to sexual cues. Men with low testosterone concentrations (e.g., because of aging), in contrast, tend to show increased interest in sex and heightened sexual arousability when administered testosterone, but whether or not the frequency of intercourse increases depends on prior sexual experience and on the nature of the relationship with their partner (Bancroft, 2005).

Brain-imaging studies indicate that when men view sexual activity there is increased activation of a distributed network of regions that may contribute to attentiveness to the physical attractiveness of women, as well as regions associated with erectile functions and more basic reward centers (Redouté et al., 2000; Rupp & Wallen, 2008). Many of these brain regions, as well as those associated with competition for mates, undergo developmental changes during puberty (Heany, van Honk, Stein, & Brooks, 2016; Wierenga et al., 2018), although these changes are not always related to changes in sexual behavior. The latter is probably due to social constraints on adolescent boys' ability to attract partners or compete against older adolescents or young men. In any case, these changes are consistent with puberty as a transitional period that bridges childhood and adulthood and the associated hormonal changes influence brain systems that contribute to sexual motivations and responsiveness to sexual opportunity, as well as changes associated with male–male competition.

Risk Taking

Risk taking is an important component of status striving and should be particularly evident in domains that are tied to cultural indicators of success and to activities that are potentially costly but also result in reputation enhancement, should they become known (e.g., through gossip) by others in the group. Theoretically, a sex difference in risk taking follows from the more intense reproductive competition among men than among women and the associated differences in the cost–benefit trade-offs of these activities. Indeed, there is a well-documented sex difference in the preference for taking risks, including making risky decisions (e.g., financial risks) and engaging in behaviors that could result in injury (Byrnes, Miller, & Schafer, 1999; A. Falk & Hermle, 2018). Byrnes et al.'s (1999) meta-analysis revealed a small sex difference, favoring boys and men, in risk taking in a variety of contexts. There were no sex differences in engagement in some risky behaviors, such as self-reported smoking, but moderate differences in engagement in intellectual and physical risks. Overall, about 2 out of 3 men engage in these behaviors more often than does the average woman. The sex difference is even larger when it comes to financial risk taking, with women investing between 20% and 50% less than men when the outcomes are ambiguous (Charness & Gneezy, 2012).

Across ages, risk taking is much more common when an audience is present, as would be expected if it enhanced social reputation (Ginsburg & Miller, 1982; D. C. Miller & Byrnes, 1997; M. Zuckerman & Kuhlman, 2000). Psychologically, these sex differences are related in part to the different ways in which men and women assess the costs and benefits of risk taking. C. R. Harris, Jenkins, and Glaser (2006), for instance, found that women focus more on the potential costs of risky behaviors and men focus more on the benefits and enjoyment of the activity. Men understand the potential costs, but rate these as less severe and less likely to happen than do women. These types of psychological and economic studies, though informative, do not fully address evolutionary questions regarding the cost–benefit trade-offs of risk taking, because they are conducted with people living in low risk developed nations.

In an evolutionarily grounded analysis, Mata, Josef, and Hertwig (2016) assessed the risk preferences of nearly 150,000 people across 77 nations. Overall risk taking for men, women, and young and older adults increased as life became more difficult (e.g., lifespans are shorter; M. Wilson & Daly, 1997). The key finding for the current discussion is that young men throughout the world were the most prone to taking risks, in keeping with an increase in the frequency of high-risk behavior as men enter the early stages of status striving and reproductive competition (M. Wilson & Daly, 1985; see also Chapter 14, this volume). Even the Mata et al. study likely underestimates the sex difference in risk taking, because the risk assessment included endorsing wanting to have an exciting life which could be interpreted differently by men and women.

The extent to which men are willing to engage in risky behaviors and the real underlying sex difference in tolerance of risk can only be understood in the context of actual reproductive competition in traditional cultures. To illustrate, consider the nomadic raiders mentioned previously. These raids were undertaken by men who were risking death but also obtained substantial material and reproductive benefits if the raids were successful (Betzig, 2012; Hirschfeld, 2015; P. Turchin, 2009). These types of raids are largely a relic of ancient history but still occur in some parts of the world today. For the Turkana pastoralists of East Africa, ownership of livestock (e.g., cattle) is a measure of wealth and contributes to men's ability to marry (Mathew & Boyd, 2011). Small-scale to large-scale (potentially including hundreds of combatants) raids on other groups are common, with the goal of stealing livestock, gaining access to grazing lands, or to exact revenge. These types of raids have a long history in this group and were associated with territorial expansions during the 18th and 19th century (Lamphear, 1988).

In more recent history, about 1 in 5 Turkana men die as a result of participation in these raids or while defending their village during raids by other groups, clearly making them risky endeavors (Mathew & Boyd, 2011). Participating in a successful raid can yield individual combatants with substantial material rewards (e.g., 11 cows on average for successful large-scale raids) and an enhanced reputation. Moreover, cowardice or desertion during a raid results in loss of reputation, including reduced desirability as a marriage partner, and sometimes physical punishment, increasing the costs of not participating in these risky activities (Mathew & Boyd, 2014). Men distribute the gains from raids among participants and older men receive more than younger ones. The result is no immediate reproductive advantage to young men, but frequent raiders eventually grow their reputations and their herds, and in the long term they have more wives and children than their more cautious peers (Glowacki & Wrangham, 2015). In fact, in many traditional cultures and developing nations, risk taking (including social surgency and extroversion) is associated with higher reproductive prospects for men but not for women, and cautiousness is associated with lower prospects for men but not for women (Alvergne, Jokela, & Lummaa, 2010; D. H. Bailey et al., 2013; V. Berg, Lummaa, Lahdenperä, Rotkirch, & Jokela, 2014; Gurven, von Rueden, Stieglitz, Kaplan, & Rodriguez, 2014).

As might be expected on the basis of the relationship between risk taking and reproductive outcomes in traditional contexts, adolescent boys' increase in risk taking and men's engagement in risky behaviors is related, in part, to circulating testosterone concentrations. Kurath and Mata's (2018) meta-analysis confirmed a modest but consistent relation between basal testosterone concentrations and a tendency to make risky decisions and to engage in risky behaviors. The relation was the same for men and women, but men's substantially higher basal testosterone concentrations will contribute to the sex difference in risk taking: The relationship between hormones and women's behavior is discussed in a following section. The pubertal increase in testosterone concentrations is associated with an increased sensitivity of the brain's natural reward center (i.e., the nucleus accumbens; Braams, van Duijvenvoorde, Peper, & Crone, 2015), making risky activities more exciting and rewarding. High testosterone concentrations also contribute to the discounting of the potential costs of failure and overestimating the potential benefits of success (van Honk et al., 2004). The discounting of costs can result in impulsive and ill-advised decisions and behaviors in many contexts (Reavis & Overman, 2001) but also large gains should the risky decision prove to be the correct one (Coates & Herbert, 2008).

Sperm Competition

Although paternity is never certain, it is unusually high in humans given our multimale–multifemale communities, as was covered in Chapter 6 of this volume. Nevertheless, cuckoldry or failed attempts to mate switch do occur at potentially meaningful levels in some lower SES communities where women often obtain resources from several men, and it occurs in some traditional contexts (Cerda-Flores, Barton, Marty-Gonzalez, Rivas, & Chakraborty, 1999; Neel & Weiss, 1975; Scelza, 2011; Strassmann et al., 2012). Whether the woman is explicitly trying to cuckold her partner (attempting to get good genes) or attempting to mate switch, she is often maintaining several simultaneous sexual relationships which creates an opportunity for sperm competition. This will occur if she copulates with her primary partner and her other partner within a few days of each other and when the probability of conception is high, as described in Chapter 3 of this volume.

Bellis and Baker (1990) found that when women initiate an infidelity it often occurs during the time of high fertility. In this study, 7% of women's copulations around the time of ovulation were with an extra-pair man, but this study was not based on a representative sample of women. A more representative assessment of the sexual behavior of adults (Great Britain) revealed that 15% of 16- to 24-year-old women and 8% of 25- to 34-year-old women engaged in concurrent sexual relationships during the past year (A. M. Johnson et al., 2001). These relationships set the stage for sperm competition, although the use of birth control will often keep the competitors from leaving the starting gate (at least with the use of condoms). Even with the availability of birth control, the occasional finding of dizygotic (two ova) twins being fathered by two different men leaves no question that sperm competition occurs in humans (W. H. James, 1993; Wenk, Houtz, Brooks, & Chiafari, 1992). W. H. James (1993) estimated that about 1 in 400 dizygotic twins are fathered by different men. Wenk et al. (1992) reported that bipaternity is found in 1 in 42 cases in which the paternity of dizygotic twins has been questioned by one of the fathers. In these cases, the competition is technically a draw.

Although these findings confirm that sperm competition occurs, the extent of such competition and its importance in shaping the evolution of human reproductive behavior is debated (Baker & Shackelford, 2018; Shackelford & Goetz, 2006). A common approach to the reconstruction of this evolutionary history is to first identify physical (e.g., testicle size) and behavioral (e.g., female promiscuity) traits for species in which sperm competition is common, and then compare and contrast these traits with those of species in which it is uncommon (Shackelford & Goetz, 2006). A contrast of the chimpanzee and gorilla (*Gorilla gorilla*) provides an apt illustration. The intense sperm competition in chimpanzees is associated with large (relative to body size) male testicles and conspicuous estrous swelling in females, the latter incites male sexual interest and is associated with copulation with multiple males. Single male harems substantially reduce the chances of sperm competition in gorillas and are associated with small male testicles and minor estrous swellings in females (R. L. Smith, 1984). In terms of testicle size, men fall in between the values for chimpanzees and gorillas, but closer to the gorilla, and women are much closer to gorillas than to chimpanzees in terms of their sexual behavior.

On the basis of these patterns and consistent with Chapter 5 of this volume, R. L. Smith (1984) proposed that the reproductive behavior of our australopithecine ancestors was similar to that found in modern gorillas, and that sperm competition was not a significant factor in human evolutionary history until the emergence of *Homo*. R. L. Smith's argument was that males used hunted meat to entice female copulations and that separation during hunts provided females with the opportunity for extra-pair sex. Sperm competition is comparatively recent, but the key change was the formation of male coalitions and the corresponding emergence of multimale–multifemale communities. As detailed in Chapter 5 of this volume, the formation of these communities likely increased the number of females that were mated with lower quality males and, at the same time, increased the opportunity for these females to seek higher quality, extra-pair mates and attempts to mate switch.

If this is correct, inciting sperm competition is not the primary reproductive strategy of women and never has been. It can occur in situations in which the woman is attempting to switch mates and maintaining multiple relationships before the switch or cannot switch mates but is nonetheless having extra-pair sex with a man of higher quality than her social partner. As was discussed in Chapter 7 of this volume, there are many other reasons (e.g., high male mortality risks) for women to maintain multiple sexual relationships and through this a more reliable flow of resources to themselves and their children (Scelza, 2013; Starkweather & Hames, 2012). In these situations, there may be no intention of mate switching or cuckolding their primary partner, but these simultaneous relationships still create opportunities for sperm competition to occur and the potential for the evolution of men's strategies to reduce associated cuckoldry risks (Barbaro et al., 2019; Pham, DeLecce, & Shackelford, 2017). In all, sperm competition clearly occurs in humans and can contribute to reproductive outcomes in some contexts, but nevertheless does not appear to be a central feature of human reproductive dynamics.

Population Genetics

Advances in our understanding of genetic variation and in the ease of measuring this variation have shed a clarifying light on the study of sexual selection. Studies of the distribution of these genetic variations within and across populations provide insights into larger-scale aspects of human social dynamics, including migration patterns (Seielstad, Minch, & Cavalli-Sforza, 1998) and patterns of social competition (G. Wyckoff, Wang, & Wu, 2000; Zeng, Aw, & Feldman, 2018). Of particular importance for us is the geographic distribution and variability of mutations in mitochondrial DNA (mtDNA) genes and genes on the Y chromosome. Children inherit mtDNA genes from their mother and boys inherit the Y chromosome from their father. Because of this, the geographic distribution and variability of mtDNA and Y chromosome genes can be used to make inferences about the migration patterns and reproductive dynamics of our maternal and paternal ancestors, respectively.

Philopatry

Geary and Flinn (2001) argued that our australopithecine ancestors were more like modern-day gorillas than chimpanzees, with family groups consisting of a dominant male, several females, and their offspring. As discussed in Chapter 5 of this volume, multimale–multifemale communities formed when related males began to cooperate to better compete against other males. In this view, the cooperation of male kin resulted in the merging of their families to create larger communities. With respect to male–male competition, males would be advantaged if they stayed in their birth group and females migrated to other groups at maturity. This is because the sex that stays in the birth group is more likely to evolve a bias to form coalitions that are composed of more than two individuals, and because larger coalitions are advantaged in competition with smaller ones. Males tend to stay in their birth group and females migrate to other groups in our two closest relatives, chimpanzees and bonobos (*Pan paniscus*), and sometimes in gorillas (see Chapter 5, this volume) and possibly in australopithecines (Copeland et al., 2011).

Humans in traditional groups today, however, are much more flexible in their social organization. A married couple may reside with paternal or maternal kin, and the bands in which they reside often include many friends and nonkin with whom they cooperate (K. R. Hill et al., 2011). The previously described large-scale raids by Turkana men necessarily involve cooperation among very distantly related men, many of whom have never met (Mathew & Boyd, 2011). These patterns speak to the importance of human cooperation with nonkin, called peer relationships or friendships by psychologists and these are the primary focus of Chapter 11 of this volume (see also Chapais, 2009).

At the same time, small-scale Turkana raids involve more closely related men and, among extant hunters–gathers, brothers are more likely to reside in the same band than are sisters (K. R. Hill et al., 2011; Mathew & Boyd, 2011). Murdock and White's (1969) classic analysis of descent rules indicated a male bias (patrilineal descent) in sub-Saharan Africa (68% of societies follow patrilineal descent), in societies around the Mediterranean (61%), and in Eurasia (59%), with more bilateral descent (both sides of family) in North America (61%) and Central and South America (66%). Even within the same region of the world, variation is found in residence patterns that are related at least in part to the nature of conflict between groups and whether the conflict is with local groups or involves more distant warfare (Ember & Ember, 1994; Moravec et al., 2018)

Even if a man resides in a community outside of his birth group, he will often maintain alliances with kin and form alliances with men who are related in other ways (e.g., through marriage; Chapais, 2009; Pasternak, Ember, & Ember, 1997). Macfarlan and his colleagues (2018; see also Macfarlan, Walker, Flinn, & Chagnon, 2014) found that raids and ambushes conducted by Yanomamö and Waorani (Ecuador) men can be composed of fraternal kin (e.g., brothers), kin by marriage (e.g., brother-in-law) and distantly related men (e.g., cousins) of similar age who have similar motives (e.g., enhanced reputation) for engaging in the raid or are potential brothers-in-law. In the latter case, each of these men would often marry the others' sister. These patterns highlight the flexibility of social relationships among men as a means of increasing coalition size and gaining competitive advantage, but also highlight the importance of kinship as an anchor to many of these coalitions.

At the same time, the studies of existing groups do not necessarily inform us about the deeper evolutionary history of group-level social dynamics, and this is where population genetic studies become particularly useful. Many of these studies reveal sex-specific patterns of population expansion and migration (Heyer, Chaix, Pavard, & Austerlitz, 2012), with the latter related in part to whether the local custom is to reside with paternal or maternal kin (Oota, Settheetham-Ishida, Tiwawech, Ishida, & Stoneking, 2001). A common finding is fewer male than female ancestors in many populations, consistent with more variability in men's than women's reproductive success, as well as stronger genetic relatedness among men than women in many local communities (Mittnik et al., 2019; Mona, Mordret, Veuille, & Tommaseo-Ponzetta, 2013; R. S. Wells et al., 2001; J. F. Wilson, Weiss, et al., 2001).

A strong genetic relatedness among men is consistent with an evolutionary history of male philopatry but neither the genetic nor ethnographic studies indicate that male philopatry was always the case, nor would we expect it to be (K. R. Hill et al., 2011; Wilder, Kingan, Mobasher, Pilkington, & Hammer, 2004). Male-biased philopatry would be most advantageous in groups with a long history of warfare. In a combined genetic and ethnographic study of central Asian populations, Heyer et al. (2015) found less genetic diversity among men in patrilocal groups than in groups with more mixed residence patterns. In other words, the presence of male kin improves men's reproductive prospects, consistent with a deeper history of competition among male lineages in patrilocal societies (see also Zeng et al., 2018). As warfare increased in scale and coalitions became larger, the genetic relatedness among men within the coalition necessarily became lower, but still appears to have been biased toward more distant relatives who would speak the same language and share the same cultural history.

Male–Male Competition

If male–male competition has been more intense than female–female competition during our evolutionary history, then there will be less variation in Y chromosome genes than in mtDNA genes. As an example, in a monogamous society, 10 of Shinbones' 11 wives would have each reproduced with a different man, resulting in male descendants with Y chromosomes from 11 men rather than only from Shinbone. The results from population genetic studies indicate that Shinbone was not alone. In many populations throughout the world, people have fewer male than female ancestors (Underhill et al., 2000; R. S. Wells et al., 2001; J. F. Wilson, Weiss, et al., 2001; Zerjal et al., 2003). The extent to which this pattern emerges varies across populations and historical time but has been extreme and widespread during certain prehistoric and historic epochs. Zeng et al. (2018), for instance, found evidence for an extreme contraction of men's genetic variability 5,000 to 7,000 years ago from Africa to Europe to East Asia, with little change in women's genetic variability. Genetically, the population size of women was 17 times larger than that of men. This does not mean that there were 17 women to every man, but rather a large proportion of male lineages disappeared during this time frame and other lineages substantially expanded. The diversity of women's lineages rules out two of the Horsemen of the Apocalypse, Famine and Plague. All that is left is War and the selective Death of most men, almost certainly because of male–male kin-based coalitional competition. If the competition did not have a kin basis to it, then Zeng et al. would have found much more variation in male lineages (Y chromosome) than they did.

The most extreme historical example of reproductive domination comes from Zerjal et al.'s (2003) analyses of the Y chromosome genes of 2,123 men from regions throughout Asia. They found that 8% of the men in this part of the world have a single common ancestor who emerged from Mongolia and lived about 1,000 years ago. The geographic distribution of these genes fits well with the historic boundaries of the empire of Genghis Khan (c. 1162–1227), who was known to have had hundreds of wives and many hundreds of children. They estimated that Genghis Khan and his close male relatives are the direct ancestors of 16 million men in Asia, ranging from northeast China to Uzbekistan, and the ancestors of about 0.5% of the world's total population. To achieve this feat, it is estimated the Khan's armies contributed to the deaths of about 40 million people, one of the most devastating examples of a dominance-based reproductive strategy in human history (M. White, 2012).

Although not on the same scale as Khan, Underhill et al.'s (2000) analysis of Y chromosome genes from 1,062 men from all over the world indicates a repeating pattern of one population of male kin replacing another in Africa, Europe, and Asia, with other studies revealing the same pattern (Poznik et al., 2016; Unterländer et al., 2017; J. F. Wilson, Weiss, et al., 2001). However, the extent of replacement of one male lineage by another can vary from one region to the next and from one historical time period to the next (e.g., Capelli et al., 2003). Some analyses also suggest an overall increase in Y chromosome variation since the extreme contraction documented by Zeng et al. (2018; Dupanloup et al., 2003). Despite evidence for extensive resource-based polygyny, as with Genghis Khan and other early empires (Betzig, 2012), population expansions and the advent of agriculture and urban settlements, as well as the eventual suppression of dominance-based reproduction, resulted in an increase in the proportion of men who are reproducing, consistent with a reduction in polygyny and increase in monogamy.

Genetic and historical records indicate that distant migrations are initiated by men in search of material resources, social status, and reproductive opportunity (Carvajal-Carmona et al., 2000; Semino et al., 2000). An example is provided by Carvajal-Carmona et al.'s (2000) assessment of mtDNA and Y chromosome patterns in a Colombian (South America) population that was established by European settlers in the 16th and 17th centuries. The results revealed that the maternal ancestry is largely Amerindian (>90%), whereas the paternal ancestry is almost entirely European (94%). When combined with the historical record of this population, these genetic patterns paint a picture of male–male competition in which European men displaced Amerindian men to the reproductive benefit of the former and at a large cost to the latter. Related studies have found similar though fewer extreme patterns in other Amerindian populations (Merriwether et al., 1997), as well as in populations in Melanesia, South Asia, the middle East, and southern China (Kayser et al., 2003; Quintana-Murci et al., 2004).

FEMALE–FEMALE COMPETITION

As covered in Chapter 3 of this volume for species generally and in Chapter 5 of this volume for primates in particular, female-on-female aggression is much more common than C. Darwin (1871) initially believed. Female–female competition is essentially over access to and the control of resources that improve their survival prospects and those of their offspring, whether these resources are mates or high-quality foods (Clutton-Brock, 2009; Kraaijeveld, Kraaijeveld-Smit, & Komdeur, 2007; West-Eberhard, 1983). The intensity of the competition rarely reaches that found in males, but it can still result in reproductive variance among females; females that are successful at achieving resource control have more surviving offspring than their less successful peers (Silk, 1993; Smuts, 1987). Men's potential to contribute to the well-being of children was documented in Chapter 6 of this volume, and this potential makes many men a resource over which women compete (D. M. Buss, 2016). The focus of this section is on women's competition over prospective mates, as contrasted with other resources.

The dynamics of female–female competition can be expressed among single women in monogamous societies or among cowives in polygynous marriages. The competition can manifest in many different ways, as with that of men. Women's competitive strategies can range from the enhancement of traits that men find attractive (see Chapter 7, this volume) to the social manipulation and exclusion of potential competitors to physical violence. In societies with socially imposed monogamy, women's financial contributions to the marriage (e.g., dowry) can be another form of female–female competition. This section begins with the different ways that women can compete and closes with discussion of the influence of sex hormones on this competitiveness.

Dressed to Kill

Women and men in many traditional societies are not typically free to choose and compete for the spouse of their choice, although it is more freely expressed in the context of extra-pair relationships and second marriages (see Chapter 7, this volume). In contrast, in many developed nations with socially imposed monogamy, the burden of finding a spouse is largely on the would-be bride and groom. These are contexts in which male–male dominance-based competition is suppressed. The latter, in combination with liberal mores that emphasize individual freedom have the effect of increasing the importance of female and male choice. In these contexts, the mate-choice preferences of the opposite sex are particularly important, and as a result many people put considerable effort into enhancing the traits that members of the opposite sex find attractive (N. P. Li, 2007).

For women in these contexts, female–female competition often includes enhancing or bringing attention to the physical traits that influence men's mate choices (see Chapter 7, this volume), as well as the derogation of these same traits in potential competitors (D. M. Buss, 1988; Jonason, 2007; Schmitt & Buss, 1996; S. Walters & Crawford, 1994). The wearing of high heels provides one example (Morris, White, Morrison, & Fisher, 2013; Prokop & Švancárová, 2020). Walking in these types of shoes changes women's gate (exaggerating hip movement) and changes the curvature of their back which often captures men's attention (D. M. Lewis et al., 2017; Morris et al., 2013). Facial cosmetics that highlight the eyes and mouth can also improve the perceived attractiveness of women (Kościński, 2012). For self-applied makeup, the average woman can move her perceived facial attractiveness from the 50th percentile to about the 60th percentile (A. L. Jones & Kramer, 2015), and well beyond this with professionally applied makeup (A. L. Jones & Kramer, 2016).

If women's enhancement of their appearance is related to competition for prospective grooms or to keep their current partner interested in them, then women should be critical of other women who do the same (e.g., dress provocatively) or who are attractive without using cosmetics or wearing high heels (D. M. Buss, 1988; Schmitt & Buss, 1996). These are women who disproportionately attract the attention of men, and indeed other women notice this and often seek to undermine the reputations of these women through relational aggression, as described in the next section (D. M. Buss, Shackelford, Choe, Buunk, & Dijkstra, 2000; Försterling, Preikschas, & Agthe, 2007; Gutierres, Kenrick, & Partch, 1999). D. M. Buss et al. (2000) asked young adults in Korea, the Netherlands, and the United States to rate the traits of a same-sex rival from most to least distressing. In all three nations, a rival with an attractive face or an attractive body was rated as more distressing to women than to men. About 2 out of 3 Korean women rated a same-sex rival with an attractive face as more distressing than did the average Korean man, whereas 17 out of 20 Dutch women rated a rival with an attractive body as more distressing than did the average Dutch man. The magnitude of each of the remaining sex differences was in-between these extremes.

Gutierres et al. (1999) asked young women and men to rate same-age peers on several desirability dimensions. These peers varied in terms of social success and physical attractiveness. The social success of peers was represented by high- and low-success vignettes (e.g., editor of a university newspaper vs. writing a letter to editor), and their physical attractiveness by facial photographs. These young adults then completed self-assessments in these same domains. Women who viewed photographs of attractive same-sex peers rated themselves as less desirable as a marriage partner than did women who read vignettes of socially successful women, whereas men showed the opposite pattern. Overall, about 2 out of 3 women rated themselves as less desirable as a marriage partner after brief exposure to a physically attractive woman.

The use of physical attractiveness as a way to compete with other women depends on the nature of the woman's current relationship and the number of well-off men in the local community (K. R. Blake, Bastian, Denson, Grosjean, & Brooks, 2018). D. M. Buss and Shackelford (1997) found that the same tactics used by single women to attract mates were often used to keep them once they were married. Women married to culturally successful men (e.g., ambitious men with relatively high incomes) use more mate retention tactics, including enhancing their appearance and monitoring his activities, than do women married to less successful men. In an analysis of nearly 70,000 "sexy selfies" (sexualized self-portraits) that were posted on social media, K. R. Blake et al. (2018) found that women posted them more frequently in areas with higher income inequality. The same pattern emerged across localities within the United States and across 113 nations. Large income inequality means that there is considerable variation in men's wealth and as a result more intense competition for the wealthier men.

Women's Aggression

In the vast majority of species, female–female competition is subtler, less risky, and oftentimes more strategic than male–male competition (Stockley & Campbell, 2013). Escalation to potentially injurious physical fights does not yield the same benefits as it does for males and likely results in reproductive costs to females. The strategic component means that female–female competition will be more variable across contexts, depending on local social and ecological (e.g., food availability) conditions, as described in Chapter 3 of this volume. Competition among adolescent girls and women follows the same general pattern found in most other species. The following sections first describe how this manifests in developed nations, in which most of this research has been conducted. Then, the dynamics of female–female competition are explored in the context of polygynous marriages, a situation that has a longer evolutionary history than does socially imposed monogamy.

Developed Nations

Women and girls might not injure and kill one another as frequently as men and boys do, but they manipulate relationships and spread malicious gossip at least as frequently, if not more so, than do boys and men (Archer & Coyne, 2005; Björkqvist, Osterman, & Lagerspetz, 1994; Card, Stucky, Sawalani, & Little, 2008; Feshbach, 1969; Grotpeter & Crick, 1996; Rose & Rudolph, 2006). Girls' and women's gossip typically focuses on same-sex friends, same-sex foes, or potential romantic partners (McAndrew, 2014). The gossip helps girls and women to form the friendships that provide them with social and emotional support, but it is also a primary means of undermining potential competitors. The latter involves social tactics that are called *indirect*, *social*, or *relational aggression*. Relational aggression can be an effective strategy, because humans are a very highly social species and are dependent on the social support and goodwill of others in their community. Relational aggression is an attack on another individual's core relationships and an attempt to undermine their wider social capital (e.g., the extent to which others trust them). When effective, relational aggression will erode the strength of victims' interpersonal relationships, including romantic relationships, and isolate them from the support of other members of the local community. These would be serious consequences in the small-scale communities that comprise traditional cultures (Boehm, 2009).

Relational aggression is primarily focused on same-sex peers and is basically a form of status striving that functions to provide competitive advantage over the victim. The behaviors include withholding positive information about competitors and strategically using negative information (e.g., they have been unfaithful to a romantic partner) against rivals, whether or not it is true, in the context of gossip. These strategically placed bits of information function to undermine the status and attractiveness of same-sex competitors (T. Reynolds, Baumeister, & Maner, 2018) and to exclude them from the social group (Benenson, 2013, 2014). If done well and judiciously, engaging in gossip can also enhance one's own status within the group or solidify existing friendships (McAndrew, Bell, & Garcia, 2007).

Although this form of aggression emerges during the preschool years, it becomes especially prominent during adolescence and is often focused on competition over romantic relationships (Bond, Carlin, Thomas, Rubin, & Patton, 2001; Crick, Casas, & Mosher, 1997; R. L. Smith, Rose, & Schwartz-Mette, 2010). As adolescent girls move into adulthood, they become increasingly skilled at using relational aggression in ways that are plausibly deniable; they phrase comments in ways that can be denied as being intentionally hostile if they are confronted by the victim (e.g., "I'm worried about Sally because she's sleeping with so many men").

To be sure, both sexes use relational aggression to undermine the attractiveness of competitors to romantic partners, with men derogating the cultural success (e.g., income) of competitors and women derogating the attractiveness and sexual fidelity of competitors (D. M. Buss & Dedden, 1990; J. P. Wyckoff, Asao, & Buss, 2019). Men also use relational aggression as a means to move up the male hierarchy by questioning the ability of their rival to contribute to the overall goals of the group (e.g., win a competition; Winegard, Winegard, & Geary, 2014). At the same time, relational aggression can be especially pernicious among girls and women. This is because they reveal more personal and potentially more embarrassing information to their best friends than do boys and men and are more dependent on these forms of intimate same-sex relationships for social and emotional support (see Chapter 11, this volume). The heightened interpersonal intimacy among girls and women comes at a cost of greater vulnerability to social manipulation and other forms of relational aggression should the relationship dissolve (Bond et al., 2001; Murray-Close, Ostrov, & Crick, 2007), as it often does (Benenson & Christakos, 2003).

The sex difference in vulnerability to relational aggression is illustrated in a study of more than 2,500 adolescents. Bond et al. (2001) determined that girls who are victimized by relational aggression are 2.6 times more likely to later suffer from depression or anxiety than are girls who are not victimized or boys who are victimized (see Chapter 14, this volume). The risk for girls continues into adulthood and is especially high if the girl or woman is isolated from friends and family, which is the goal of relational aggression (Kendler, Myers, & Prescott, 2005). A study of 2,319 adolescents confirmed higher levels of depression in the victims of relational aggression and that physically attractive girls, but not boys, are victimized more often than their less attractive peers. Leenaars, Dane, and Marini (2008) concluded that "a one standard deviation increase in physical attractiveness increased the odds of females being indirectly victimized by 35% . . . and decreased the odds of males being victimized by 25%" (p. 410). So, an adolescent girl at the 80th percentile of attractiveness will receive 35% more derogatory remarks either directly or through gossip than will a girl of average attractiveness, and this will increase to 70% more derogatory remarks for the most attractive girls. In a study of more than 7,500 adolescents, J. Wang, Iannotti, and Luk (2010) found that thinner girls are the primary targets of relational aggression, whereas smaller boys are the targets of physical bullying. In a series of five experiments, T. Reynolds et al. (2018) confirmed that attractive women or women who dress provocatively are more frequent targets of relational aggression than are other women (Vaillancourt & Sharma, 2011).

All of these findings follow from the patterns described previously. Women often compete on the basis of physical attractiveness and those with an advantage are targeted for social and reputational attacks. Although the harm to the victims of relational aggression is well documented, the benefits to perpetrators are not as well understood. As with adolescent boys and men, adolescent girls and women differ in how much they desire social influence and status. T. Reynolds et al. (2018) found that the most ambitious women were also the most likely to engage in relational aggression, in keeping with this as a status-related social strategy (G. L. Carter, Montanaro, Linney, & Campbell, 2015). As with men's status striving, sometimes it works and sometimes it backfires. Many aggressors wind up excluded from the very groups they are trying to control, but others appear to be more successful (Hawley, 2003; Rose, Swenson, & Waller, 2004).

LaFontana and Cillessen (2002) found that as children move into adolescence the use of relational aggression becomes associated with peer popularity—aggressive girls achieve social visibility and influence (Vaillancourt, 2013). Socially aggressive and popular peers, however, are not always well liked, especially by other girls. For adolescents, R. L. Smith et al. (2010) found that relationally aggressive adolescent girls largely directed their aggression toward other girls and were more popular among boys than were other girls. We might speculate that these aggressive girls used different social tactics in their relationships with other girls compared with their relationships with boys. Whatever they are doing, their social skills provide them with an advantage in the context of their peer group.

Although girls and women attempt to mask their relational aggression, they are not always successful at doing so. If the victim discovers the source of the rumor, female-on-female aggression can escalate to physical violence (A. Campbell, 1995, 1999). This is especially true in contexts in which there are few successful or attractive men, and the competition among women over these men is intense. A. Campbell (1995) described how in many of these contexts, including low-income neighborhoods in developed nations, being called a "slut" is fighting words:

> She started spreading rumors about me saying that I used to sneak out in the middle of the night in my night-dress and meet ten boys or something, really stupid. . . . Well we were arguing with each other about the rumor mainly and she was saying she didn't say it . . . and then she started calling me names like that and then she started to walk off across the road and she said "I'll get you some time, you fucking bitch." And that made me mad because if she was going to get me she was going to get me there and then, I mean there was no point in getting me later and so I kicked her in the back and she fell flat on her face . . . and we started fighting. (pp. 115–116)

It is not simply name calling and large differences in men's wealth that spark physical confrontations among adolescent girls and women. These also tend to be contexts with higher male mortality and high male incarceration rates that in turn skew the operational sex ratio and further intensify the competition among women (A. Campbell, 2013). These escalated conflicts have been documented in various parts of the world and are not confined to low-income neighborhoods in developed nations. A. Campbell (2013) noted that in

> China and Zambia . . . female aggression is principally driven by competition over resources and often includes men. The degree of female economic and social dependence on men is related to the intensity with which women are prepared to fight to secure high-status men. (p. 116)

Polygynous Societies

Social manipulation and an occasional fight over a would-be boyfriend or husband in a developed nation is one thing, but competition among cowives or with other women (e.g., sister- or mother-in-law) in polygynous households or compounds is often at another level of seriousness. As described in Chapter 7 of this volume (see Table 7.2), polygyny is common across human societies and has been an important feature of human evolution for at least 4 million years (see also Chapter 5, this volume). One result is that women often have to contend with the competing interests of the other wives of their husbands, as well as with their husbands' female kin if they move into his village. The nature and intensity of this competition varies with whether or not a cowife is a sister, the extent to which cowives must cooperate to produce food, and oftentimes age differences between the women (D. R. White & Burton, 1988). With regard to the latter, postmenopausal cowives are often less engaged in competition with younger wives than are younger wives with each other, in part so that younger wives will provide some care for them in their old age (Jankowiak, Sudakov, & Wilreker, 2005).

Whatever the specifics, in many contexts the children of polygynously married women are often less healthy and suffer higher mortality risks than do the children of monogamously married women, although the reasons for this are not fully understood (Josephson, 2002; Lawson & Gibson, 2018;

Strassmann, 1997; Strassmann & Gillespie, 2002). Omariba and Boyle's (2007) analysis of more than 500,000 children across 22 sub-Saharan nations indicated that a child's chances of dying before the age of 5 years was 24% higher if their mother was in a polygynous as compared with a monogamous marriage. The children of polygynous unions were also more likely to die than were the children of single mothers (24% higher vs. 16% higher, respectively, than children from monogamous marriages). Even when the amount of income per child was taken into consideration, the children of polygynously married women were still 17% more likely to die than were children from monogamous families. This is not to say that polygyny is always harmful to children. In some situations, children are better off if their mothers are married to a wealthy polygynous man relative to children from poor monogamous households (Lawson et al., 2015).

Even so, ethnographic studies of polygynous marriages indicate that the relational aggression described in the previous section is common in the relationships among cowives in hunger–gatherer, agricultural, and other societies (Burbank, 1987; Jankowiak, 2008; Jankowiak et al., 2005). Burbank's (1987) survey of 137 societies indicated that verbal abuse and insults are the most common form of women's aggression. "One of the most striking findings of this survey is that women are by far the most common targets of female aggression. . . . The most frequent contenders are cowives, sexual revivals, a wife, and the 'other woman'" (Burbank, 1987, pp. 82–83). The most common instigators of arguments among cowives are jealousy, unequal treatment by the husband, and the introduction of a new cowife into the family. The addition of a cowife often triggers physical fights among the cowives, as this results in a substantial reduction in the amount of resources that each of the cowives will receive from their husband. In effect, most polygynously married men do not have the material and emotional resources needed to meet the expectations of each of their wives, and this shortfall is what drives the competition among them.

Strassmann (1997, 2011; Strassmann & Gillespie, 2002) provides one of the more thorough assessments of this pattern, with her study of the lifetime reproductive success of monogamously and polygynously married Dogon (Republic of Mali) women. For women, the reproductive disadvantage of polygyny is largely due to a sharply higher mortality rate for their children: Even with increased mortality, men still reproductively benefit from polygyny. After controlling for the age and sex of the child, the number of children in the family compound, and the overall economic well-being of the family, the odds of premature death were 7 to 11 times higher for children from polygynous marriages than from monogamous marriages (Strassmann, 1997). The premature mortality was not due to diminished resources per child but may have been related to less paternal investment and the resulting competition from cowives for the investment that was provided. "In addition to neglect and mistreatment, it was widely assumed that cowives often fatally poisoned each other's children. . . . Cowife aggression is extensively documented in

Malian court cases with confessions and convictions for poisoning" (Strassmann, 1997, p. 693).

Murdering the children of cowives not only increases the immediate resources available to their own children, it also reduces the number of heirs to their husbands' land. As with the Kipsigis (see Chapter 6, this volume), sons inherit and divide the land of their father and therefore the sons of cowives are direct competitors for the land each woman's sons will need to attract wives. This competition may explain why the mortality of Dogon boys is 2.5 times higher than that of their sisters. Ji et al.'s (2013) study of the Mosuo (China) confirms the importance of resource control for women's reproductive success. In this matrilineal society, women live with their sisters in family compounds and they, not cowives, are the primary competitors for resources produced by the family's farm. As the number of sisters increases, the number of children each woman has decreases, especially among younger and subordinate women. Other studies suggest that competition among coresident women who are not cowives (e.g., wives of brothers) is particularly important during the child's first 2 years of life, when mortality risks are the highest (Pettay, Lahdenperä, Rotkirch, & Lummaa, 2016).

Clearly, it's not always the case that children in polygynous households are disadvantaged relative to children from monogamous ones or that all cowife relationships are fraught with competitive tension. Nevertheless, it is clear that in many contexts competition among cowives can be intense and occasionally deadly. These types of dynamics have more likely than not been an important contributor to the evolution of female–female competition in humans (Geary et al., 2014). If they were not important, women should be emotionally indifferent to whether their husband or romantic partners had one or several other mates, but this is clearly not the case, as was discussed in Chapter 7, this volume.

Resources and Cultural Success

Although brideprice and brideservice are common in traditional societies, the bride's family providing a dowry to the couple or to the groom's family is uncommon, occurring in less than 6% of societies (Dickemann, 1981; Gaulin & Boster, 1990; Murdock, 1981). Dowries are primarily found in highly stratified societies with socially imposed monogamy, in which wealthy men invest the bulk of their resources in a single woman and their children, rather than in many wives and families. The net effect is the mate value of wealthy men is much higher in societies with socially imposed monogamy than in polygynous ones. Gaulin and Boster (1990) argued that dowry is a form of female–female competition to attract these high-status men as marriage partners. Indeed, in societies without a traditional dowry but with socially imposed monogamy, a woman's financial prospects contribute to her attractiveness as a marriage partner. In the United States, for instance, men rate the financial prospects of a potential marriage partner as important, but not as important as her physical attractiveness and not as highly as women rate the financial prospects of men (Kenrick, Sadalla, Groth, & Trost, 1990).

But do woman's financial and other forms of cultural success translate into reproductive success, as they do for men? Recall that in traditional and developing societies, including those in which dowry was once common (e.g., Western Europe), the SES of the family substantially influenced children's risk of premature mortality (see Chapter 6, this volume). All else being equal, a woman's contribution to the income of her family might then result in a reproductive advantage in terms of more surviving children. All else is not equal, however, because attaining cultural success in the modern world results in different life-history trade-offs for women than for men (Hakim, 2002; Low, Simon, & Anderson, 2002).

Using a nationally (United States) representative sample of 3,902 women age 45 years and older, Low et al. (2002) found a trade-off between years of education and earnings potential and number of children. Throughout much of the 20th century, women with a high school diploma had, on average, 2.8 children, whereas women with a postgraduate degree had 1.8 children. The pattern for childlessness is the opposite of that described for men: Compared with high school graduates, 3 times as many women with postgraduate degrees never had children (9% versus 27%). The same pattern is found in other large-scale studies conducted in the United States and in various European nations (Goodman & Koupil, 2010; Hopcroft, 2006; Nettle & Pollet, 2008), although the effect is less dramatic in Sweden (Fieder & Huber, 2007a). These SES differences in lifetime number of children are largely due to the delay in childbirth commonly associated with obtaining a higher education (beyond a 4-year degree) in developed nations. These same results emerge when comparing women who prefer to work and compete for cultural success (about 1 in 5 to 1 in 6 women) with other women (Hakim, 2002; von Stumm et al., 2011): career-focused women (whatever their education level) earn more money but have fewer children, on average, than do other women.

Hormones and Women's Competitiveness

As was discussed in Chapter 4 of this volume, much less is known about the relation between sex hormones and female aggression than about hormones and male aggression. Even in species in which females are more aggressive than males, males typically have higher circulating testosterone concentrations than do females, indicating there are some differences in the biological mechanisms that influence male and female competitiveness. There is nevertheless evidence that prenatal exposure to androgens and perhaps a heightened sensitivity to testosterone or related hormones (e.g., androstenedione) contribute to the aggressiveness of mammalian females (J. A. French, Mustoe, Cavanaugh, & Birnie, 2013). Similarly, there is some evidence that women's status striving and dominance orientation is influenced by prenatal exposure to testosterone (Madison, Aasa, Wallert, & Woodley, 2014; Pasterski et al., 2007), but this needs further study.

Most of the research on the relation between sex hormones and women's competitiveness has focused on circulating hormone concentrations. The winner–loser effect found among men is not likely to be very strong in women, generally, because women's testosterone concentrations tend to be more stable (and much lower) than those of men and are less reactive to social context (Handelsman et al., 2018; Lobotsky, Wyss, Segre, & Lloyd, 1964). Indeed, Geniole et al.'s (2017) meta-analysis suggested that unlike men, there is no relation between women's testosterone concentrations and performance in lab-based competitions, but a potentially larger relation is sometimes found in real-world competitive settings. For the latter, the two largest winner–loser effects were found for women competing in professional or semi-professional sporting events (Jiménez, Aguilar, & Alvero-Cruz, 2012; T. Oliveira, Gouveia, & Oliveira, 2009), but other studies of elite women athletes have not found these effects (Edwards, Wetzel, & Wyner, 2006; L. D. Hamilton, van Anders, Cox, & Watson, 2009).

The relationship between testosterone concentrations and status striving also appears to be weaker in women than in men (Dekkers et al., 2019; Schultheiss et al., 2004), as is the case in most other mammals (J. A. French et al., 2013). Instead, young women's status striving and social assertiveness appears to be more strongly related to estradiol than to testosterone concentrations (K. R. Blake, Bastian, O'Dean, & Denson, 2017; Stanton & Edelstein, 2009). Across studies, Schultheiss and colleagues have found that higher circulating estradiol concentrations are associated with stronger implicit social-power motives for single, but not romantically involved women (Schultheiss, Dargel, & Rohde, 2003; Stanton & Schultheiss, 2007). The latter result is consistent with estradiol concentrations being related to competitiveness over mates, although not necessarily in the challenge–response manner. As described in Chapter 7 of this volume, the increase in estradiol concentrations that contribute to ovulation is associated with an increase in women's sexual motivation and attentiveness to men and these latter changes may be driving women's competitiveness, at least for women in search of a romantic partner.

CONCLUSION

Humans compete in a variety of creative and seemingly evolutionarily novel ways (G. F. Miller, 2000; Winegard et al., 2018), but careful consideration of this variation reveals a core structure. As with the males of most other species, the core issue for men is their status relative to other men. The primary difference is that men's status can be achieved in many more ways than in other species, from the intimidation and murder of competitors to the control of the ecological (e.g., land) and biological (e.g., cattle) resources that women need to reproduce to the attainment of a college degree and the securing of a well-paid job. The reason is simple: status matters. Men at the top of their society's hierarchy are better able to realize their mating preferences, and men at the bottom are at serious risk of being completely shut out of the reproductive pool. Unlike most other species, men need other men to achieve and maintain status—men compete as coalitions and strive for status within their coalition. Men, of course, vary in the risks they are willing to take and the costs they are willing to pay to achieve status. Some men are satisfied with being in the middle of the pack; they have enough status to marry but not enough to incur the wrath of the most competitive men. Other men want absolute control and dominance, but fortunately most of these would-be despots do not achieve this goal.

In societies characterized by kin-based or ideological coalitions, men cooperate with one another to control the social and material resources of the society. If any such coalition gains control, the men that compose the coalition use the society's resources and their social power to actualize their reproductive preferences. These are situations that give rise to despotic regimes (Betzig, 1986; Hirschfeld, 2015). In many of these societies, coalitions of high-status men achieve social control by means of violence or threats of violence and use this control to reproduce at the expense of low- and middle-status men and with little regard for the preferences of women. These societies stand in sharp contrast to societies in which monogamy is ecologically or socially imposed (Betzig, 1986; Flinn & Low, 1986): the latter are often WEIRD nations (Henrich et al., 2010). Monogamy in turn reduces reproductive skew among men (i.e., differences in the number of children sired by elite and low-status men) and thereby reduces the willingness of men to pay the costs to achieve high status through physical aggression. Men's competition in these societies essentially shifts from the use of dominance-based physical violence to the accumulation of prestige-based competencies that are indicators of cultural success (Henrich & Gil-White, 2001; Irons, 1979). Achieving cultural success is simply another means of achieving control and increasing the ability to exercise one's reproductive preferences, but this influence is not achieved by force.

Monogamous societies are also characterized by a fuller expression of female choice, and more exacting male choice. As described in Chapter 6 of this volume, when men are restricted to one wife at a time they become choosy when it comes to a marriage partner and typically invest more in parenting than in mating. This is associated with increased competition among single women for the most desirable bachelors, often by enhancing the physical traits that men find the most attractive. Women also compete through relational aggression by manipulating the social relationships of competitors and emotionally harassing them (A. Campbell, 2013). Women in polygynous societies do the same, especially if their husband is married to one or several other women (Burbank, 1987). The subtlety of relational aggression compared with physical aggression follows from the sex difference in the cost–benefit trade-offs of competition. Most women will have the opportunity to marry and reproduce, whether or not she is culturally successful. To be sure, it is better to be successful for women and men but is it not as critical for women's reproductive success as it is for men's reproductive success.

9

Evolution and Development of the Human Mind

The main points of the preceding chapters can be summarized in terms of the core differences between men and women. Men have evolved to attempt to organize their social world and life trajectory in ways that increase their social status and influence within the wider communities in which they live, and they have evolved to attempt to gain access to and control of culturally important resources. On the surface, men in different cultures and across different historical periods often seem to be engaged in very different activities, from Genghis Khan's rampage through Asia to monogamous men's high levels of investment in marriage and children. These are of course very different behaviors and reflect the extremes of dominance-based and prestige-based approaches to status striving and reproduction (Henrich & Gil-White, 2001). Different cultural contexts, especially the social imposition of monogamy and the suppression of male-on-male violence, close some pathways to cultural success and open others and, in doing so, change the mix of men who are likely to be successful or not. Nonetheless, underneath this variation is the same motive to gain social recognition and influence and to gain access to and control of culturally important material resources.

Women have evolved to attempt to create networks of social relationships that provide them and their children with social and emotional support and that enhance their access to and control of culturally important resources. The relational aggression described in Chapter 8 of this volume is the dynamic that emerges as multiple women work to organize the pattern of relationships in the social groups in which they are embedded. Of course, some women

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Male, Female: The Evolution of Human Sex Differences, Third Edition, by D. C. Geary

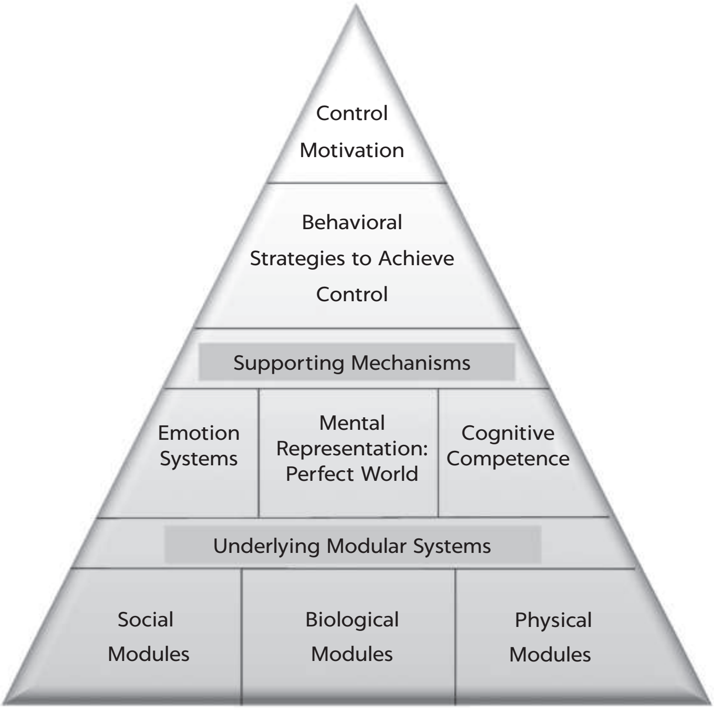
seek social status and direct access to resources, but the costs and benefits of this have been much stronger for men than for women during recorded history and almost certainly during human evolution. The costs (e.g., premature death) have lessened in societies with socially imposed monogamy and with the suppression of male-on-male violence, but even here women spend less effort (on average) devoted to achieving cultural status than do men (Hakim, 2002; see Chapter 14, this volume).

The goal of this chapter is to build a bridge from the sex differences in parenting (Chapter 6, this volume), mate choices (Chapter 7), and competition for mates (Chapter 8) to the sex differences in development (e.g., friendships, play patterns) and in brain and cognition, which are covered in the following chapters. In building this bridge, sex differences in motivational focus and emotions are weaved into a framework for linking reproductive behaviors with psychological and cognitive evolution and development. This framework was introduced in the first edition of this book (Geary, 1998b) and elaborated on in *The Origin of Mind* (Geary, 2005). The mind is organized in a way that results in biases to attend to and process evolutionarily significant forms of information (e.g., angry facial expressions) and includes corresponding behavioral, emotional, and motivational biases (R. Gelman, 1990; Simon, 1956). All of these biases converge in ways that result in attempts to gain social influence and to gain access to and control of the forms of biological (e.g., high-quality food) and physical (e.g., resource-rich ecology) resources that enhanced survival and reproductive prospects during our evolutionary history.

The apex of the triangle in Figure 9.1 represents this fundamental motivation to achieve control. The midsection shows the supporting emotion systems, mental representations, and cognitive competencies that support the corresponding behavioral attempts to gain social influence and control resources. The base represents the classes of cognitive module (e.g., universal cognitive abilities and knowledge) that facilitate the processing of evolutionarily salient social, biological, and physical information. The general structure shown in Figure 9.1 provides a conceptual framework for studying behavior and cognition across species, although the specifics (e.g., specific information processed by the social modules) will differ from one species to the next (see Geary, 2005).

It is assumed that men and women and boys and girls are more similar than different when it comes to the basic structure of these systems. For instance, women and men have cognitive systems for processing facial information that have largely been shaped by natural selection. If any of the associated abilities (e.g., sensitivity to subtle variation in facial expressions) have been more important for one sex as related to competition for resources or social influence, then that sex should have an advantage for this ability. Relational aggression, for instance, is more subtle than physical aggression and is more critical to women's social potency. The subtlety of relational aggression puts a premium on detecting slight changes in facial expressions, vocal intonation, and other social cues. Relational aggression would then result in the evolution of an advantage for women in these areas, just as physical competition has resulted in taller and more muscular men (Geary, Winegard, & Winegard, 2014).

FIGURE 9.1. Motivation to Control



The apex represents the proposal that human behavior is fundamentally driven by a motivation to control the social, biological, and physical resources that have tended to improve survival and reproductive outcomes during human evolution. The midsection shows the supporting emotion or affective systems, mental representations, and cognitive competencies that support the motivation to control and operate on the modular systems shown at the base. Reprinted from *The Origin of Mind: Evolution of Brain, Cognition, and General Intelligence* (p. 74), by D. C. Geary, 2005, Washington, DC: American Psychological Association. Copyright 2005 by the American Psychological Association.

In fact, girls and women do have advantages over boys and men in the social-cognitive competencies related to relational aggression (see Chapter 12, this volume).

In the first section of this chapter, the motivation to control is fleshed out, and sex differences in motivational and emotional processes are weaved into the framework. Then, an overview of universal cognitive abilities, called folk domains, is provided, which are the focus of the following chapters on sex differences in brain and cognition.

MOTIVATION TO CONTROL

For all species, selection will favor the evolution of traits that enable individuals to achieve some level of access to and control of the types of resources that supported survival and reproduction during the species' evolutionary history. This is not an explicit desire to control, but rather reflected in the many adaptive traits that result in resource control (or that help to avoid becoming a resource for another species) and for many species, this includes social influence. The point can be illustrated by the beak evolution in Darwin's finches (see Chapter 2, this volume). Beak size and shape evolved to allow the different species of finch to exploit different sources of food (P. R. Grant & Grant, 2014). Beak structure, and presumably a perceptual sensitivity to food sources that can be handled by the beak, along with behavioral foraging for these foods can be encompassed under the motivation to control. This functional constellation of adaptive traits results in the ability of these birds to identify the right type of food and to control or use these foods for their survival. These physical, perceptual, and behavioral traits are integrated together in ways that result in successful foraging.

When conceptualized in this way, the behavioral, emotional, representational, and cognitive (i.e., working memory and folk modules) adaptations described below enabled our ancestors to monitor and influence social dynamics and to gain access to the biological (e.g., food) and physical (e.g., territory) resources that enhanced their survival and reproductive prospects (Geary, 2005). C. Darwin's (1859) conceptualization of natural selection as resulting from a "struggle for life" (p. 115) is more precisely defined as a struggle for control of the resources that support life and that allow one to reproduce. The motivation to control is essentially a rule-of-thumb or heuristic for integrating evolved adaptations into functional systems that result in outcomes related to survival and reproductive prospects. In the following sections, this heuristic is integrated with psychological theories of human motivation, sex differences in the foci of control, and supporting mechanisms for achieving control.

Psychological Theories

The motivation to control heuristic is not meant to be a psychological theory of human motivations but is nevertheless consistent with many such theories (e.g., Bandura, 2001; Dweck, 2017; Maslow, 1943; R. M. Ryan & Deci, 2017; Sheldon, 2011). Bandura's (2001) influential theory of human agency captures the gist of this heuristic, "The capacity to exercise control over the nature and quality of one's life is the essence of humanness" (p. 1). There are also important similarities to R. M. Ryan and Deci's (2017) tripartite self-determination theory, which includes fundamental motives for autonomy, competence, and relatedness. The autonomy component is the ability to pursue one's intrinsic interests without interference from external influences (e.g., other people), which is similar to Bandura's agency. The competence component, as well as Maslow's (1943) need for esteem, fit nicely with Henrich and Gil-White's (2001) distinction between dominance-based and prestige-based status. An inherent motivation to become skilled at culturally important activities creates competence and prestige, which in turn often confers reproductive benefits, especially for men (see Chapter 8, this volume). Maslow's self-actualization (e.g., creating music for its own sake) is likely an aspect of prestige-based status striving in developed nations (Kenrick, Griskevicius, Neuberg, & Schaller, 2010; G. F. Miller, 2000; Winegard, Winegard, & Geary, 2018).

R. M. Ryan and Deci's (2017) relatedness is similar to Baumeister and Leary's (1995) need to belong and to Maslow's (1943) love, affection, and belongingness needs; humans want to be part of and valued by a larger social group. There are specific social relationships that are prioritized over others (e.g., children, mates), but all are captured by a core bias to develop a network of relationships (Kenrick et al., 2010). The same is true for any primate that lives in a large social group. It is also the case that status hierarchies emerge in all of these groups and species and influence access to mates and to high-quality food, as was discussed in Chapter 5 of this volume. C. Anderson, Hildreth, and Howland (2015) showed that humans are no different; a desire to achieve some level of status is a fundamental human motivation. For nonhuman primates, there is very little if any self-reflection on their own status or their conscious desire to achieve it, but they behave in ways that will enhance their status, if successful. The status-related behaviors of nonhuman primates are dominance-based, with little evidence of empathy for the plight of the dominated (Boehm, 2009).

People who consistently use these types of strategies are often considered to have some type of personality disorder or manifest the "dark" aspect of personality: The "*general tendency to maximize one's individual utility—disregarding, accepting, or malevolently provoking disutility for others—accompanied by beliefs that serve as justifications*" (Moshagen, Hilbig, & Zettler, 2018, p. 656, italics in original). Genghis Khan would certainly fit this profile, as would the well-studied despots of history (e.g., Adolf Hitler; Kershaw, 1998). Nonhuman primates of course do not make these self-serving justifications, and for people these are essentially attempts to diminish or justify the harm caused to others and to mitigate retribution (Henriques, 2003; Mercier & Sperber, 2011). Thankfully, these dark features of personality are only fully expressed in a small percentage of people but are almost certainly the evolutionarily ancient basis for status striving. The benefits of social cooperation (e.g., to suppress the status striving of would-be alpha males) and associated emotions (e.g., empathy, guilt) keep these in check and help to divert their expression to prestige-based status striving, depending on context.

Even so, the basic outcomes are the same, success at achieving status results in an enhancement of social influence and increased control of culturally important resources. This is the key point of the motivation to control heuristic. Social, behavioral, and cognitive traits that result in these basic outcomes will be organized together and enhanced over evolutionary time, and their expression can be interpreted as reflecting a finite set of human motives. Critically, the outcomes should map into the basic issues covered in previous chapters; they should be related to investment in children (Chapter 6, this volume), mate choices (Chapter 7), and competition for mates (Chapter 8). For instance, the relational aggression described in Chapter 8 of this volume can be an effective strategy for enhancing status and resource control (e.g., access to romantic partners), because it directly undermines the victims' social relationships and social capital and results in a relative advantage for the aggressor. From the perspective of psychological theories of motivation, relational aggression works because it disrupts the pattern of social relationships that contributed to survival and reproductive outcomes during our evolutionary history. More precisely, this form of aggression interferes with the victims' need to belong, esteem, or relatedness motives and through this creates psychological distress (e.g., depression; R. M. Ryan & Deci, 2000).

Any trait that provides an advantage in terms of engaging in or defending against relational aggression will be enhanced over evolutionary time and more so for women than for men. Critical for understanding later chapters are the goals that have been achieved by these strategies (e.g., enhanced social influence), and less so the underlying motivational systems.

Sex Differences

There is no question that women and men benefit by having some level of influence in social relationships, access to material resources, and status within their community (Marmot, 2004). As a result, the sexes will be more similar than different when it comes to wanting some degree of success in these endeavors or some degree of agency from Bandura's (2001) perspective or autonomy from R. M. Ryan and Deci's (2017) perspective. The key differences are the ways in which women and men want to organize their social relationships and communities and in the distribution of wealth within those communities. Sex differences in the social motives and preferences of women and men illustrate this point.

Studies of personal values and social interests reveal a consistent pattern of sex differences, with women valuing the development of altruistic, reciprocal relationships with other people and men being "interested primarily in power, competition, and struggle" (i.e., politics; Willingham & Cole, 1997, p. 144). Overall, 4 out of 5 women value the development of reciprocal social relationships more than the average man, whereas 3 out of 4 men value political activities more than the average woman. These sex differences are found across historical periods and across cultures (Tiger & Shepher, 1975; Van Vugt & Spisak, 2008; von Rueden, Alami, Kaplan, & Gurven, 2018; Willingham & Cole, 1997) and appear to have become exaggerated with the advent of large-scale agriculture and animal domestication (Carmichael & Rijpma, 2017; Dong et al., 2017). These are the conditions that supported early empires and increased the reproductive gains for successful male coalitions (Betzig, 1986, 2012; see Chapter 8, this volume).

Politics is essentially about organizing social support to better gain control over the behavior of other people and their resources. Across human cultures, politics is largely a manifestation of competition between coalitions of men but includes some women in democratic and egalitarian societies (Bowser &

Patton, 2010). Socially dominant men in these coalitions have more wives and mistresses and more children than do subordinates or members of losing coalitions (Chagnon, 1988; Gómez, Verdú, González-Megías, & Méndez, 2016; Raffield, Price, & Collard, 2017; von Rueden & Jaeggi, 2016). The bottom line is that men usually have more to gain, reproductively, by engaging in political activities. The corresponding sex difference in interest and engagement in the political arena is a reflection of a more basic sex difference in orientation toward social dominance and comfort with an unequal distribution of the groups' resources versus social equality in decision making and resource distribution (Sidanius, Pratto, & Bobo, 1994).

Across nations, generations, political ideologies, and income levels, men have a stronger social dominance orientation and women have a stronger social equality orientation (Pratto & Hegarty, 2000; Sidanius, Pratto, & Bobo, 1994), although paradoxically the sex differences are larger in wealthy nations with egalitarian norms and high rates of women's participation in politics and the labor market (I. C. Lee, Pratto, & Johnson, 2011). Overall, about two out of three men endorse the importance of social dominance more strongly than does the average woman, and almost three out of four women endorse the importance of social equality more strongly than does the average man. Men who are high in the desire to achieve social dominance also express a desire for multiple mating partners and have less interest in parenting, as would be expected if the motivation to achieve dominance is implicitly related to reproductive interests. Socially dominant women, in contrast, are more interested in marrying high-status men than in finding multiple mates (Pratto, 1996; Pratto & Hegarty, 2000).

Tiger and Shepher's (1975) study of the social-egalitarian Kibbutzim revealed greater voluntary participation of men in politically influential committees, and more extramarital affairs by the dominant men on these committees but not by the dominant women on the same committees. In terms of social policies and consistent with their social dominance orientation, men are more inclined to advocate policies associated with group dominance (e.g., military spending). Consistent with their social equality orientation, women are more inclined to advocate policies that result in a more equitable distribution of social resources (e.g., higher taxes to pay for social welfare) and a greater investment in children (e.g., public day care; Pratto, 1996).

The tendency of women to value social equality and reciprocal social relationships more so than men might reflect, in part, a stronger preference for reducing conflict through nonviolent means and maintaining stability within the social community. As has been repeatedly shown throughout human history, the struggle for despotic control of a social or political region often results in the wholesale destruction of entire communities (Keeley, 1996; M. White, 2012). The frequency of these events has declined over time but are not a complete relic of the past (Pinker, 2011). A United Nations report concluded that from 1985 to 1996, 2 million children were killed worldwide and 6 million were seriously injured during large-scale wars to smaller-scale ethnic conflicts, and millions more suffered from malnutrition and illness, among other deleterious consequences as a result of these conflicts (Machel, 1996). Of course, there are millions of women who are similarly affected during these male–male conflicts. In other words, coalitions of men have the most to gain through the use of violence, but these coalitional struggles for control can disrupt entire communities and in doing so, impose substantial costs on women and their children.

Even relatively subtle levels of social instability can have adverse effects on the physical well-being of children (Flinn, 2006; Flinn & England, 1997; Picard, Juster, & McEwen, 2014; Theall, Brett, Shirtcliff, Dunn, & Drury, 2013), which will be of greater concern for women than men. Children living in unstable social environments tend to have abnormal (elevated or highly variable) stress hormone profiles (i.e., cortisol), are ill more frequently, and weigh less than children living in more stable households and communities, and they show more signs of accelerated cellular aging. Growing up in a socially unstable environment increases health and mortality risks in adulthood and, as a result, can shorten the lifespan (Marmot, 2004). Within relatively small communities, stable social relationships can be achieved by engaging in activities that suppress male–male competition, result in a more equal distribution of resources, and promote cooperative childcare and the economic interdependence of women and men (Boehm, 2009, 2012; Hewlett, 1992).

Stated bluntly, there are consistent sex differences in the ways in which men and women would prefer to organize their social worlds and in the strategies they use to achieve this organization (e.g., physical violence). These sex differences are reflected in social motives and political interests and activities and are consistent with the relative focus of men on mating effort and women on parental effort. Men seek to achieve social dominance and are more concerned with social status (cultural success) than are women, because today and throughout our evolutionary history the achievement of dominance and status results in more wives and more children. Women typically cannot improve their reproductive success by gaining additional husbands, but they can improve their reproductive success by organizing the social community in a way that would enhance the well-being of their children. These communities are socially stable and have sufficient material and social resources to provide a "safety net" for families and children who are in difficult circumstances. The strength of this preference will vary with the level of available resources. As described in Chapter 7 of this volume, when women compete for a limited and valuable resource, they can be vicious and not at all interested in equality.

Men are more likely to benefit from substantial increases in status and wealth, especially in polygynous societies, and the relative benefits to women are mitigated by the costs associated with male coalitional conflicts over the distribution of this wealth. By advocating social policies that suppress male–male competition (e.g., political opposition to warfare), women might be able to reduce the overall level of socially disruptive violence in the society, including male-on-female aggression. From this perspective, women's focus on social equality is just as functionally self-serving as the dominance-oriented social motives of men. As with men, women work to organize and control social relationships and dynamics, but the sexes do so in different ways.

Supporting Mechanisms

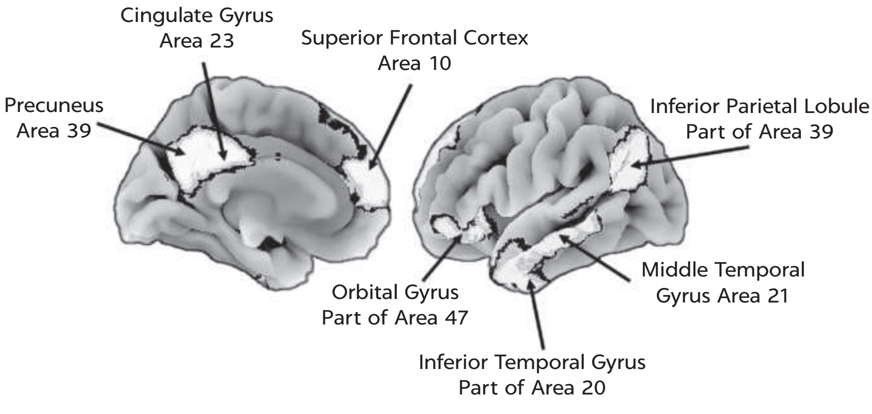
People use the competencies in the middle sections of Figure 9.1—the emotion systems, mental representations, and cognitive competencies—to help them align the social and material world to better meet their interests. The modular systems in the Folk Domains are described in a separate section.

Mental Representation of the Perfect World

A brief overview of the mechanisms that support the generation of mental representations of the "perfect" world, in which an individual has social influence and access to culturally important resources, are presented next. The sex differences in the content of this world are then discussed.

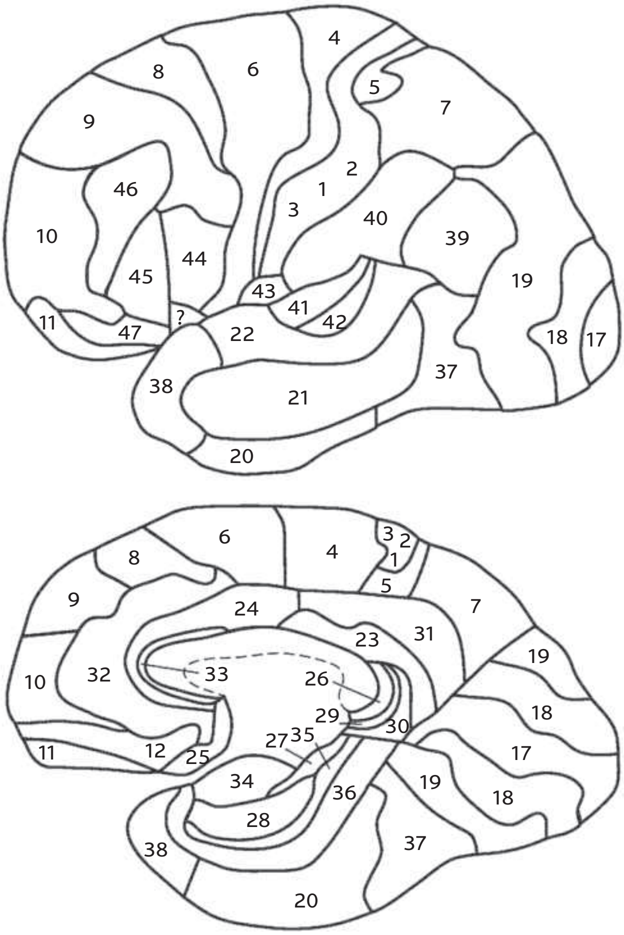
Mentally representing the world. An evolutionarily ancient network of brain regions, called the *default mode network*, is involved in integrating the emotional (e.g., anxiety levels) and motivational state of individuals with self-referential thoughts (e.g., evaluating whether they are "helpful" people) and memories of past experiences. The key areas in this brain network are shown in Figure 9.2, and the corresponding Brodmann (1909) map areas are shown in Figure 9.3. The network is active during relaxed states and results in self-relevant reflections about past memories and future goals and provides

FIGURE 9.2. Key Brain Areas of the Default Mode Network Support the Construction of Self-Centered Mental Representations of the World



This includes potential future states. To the left is the medial (center) view of the brain and to the right is the lateral (outer side surface) view. The numbers next to the labels are Brodmann (1909) map coordinates.

FIGURE 9.3. Maps of Brodmann's Areas of the Human Neocortex



The top section is the lateral (outer) view of the cortex, whereas the bottom section is the medial (center) view. Many of these areas can be subdivided into specialized subregions that may process different forms of information. Very generally, Brodmann Areas 1, 2, 3, 5, 31, and 43 are part of the parietal cortex and support a variety of functions including sense of body position, attention, and spatial competencies. Brodmann Areas 17, 18, and 19 are part of the occipital cortex and support simple and complex visual perception. Brodmann Areas 22, 41, 42, and subregions of Areas 40 and 38 are part of the temporal cortex and support simple and complex auditory and speech perception. Brodmann Areas 20, 21, 26–28, 34–37, and 52 are part of the temporal lobe and support a variety of complex visual competencies. Brodmann Areas 4, 6, and 8 are involved in complex motor movements and are part of the frontal cortex. Brodmann Area 44 and subregions of Area 45 are involved in speech generation and gesture and are part of the frontal cortex. Brodmann Areas 9, 10, 11, 25, 46, 47, and subregions of Area 45 are part of the prefrontal cortex and support behavioral control, executive function, and many complex social competencies. Brodmann Areas 23, 24, 30, (parts of 31), 32, and 33 are part of the cingulate cortex and support attentional and emotional functions. Illustration by Mark Dubin. Reprinted with permission.

"a self-centered predictive model of the world" (Raichle, 2015, p. 443). Although the network is ancient, substantial evolutionary changes have resulted in a uniquely complex system in humans relative to nonhuman primates. For instance, one area of the network, the precuneus, is involved in feelings of agency, self-awareness, personal memories, and thinking about the world in ways that involve the self (Andrews-Hanna, Smallwood, & Spreng, 2014; Cavanna & Trimble, 2006; Rugg & Vilberg, 2013). Other areas, like the medial prefrontal cortex, are especially important during conscious reflections about the self, including explicit goal-directed self-evaluations (Davey, Pujol, & Harrison, 2016). The default mode network in combination with the executive and attentional control network involved in explicit problem-solving enable people to generate a conscious representation of themselves in the context of past and future social scenarios, among other contexts (Andrews-Hanna, Smallwood, & Spreng, 2014). These thoughts provide clues about its evolutionary function:

> The content of self-generated thoughts suggests that they serve an adaptive purpose by allowing individuals to prepare for upcoming events, form a sense of self-identity and continuity across time, and navigate the social world. On average, adults tend to rate their thoughts as goal oriented and personally significant, yet thoughts also commonly involve other people. (Andrews-Hanna et al., 2014, p. 32)

The content of these automatically generated thoughts is consistent with evolutionary models that have focused on social strategizing and social competition as the primary drivers of the large increases in brain size since *Australopithecus* (see Chapter 5, this volume; Alexander, 1989; D. H. Bailey & Geary, 2009; Dunbar, 1993; Flinn, Geary, & Ward, 2005; Geary, 2005; Humphrey, 1976). These thoughts often involve a form of mental time travel, which is the mental simulations of past, present, or potential future states that can be cast as images, in language, or as episodic memories (i.e., memories of personal experiences; Rugg & Vilberg, 2013; Suddendorf & Corballis, 2007; Tulving, 2002). The integration of social competition, mental time travel, and the use of mental models for problem-solving (Johnson-Laird, 1983) results in what appears to be the uniquely human ability to construct self-centered representations of past, present, and potential future worlds and to engage in effortful reasoning and problem-solving on the content of these representations. The future that people think about often involves a mental representation of a desired or fantasized state that then can be compared with a mental representation of the current situation. In this future state, people typically have enhanced social status, influence, and access to culturally important resources relative to their current condition. This future state is a goal to be achieved, and explicit social strategizing and problem-solving enable people to plan ways to reduce the difference between where they are today and where they want to be in the future (Geary, 2005).

Mental models of current or future states often include explicit beliefs and attributions about the self, others, or group dynamics. The attributions are attempts to understand the behavior of other people in terms of their emotions and intentions. These attributions do not need to be factually accurate, only helpful in moving one closer to the fantasized future state. Attributions about favored ingroup members and disfavored members of an outgroup are an example, and a bias that would have easily evolved in the context of coalitional competition. Indeed, these biases are particularly salient during times of intergroup competition and hostilities (Choi & Bowles, 2007; Fiske, 2002; L. T. Harris & Fiske, 2006). Horowitz's (2001) seminal analysis of ethnic conflict in the real world shows that these biases are salient during conflicts over resource control and social influence. In these situations, unfavorable attributions about the character and intentions of members of the outgroup often include rumors of an intended attack or conspiracy to attack (e.g., poison the ingroup's food supply, attack women of the ingroup). These attributional biases justify, facilitate, and precede violence in many instances of real-world ethnic conflict. The result is often deadly and results in the self-serving elimination of economic or social competitors. The attributional biases not only justify this self-serving violence, they protect individuals from the emotional consequences (e.g., guilt) that could result if the violence were directed against members of the ingroup (Böhm, Rusch, & Baron, 2018).

People also have a system of attributional biases that support attempts to achieve some level of control (Bandura, 2001; Heckhausen & Schulz, 1995). These control mechanisms are important, because the failure of these mechanisms appears to result in depression and behavioral inhibition (i.e., a cessation of attempts to achieve control; Shapiro, Schwartz, & Astin, 1996). One important function is to maintain control-oriented behaviors in the face of failure (Heckhausen & Schulz, 1995). These mechanisms include attributions that allow people to interpret personal failure in ways that maintain their sense of self-efficacy or their belief that they can achieve the goal in question. Such interpretations might involve attributing failure to external causes (e.g., "It wasn't my fault") or maintaining an illusion of control by interpreting the outcome as predictable (e.g., "I knew that this would happen"). Other cognitive factors that help to maintain control and a focus on the desired goal include the development of subgoals to be achieved along the way and mentally imagining the end result (Duckworth, Milkman, & Laibson, 2018). Many other common aspects of daily life, including rituals, reliance on third-party intervention, belief in psychic powers, and so on serve the function of providing a sense of a coherent and orderly environment, help to predict and control potentially significant life events (e.g., the health of kin), and mollify the fear and anxiety associated with not having complete control over these events (Landau, Kay, & Whitson, 2015).

Sex differences. Both sexes construct and use mental representations of potential future worlds to strategize about improving their conditions in life. The core difference is in the types of worlds that men and women construct. These differences are illustrated by the content of their representations or fantasies and, critically, these often align with the sex differences discussed in previous chapters. As an example, creating the perfect world is fraught with frustration, largely because of the competing interests of other people who are working to organize their own worlds. Navigating these difficulties requires attributions about who or what is thwarting an individual's goals or who is the primary threat to an individual's well-being.

At the extreme, these attributions can result in psychiatric delusions of persecution and these in turn align with topics discussed in previous chapters. In keeping with the mortality risks associated with coalitional male–male competition (see Chapter 8, this volume), men with these delusions frequently fear physical attack by groups of unknown men (Walston, David, & Charlton, 1998; Zolotova & Brüne, 2006). Women, in contrast, are concerned about physical or relational aggression perpetrated by people they know, sometimes other women and at other times men. Walston et al. (1998) found that women were more concerned about family and friends gossiping about them, although this concern is not as high as that associated with their physical safety (Zolotova & Brüne, 2006). Women are also more likely to have delusions about being loved (Brüne, 2001). Women with these delusions are much more likely (78%) than men (25%) to enhance their physical attractiveness and feel desired by an older, higher status man. The latter mirrors the content of popular fiction stories that women find more appealing than do men and that if achieved would improve their well-being and that of their children (see Chapter 7, this volume).

The sex difference in sexual fantasy provides a more typical example of how mental representations align with evolutionarily important themes (see Chapter 7, this volume). The point is illustrated by B. J. Ellis and Symons' (1990) finding that nearly 1 out 3 young men but less than 1 out of 10 young women report having fantasized about sexual relationships with more than 1,000 members of the opposite sex. The fantasies reflect the sex difference in the motivation to seek multiple sex partners, and the associated reproductive benefits should these fantasies be achieved (Symons, 1979). Fantasizing about sexual relationships is not only a reflection of this motive; it may provide a means for rehearsing strategies for achieving this end. In the absence of birth control, men who have such fantasies tend to seek multiple relationships and will leave more descendants on average than their less imaginative peers. In this view, the reproductive motivation of despots and many young college men is the same, although they clearly differ in the ability to realize their fantasies and in the strategies used during the pursuit of this reproductive goal.

Cognitive Competencies

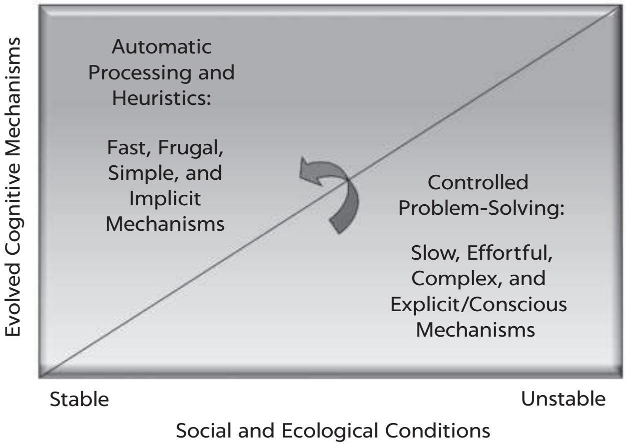
Cognitive competencies include a suite of domain-general abilities that can be used for learning and problem-solving across areas, from social strategizing to tool making to algebra. Executive function is a core domain-general ability that is composed of working memory (i.e., the ability to hold something in mind while engaged in another process) and task switching (i.e., changing from one set of tasks to another), both of which are dependent on the ability to inhibit the processing of goal-irrelevant information and behaviors (Baddeley, 1986;

Bjorklund & Harnishfeger, 1995; Cowan, 1995; Miyake & Friedman, 2012; Miyake et al., 2000). These competencies also contribute to fluid intelligence (i.e., the ease of learning novel information; Shipstead, Harrison, & Engle, 2016). Fluid intelligence is typically understood in terms of learning in evolutionarily novel domains, such as reading and arithmetic (Cattell, 1963; Geary, 1995a, 2007), but also is important for devising strategies to cope with ecological change (e.g., seasonal change in weather) and with variation and change in social dynamics (Ash & Gallup, 2007; Geary, 2005; R. Potts & Faith, 2015).

The interface between these competencies and the automatic processing and monitoring of an individual's well-being that occurs via the default model network is shown in Figure 9.4. The former includes many heuristics (e.g., the biased attributions about outgroups) that occur without conscious deliberation and are particularly useful for conditions that are stable across time (Kahneman, 2011). When people come across a situation that they cannot automatically understand or with which they cannot cope, as shown by the unstable end of Figure 9.4, there is an attentional shift and an engagement of these domain-general competencies in ways that enable the explicit problem-solving needed to devise a strategy to cope with the new situation (J. Evans, 2002; Stanovich, West, & Toplak, 2016). The repeated use of this new strategy results in its memorization, and then it becomes part of the automatic problem-solving repertoire of the individual, as represented by the curved arrow in Figure 9.4.

The key idea here is that organizing a perfect world requires the evolution of and frequent engagement of domain-general competencies. This is because

FIGURE 9.4. Evolved Heuristics and Controlled Problem-Solving



People automatically engage in most day-to-day activities without consciously thinking about them and similarly use heuristics, or rule-of-thumb explanations, to provide coherence to their experiences. These are represented by the stable end of social and ecological conditions. Situations that deviate from the norm trigger attentional shifts and engagement of more effortful and explicit problem-solving that is dependent on domain-general competencies.

individual relationships, the pattern of social relationships within the ingroup, and coping with the competing interests of outgroups are never completely predictable, and individuals who are unable to understand and respond to changes in these dynamics are at a considerable disadvantage (R. D. Alexander, 1989; Humphrey, 1976). The engagement of these domain-general competencies for the top-down evaluation and manipulation of self-centered mental representations of the social world creates the ability to mentally simulate potential future social scenarios, to use problem-solving to generate a variety of potential responses to these situations, and to mentally rehearse these responses (Geary, 2005). In other words, an evolutionary history of complex and ever-changing patterns of social cooperation and competition has resulted in a high level of social unpredictability. The resulting evolutionary solution is to mentally generate potential variations of these conditions and to then rehearse behavioral strategies for controlling outcomes associated with each of these variations. Variation in ecological conditions (e.g., weather changes, migration patterns of hunted species) also contributed to the evolution of these systems, but the contents of thoughts generated by the default mode network suggest social dynamics were particularly important for their evolution.

Emotions

The emotion system provides critical information to others and to the self about an individual's current well-being and social status, and it is essential for the development and maintenance of relationships with friends and family and for adaptively responding to changing social dynamics (Cosmides & Tooby, 2013). For example, all people are embedded in a network of social relationships, and they value the welfare of their friends and kin that compose this network. The intensity of one's emotional responses to these individuals will vary on the basis of how much their welfare contributes to one's own proximate (i.e., here and now) and reproductive well-being. Threats to a child will elicit stronger emotions than will threats to a friend, and threats to a friend will elicit stronger responses than will threats to a stranger. Emotions are also important for updating the relative valuation of these relationships. Support from a friend during a difficult time typically results in gratitude that, in turn, increases the valuation of the welfare of the supportive individual and a person's relationship with them (Forster, Pedersen, Smith, McCullough, & Lieberman, 2017). A brief overview of emotion systems is provided next, followed by a review of the associated sex differences and a discussion of these sex differences in evolutionary context.

Emotion and mental representations. Emotions can be understood in terms of observable behaviors (e.g., facial expressions), as well as the corresponding feelings that are the personal experiences of an emotional state (Damasio, 2003). Emotions provide observable feedback to others (e.g., frowns signal disapproval) and feelings provide unobservable feedback to the individual (Campos, Campos, & Barrett, 1989). The latter is a useful indicator of the effectiveness of control-related behavioral strategies and of the potential benefits of a simulated behavior. Positive feelings provide reinforcement when strategies result in the achievement of significant goals or at least a reduction in the difference between the current and desired future state. Negative feelings promote disengagement when behaviors do not result in this end (J. A. Gray, 1987). The supporting brain systems (e.g., the amygdala) function in part to amplify attention to evolutionarily significant forms of information, like facial expressions, and to produce observable emotional expressions, subjective feelings, and corresponding behavioral biases that are focused on reproducing outcomes that were associated with survival or reproductive prospects during human evolution (Lazarus, 1991; Öhman, 2002). Kensinger (2007) described how memories for emotionally threatening or potentially harmful objects or events engage the amygdala and the hippocampus (involved in forming long-term memories, among other things) more strongly than do neutral or positive events:

> Although emotional memories are susceptible to distortion, negative emotion conveys benefits on memory for detail. These benefits make sense within an evolutionary framework. Because a primary function of emotion is to guide action and to plan for future occurrences, it is logical that attention would be focused on potentially threatening information and that memory mechanisms would ensure that details predictive of an event's affective relevance would be encoded precisely. (p. 217)

Positive emotions are evolutionarily functional as well. It is not a coincidence that happiness is strongly related to the strength of reciprocal and romantic relationships (Diener & Seligman, 2002), the former being sources of social support and the latter related to reproductive goals. Negative and positive emotions also contribute to niche seeking activities, such that individuals pursue evolutionarily significant goals in ways that are most adaptive for them (Rowe, 1994; Scarr & McCartney, 1983). Adaptive niche seeking would require the individual to pursue goals in ways that capitalize on their personality and their social, cognitive, or behavioral strengths by using competencies for which they have a relative advantage over other people (Dweck, 2017; Lubinski & Dawis, 1992). The use of these strengths is more likely to result in success, and the corresponding positive emotions reinforce use of these competencies (Izard, 1993). An apt example is the increase in testosterone concentrations and positive emotions that men experience when they win a competition that is important to them (Geniole, Bird, Ruddick, & Carré, 2017). These successes result in a subjective feeling of pride that is a cue to an increase in social status (Durkee, Lukaszewski, & Buss, 2019). The combination of increases in testosterone and pride reinforce the use of the strategy that produced the win and prompt further status striving.

Sex differences. Emotions and feelings help to guide women and men in their attempts to organize their world in ways consistent with their best interests. As described for fantasies, sex differences in emotional responses often align with sex differences described in previous chapters (D. M. Buss, 1989a; Vigil, 2009). The sex difference in emotional reactions to casual sex described in Chapter 7 of this volume provides one example. These include more intense feelings of moral disgust and guilt on the part of women than men (A. Campbell, 2008; Kennair, Wyckoff, Asao, Buss, & Bendixen, 2018) and the development of feelings of emotional dependency and anxiety about their partner's emotional investment in them, even among women who have liberal sexual attitudes (J. M. Townsend, Kline, & Wasserman, 1995). These sex differences follow from the higher costs for women if there is an unwanted pregnancy and from women's preference for men who will invest in them and their children.

To further illustrate the point, consider the sex difference in risk taking as related to men's status striving (see Chapter 8, this volume). By definition, risk taking involves making decisions and engaging in behaviors that could be harmful, especially in traditional contexts where risk taking and escalation of male-on-male conflicts can end in injury or death. The experience of fear and anxiety that would typically keep exuberant risk taking and conflict escalation in check are suppressed by the rise in testosterone concentrations during adolescence (Stanton, Wirth, Waugh, & Schultheiss, 2009). The suppression of these harm-avoidance feelings does not occur in women and results in a protective avoidance of the associated risks and as a consequence, a much lower prevalence of serious injury and premature death (A. Campbell, 2013; Owens, 2002). In many traditional contexts, men who avoid these risks are lower status and less likely to marry than are their more adventurous peers (e.g., Glowacki & Wrangham, 2015), but women who avoid unnecessary risks and potential injury are better able to invest in their children (Sear & Mace, 2008).

There are also sex differences in expressed emotions. These are the social signals (e.g., facial expressions) that typically but not always correspond to experienced feelings. The majority of associated studies reveal that women express these signals more frequently and intensely (e.g., wider smile) than do men (Buck, Savin, Miller, & Caul, 1972; Fischer & LaFrance, 2015; Kring & Gordon, 1998), and that these sex differences generally become larger as children move into adolescence (Chaplin & Aldao, 2013). J. J. Gross and John (1998) identified five subdomains that are common areas in which emotions are expressed. These include expressive confidence (i.e., the ability to act out emotions without feeling them), positive expressivity (i.e., the expression of positive emotions), negative expressivity, impulse intensity (i.e., strong feelings and difficulty controlling their expression), and masking (i.e., suppression of emotional expression). In this analysis, there was no sex difference in expressive confidence, but about 3 out of 4 women reported more positive expressivity than did the average man, and 2 out of 3 women reported more negative expressivity than did the average man. Among children, impulse intensity is higher in boys than in girls, but this reverses in adolescence (Chaplin & Aldao, 2013).

Overall, there is no sex difference in tendency to express anger (Archer, 2004), but boys and men are more likely to become physically aggressive in provocative or stressful situations (A. Campbell & Muncer, 2008; Knight, Guthrie, Page, & Fabes, 2002). In a meta-analysis of 122 samples of children and young adults, Knight et al. (2002) found that, independent of age, about 2 out of 3 boys and men behaved more aggressively (e.g., hit another person) than did same-age girls or women. These sex differences were most pronounced following mild to moderate provocations (e.g., subtle insults), where 7 out of 10 boys or men responded more aggressively than did the average girl or woman. Under conditions of low or high provocation, the sex differences were much smaller. When women are directly provoked and there is little risk of retaliation, they can behave nearly as aggressively as men. Men also tend to be more overtly aggressive in stressful situations, even when they are not directly provoked (Verona & Curtin, 2006). These sex differences are due in part to boys' and men's tendency to use aggression instrumentally or as a dominance-based strategy to control social dynamics and to get what they want, whereas girls' and women's tendency is to avoid escalation of physical conflict (A. Campbell, 2013; A. Campbell & Muncer, 2008).

In contrast to the study of emotional expression, it is more difficult to study sex differences in the personal experience of emotion. Women self-report more intense feelings than do men (Buck, Miller, & Caul, 1974; M. Grossman & Wood, 1993). Using diary methods, Barrett, Robin, Pietromonaco, and Eyssell (1998) found that women and men reported a similar range of emotions during day-to-day social interactions, but women rated the intensity of their accompanying feelings higher than did men. In their analysis of multiple emotions and feelings scales, J. J. Gross and John (1998) found that 6 out of 7 women reported more intense emotional states than did the average man, whereas 2 out of 3 men reported more masking than did the average woman.

Physiological and brain-imaging studies of emotion processing reveal a much more nuanced picture than do the self-report studies. Sometimes women show more intense physiological reactivity (e.g., sweating) in emotion eliciting situations (e.g., viewing an injury), consistent with their reports of more intense feelings, but sometimes they do not (Eisenberg & Lennon, 1983; Gard & Kring, 2007; Wager, Phan, Liberzon, & Taylor, 2003). Buck et al. (1974) found disconnections between expressed emotions, reported intensity of accompanying feelings, and physiological indicators of emotional reactivity. In situations designed to elicit a range of reactions, more women than men expressed emotions and reported intense feelings but showed little physiological indication of reactivity. In support of J. J. Gross and John's (1998) finding that men report more masking, Buck et al. found more men inhibited observable emotional expressions (e.g., facial expression) and reported less intense feelings but showed strong physiological reactivity to the situation. At the same time, there are also women who report intense feelings and have just as intense physiological reactions, as there are men who report little emotional reactivity and show few physiological reactions (see also Kring & Gordon, 1998).

Lebron-Milad et al. (2012) found no sex differences in basic physiological reactions to fear-inducing situations, but stronger brain activation in areas associated with emotion processing in women than in men. They suggested that their results imply "that men and women use different neural strategies to produce homeostasis in the brain in response to fear" (Lebron-Milad et al., 2012, p. 8). A recent meta-analysis of 56 brain imaging studies confirmed sex differences in the system of brain regions when viewing emotion-eliciting visual scenes (e.g., facial expressions of disgust or anger; Filkowski, Olsen, Duda, Wanger, & Sabatinelli, 2017). For men, the engaged regions suggested that they were exerting more effort at the top-down regulation of feeling states, consistent with masking and enhanced emotional regulation. For women, the engaged regions suggested increased vigilance and attention toward emotion cues and heightened stress and threat responses. Women also show stronger activation of areas (e.g., hippocampus) that would result in a better memory for the event (Cahill et al., 2001; Cahill, Uncapher, Kilpatrick, Alkire, & Turner, 2004). These sex differences are larger for negative or threatening images than for positive ones. In contrast, men show stronger neural responses in emotion-processing areas than do women when viewing amusing or erotic images or films (Stevens & Hamann, 2012).

Emotion in evolutionary context. In many contexts, the expression of fear, anxiety, and even empathy for opponents will undermine adolescent boys' and men's status within their group and will often provoke hostile reactions from their peers (Winegard, Winegard, & Geary, 2014). Their status striving and risk taking within these groups are facilitated by the testosterone-based dampening of emotional expression and the muting of their experienced feelings and stress (Stanton et al., 2009). The hormonal dampening of these systems, as well as men's tendency to consciously suppress their feelings and mask emotional expression, is consistent with the harsh rites of passage that boys in war-like societies are expected to endure (Sosis, Kress, & Boster, 2007; see Chapter 8, this volume).

This dampening also is important for the maintenance of emotional composure under the stressors of male–male competition in traditional contexts. As a Yanomamö (Venezuela, Brazil) warrior and headman, Kaobawä related to Chagnon (1997), "Never show fear to your enemy! Be strong and calm. The moment you reveal that you are afraid, you are in mortal danger! That is when your enemy will kill you" (p. 256). During the age of empires and clashes of organized militaries, a common tactic was to attempt to incite fear and panic in the opponent that would then "break rank" and lose the advantage of a coordinated defense or attack (R. Petersen & Liaras, 2006). The next chapter describes how socialization practices vary with the intensity of male–male competition in the wider society and how these practices can further suppress boys' tendency to express fear, pain, empathy, and other feelings that could interfere with their ability to compete in these contexts. Chapter 14 describes how this emotional dampening contributes to the sex differences in externalizing disorders (e.g., conduct disorder) and in accidental injury and premature death.

As noted, girls' and women's intense feelings of fear, anxiety, and stress in potentially dangerous circumstances increase their vigilance in these contexts and prompt self-protective defensive behaviors (e.g., withdrawal, avoidance; Archer, 2019; A. Campbell, 2013). As with boys' and men's risk taking, these biases can have downsides, including heightened risk for anxiety and depressive disorders for adolescent girls and women (see Chapter 14, this volume). Even so, some women show a disconnect between expressed emotions and their underlying feelings and physiological state that suggests the strategic use of emotional expressions. These women are not experiencing the corresponding feelings, but are expressing the emotions for social reasons, probably in the context of female–female relational aggression and to better manage relationships with men and same-sex friends.

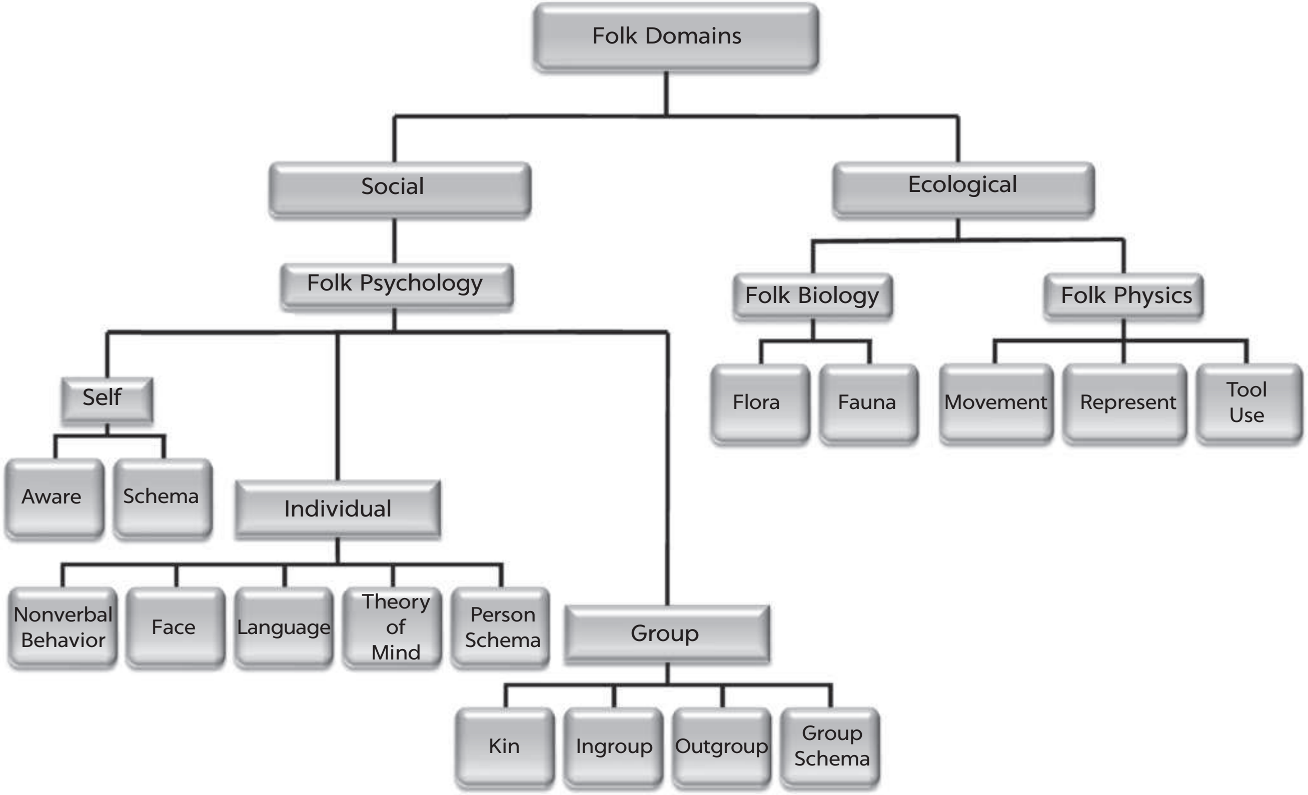
Even with the strategic use of emotional expressions, girls and women are on average more genuinely expressive than are boys and men (Archer, 2019; Rose & Rudolph, 2006). The result is more transparency in the context of many of their relationships. As is described in Chapter 11 of this volume, transparency is particularly important for the development and maintenance of the same-sex friendships that are central sources of social and emotional support for girls and women.

FOLK DOMAINS

This section focuses on the base of the triangle in Figure 9.1 and the corresponding folk domains shown in Figure 9.5. These organize our understanding of evolved biases in the human brain and cognition and provide the scaffolding for the discussion of corresponding sex differences in Chapters 12 and 13 of this volume. These folk domains represent universal cognitive abilities (e.g., language), clusters of knowledge (e.g., about the self), and cognitive biases (e.g., attributions about outgroups) that are needed to navigate various social relationships and to cope with myriad ecological challenges that confront people living in traditional contexts. The ways in which these are expressed can vary from one culture to the next, but people in all cultures have a core set of competencies in these domains (ojalehto & Medin, 2015).

The highest level in Figure 9.5 represents abilities and knowledge organized around the areas of folk psychology, folk biology, and folk physics (e.g., Medin & Atran, 1999; Pinker & Bloom, 1990; Spelke, Breinlinger, Macomber, & Jacobson, 1992; Wellman & Gelman, 1992). The second level of Figure 9.5 (social and ecological) is a reflection of the evolutionary salience of other people and their behavior (Brothers, 1990; Brothers & Ring, 1992; Geary & Flinn, 2001; Humphrey, 1976) and the biological and physical ecologies that support survival and reproductive activities (Kaplan, Hill, Lancaster, & Hurtado, 2000). The third level represents functional systems that compose

FIGURE 9.5. Evolutionarily Salient Abilities, Knowledge Domains, and Cognitive Biases Coalesce Around the Domains of Folk Psychology, Folk Biology, and Folk Physics



These enable the navigation of core social relationships and the common ecological demands (e.g., hunting) of people living in traditional contexts. Adapted from *The Origin of Mind: Evolution of Brain, Cognition, and General Intelligence* (p. 129), by D. C. Geary, 2005, Washington, DC: American Psychological Association. Copyright 2005 by the American Psychological Association.

key folk domains. Functional means that different combinations of abilities and knowledge can be put together in building-block form to meet current social or ecological demands (Geary, 2005; Geary & Huffman, 2002; Marcus, 2004). For instance, the Individual level under folk psychology captures the abilities (e.g., language, face processing) and knowledge (e.g., person schema) that are engaged during social interactions with other people.

These can be considered modular in the sense that they represent coherent abilities and knowledge domains, but they are not cognitive modules in the sense used by some evolutionary psychologists (e.g., for detecting social cheaters; Cosmides, 1989). Rather, they rather reflect more basic knowledge domains and abilities, but even so there is not a one-to-one correspondence between them and a single region in the brain. Language, for instance, is a coherent and functional social-cognitive ability but is supported by a system of regions that are distributed across various areas in the brain (Gernsbacher & Kaschak, 2003), and it is highly integrated with other social competencies, like the use of gesture (Skipper, Goldin-Meadow, Nusbaum, & Small, 2007). Moreover, folk abilities and domains are different from the academic competencies (e.g., reading, arithmetic) that are dependent on schooling and not needed for survival or reproduction in traditional contexts. The relation between folk domains and academic development is discussed elsewhere (Geary, 1995a, 2007, 2008; Geary & Berch, 2016), and any associated sex differences are covered in Chapter 14 of this volume. The goal here in differentiating folk cognition from these culturally specific forms of academic competence is to provide a more nuanced examination of sex differences than has been provided in research and theory on human sex differences in brain and cognition (e.g., D. F. Halpern, 2000).

Folk Psychology

The taxonomy of folk psychological domains supports the competitive and cooperative social dynamics that are common in humans (Bugental, 2000; Caporael, 1997). Although these are separated in terms of self-, individual-, and group-level systems, simultaneous activation of multiple systems is common in day-to-day life. People's sense of self, for instance, is influenced by their group memberships (e.g., ethnicity, political affiliation; Ashmore, Deaux, & McLaughlin-Volpe, 2004). Nevertheless, each of these folk systems has distinct features and different patterns of sex differences, as is covered in Chapter 12 of this volume.

Self

Self-awareness is the ability to consciously represent the self as a social being, is integrally related to the ability to mentally time travel, and may be unique to humans (Suddendorf & Corballis, 2007; Tulving, 2002). Self-awareness is supported by aspects of the default mode network and executive processes acting on autobiographical memories and other representations of the self.

These memories and representations are important for processes such as social comparisons or projections of the self into the future (Andrews-Hanna et al., 2014; LeDoux & Brown, 2017; Raichle, 2015). The *self-schema* is a long-term memory network of information that links together autobiographical memories with knowledge and beliefs about the self, including positive and negative traits (e.g., friendliness) and personal evaluations of competence or self-efficacy in various areas (Bandura, 2001; Fiske & Taylor, 1991; Markus, 1977; R. M. Ryan & Deci, 2017). Self-awareness of an individual's strengths and weaknesses, personality, and so forth can be used to form social strategies for increasing social influence and access to culturally important resources (Geary, 2005), and it appears to engage a part of the default mode network (Meyer, 2019; Qin & Northoff, 2011).

Although the evidence is mixed, self-schemas might contribute to the regulation of goal-related behaviors (Bandura, 2001; Sheeran & Orbell, 2000). Self-regulation results from a combination of implicit and explicit processes that influence social comparisons, self-efficacy, valuation of different forms of ability and interests, and the formation of social relationships. When evaluating the competencies of others, people focus on attributes that are central features of their self-schema and prefer relationships that provide feedback consistent with their self-schema. Athletes implicitly compare and contrast themselves with others on dimensions that involve physical competence, whereas professors focus more on intellectual competence (Fiske & Taylor, 1991). People value competencies for which they excel and discount those for which they are at a competitive disadvantage (S. E. Taylor, 1982). The combination may facilitate niche seeking and the development of niche-relevant competencies. In modern contexts, for instance, knowledge of one's own personal interests and personality (e.g., degree of extroversion) can influence his or her career choices, and therefore the pursuit of one prestige-based route to cultural success or another.

Individual

There are several types of universal one-on-one relationships in humans, including attachment between a parent and a child, and friendships (Bugental, 2000; Caporael, 1997). Despite motivational and emotional differences across these relationships, they are all supported by the same suite of cognitive competencies, including the ability to read nonverbal communication signals (e.g., gesture), facial expressions, language, and theory of mind (Adolphs, 1999; Brothers & Ring, 1992; Humphrey, 1976; Leslie, 1987; Pinker & Bloom, 1990). *Theory of mind* represents the ability to make inferences about the intentions, beliefs, emotional states, and likely future behavior of other individuals; it may be especially developed in humans, and is related to social competencies (Imuta, Henry, Slaughter, Selcuk, & Ruffman, 2016; Leslie, Friedman, & German, 2004). The functional individual-level system is also engaged during the dynamics of one-on-one social interactions, providing cues to the online emotions and intentions of other people.

The integration of these modular systems with motivational and emotional systems provides the basis for the development and maintenance of long-term relationships. In these relationships, the *person schema* becomes important. People develop such schemas of familiar people and people for whom future social relationships are expected (Fiske & Taylor, 1991). The schema is a long-term memory network that includes representations of the other persons' physical attributes, especially race, sex, and age, as well as memories for specific behavioral episodes, and more abstract trait information. The latter typically varies across two continuums, sociability (warm–emotionally distant) and competence (D. J. Schneider, 1973). The person schema will also include information about the person's theory of mind (Adolphs, 1999; Leslie, 1987). This would include memories and trait information about how the person typically makes inferences, responds to social cues, his or her social and other goals, and so forth. The person schema is also likely to include emotional dimensions, including memory representations that elicit a sense of familiarity and specific feelings on the basis of memories of prior experiences with a person (Brothers, 1990).

Group

People readily demarcate their world into social groups that reflect the evolutionary significance of kin, the formation of ingroups and outgroups, and ideologically based social identification (R. D. Alexander, 1979; Dunbar, 1993; Eagly, 1987). An evolved bias to differentially favor kin over nonkin is found in all species (Hames, 2016; W. D. Hamilton, 1964; Lukas & Clutton-Brock, 2018; Perry & Daly, 2017) and is illustrated by the parental investment discussed in Chapters 4 and 6 of this volume. The following sections outline the basics of the evolution and social psychology of ingroups and outgroups and group identification or group schemas. The latter is illustrated with a discussion of the ideology of gender.

Ingroups and outgroups. Group-level, coalitional competition is common across human societies and almost certainly has a deep evolutionary history (Böhm et al., 2018; Choi & Bowles, 2007; see Chapter 8, this volume). Coalitional competition also is found in some other primates, among other species, and is characterized by cooperation among members of the ingroup to more effectively compete against outgroups for control of survival-related (e.g., fruit trees) or reproduction-related (e.g., mates) resources (see Chapter 5, this volume). Contrasting species that form coalitions to their more solitary cousins provides a means to test the hypothesis that the cognitive competencies and brain systems that govern coalition formation have evolved. Such contrasts have consistently revealed that species in which coalitions form have a larger neocortex and more complex social-cognitive competencies than do evolutionarily related solitary species (D. A. Clark, Mitra, & Wang, 2001; Dunbar, 1993; Dunbar & Bever, 1998), although brain size in primates is also influenced by nonsocial factors (e.g., foraging complexity; DeCasien, Williams, & Higham, 2017).

The initial evolutionary basis for large-scale human coalitions was most likely male philopatry and the formation of kin-based coalitions among males (see Chapters 5 and 8, this volume). In traditional societies, group size can vary in response to the opportunities and demands of the local habitat that supports the group, but usually does not exceed 150 to 200 individuals (Dunbar, 1993). These groups are hierarchically organized and day-to-day activities (e.g., hunting) usually occur in smaller bands of about four families that include about 15 to 20 people (M. J. Hamilton, Milne, Walker, Burger, & Brown, 2007; K. R. Hill et al., 2011), with the larger group coming together at times, including those times of intergroup conflict (Mathew & Boyd, 2011). The individuals that compose these groups will include kin and allies who share beliefs (e.g., origin myths) that not only distinguish them from other groups but often, if not always, assign special significance to their own group (D. E. Brown, 1991). When a group's status or resources are threatened by the activities or perceived hostile intentions of other groups, the human tendency to form ingroups and outgroups and process information about group members that are favorably biased toward the ingroup and negatively biased against the outgroup is exacerbated (Hewstone, Rubin, & Willis, 2002; Horowitz, 2001; Riek, Mania, & Gaertner, 2006). Hewstone et al. (2002) concluded that "threat is a central explanatory concept in several of the theories . . . and literature on intergroup bias" (p. 586). Ingroups and outgroups are defined by differing social and moral ideologies that favor ingroup members (kin and friends) and devalue outgroup members (L. T. Harris & Fiske, 2006).

One key condition for effective competition against an outgroup is the disengagement of the emotional and moral mechanisms that reduce conflict and foster cooperation within ingroups (Haidt, 2007). Although some level of ingroup conflict is anticipated, especially when there are no current competing outgroups, it appears that feelings such as guilt and empathy moderate this conflict in the service of mutually beneficial cooperative exchanges (Baumeister & Leary, 1995; Trivers, 1971), as does the belief that reciprocal relationships are often in a person's best interest (Baron, 1997). When directed toward outgroups, these same emotional biases would result in a competitive disadvantage. In other words, when the competition between groups affected reproduction and survival, individuals who were able to dehumanize outgroups, in extreme cases, were likely at a competitive advantage.

The basic point should be clear: The cognitive and behavioral processes involved in the formation of ingroups, outgroups, and social identification are readily interpretable in terms of social selection pressures. These social–psychological phenomena are the proximate mechanisms that facilitate the formation of cooperative coalitions that, in turn, function to gain access to or control of the social and ecological resources that enhance the well-being of ingroup members. Enhancement is essentially about control of the resources that facilitate the health and well-being of the individual and her or his kin, and about improving reproductive options (see Chapter 8, this volume). When viewed in terms of mental models and the motivation to control, explicit representations of group-level dynamics allow for the simulation of potential future relationships among groups, as well as the development of competitive strategies. These mental simulations are capitalized on in military strategy and many competitive games (e.g., chess).

Group schema. Social psychologists have studied group identification for much of the 20th century and continue to do so. Much of this research has focused on the personal identification with members of a perceived ingroup under conditions of threat by and competition with an outgroup (Fiske, 2002; Fiske & Taylor, 1991; Hewstone et al., 2002). Ingroup identification is facilitated by a shared system of beliefs and moral rules that are often symbolically represented, as in national flags or religious images. These shared beliefs are central to the social identification processes underlying group formation and competition (Abrams & Hogg, 1990) and are critical to the formation of larger and more competitive groups than would otherwise be possible (K. MacDonald, 1988).

The initial pressure for the evolution of the emotional and cognitive biases that support this identification process might have been ancestor worship and the cross-generational transfer of myths about these ancestors and, as groups enlarged, eventually the emergence of deities that punished failures to cooperate with distant ingroup members (Palmer, Ellsworth, & Steadman, 2009; Purzycki et al., 2018). In any case, the formation of groups on the basis of these ideologies define the perceived mutual self-interest of individuals that compose these groups and is the basis for the intragroup cooperation that facilitates large-scale between-group conflict (Atran & Ginges, 2012; Norenzayan & Shariff, 2008). Supporting evidence comes from studies that enhance mortality cues, as well as less severe threats. These contexts increase people's endorsement of ingroup ideologies and result in harsher evaluations of outgroup members (Arndt, Greenberg, Pyszczynski, & Solomon, 1997). In other words, people rally around ideologies when they are threatened.

Ideology of gender. There is no question that humans socially categorize each other on the basis of biological sex and begin to do so very early in life (Maccoby, 1988; Martin, Ruble, & Szkrybalo, 2002). Kujawski and Bower (1993), for instance, showed that infants as young as 10 months distinguish the sex of other infants on the basis of differences in the other infants' movement, as measured by looking patterns. Cognitive and brain imaging studies reveal that people can categorize others' sex in less than 1 second on the basis of a few facial features, and when they do so they engage different brain regions relative to the processing of other facial information (e.g., familiarity; Cabeza & Nyberg, 1997; Schyns, Bonnar, & Gosselin, 2002). People have a number of stereotypes about boys and men and girls and women, but most of these stereotypes are accurate and, if anything, they often underestimate the magnitude of the actual sex differences (D. F. Halpern, Straight, & Stephenson, 2011; Jussim, 2017; Löckenhoff et al., 2014; Swim, 1994).

Many people also have a system of beliefs called *gender roles* that descriptively captures the behaviors, attitudes, social expectations, and social position of boys and men and girls and women in most societies (Eagly, 1987; see also Chapter 10, this volume). Eagly (1987; see also W. Wood & Eagly, 2002) proposed that these beliefs include descriptive and injunctive norms. The former are descriptions of stereotypical sex differences (e.g., men are more physically aggressive than women), and the latter are expectations about how boys and girls and men and women ought to behave. Both types of norms are organized, in part, in terms of communion and agency. Women have, on average, more communal traits as "manifested by selflessness, concern with others, and a desire to be at one with others" (Eagly, 1987, p. 16), whereas men have, on average, more agentic traits as manifested by "self-assertion, self-expansion, and the urge to master" (Eagly, 1987, p. 16).

These theorists argue further that sex differences in communion and agency are influenced by the different social and economic roles that men and women occupy in most if not all societies to varying degrees. Of particular importance is women's greater involvement in domestic activities (e.g., childcare) and men's greater involvement in paid employment or physically demanding resource acquisition (e.g., hunting). These roles in turn are influenced by a combination of physical sex differences (e.g., men are larger than women), contextual factors, and modes of economic activity (e.g., agriculture). In addition to the greater communal demands of domestic activities and the greater agency demands of employment-related activities, women and men tend to differ in social status, including a greater frequency of men than women in high-status occupations and in key political positions. The argument is that the greater social status of men than women not only further reinforces the communal and agentic roles of women and men, respectively, but influences the emergence of sex differences (through injunctive norms) in those social behaviors associated with dominance and submission (Eagly & Karau, 2002). Whereas Eagly (1987) acknowledged that many factors contribute to these sex differences—"the requirements of the economy and social structure interact with the biological attributes of women and men and with the political ideologies of societies to produce differential role occupancy" (p. 31)—the gist of her theory is that most sex differences are caused by injunctive norms.

In theory, women and men use these norms to evaluate their own social behavior and that of other people, and in fact social psychological studies confirm these evaluations (e.g., Eagly & Karau, 2002). It is not that boys and girls simply internalize injunctive norms, but in addition, other people mete out rewards and punishments for adherence to and violations of these norms. This section cannot do complete justice to the nuances of the social role model but argues that we do not fully understand the cause and effect of these relations. The normative stereotypes are found in all cultures in which they have been studied (Best & Williams, 1983), and some of these reflect biologically influenced sex differences. Men are in fact more physically aggressive than women, and women do in fact invest more in children. The extent to which sex differences are caused by injunctive norms and other social processes as contrasted to or interacting with biological biases in these behaviors, cognition, and so on, is not well understood. These theorists have downplayed the potential importance of sexual selection for understanding human sex differences (W. Wood & Eagly, 2002), and some theorists have incorrectly characterized evolved biases as deterministic, in that they cannot be expressed in different ways in different contexts (Bussey & Bandura, 1999).

From the motivation to control perspective, the argument that sex differences are largely the result of injunctive norms is appealing to many people because such theories create an illusion of control and are more politically palatable (Jussim, 2017). If gender-role theories are largely correct, then all sex differences in social status, social behavior, and so on can be potentially eliminated by modifying the social expectations for girls and women and boys and men. Although appealing, strong versions of this view are almost certainly wrong, as Eagly (2018) conceded. The communal-agency distinction can be applied to nearly all of the sex differences described in Chapter 5 of this volume for nonmonogamous primates and in other chapters for many other species. Male–male competition to establish social dominance or agency is a salient feature of nearly all of these primate societies, as is the fact that most "domestic" activities, in particular the care of offspring, are the domain of females (Andersson, 1994; Whitten, 1987). Even young children notice these differences and begin to state them (e.g., "Girls like to play with dolls"), but the statements need not be indicators of normative or injunctive norms (S. A. Gelman, Taylor, & Nguyen, 2004), but rather descriptions of differences that emerge as children play and socialize in ways that are the most engaging for them (see Chapters 10 and 11, this volume). In this view, these norms are not the primarily casual factors in creating sex differences, but largely descriptions of them.

In keeping with this argument, the social roles of women and men differ in societies in which there are no explicit gender roles, such as the Batek of Malaysia (Endicott, 1992; Murdock, 1981). The same general pattern of sex differences emerges in societies that are socially isolated from one another and similarities across these societies cannot be explained in terms of shared cultural ideologies about the gender roles of women and men (D. E. Brown, 1991; Eibl-Eibesfeldt, 1989). In a review of sex differences in the division of labor across 224 societies, Daly and Wilson (1983) reported that the agentic activity of weapon making was an exclusively male activity in 121 of the 122 societies in which this information was available, whereas the communal activity of cooking was an exclusively female activity in 158 of the 201 societies surveyed.

Pratto (1996; see also Pratto, Stallworth, Sidanius, & Siers, 1997) has also shown that a combination of factors influence the occupational differences that are prominent in Eagly's (1987) theory. In addition to stereotypes about the relative communal and agentic orientations of women and men, the distribution of women and men into different status-related occupations is related to self-selection (see also Hakim, 2002; Stoet & Geary, 2018; see Chapter 14, this volume). When given a choice, men, on average, prefer dominance-oriented occupations, those emphasizing hierarchical social relationships and the control of other people. Women, on average, prefer to work in hierarchy-attenuating jobs, those that involve working with people, especially the disadvantaged and underprivileged (Pratto et al., 1997). These differences are in keeping with the ways in which men pursue cultural success in developed nations and with the tendency for women to avoid direct competition and their more communal orientation. The latter reflects women's higher investment in children and families.

Regardless, social ideologies can influence human behavior and there is no reason to expect that gender will be immune from such influence. Still, the construction of gender ideologies is at times an attempt at social and political manipulation. The tendency of some scholars to describe girls and women as passive and boys and men as active might represent an implicit attempt to suppress female choice and maintain the status quo (i.e., male control of social and material resources). Boys and men are in fact more physically active than are girls and women (see Chapter 10, this volume), but both sexes actively pursue their self-interests.

Similarly, the ideological prescriptions of some feminist scholars appear to be implicitly designed to disrupt the formation of male coalitions, suppress male–male competition (i.e., suppress the establishment of dominance hierarchies), and, at the same time, increase female choice and female control of essential resources (see American Psychological Association, 2018; G. C. H. Hall & Barongan, 1997). These prescriptions reflect the expression of sexual politics, which includes conflict over the different reproductive preferences of men and women through human language. These are essentially strategies that function to persuade other people to join an ideological group, and if enough people are persuaded the result will be a change in the flow of resources within the culture or social group. Any such strategies may successfully convince some other people, but biology is indifferent to them.

Folk Biology

As with beak specialization in Darwin's finches (see Chapter 2, this volume), there is considerable evidence for species-specific brain, cognitive, behavioral, and physical specializations that enable the location and manipulation of edible plants, fruits, and nuts (e.g., raccoons, *Procyon lotor,* cleaning of food), as well as the location and capture of prey species (Barton & Dean, 1993; Huffman, Nelson, Clarey, & Krubitzer, 1999). The folk biological modules shown in Figure 9.5 represent the most rudimentary cognitive specializations that support humans' ability to learn about, identify, and secure biological resources in the wide range of ecological niches occupied by our species (Caramazza & Shelton, 1998; Malt, 1995; Medin & Atran, 2004). Children appear to have an inherent but skeletal set of perceptual (e.g., attention to self-generated motion) and cognitive biases (e.g., inference that living things have agency) that orient them toward living things and enable increasingly sophisticated and accurate inferences about them (Atran, 1998; Margett-Jordan, Falcon, & Witherington, 2017; Setoh, Wu, Baillargeon, & Gelman, 2013). By adolescence, these coalesce into functional competencies that support hunting, gathering, horticulture, and in many contexts, animal domestication.

Analogous to variation in the surface structure of human languages and a universal grammar (Pinker, 1999), there is cross-cultural variation in the extent and organization of folk biological knowledge but also a universal core (ojalehto & Medin, 2015). As a reflection of this core, humans throughout the world are able to categorize the flora and fauna in their local ecologies and show similar categorical and inferential biases when reasoning about these species (Atran, 1998; Berlin, Breedlove, & Raven, 1966; J. M. Diamond, 1966). Through ethnobiological studies, "it has become apparent that, while individual societies may differ considerably in their conceptualization of plants and animals, there are a number of strikingly regular structural principles of folk biological classification which are quite general" (Berlin, Breedlove, & Raven, 1973, p. 214). Bailenson, Shum, Atran, Medin, and Coley (2002) asked groups of novices and bird experts from the United States and Itza' Maya Amerindians (Guatemala) to classify about 100 birds from their region and from the region of the other group. There were similarities in the classifications of all three groups, as well as differences. The classification system of U.S. experts and the Itza' Maya were more similar to the scientific taxonomy of these species than was that of the U.S. novices:

> The Itza' data are dramatic in that despite not being exposed to either western science in general or formal taxonomy in particular, their consensual sorting agrees more with (western) scientific taxonomy than does the consensual sort of US non-experts. This difference held for both US birds and Tikal birds. (Bailenson et al., 2002, p. 24)

Bailenson et al.'s (2002) findings for novices are not unique and highlight the importance of experience for fleshing out inherent skeletal competencies and for focusing on one aspect of folk biology or another (Busch, Watson-Jones, & Legare, 2018). Without sufficient experience with the natural world, as with Western college students or children living in modern urban areas, only rudimentary aspects of folk biology develop (Medin & Atran, 2004). With sufficient experience, people develop at least a three-level organization to their knowledge of the biological world. The most general level corresponds to the kingdom level in the scientific classification and is the only level shown in Figure 9.5. People further subdivide flora and fauna into groups of related species that correspond to the class level, such as birds, mammals, and trees, and then more specific species, such as bluebirds (*Sialia*) and robins (*Turdus*). Cross-cultural variation is largest for knowledge of species that are specific to the local ecology and that are of functional importance to the local population (Atran, 1998; Malt, 1995). This species-specific knowledge can then be used to make inferences about the behavior, growth, and so forth of less familiar but related species.

Knowledge of the species' morphology, behavior, growth pattern, and ecological niche (e.g., arboreal versus terrestrial) help to define the essence of the species (Atran, 1994; Malt, 1995). The essence is a species-specific schema that includes knowledge of salient and stable characteristics, including the species' relationships with other species in the wider ecology (e.g., Medin et al., 2006). Biological essence may also be analogous, in some respects, to people's theory of mind. This is because mental models of flora and fauna would be well suited for representing and predicting the likely behavior of these organisms (e.g., seasonal growth in plants). The combination of folk biological categories, inferential biases, and knowledge of the species' essence allows people to capture and use these species to increase their survival prospects (Figueiredo, Leitão-Filho, & Begossi, 1993, 1997; see Chapter 13, this volume).

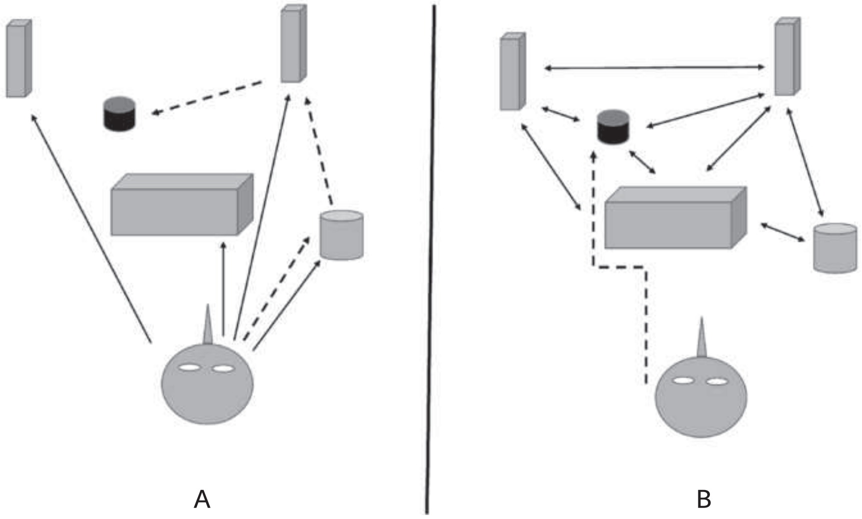
Folk Physics

Folk physics is supported by brain and cognitive systems that enable organisms to engage with the physical world. At the most basic level, animals need ways to determine where they are, where they are going, and how to get back, as related to seeking food, shelter, or mates and to avoid threats (e.g., predators) to their well-being. The movement and representation modules shown in the rightmost portion of Figure 9.5 represent the most fundamental systems that support these abilities. These systems interact but also have components that are functionally and anatomically distinct (Milner & Goodale, 1995), and in nonhuman species support navigating in the ecology, prey detection and tracking, prey capture, predator avoidance and other key survival-related behaviors (e.g., Barton & Dean, 1993; Gallistel, 1990; O'Keefe & Nadel, 1978; Shepard, 1994).

The most critical brain and cognitive systems are those that support the representation of and movement in three-dimensional space. The core function of movement is to navigate from one place to another and there are two systems for doing so (Byrne, Becker, & Burgess, 2007; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; O'Keefe & Nadel, 1978). As illustrated by section A of Figure 9.6, the first is based on an egocentric view of what the organism sees, including objects with respect to the self. Egocentric navigation is especially dependent on a part of the brain called the caudate nucleus, and is part of an evolutionarily old subcortical network that is involved in movement and reward processing. Egocentric representations position the individual relative to objects in the ecology and the individual uses these to determine where to go and when to change direction. Navigation then involves moving to one landmark, making some type of change in direction (e.g., turn left), moving to the next landmark, changing direction and so on until the goal is reached. This is essentially a stimulus-response type of strategy that is based on familiarity with the navigated ecology.

As illustrated by section B in Figure 9.6, allocentric navigation is dependent on forming a spatial map of the relations among landmarks in the ecology

FIGURE 9.6. Egocentric and Allocentric Navigation



Section A illustrates egocentric navigation which is based on viewing landmarks in the current environment, as represented by solid lines. The dashed lines show navigation that involves moving to one landmark, changing direction to reach the next, and changing direction again to reach the goal. Section B shows allocentric navigation which involves forming a spatial map of the relations among key landmarks in the environment, as shown by solid lines. Navigation is based on the location of the goal relative to its position among the landmarks, as shown by the dashed line.

(O'Keefe & Nadel, 1978). This is another evolutionarily old system and is dependent on the hippocampus (especially in novel environments), surrounding areas, and several areas in the occipital and parietal lobes (Boccia, Nemmi, & Guariglia, 2014; Broglio et al., 2015). The spatial map is composed of large-scale geometric relations and positioning of objects in space independent of the organism, providing a type of "bird's-eye view" understanding of where things are in relation to one another. This is a very flexible system that allows for the location of and navigation to the goal on the basis of its location relative to other landmarks (rather than the self) in the ecology (Gallistel, 1990). Both egocentric and allocentric navigation are also dependent on several areas of the parietal cortex, such as parts of Areas 7 and 40 in Figure 9.3, that can also integrate these strategies while the individual is moving from one place to another (Boccia et al., 2014; Maguire et al., 1998; Maguire, Frackowiak, & Frith, 1996; Whitlock, 2017). These areas are integrated with areas that support actual movement in and acting on the environment and these include the several motor areas of the neocortex (e.g., Areas 4 and 8 in Figure 9.3) and the cerebellum (not shown in Figure 9.3; Therrien & Bastian, 2019).

A few species can also generate explicit mental representations of egocentric and allocentric physical space in working memory. Kuhlmeier and Boysen (2002), for instance, demonstrated that many chimpanzees (*Pan troglodytes*) can form a correspondence between the location of a miniature object in a scale model of an enclosure and the location of the actual object in the enclosure. The ability to do this suggests that some chimpanzees are able to generate an explicit mental representation of the location of objects that are not currently being viewed. Other experimental manipulations suggested that these chimpanzees form a mental representation of the location of objects on basis of both landmark information (e.g., the object is next to another object) and geometric coordinates (e.g., the object is northeast of another object). As is reviewed in Chapter 13 of this volume, humans are exceptional in both regards. For now, it is noted that some of the same brain regions (e.g., Areas 7 and 40 in Figure 9.3) that are engaged during actual movement in space are engaged during the generation and mental manipulation (e.g., rotation) of visual images (Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Zacks, 2008).

Tool use is a human universal that enables people to more fully exploit biological resources in the local ecology (Murdock, 1981). On the basis of brain imaging and cognitive deficits following brain injury, Johnson-Frey (2004) concluded that homologous (from a common ancestor) brain regions are involved in basic object grasping and manipulation in humans and other primates. These include parts of Area 40 as well as areas involved in coordinated movement and object recognition (e.g., Areas 6 and 37 in Figure 9.3; Ishibashi, Pobric, Saito, & Lambon Ralph, 2016). At the same time, it is clear that humans have a much better conceptual understanding of how objects can be used as tools than do other primates (Povinelli, 2000). This knowledge is based on a distributed network of brain regions, with parts of Area 40 on the left side of the brain supporting the forms of mechanical reasoning that are unique to humans (Reynaud, Lesourd, Navarro, & Osiurak, 2016). People's understanding of how these objects can be used is also influenced by the inferred intentions of potential tool users (Bloom, 1996). At the core, human tool use involves the ability to mentally represent an object as a potential tool, to manipulate this mental representation to explore the different ways in which the object might be used, and finally to integrate such representations with active tool use (Lockman, 2000).

Foley and others have detailed the relation between advances in the sophistication of tools used for food extraction (e.g., digging sticks) and hunting with the appearance of species since *Australopithecus afarensis* (Foley, 1987; Foley & Lahr, 1997). There is evidence that *Homo habilis* used simple stone tools and that increases in the complexity of stone tools and their geographic distribution coincided with the emergence and migration patterns of *Homo erectus*. Further increases in the complexity of stone tools and again their geographic distribution coincided with the emergence and migration patterns of early modern humans. The most complex stone tools are found in archaeological sites dating less than 50,000 years ago and are found with the fossils of modern humans and *Homo neanderthalensis* (Foley & Lahr, 1997). The pattern of tool "evolution" and the likely function of these tools, including hunting and other forms of food extraction (e.g., digging up edible roots), appears to be consistent with an increase in reliance on hunting during recent human evolutionary history. The recent emergence of hunting contrasts sharply with the sex difference in physical size—an indicator of physical male–male competition—that extends back at least 4 million years ago (see Chapter 5, this volume).

Folk Heuristics

The explicit mental representations at the center of Figure 9.1 and the implicit knowledge represented in folk modules have been discussed elsewhere (see Geary, 2005). Implicit knowledge is inferred by regularities in the behavior of organisms, but the principles governing these regularities cannot always be explicitly articulated (Gigerenzer, Todd, & ABC Research Group, 1999; Rozin, 1976; Simon, 1956). Barton and Dean's (1993) analysis of the brain's visuomotor pathway as related to prey-capture in mammals illustrates this point. Cells in this system are likely to be sensitive to the movement patterns of prey species and enable the coordination of the behaviors necessary to capture this prey, such that the functioning of this module can be said to reflect an implicit understanding of how to catch prey. The organization of prey-catching behavior indicates a form of knowledge that is represented in the structure and function of the underlying neural systems, and there is no need for an explicit awareness of how prey are identified and caught. The same is true for prey species, whereby the detection of a predator automatically triggers a defensive response (e.g., freezing) without any need for the animal to consciously experience fear (LeDoux & Brown, 2017). All that is needed for the defensive response to evolve is for it to work most of the time.

The evolution of these systems results in outcomes that are not typically optimal but rather just good enough to yield the desired outcome. Much of human behavior is influenced by similar implicit or "intuitive" mechanisms (Kahneman, 2011). Children, for example, form and maintain friendships on the basis of reciprocity or the give-and-take of these relationships, without having read Trivers' (1971) seminal article on the evolution of reciprocal altruism. Despite this, the social behavior of children indicates they understand implicitly the reciprocal core of long-term social relationships, such that children who do not reciprocate are socially rejected (Youniss, 1986). Reciprocity results from the organization of folk psychological modules, the pattern of emotional reactions to social relationships, and more or less automatically results in an implicit understanding of the costs and benefits of friendships and in mechanisms for their formation, maintenance, and, in many cases, dissolution. The explicit understanding of these same principles, in contrast, was only achieved through considerable scientific effort.

The explicit representation of social and other forms of information in working memory and the formation of self-centered mental simulations of the world is only necessary when the folk systems do not result in the desired outcome or when there is a mismatch between knowledge implicit in these systems and experience (Geary, 2005). During social interactions, the knowledge represented in the person schema is implicit; there is no conscious representation of this information (e.g., where the person is on the sociability trait), but it nonetheless influences the dynamics of the interaction (Fiske & Taylor, 1991). However, when the behavior of this other person is inconsistent with the schema, then attention is drawn to the inconsistency, and the behavior is explicitly and consciously represented in working memory. The explicit representation allows inferences about the likely source of the inconsistency and facilitates incorporation of the behavior into the person schema.

The person schema is also related to the use of mental simulations to make judgments about how the person might react in various situations, called the simulation heuristic by Kahneman and Tversky (1982). For instance, variation in an individual's traits (e.g., warm–emotionally distant) influences how easy it is to generate one type of behavioral sequence or another. It is easier to mentally simulate the dynamics of a socially warm friend making a good impression when first meeting your family than it is to imagine the same outcome with an emotionally distant friend. The person schema allows for seamless interactions in most situations. When the dynamics or outcomes are not certain, the combination of the person schema and the ability to form mental representations of potential future states allows one to simulate how other people will likely respond in these situations and enables better predictions of other people's behavior and the rehearsal of related social strategies.

THE DEVELOPMENT OF FUNCTIONAL SYSTEMS

Consider the life history topics discussed in Chapter 4 of this volume, specifically, the evolved functions of experiences during development, phenotypic plasticity, and play. Consideration of the developmental period is critical for understanding humans and human sex differences. The length of this period appears to have nearly doubled since *Homo erectus* (C. Dean et al., 2001), has coevolved with the malleability or plasticity of folk modules, and has coevolved with the corresponding ability to transmit cultural information across generations (e.g., Darwin's natural selection, Mozart's 25th symphony; Geary, 2007; Richerson & Boyd, 2005). The human ability to adapt to an unusually wide range of ecological and social niches is dependent on the plasticity of folk modules, the ability to explicitly problem solve to cope with social dynamics and to modify the ecology in self-serving ways (e.g., build shelters), and a corresponding ability to create cultural scenarios that support large-scale societies. At the same time, and as every parent knows, there are limits on adults' ability to influence developing children. This is because children have inherent biases to seek certain types of experiences and to build their own social and cultural niches, as is covered in Chapters 10 and 11 of this volume.

Children's Niche Seeking

All of us desire some level of control over the social relationships that are important to us and over access to culturally important resources (Heckhausen

& Schulz, 1995), but the specifics of these social and cultural contexts vary considerably from one place (or time) to another. Social and ecological variability in turn results in pressures for the evolution of brain and cognitive systems that can adapt themselves, so to speak, to changing circumstances (Siegler, 1996; Tooby & Cosmides, 1990a). The ontogenetic or developmental adaptation of an evolved cognitive system to local conditions appears to reflect the operation of what Mayr (1974) called an open genetic program, or phenotypic plasticity, as was discussed in Chapter 4 of this volume. A closed program results in a perceptual, cognitive, or behavioral trait that cannot be modified by experience. With an open program "new information acquired through experience is inserted into the translated program in the nervous system" (Mayr, 1974, p. 651), although an "open program is by no means tabula rasa; certain types of information are more easily inserted than others" (Mayr, 1974, p. 652). The longer the lifespan of an individual, the greater will be the selection

> premium on replacing or supplementing closed genetic programs by open ones. . . . A subsidiary factor favoring the development of an open program is prolonged parental care. When the young of a species grow up under the guidance of their parents, they have a long period of opportunity to learn from them—to fill their open programs with useful information on enemies, food, shelter, and other important components of their immediate environment. (Mayr, 1974, p. 657)

Mayr's (1974) description of an open program is consistent with research in the developmental sciences. It is now known that many of the early competencies of infants and young children reflect innate but skeletal knowledge (R. Gelman, 1990; S. A. Gelman, 2003; Spelke et al., 1992). Skeletal means the underlying brain and perceptual systems provide the initial structure of folk competencies that are then fleshed out and adapted to local conditions during the developmental period (R. Gelman, 1990; Gopnik & Wellman, 2012; Keil, 1992). For these processes to operate, early attentional, perceptual, and cognitive biases must be coupled with a motivational bias for children to engage the ecology and the social world in ways similar to those in which the biases originally evolved (Bjorklund & Pellegrini, 2002; Scarr, 1992). Behavioral engagement is predicted to generate evolutionarily expectant experiences that provide the feedback needed to adjust the architecture of folk systems to nuances in evolutionarily significant domains (Greenough, Black, & Wallace, 1987), such as allowing the individual to discriminate one face from another (Pascalis, de Haan, & Nelson, 2002). These behavioral biases are expressed as common childhood activities, such as social play and exploration of the ecology, as described in Chapter 4 of this volume and elaborated on for boys and girls in the following chapter.

The interaction between infants' language perception and their early exposure to language illustrates how early experiences can shape the architecture of an evolved brain and cognitive system. Infants born into all cultures respond to the same basic phonemes (language sounds), including those that are not in their parents' native language, and can discriminate these language sounds from other categories of sound, such as musical notes (Kuhl, 2010). The neural, perceptual, and cognitive systems that allow infants to respond to the phonemes of all languages are part of the skeletal structure of the language domain. In this case, language exposure during the first year of life results in a trimming of the range of phonetic sounds to which the system responds (Kuhl et al., 1997). The net result is that the functional features of the system (i.e., the language sounds that can be comprehended and produced) correspond to the local language. A similar skeletal structure is evident for face processing and becomes refined and fleshed out with infants' and children's exposure to variation in faces, across people and for different emotions (M. H. Johnson, Senju, & Tomalski, 2015). It is very likely, in fact, that a skeletal structure that is elaborated on through natural developmental activities is in place for most, if not all, of the folk domains shown in Figure 9.5.

Parents and Culture

It is an all too common and rather naive assumption that parents, social injunctions, and other cultural information drive children's experiences and thereby shape their cognition, motivations, and even their brain architecture (Hyde, 2007; W. Wood & Eagly, 2002). As described in Chapter 6 of this volume, parents can have a profound influence on the well-being of their children, but the relationship between parenting and the social, psychological, and cognitive development of children is considerably weaker than many people assume (J. R. Harris, 1995; Lytton & Romney, 1991; Rowe, 1994; Scarr, 1992). Nevertheless, cross-cultural comparisons do suggest that parents and other socializing influences can affect the social and psychological development of children, although the magnitude of these effects appears to be small to moderate (Low, 1989); these are elaborated on in Chapter 11 of this volume. In fact, children are predicted to have some degree of receptivity to parental and socializing influences, given the unusually long developmental period and the cross-generational transmission of cultural knowledge. Much of this transmission however occurs through social learning and imitation and not any type of direct instruction by parents (Lancy, 2014).

Still, some aspects of child-rearing practices appear to reflect parental knowledge of the demands of adult life, as well as more subtle, implicit influences, as was discussed in Chapter 6 of this volume. For instance, parent–child warmth, a component of attachment between parents and children, may vary in ways that prepare children for adult life (Low, 1989; Whiting & Whiting, 1975). K. MacDonald (1992) proposed that the degree of parental warmth modifies the neurobiological systems that underlie emotional reactions to social dynamics, much like early language exposure modifies aspects of the language system. These modifications result in children becoming more or less sensitive to other people, influencing the extent to which their behavior is relatively self-serving or cooperative. Harsh treatment, such as repeated physical beatings, may "shut down" the systems that generate the feelings that facilitate empathy and social cooperation, resulting in a relatively self-serving social style. As with many traits, the cost–benefit trade-offs associated with a relatively cooperative or self-serving approach to social relationships depends on context and cannot be known ahead of time. Parental experience of relatively more cooperative or more self-serving relationships among adults biases their treatment of children that in turn emotionally prepares the children for the same types of relationships when they become adults.

CONCLUSION

The main thesis of this chapter is that evolution results in a constellation of traits that allow organisms, including humans, to attempt to achieve some level of control over the social, biological, and physical resources that have enhanced survival and reproductive prospects during the species' evolutionary history (Geary, 2005). The corresponding motivation to control is a heuristic rule of thumb that I use to attempt to better understand how human behavior and other traits are organized and how they may have evolved. If gaining some level of control over the dynamics of social discourse, for instance, provided survival and reproductive benefits during human evolution, then selection will favor the emergence of social-cognitive competencies that process associated information (e.g., facial expressions). The processing of this information is necessary but not sufficient to ensure adaptive responses to local conditions, however. To be functional, the systems must also include emotional and behavioral components. The emotional components provide feedback to others and to the self about relative success at gaining some level of control (Damasio, 2003), and behavioral components are needed to actually achieve corresponding goals.

Behaviors, cognition, and emotions are organized together as functional systems that focus on recreating the conditions that improved survival and reproductive prospects during human evolution. These conditions were discussed in previous chapters, as related to sex differences in relative investment in parenting, competition to attract the attention of would-be mates, as well as direct competition with members of the same sex over access to mates and culturally important resources. As mentioned, relational aggression among adolescent girls and women is often centered on romantic relationships and functions to undermine the social support of competitors and to drive them from the social group (Benenson, 2013, 2014). These dynamics are in effect attempts to organize the local network of social relationships in self-serving ways. Genghis Khan and his allies did the same on a much larger scale and used dominance-related violence to do so, rather than gossip and innuendo. In any case, this framework allows us to merge the sex differences described in earlier chapters with those that emerge during human development and that are found for the brain and cognitive systems that support folk domains, as is discussed in the following chapters.

10

Sex Differences in Infancy and Play

This chapter melds human sex differences in general physical development, during infancy, and in play with the life history perspective reviewed in Chapter 4 of this volume. It also melds these differences with sex differences in parenting, mate choices, and competition for mates. The following chapter integrates this with a focus on the social development of boys and girls and the influence of parents and culture on the expression of the associated sex differences. The organizing framework is shown in Figure 10.1, whereby the developmental activity component of Figure 4.1 (see Chapter 4, this volume) is expanded to embed research on human sex differences within the broader theories of life history and sexual selection. Most of the sex differences documented by developmental psychologists over the past century can be easily incorporated into evolutionary theory and this chapter illustrates how this can be done.

The well-known relationship between sexual selection and physical development in other species is readily applied to sex differences in the physical development of boys and girls as described in the first section. The discussion then moves to infancy. As C. Darwin (1871) observed, sex differences become exaggerated with the approach of reproductive maturation, with smaller or no differences early in development. This is generally true for humans, but there are some intriguing differences in infancy that are the roots of sex differences described in the following chapters and are understandable in terms of sex differences described in previous ones. Children's play is discussed next. Play is particularly interesting because children's self-directed activities

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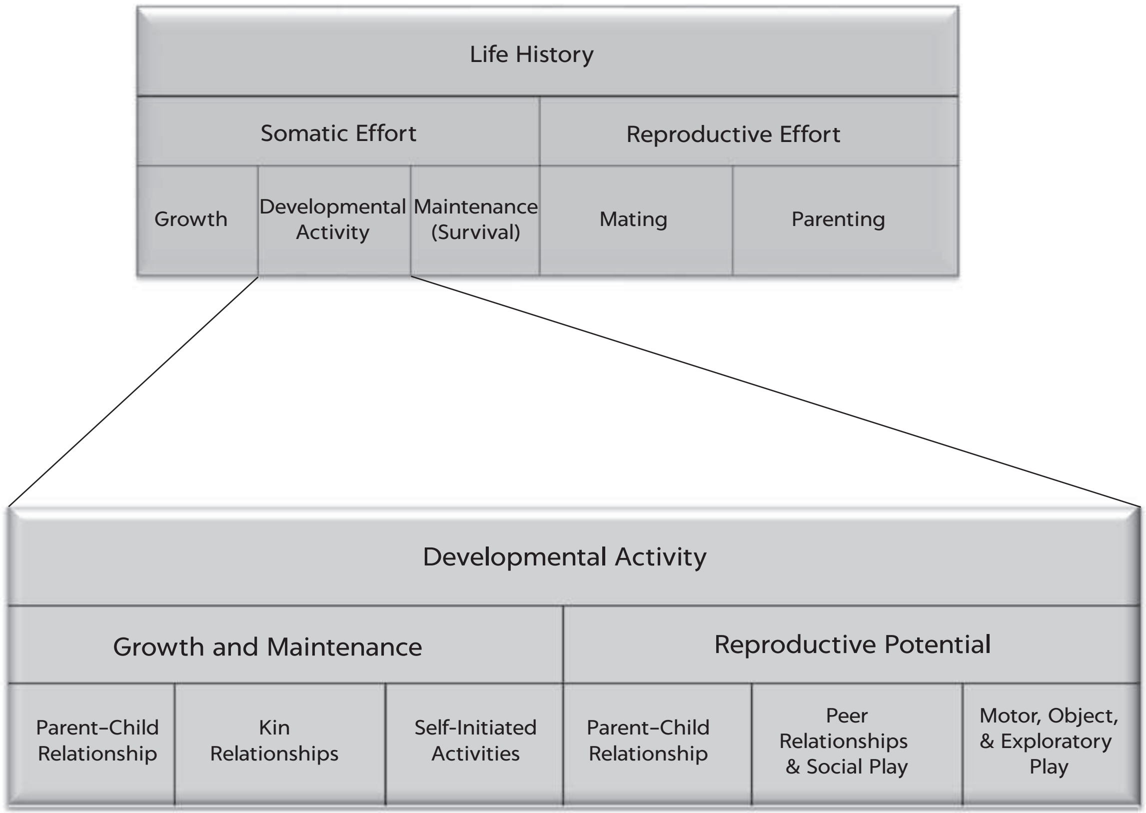
FIGURE 10.1. Components of Developmental Activity Based on Life-History Theory



Parent–offspring relationships emerge from parents' reproductive effort and the efforts of offspring to obtain parental resources. Kin relationships represent investment in the child from the wider kin-group. Self-initiated activities refer to the child's foraging and related behaviors that contribute to physical growth and maintenance; the parent–child relationship can also contribute to the child's reproductive potential (e.g., through educational and cultural success). Peer relationships and various forms of play provide experiences that flesh out folk domains and adapt them to local circumstances.

reflect our evolutionary history and help children to adapt folk abilities to local conditions. The chapter closes with discussion of the relation between prenatal and early postnatal exposure to sex hormones and the many sex differences discussed in this chapter.

PHYSICAL DEVELOPMENT

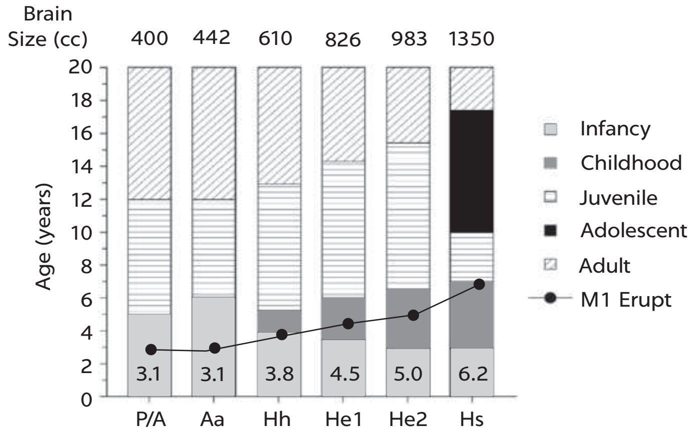
The key functions of developmental experiences are to adapt folk competencies to local conditions (R. Gelman, 1990; Mayr, 1974), and in doing so the associated physical, behavioral, and social skills are tailored to the demands of adulthood in the context of these conditions. The demands of adulthood are those which our ancestors faced, not the school-dependent occupations found in developing and developed nations today. The relationship between development and preparation for adulthood in these societies is discussed elsewhere (Geary, 1995a, 2007). This section begins with a discussion of evolutionary change in the length of the human developmental period and then moves to a review of sex differences in physical development and physical competencies.

Evolution of Childhood and Adolescence

Evolutionary change in the pattern and length of life history development indicates a change in selection pressures, such as changes in diet, ecology, or intensity of social competition (Antón, Potts, & Aiello, 2014). Slower development, larger brains, and longer lifespans tend to go together in primates and suggest that slower development provides more opportunities to learn or refine skills that are needed for survival and reproduction in adulthood. The question of exactly what these nonhuman primates need to learn during their development ranges from the complexities of finding high-quality foods (e.g., fruits) to the demands of social competition and learning from others (DeCasien, Williams, & Higham, 2017; Street, Navarrete, Reader, & Laland, 2017), and the questions remains to be resolved (Powell, Isler, & Barton, 2017).

With respect to hominin evolution (see Chapter 5, Figure 5.5, this volume), McHenry (1994a) and Bogin (1999) estimated the ages of maturation for *Australopithecus afarensis* and *Australopithecus africanus* to have been similar to that found in the modern chimpanzee (*Pan troglodytes*), which is 10 to 12 years old. There is disagreement about the specific age of maturation for species of *Homo*, but the general evolutionary pattern can be estimated with some certainty. As shown in Figure 10.2, Bogin estimated gradual increases in the length of the developmental period from *Homo habilis* to *Homo erectus* to *Homo sapiens* (see also Bogin, Varea, Hermanussen, & Scheffler, 2018). Of particular interest are differences in the evolved pattern of human development compared with that of our ancestors, specifically the unique and qualitatively different periods of childhood and adolescence (Bogin, 1999).

FIGURE 10.2. Evolution of Hominid Life History During the First 20 Years of Life



Mean brain sizes are given at the top of each histogram. Mean age at eruption of the first permanent molar (M1) is graphed across the histograms and given below the graph. P/A = *Pan troglodytes* (e.g., chimpanzee) and *Australopithecus afarensis*; Aa = *Australopithecus africanus*; Hh = *Homo habilis*; He1 = early *Homo erectus*; He2 = late *Homo erectus*; Hs = *Homo sapiens*. From *Patterns of Human Growth* (2nd ed., p. 15), by B. Bogin, 1999, Cambridge, England: Cambridge University Press. Copyright 1999 by Cambridge University Press. Reprinted with permission.

Chimpanzees and our early ancestors had three broad and relatively distinct developmental periods, as with other mammals. *Infancy* is the time of suckling, and *juvenility* is the time between weaning and reproductive maturation. For most primates, the juvenile period is initiated with the eruption of the first molar and independent feeding. Unlike most other primates, chimpanzees have a 12- to 18-month delay between the age of first molar eruption and weaning. During this time they learn, through observation and imitation, how to “fish” for termites, crack open nuts, and other survival-related skills (Goodall, 1986). Bogin (1999) proposed that human childhood emerged between infancy and juvenility and extends from 2 to 3 years old (i.e., age of weaning in traditional societies) to the age of eruption of the first molar at 6 to 7 years old. Weaning is typically followed by a new pregnancy in traditional societies, leaving the 3-year-old dependent on a wider range of adults for food preparation, feeding, and care. As described in Chapter 6, this volume, this community of adults often includes grandparents (e.g., maternal mother) and the father.

Age of first molar eruption is interesting because it is tightly related to adult brain size and brain development (J. Kelley, 2004). The human brain is very large and is expensive to build and maintain. In most primates, the brain consumes 8% to 9% of resting metabolic calories, but this jumps to 20% to 25% in humans (W. R. Leonard & Robertson, 1994). The share of calories devoted to the developing brain is still larger, especially during infancy and childhood (Kuzawa et al., 2014). A 5-year-old, for instance, will devote 44% of basal metabolic calories to brain development and functioning (Bogin, 1999). Although it does not get much larger in terms of volume, the human brain continues to develop (e.g., generating and then pruning axonal connections between regions) through adolescence and into early adulthood (Foulkes & Blakemore, 2018).

The juvenile period is the same as that found in other primates and lasts from age 7 years old to the onset of the hormonal changes that begin puberty and reproductive maturation (e.g., 11–13 years old). Boys and girls show marked skeletal growth following the onset of puberty, along with increases in muscle mass and fat tissue. The growth spurt in other primates is different in that it is largely due to increased muscle mass and little if any change in skeletal growth (Bogin, 1999; Leigh, 1996). These differences in physical development and the social behavior of teenagers mark the evolutionarily novel period of *adolescence*.

This human developmental period coevolved with increases in brain size (see Chapter 5, this volume), a corresponding increase in the range of ecologies occupied by our ancestors, and a likely increase in the complexity of social relationships, including intrasexual competition (Joffe, 1997). The 15- to 20-year period between weaning and reproduction in traditional societies—compared with the 5- to 7-year period in chimpanzees and our early ancestors—is intriguing and indicates that activities during this developmental period are of critical evolutionary significance. The self-initiated activities and preferences of children and adolescents provide us with insights into the nature of these selection pressures. This is because developmental activities prepare children and adolescents to be successful in the adulthoods of our ancestors and what happens during development provides insights into these adulthoods (Geary, 1992; Tooby & Cosmides, 1990b).

Sex Differences

Next, the general pattern of sex differences in physical development and physical competencies as potentially related to sexual selection is examined. For extensive reviews of sex differences in physical development, see Tanner (1990) and Bogin (1999).

Development Pattern

The development of secondary sexual characteristics can be costly, especially for males (see Chapter 4, this volume). These costs include potential suppression of immune functions, increased risk of predation (e.g., for brightly colored males), and increased aggression from same-sex adults. These costs create substantial benefits for delaying the emergence of reproductive maturation and any corresponding sex differences until the individual has gained the physical (e.g., weight), social, behavioral, or cognitive competencies needed for successful intrasexual competition or intersexual choice. C. Darwin (1871) described this pattern 150 years ago:

> There is . . . a striking parallelism between mammals and birds in all their secondary sexual characteristics, namely in their weapons for fighting with rival males, in their ornamental appendages, and in their colours. In both classes, when the male differs from the female, the young of both sexes almost always resemble each other, and in a large majority of cases resemble the adult female. In both classes the male assumes the characters proper to his sex shortly before the age for reproduction. (p. 297)

Consider the northern elephant seal (*Mirounga angustirostris*) and the satin bower bird (*Ptilonorhynchus violaceus*). Male elephant seals mature at around 8 years old, as compared with 3 years old for females (Clinton & Le Boeuf, 1993). Among other things, the males' relatively long maturational period allows them to gain the body mass and fighting skills (i.e., reproductive potential) needed to compete for a harem. Male satin bower birds do not achieve full-adult blue plumage until they are 7 years old and do not typically reproduce until 10 years old, as compared with 2 years old for females (Collis & Borgia, 1992). During development, young males do not differ significantly in appearance from young and adult females. During their juvenile period, "young males spend a great deal of time observing older males at their bower, and practice bower building and display behaviors when the owner is absent" (Collis & Borgia, 1992, p. 422). Young males also engage in fighting with their same-age peers, which provides the experience needed for serious dominance-related encounters in adulthood. Delayed maturation allows males to grow larger and gain the social and behavioral competencies needed to compete for and attract mates.

Humans are no different. Many physical sex differences do not emerge until puberty and adolescence, and many of the earlier-emerging differences are comparatively small (Bogin, 1999; Tanner, 1990). As with male northern elephant seals and bowerbirds, boys develop more slowly than do girls:

> [Overall,] girls grow up faster than boys: that is, they reach 50% of their adult height at an earlier age, . . . enter puberty earlier and cease earlier to grow. . . . At birth the difference corresponds to 4 to 6 weeks of maturation and at the beginning of puberty to 2 years. (Tanner, 1990, p. 56)

The most prominent sex differences to emerge during puberty are a widening of the hips and pelvis in girls—the development of which is not complete until about 17 years old (Bogin, 1999)—and a widening of the width of the shoulders in boys:

> [Boys also] develop larger hearts as well as larger skeletal muscles, larger lungs, higher systolic blood pressure, lower resting heart-rate, a greater capacity for carrying oxygen in the blood, and a greater power of neutralizing the chemical products of muscular exercise. . . . In short, the male becomes more adapted at puberty for the tasks of hunting, fighting, and manipulating all sorts of heavy objects. (Tanner, 1990, p. 74)

The changes in lean muscle mass and the percentage of body fat are dramatic. At 9 years old, boys have about 8% more muscle than girls (J. Kim et al., 2006).

During the next 6 years, girls' lean muscle mass will increase about 50%, but this increase is more than double for boys. At 15 years old, boys have about 70% more muscle tissue than girls and nearly all boys have more muscle mass than does the average girl. These differences increase over the next several years because muscle growth is nearly complete in girls and continues for at least 3 more years in boys (Lassek & Gaulin, 2009; Tanner, 1990). At age 9, girls have about 25% more body fat than boys, but this increases to about 60% more body fat than boys by age 15 (J. Kim et al., 2006). The facial features that women find attractive in men also emerge during this time but there are less marked changes in girls' faces; "in some girls scarcely any detectable spurt in face dimensions occurs at all" (Tanner, 1990, p. 68). These more minor changes result in the retention of the youthful appearance that men find attractive in women's faces.

As with other species, these physical changes are related to the increase in sex hormone concentrations that occurs during puberty (Tanner, 1990). For instance, there is a 20-fold increase in testosterone concentrations as boys move from childhood into adolescence. One result is 15 times more plasma (blood) concentrations of testosterone in young men than in young women (Handelsman, Hirschberg, & Bermon, 2018). For girls, the increase in concentrations of estrogens (e.g., estradiol) and other hormones trigger their physical maturation, including the increase in the percentage and distribution of body fat (de Ridder et al., 1992).

Physical Competencies

Although boys and girls are more similar than different before puberty, there are a few early differences. During childhood and juvenility, boys have small to moderate advantages in grip strength, jumping distance, and running speeds, and these differences increase substantially during adolescence (Thomas & French, 1985). For 17-year-olds, more than 9 out of 10 men outperform the average woman in these areas. The exaggeration of the sex differences in lean muscle mass that occurs during adolescence translates into substantial differences in lower and especially upper body strength by early adulthood (Pheasant, 1983). From 10 to 16 years old, boys' raw upper body strength increases nearly fourfold and their lower body strength by nearly threefold (Carron & Bailey, 1974), as compared with much more modest changes in girls (Round, Jones, Honour, & Nevill, 1999). Activity levels differ as well: About 3 out of 5 infant boys are more physically active than are same-age girls, and this difference increases over time. By adolescence, about 7 out of 10 boys are more physically active than are same-age girls (Eaton & Enns, 1986; Nilsen, Anderssen, Ylvisaaker, Johannessen, & Aadland, 2019).

Because of the sex differences in leg length, muscle mass, and cardiovascular capacity, men can run faster than women on average (Cheuvront, Carter, Deruisseau, & Moffatt, 2005), but by far the largest differences are for throwing distance and throwing velocity (Thomas & French, 1985). Between the ages of 4 and 7 years old, 9 out of 10 boys have higher throwing velocities than the average same-age girl. By 12 years old, the very best girls have throwing velocities that are comparable with those of the least skilled boys. The sex difference is even larger for throwing distance. By 2 to 4 years old, more than 9 out of 10 boys can throw farther than the average girl, and by 17 years old only the very best girls can throw as far as the least skilled boys. By early adulthood, men also have moderate to large advantages in visual acuity, throwing accuracy, and in the ability to track and block objects thrown at them. In these areas, about 3 out of 4 men outperform the average woman (Jardine & Martin, 1983; Watson & Kimura, 1991).

The sex differences in throwing skills are related to differences in the structure of the supporting skeletal system. Relative to overall body height, boys have a longer ulna and radius (i.e., forearm), on average, than do girls (Gindhart, 1973). The radii of 3 out of 4 newborn boys is longer than those of the average newborn girl, and by adolescence, the radii of more than 19 out of 20 18-year-old men is longer than those of the average 18-year-old woman. There are also sex differences in the timing and pattern of skeletal ossification in the elbow and in the length and robustness of the humerus (i.e., upper arm; Benfer & McKern, 1966; Tanner, 1990), all of which contribute to men's throwing advantage.

These differences in skeletal structure and associated throwing competencies, combined with the large male advantage in arm and upper body strength, indicate strong selection pressures for these traits in men. These sex differences in fact provide further support for the hypothesis that the evolution of male–male competition in humans was influenced by the use of projectile weapons (e.g., spears) and blunt force weapons (e.g., clubs; Keeley, 1996; see Chapter 8, this volume). Coincident with the emergence of these physical sex differences are widening sex differences in sensitivity to pain. Men have a higher threshold and greater tolerance for physical pain than do women (Bartley & Fillingim, 2013), and especially when their tolerance is gauged against that of other members of their ingroup (A. H. Buss & Portnoy, 1967).

Despite the converging evidence for the importance of male–male competition for the evolution and expression of these sex differences, some theorists have argued that they evolved from the division of labor, including men's hunting (e.g., Kolakowski & Malina, 1974; W. Wood & Eagly, 2002). As described in Chapter 5 of this volume and elaborated on in Chapter 13 of this volume, the division of labor hypothesis is incorrect. In addition to the reasons outlined in these sections, sex differences in pubertal development are closely tied to sex differences in intrasexual competition and the corresponding sex differences in physical size. Across polygynous primates with intense male–male competition, there is a characteristic pattern of female and male growth. When it occurs, the female growth spurt begins at an earlier age, reaches its peak more quickly, and lasts for a shorter period than that of males. The human sex differences fit this pattern (Leigh, 1996; Tanner, 1990).

Of course, some physical sex differences have evolved through natural rather than sexual section, such as the wider pelvic region in women to accommodate infants with larger cranial size. Once the large pelvis evolved, the waist-to-hip ratio that men find attractive emerged and began to be shaped by male choice (see Chapter 7, this volume). Girls are also more physically flexible than are boys and have an advantage in fine eye-motor coordination. Unlike many of the advantages shown by boys, the advantage of girls in these areas does not change substantively during adolescence, suggesting they are not related to sexual selection. In any case, about 3 out of 5 girls outperform the average boy in these areas (Thomas & French, 1985). Kimura (1987) argued that the advantage of girls and women might be related to manipulating objects “within personal space, or within arm’s reach, such as food and clothing preparation and child care” (p. 145). Coss and Goldthwaite (1995) argued the greater flexibility of girls and women, among several other traits, are evolutionarily old adaptations related to an arboreal life. As found in orangutans (*Pong pygmaeus*), the smaller female *Australopithecus* appears to have had adaptations (e.g., greater flexion in ankle joints) that facilitated movement in trees, which is a predator avoidance strategy.

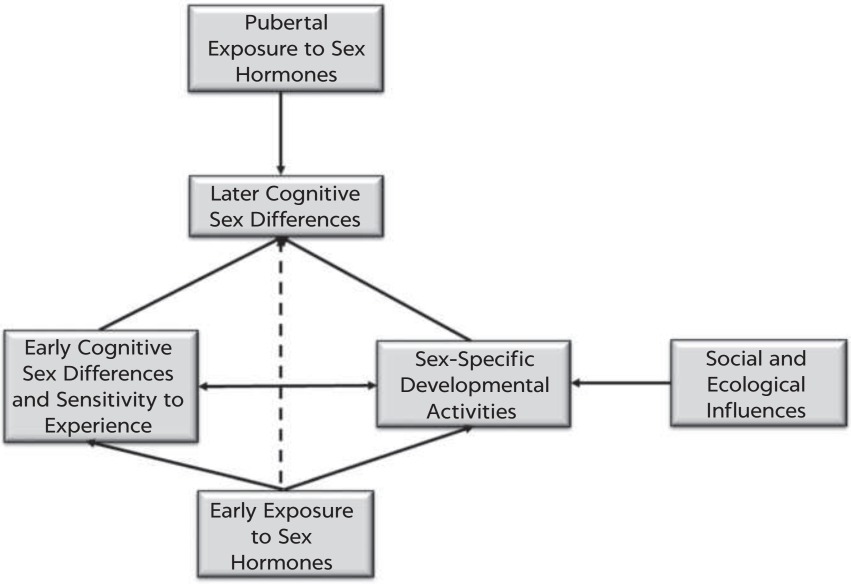
INFANCY

C. Darwin’s (1871) cross-species observation that the sexes are more similar than different early in life applies to humans. There are, however, several intriguing patterns in the infancy literature that suggest the skeletal structure of at least some later sex differences are evident in the 1st year or 2 of life and possibly in the first few days of life. G. M. Alexander (2003) hypothesized that some of the early sex differences in orientation toward people (more in girls) or things (more in boys) reflect the evolved skeletal structure of the visual system and biases in the “what,” “where,” and “how” visual pathways (see Chapter 12, this volume). For the where pathway, prenatal and early postnatal exposure to androgens (i.e., male hormones) appears to result in an attentional and perceptual bias to focus on spatial location and object motion. More recently, Handa and McGivern (2015) proposed that the where pathway includes a how component that will support competence in the use of objects as tools. The what pathway is enhanced in the absence of early exposure to androgens and results in an attentional and perceptual bias for processing faces and color variation in the green to red spectrum, among other things.

The actual processing of these different types of information is not that clear cut, however, but many of these biases emerge before infants can recognize themselves and cannot be influenced by any socially imposed gender schemas (Campbell, Shirley, Heywood, & Crook, 2000). These early biases in turn appear to result in experiences that selectively maintain or prune the corresponding neural pathways, leading to a developmental increase in the magnitude of the corresponding sex differences.

The basic idea is shown in Figure 10.3, whereby early exposure to sex hormones results in early sex differences in folk domains (e.g., attention to moving objects) as well as sex differences in sensitivity to the experiences that emerge from engagement in sex-typical play and other activities. The

FIGURE 10.3. Developmental Sex Differences in Folk Domains



Developmental sex differences in folk domains emerge through a combination of small early-emerging differences, a sensitivity to experiences that will lead to their elaboration, and engagement in sex-typical behaviors. The latter can be amplified or diminished by social and ecological factors. The dashed line represents organizational effects on the brain systems that support cognitive sex differences that, in turn, are activated by pubertal hormones.

latter might also be influenced by social and ecological factors. The adult sex differences in folk domains (covered in Chapters 12 and 13, this volume) emerge from a combination of early and pubertal exposure to sex hormones and biologically and socially influenced differences in developmental experiences, as well as sex differences in sensitivity to one type of experience or another.

Attention to People

Studies of infants' brain activity while they view social information, such as faces, confirm that at least some of the skeletal structures of the folk-psychological systems are in place very early in life and become fine-tuned with development and social experience (e.g., discriminating one face from another; M. H. Johnson, Senju, & Tomalski, 2015). The use of a variety of behavioral measures also reveals this early social bias, and that girls orient to other people more frequently than do boys (G. M. Alexander, 2014; Connellan, Baron-Cohen, Wheelwright, Batki, & Ahluwalia, 2000; Freedman, 1974; Garai & Scheinfeld, 1968; McGuinness & Pribram, 1979). Orientation toward other people is measured in terms of the duration of eye contact, empathy for others' distress, and time spent looking at faces, among other behaviors.

Individuals and Groups

In a review of sex differences in nonverbal behavior, Haviland and Malatesta (1981) noted that "there is no doubt that girls and women establish and maintain eye contact more than boys and men. The earliest age for which this is reported is 1 day" (p. 189). Connellan et al. (2000) assessed the amount of time 102 newborns (about 37 hours old) spent looking at a face and at a mobile. Girls attended longer to the face and boys attended longer to the mobile, in keeping with a sex difference in biases toward the where system (stronger in boys) and the what system (stronger in girls). In one of the largest studies of this type, Osofsky and O'Connell (1977) assessed 328 newborns (2–5 days old) on a variety of behavioral and orienting tests, including orientating toward faces. They found that about 6 out of 10 girls oriented more to human faces, whether or not the person was speaking, than did the average boy. Hittelman and Dickes (1979) focused on eye contact in 2- to 4-day-olds and found that boys made eye contact as frequently as girls but did not hold their gaze as long. When their eyes were open, boys were in eye contact 21% of the time as compared with 31% of the time for girls. Gluckman and Johnson (2013) found the same pattern in 6-month-olds, but at this age nearly 3 out of 4 girls maintained eye contact longer than did the average boy. In other words, these sex differences become larger in the first few months of life.

Boys and men also gaze-avert more frequently than do girls and women, a sex difference that has been found as early as 6 months of age. Girls are not necessarily better at all aspects of face processing, however. Infant boys and girls scan faces differently, with boys incorporating more information on overall face shape and girls on the internal configuration of the face (e.g., eyes, mouth; Rennels & Cummings, 2013). Boys' more holistic processing may give them a short-term advantage in recognizing faces from different positions, although this usually disappears by 6 months old (Pascalis, de Haan, Nelson, & de Schonen, 1998), and girls' detail processing likely contributes to their advantage in emotion recognition. Eventually, infant girls develop a better memory for faces, although this advantage is smaller than that found in children and adults (Fagan, 1972; J. A. Hall, 1984; Haviland & Malatesta, 1981). McClure's (2000) meta-analysis revealed that infant girls have an advantage over boys in processing facial emotional expressions; in the 1st year or 2 of life about 2 out of 3 girls are more attentive to human facial expressions than is the average boy.

The typical study in this area presents infants with a single face, voice, or movement pattern or with a pair of individuals. These types of stimuli reveal infants' interest in other people but may not capture an important aspect of male sociality. As described in detail in a later section, boys organize themselves into larger groups than do girls and engage in competitive play in the context of these groups. Boys' group-level play is consistent with preparation for the coalitional male–male competition described in Chapter 8 of this volume. Benenson and her colleagues (Benenson, Duggan, & Markovits, 2004; Benenson, Markovits, Muller, Challen, & Carder, 2007) tested the corresponding hypothesis that the sex differences in social organization manifest as differences in the attentional interests of infant boys (i.e., a focus on groups) and infant girls (i.e., a focus on individuals).

In their first study, Benenson et al. (2004) presented 6- to 8-month-olds with a series of video clips of a single puppet or a group of three puppets. Girls and boys looked longer at the group than at the individual, but the bias was larger in boys (83% of boys vs. 63% of girls). The same procedure was used in the second study, but the infants watched film clips of groups of six 6-year-old boys and girls or individual 6-year-old boys or girls (Benenson et al., 2007). Again, girls and boys looked longer at the groups of children, but the difference was larger in boys. The sex difference emerged because the boy infants were especially interested in the group of older boys, with no sex difference in the amount of time spent watching the group of girls. About 3 out of 4 of the infant boys watched the boys' groups longer than did the average girl. G. M. Alexander, Wilcox, and Farmer (2009) did not, however, find a sex difference in preference for looking at groups for younger infants (about 4 months old), but boys with a large postnatal surge in testosterone concentrations spent more time looking at groups than did other boys. It may be that the sex difference in orienting toward groups does not consistently emerge until after 6 months, but either way these fascinating results are consistent with the sex differences in peer relationships described in the next chapter of this volume.

Empathy and Social Responsiveness

Empathy includes the understanding, recognition, and experience of the emotional state of others. Empathy can involve distress at seeing others in psychological or physical pain, as well as understanding and experiencing the specific emotional state of others (e.g., "I feel your pain"). Christov-Moore et al. (2014) provided an excellent review of the evolution of empathy in mammals and the associated behavioral indicators of it. The latter includes mimicry of facial expressions or body movements that signal emotional states and consolatory behavior (e.g., touching) directed toward the victims of aggression. They proposed that the length and intensity of maternal caretaking of primate infants provided the foundation for the elaboration of these empathy systems. These systems enhance females' sensitivity to subtle cues to the underlying state of the infant and in some primate species, may promote behavioral cooperation among related females that also contributes to the well-being of offspring. One result is that female primates generally show more indicators (e.g., mimicry of emotion cues) of empathy than do same-species males. On this view, we would expect girls and women to show more empathy in most contexts than boys and men, and indeed there are sex differences in the sensitivity to social cues that reflect the emotional state of others (see Chapter 12, this volume).

The question here is whether the root of these sex differences in social sensitivity is evident in the empathy of infants and young children. The associated studies do not always find early sex differences in empathy but most of them do find small but potentially important differences (Hastings, Zahn-Waxler, Robinson, Usher, & Bridges, 2000; Knafo, Zahn-Waxler, Van Hulle, Robinson, & Rhee, 2008; Noten et al., 2019; Rhee et al., 2013; Vaish, Carpenter, &

Tomasello, 2009; Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992). One indication of an evolved sensitivity is a reflexive reaction to the emotional state of others (Christov-Moore et al., 2014), and this is sometimes found with infant crying (M. L. Hoffman, 1977). Simner (1971) found that infant girls tended to cry longer than infant boys when exposed to the cry of another infant, but there was no sex difference in reflexive crying when the infants were exposed to artificial noise of the same intensity.

On average, 12- to 20-month-old girls respond to the distress of other people with greater empathic concern than do boys, as defined by "emotional arousal that appears to reflect sympathetic concern for the victim . . . manifested in facial or vocal expressions (e.g., sad looks, sympathetic statements) or gestures" (Zahn-Waxler et al., 1992, p. 129). Girls also tend to respond to distressed individuals with more consolatory behavior (e.g., comforting) and engage in more information seeking (e.g., "what's wrong?"). Boys, in contrast, are more frequently unresponsive or emotionally indifferent to the other individuals' distress. By 20 months of age, about 3 out of 5 girls respond with greater empathic concern to the distress of another person than does the average boy, whereas 2 out of 3 boys show more emotional indifference (and sometimes anger) than does the average girl. These sex differences continue into childhood and adolescence and the disregard for the distress of others becomes worse for a subset of boys (Hastings et al., 2000; see Chapter 14, this volume). Girls who show a disregard for the distress of others also have later social difficulties, but there are fewer girls than boys in this group (Vaish et al., 2009; Van Hulle, Rodgers, D'Onofrio, Waldman, & Lahey, 2007).

The social interactions between parents and infants also reveal that girls are more responsive and perhaps more sensitive to social cues than are boys (Freedman, 1974; Gunnar & Donahue, 1980; W. D. Rosen, Adamson, & Bakeman, 1992). W. D. Rosen et al. (1992) found that in ambiguous situations, 12-month-olds of both sexes approached a potentially risky unfamiliar object if their mother signaled positive emotions (e.g., smiling) in reference to the object. When mothers signaled fear through their facial expressions, girls tended to withdraw but boys still approached the object. In this study, independent coders rated the intensity of the mothers' fear signal and judged that these signals were more intense when directed toward boys, indicating the sex difference was not due to the behavior of their mothers. Rather, the tendency of boys to approach unfamiliar objects more frequently than girls might be an early manifestation of the sex difference in risk taking, as described in Chapter 8 of this volume. Mothers' more intense signaling might also reflect prior experiences with unresponsive sons.

In a related study with 6- to 12-month-olds, Gunnar and Donahue (1980) found that mothers attempted to initiate social interactions with their sons just as frequently as with their daughters, but daughters were much more responsive; Whiting and Edwards (1988) found the same pattern with older children across 7 cultures. For instance, 12-month-old girls were twice as likely (52%) as boys (25%) to positively respond to their mother's attempts to engage them in some form of social interaction. Boys and girls were equally responsive to their mother, in contrast, when she used a toy to attempt to initiate a social interaction. Girls also initiated about 30% more social interactions with their mother than did boys. Gunnar and Donahue's results suggest that the occasional finding that mothers sometimes interact more with their daughters than with their sons (e.g., Klein & Durfee, 1978) might stem from a sex difference in social responsiveness and the degree to which social interactions are initiated by girls, rather than a maternal preference for girls (Freedman, 1974).

Attention to Things

G. M. Alexander's (2003) proposal that boys have an attentional bias toward the where visual pathway should result in a preference for mechanical objects that produce nonbiological motion, like toy trucks, moving mobiles, or objects moving through space, and in an advantage in some forms of spatial ability (L. B. Cohen & Gelber, 1975; Freedman, 1974; McGuinness & Pribram, 1979). However, sex differences are not always found for interest in objects and mechanical motion (Bakker, Kochukhova, & von Hofsten, 2011; Escudero, Robbins, & Johnson, 2013), but when they are found they favor boys (G. M. Alexander, Wilcox, & Woods, 2009; Benenson, Tennyson, & Wrangham, 2011; Campbell et al., 2000; Lutchmaya & Baron-Cohen, 2002).

In Connellan et al.'s (2000) study of newborns, the sex difference in looking time was larger for the mobile than for the face. Boys not only looked longer at the mobile than at the face, about 7 out of 10 boys looked longer at the mobile than did the average girl. Boy and girl infants can track the trajectory of moving objects (S. P. Johnson, Amso, & Slemmer, 2003), but sometime between 4 and 9 months old, boys develop an advantage in the ability to track and remember the trajectory of several objects as they move behind other objects (i.e., know where they are even though they cannot see them), but same-age girls are unable to do this (T. Wilcox, Alexander, Wheeler, & Norvell, 2012). By 5 months, boys also have a better intuitive understanding than girls of what objects will look like when viewed from different angles, suggesting an early advantage in some aspects of spatial ability (Moore & Johnson, 2008). Lauer, Udelson, Jeon, and Lourenco (2015) found that infant boys with a stronger interest in objects had stronger spatial abilities than other boys, suggesting object interest and spatial ability are supported by a common brain and cognitive system, in keeping with G. M. Alexander's (2003) proposal (see also Chapter 13, this volume).

On the basis of a review of sex differences in perception, McGuinness and Pribram (1979) concluded that when "differences are found, males from 4–6 months onward respond preferentially to blinking lights, geometric patterns, colored photographs of objects and three-dimensional objects" (p. 19). A similar conclusion was drawn by L. B. Cohen and Gelber (1975) on the basis of a review of infants' visual memory:

> Males and females are processing and storing different kinds of information about repeatedly presented [visual] stimuli. Males appear to be more likely to store information about the various components of a repeatedly presented stimulus, for example, its form and color. . . . [whereas] females, unlike males, are more likely to store information about the consequences of orienting. (p. 382)

It appears that by the time they are 4 months old, boys selectively attend to the physical properties of objects (e.g., shape), whereas girls selectively attend to the consequences of orienting to objects in their environment, rather than to the details of the objects themselves, except when these objects are people. In this situation, consequences refer to how the objects might be related to the behavior of other people.

In all, there are probably more similarities than differences in infant girls' and boys' attention to and processing of nonbiological object motion, but the differences that are found are consistent with G. M. Alexander's (2003) proposal that there are sex differences in a bias toward the what and where components of the visual system. Boys' bias results in a focus on where objects are relative to other objects and a tracking of them as they move themselves (e.g., a rotating mobile) or move through space. These early sex differences may lay the foundation for the later described sex differences in object-oriented play and implicit knowledge of tool use, as well as men's advantage in tracking and responding to objects in motion (see Chapter 13, this volume).

PLAY

As is found for other species with a slow pace of life and a long developmental period (see Chapter 4, this volume), play is a universal aspect of children's behavior. Graham and Burghardt (2010) identified five common features of play: (a) it is voluntary; (b) it is not immediately functional, but may have delayed benefits; (c) it involves some components of more functional activities; (d) it is repeated; and (e) it occurs in safe environments. Humans also engage in more organized games that can involve elements of play (e.g., voluntarily organized by children) but are also constrained by rules and have a specific objective. They are included here because children's engagement in culture-specific games may provide practice for later functional activities that are important for that culture. Overall, the sex differences in play activities are nearly as large as some of the previously described physical sex differences. During the preschool years and into childhood there is very little overlap in boys' and girls' suites of play behavior (Golombok & Rust, 1993; Golombok et al., 2008; Todd et al., 2018), including differences in the frequency of engagement in rough-and-tumble play, team sports, and doll and family play, among others.

The study of sex differences in boys' and girls' play is generally organized by three relatively independent components: gender schemas, child-initiated activities, and the formation of same-sex play groups (D. E. Brown, 1991; Lever, 1978; Maccoby, 1988; Maccoby & Jacklin, 1974; Pitcher & Schultz, 1983; Sandberg & Meyer-Bahlburg, 1994; Whiting & Edwards, 1973, 1988). This section begins with a brief discussion of gender schemas and then moves to child-initiated social play, followed by discussions of locomotor, exploratory, object-oriented, and sociodramatic play. Children's segregation into same-sex play groups is discussed in Chapter 11 of this volume.

Gender Schemas

As should be clear from the discussion to this point, the specifics of peoples' mate choices (e.g., relative focus on kindness) and competition for mates (e.g., dominance vs. prestige) can vary across cultures and historical periods, as well as with local conditions (e.g., operational sex ratio). In other words, there are core human universals but also important variations in the ways in which they are expressed. The issue here is the relative influence of gender roles or gender schemas (i.e., beliefs about the normative behaviors of boys and girls) on sex differences in children's behavior. As described in Chapter 9 of this volume, these schemas include injunctive norms and other social–psychological processes that have been proposed as the key socialization mechanisms that drive the development and expression of sex differences (Bem, 1981; W. Wood & Eagly, 2002).

It is clear that children do indeed develop sex-typed knowledge or gender schemas. Infants begin to make sex-based discriminations (e.g., between men's and women's voices) by the time they are 6 months old (Martin, Ruble, & Szkrybalo, 2002). By 18 months, they are beginning to categorize some activities as male-typical and others as female-typical (Eichstedt, Serbin, Poulin-DuBois, & Sen, 2002), and they begin to talk about these as 2-year-olds (S. A. Gelman et al., 2004). In fact, by 5 years old, children have developed detailed gender schemas and are often more stereotyped and rigid in their beliefs about boys and girls than their parents and other adults (e.g., Davoodi, Soley, Harris, & Blake, 2020; S. A. Gelman et al., 2004).

Even so, parents also have stereotyped beliefs. One argument is that these beliefs (e.g., boys are more agentic, girls more communal or nurturing) influence how they treat their sons and daughters, including the types of toys they buy and their explicit or implicit approval of their children behaving in ways consistent with these beliefs (e.g., Boe & Woods, 2018; Kollmayer, Schultes, Schober, Hodosi, & Spiel, 2018; Mesman & Groeneveld, 2018). Many of these scholars acknowledge that exposure to sex hormones contributes to the developmental emergence of sex differences but at the same time argue that social influences are of overriding importance. The basic argument is illustrated by Dinella and Weisgram's (2018) summary of a series of articles on the relation between parents' gender schemas and their children's toy preferences:

> In this Special Issue, we gather together cutting-edge research on the factors that affect gender differences in children's toy interests, how subtle gender-related messages affect children's performance and behaviors, and *how adults create these gender-related messages and affect children's interests*. (p. 253; italics added for emphasis)

The irrational exuberance of these types of causal claims must, however, be tempered by reality. To be sure, there is an important relationship between parental attitudes, stereotypes, and prejudices and those of their children, in keeping with a social influence on children's beliefs and attitudes (Degner & Dalege, 2013; Tenenbaum & Leaper, 2002). Tenenbaum and Leaper's (2002) meta-analysis focused specifically on sex-related stereotypes and included results from 43 studies and more than 10,000 people. They found a modest relation between parent's stereotyped beliefs and their own children's stereotyped beliefs about men and women and boys and girls. About 3 out of 5 children whose parents have strong stereotyped beliefs will themselves have stronger than average beliefs in this area. The results were primarily for attitudes (e.g., beliefs about men's and women's behavior) and did not extend to sex-typed interests. The latter includes toy preferences and here "parents' gender schemas had a negligible association with children's gender related interests" (Tenenbaum & Leaper, 2002, p. 626).

Moreover, children's explicit knowledge of gender schemas is only weakly related to their actual play behavior and social activities (P. J. Turner & Gervai, 1995). Girls and boys segregate into same-sex groups whether or not they are engaging in sex-typed activities, and this is independent of the influence of adults (Maccoby, 1988). Children raised by egalitarian parents who actively discourage sex typing have children with less stereotyped beliefs about sex differences than do children raised in other types of families. However, the toy and play preferences of these children are sex-typical and do not differ from those of children raised by parents with stereotyped beliefs (Weisner & Wilson-Mitchell, 1990). Another example is provided by studies of biological males who had pelvic birth defects and reconstructive surgery that resulted in female genitalia (Reiner & Gearhart, 2004). All of these children were raised as girls, but they all reported male-typical play and interests (e.g., wrestling, ice hockey) and none of them reported much engagement in female-typical play (e.g., with dolls). Eight of 14 children who were raised as girls eventually changed to a male identify, five retained a female identity, and one refused to discuss it.

These types of findings do not mean that children's emerging gender schemas do not influence sex differences in behavior. Rather, they do not appear to do so in any straightforward way or as strongly as implied in many of the associated studies (Dinella & Weisgram, 2018). More implicit and subtle processes may be operating, the details of which are a source of continuing theoretical debate and remain to be fully demonstrated in children's actual behavior (see Bussey & Bandura, 1999; Martin et al., 2002). These studies and debates are best left to others, but it is noted here that gender schemas are not an alternative theory to the influence of sexual selection on human sex differences. In fact, gender schemas are highly compatible with the many different ways people compete for mates and resource control across cultures. A prestige-based path to cultural success necessarily requires the acquisition of culture-specific skills and knowledge (see Chapter 8, this volume). There must be here-and-now mechanisms that enable children to modify the expression of inherent biases so they are expressed in such culturally useful ways, and gender schemas may be one of these mechanisms.

Social Play

Rough-and-tumble play and play parenting are the two most common forms of social play in primates (see Chapter 4, this volume; Burghardt, 2005; Lonsdorf, 2017). Following the general pattern of more intense male–male than female–female competition and more female than male parenting, rough-and-tumble play is more common in male than female primates and play parenting is more common in female than male primates. The following sections show that the same pattern is found for boys and girls.

Rough-and-Tumble Play

Rough-and-tumble play or play fighting is found in many species of mammal and is more common for males than for females when physical male–male competition over mates is frequent and intense in adulthood (Power, 2000). As was detailed in Chapters 5 and 8 of this volume, it is abundantly clear that our male ancestors frequently engaged in one-on-one and coalitional male–male competition. Even if competition is typically nonviolent and prestige-based in developed nations today, we would still expect to find sex differences in play fighting. Indeed, the following sections detail research showing that boys engage in more one-on-one and coalitional rough-and-tumble play fighting than do girls.

One-on-one. Rough-and-tumble play typically occurs more frequently, with more vigor, and with greater zest among boys than among girls. The sex difference is found in all developed nations in which it has been systematically studied (Maccoby, 1988), but has not been as systematically studied in traditional cultures. In these cultures, the same sex difference is generally but not always found (Deaner & Smith, 2013; Eibl-Eibesfeldt, 1989; Konner, 2010; Whiting & Edwards, 1973, 1988; cf. Boyette, 2016). The lack of sex differences in some contexts is not surprising, because its expression is highly dependent on social context and is most evident with groups of three or more same-sex children and in the absence of adult supervision. The latter is important because adults tend to suppress this type of play in societies with less intense physical male–male competition in adulthood (Fry, 1988). Even in societies with intense competition, day-to-day social groups tend to be small, and so children often only have a few friends. These social groups tend to include boys and girls, which lowers engagement in rough-and-tumble play. As group size increases, boys and girls are more likely to segregate and engage in sex-typical activities (Lew-Levy, Boyette, Crittenden, Hewlett, & Lamb, 2019).

The highest rates of rough-and-tumble play occur in groups of unsupervised children and in safe contexts, where boys engage in various forms of playful physical assaults and wrestling 3 to 6 times more frequently than do same-age girls (DiPietro, 1981; Maccoby, 1988). In an analysis of the activities of triads of 4-year-olds, DiPietro (1981) found that boys engaged in playful hitting, pushing, and tripping 4.5 times more frequently than did girls. The sex difference in rough-and-tumble play emerges by age 3 and peaks between the ages of 8 and 10, at which time boys spend about 10% of their free time in these activities (Maccoby, 1988; Pellegrini & Smith, 1998). A 10-year longitudinal study revealed that 3-year-olds who engaged in a lot of rough-and-tumble play became adolescents who were particularly aggressive with their peers (Kung, Li, Golding, & Hines, 2018). This was true of both sexes, but the boys were much more physically aggressive than the girls.

As boys move from juvenility to puberty and adolescence (Figure 10.2), the roughness of play intensifies and the line between play and outright physical aggression begins to blur. As with the males of many other species, the relationship between boys' physical roughhousing, physical aggression (e.g., bullying), and their social dominance begins to emerge in early adolescence (Volk, Camilleri, Dane, & Marini, 2012). Pellegrini and Bartini (2001) found that between the ages of 10 and 12, bullying among boys increased at the beginning of the school year and then decreased as the year unfolded. The decrease likely resulted from the establishment of a dominance hierarchy, which typically results in a reduction in physical aggression. Unlike younger boys for whom physical aggression is often associated with social rejection, physical bullying in adolescent boys is associated with the achievement of social dominance, as defined by peers and teachers, and with a higher frequency of dating and higher rated attractiveness by girls (Bukowski, Sippola, & Newcomb, 2000; Dane, Marini, Volk, & Vaillancourt, 2017). This does not mean that these boys are necessarily liked, but they do have social presence and influence (Stassen Berger, 2007). Other studies suggest that dominant adolescents use a mix of coercive (e.g., bullying) and prosocial (e.g., taking charge) behaviors to achieve dominance, depending on context and the relationship (Hawley, 1999), as illustrated in the following chapter.

The intensity and nature of boys' rough-and-tumble play varies with the intensity of physical male–male competition, especially between-group warfare, in their social world (Ember & Ember, 1994). In societies characterized by high levels of male-on-male physical aggression among adults, the play fighting of boys is rougher than the play fighting in more peaceful societies. The intense male-on-male aggression described for the Yanomamö (Venezuela, Brazil) in Chapter 8 of this volume is complemented by young Yanomamö boys play fighting with clubs. In this society and others like it, parents (often fathers) encourage the escalation of rough-and-tumble play and inculcate aggression and emotional indifference in their sons (Ember & Ember, 1994); socialization tends to be harsh for girls as well (Barry, Josephson, Lauer, & Marshall, 1976). These are the same types of societies in which adolescent boys are often subjected to painful and often threatening rites of passage before they are considered to be men (Sosis, Kress, & Boster, 2007).

Loy and Hesketh (1995) provided a number of examples of how socialization practices prepare boys for later male–male competition, with their analysis of the war-related games of the Native American warrior societies of the central plains (United States). "Evidence suggests that all Plains Indian tribes were, to greater or lesser degrees, involved in a wide range of warring activities . . . confined primarily to small war parties, raids, forays; that is, conflicts which were brief and usually indecisive" (Loy & Hesketh, 1995, p. 80). For the Sioux, and many other Native American tribes, the activities of young boys were designed to encourage one-on-one and coalition-based aggression, as well as physical endurance:

> Games for the Sioux frequently were contrived life-situations in miniature. They ran the gamut from the more complex diversion of the Moccasin Game enjoyed by adults to the raucously rough Swing-kicking game played by young boys. . . . The Swing-Kicking Game took first place as a rugged conditioner, and there was no pretense at horseplay. Here two rows of boys faced each other, each holding his robe over his left arm. The game was begun only after the formality of the stock question, "Shall we grab them by the hair and knee them in the face until they bleed?" Then using their robes as a shield, they all kicked at their opponents, endeavoring to upset them. There seems to have been no rules, for the boys attacked whoever was closest, often two boys jumping one. Kicking from behind the knees was a good way of throwing an opponent, and once down he was grabbed at the temples with both hands and kneed in the face. Once released, the bloody victims would fight on, kicking and kneeing and bleeding until they could fight no longer. . . . As Iron Shell explained, "Some boys got badly hurt, but afterwards we would talk and laugh about it. Very seldom did any fellows get angry." . . . Throw at Each Other with Mud was a slightly more gentle spring pastime where teams of boys attacked [each other] with mud balls which they threw from the tips of short springy sticks. Each boy carried several sticks and an arsenal of mud as he advanced. "It certainly hurt when you got hit, so you must duck and throw as you attack." Sometimes live coals were embedded in the mud balls to add zest to the game. (Hassrick, 1964, pp. 127–130)

Good times! These types of games are found in many traditional cultures and are much more common among boys than girls (Deaner & Smith, 2013). Boys engage in play fighting and aggressive coalitional games, though rather tempered as compared with the Sioux, even in societies in which the majority of men do not engage in intergroup aggression or physical one-on-one competition (Rose & Rudolph, 2006). As noted, boys in these societies are often discouraged from engaging in play fighting and games that get too rough but do so anyway, at least when adults are not around.

Coalitions. The sex difference in infants' interest in groups (Benenson et al., 2004) continues into childhood and beyond. These studies confirm that boys organize themselves into much larger social groups than do girls, engage in intergroup competition once such groups are formed, form within-group dominance hierarchies, and show within-group role differentiation and specialization when engaged in group-level competition (Eder & Hallinan, 1978; Lever, 1978). Boys begin to show a preference for group-level activities over dyadic ones as early as 3 years old, show a strong bias against members of competing groups by 5 years old, and consistently form larger groups than girls by 6 years old (Benenson, 1993, 2014; Rose & Rudolph, 2006). The pattern continues into adolescence and is even found in the recreational activities of middle-age and older adults in developed nations (Deaner et al., 2012). Scalise Sugiyama, Mendoza, White, and Sugiyama (2018) found that boys' engagement in war-like coalitional games is common in hunter–gatherer societies like the Sioux and includes activities (e.g., throwing and dodging projectiles) that commonly occur during intergroup raids.

The sex difference in the bias to self-organize into large groups is illustrated by Lever's (1978) study of children's play and engagement in games. Lever asked 181 10- and 11-year-olds to record their after-school activities during the course of 1 week, resulting in 895 cases of social play. During this week, boys participated in group-level competitive activities, such as football and basketball, 3 times as frequently as did girls. Observation of these children's spontaneous (i.e., not organized by adults) play activities confirmed the pattern noted in their diaries and indicated that boys' social play involves larger groups and greater role differentiation within these groups:

> More often, boys compete as members of teams and must simultaneously coordinate their actions with those of their teammates while taking into account the action and strategies of their opponents. Boys interviewed expressed finding gratification in acting as a representative of a collectivity; the approval or disapproval of one's teammates accentuates the importance of contributing to a group victory. (Lever, 1978, p. 478)

A questionnaire-based assessment of the play activities of nearly 700 6- to 10-year-old girls and boys revealed the same pattern (Sandberg & Meyer-Bahlburg, 1994). For 6-year-olds, 44% of the boys regularly played American football, compared with 2% of the girls. For 10-year-olds, 70% of the boys regularly played American football, compared with 15% of the girls. The magnitude of the sex difference was smaller, though still substantial, for basketball; 85% of 6-year-old boys and 86% of 10-year-old boys played basketball regularly, as compared with 25% and 36% of the same-age girls. With respect to child-initiated play, these sex differences have changed little from one decade to the next and are evident whether observations, questionnaires, interviews, or diaries of leisure activities are used to assess play behavior (Deaner et al., 2012; Rose & Rudolph, 2006; Sutton-Smith, Rosenberg, & Morgan, 1963), and they are found across traditional and WEIRD cultures (i.e., Western, educated, industrialized, rich, and democratic; Deaner & Smith, 2013). A description of how boys organized themselves into coalitions is provided in Chapter 11 of this volume.

Skill development. One evolved function of the developmental period is to enable children to adapt folk systems to the nuances of the local social group and ecology (see Chapter 9, this volume). In this view, play fighting allows boys to assess their physical competencies and skills relative to those of their peers and allows them to practice the social skills needed for coalition-based intergroup warfare (Geary, Byrd-Craven, Hoard, Vigil, & Numtee, 2003; Pellis & Pellis, 2007). Stable male coalitions are important in contexts with frequent between-group fighting and, in these contexts, men tend to stay in their birth group, at least when the warring groups are nearby (Pasternak, Ember, & Ember, 1997). Under these conditions, boys' coalitional play groups will form the core of actual competitive coalitions in adulthood. The dozen or so years in which these boys have competed together in play coalitions provide an opportunity to learn about each other's strengths and weakness and how to organize their group into an effective coalition (see Chapter 11, this volume).

It is also likely that the intensity of the play fighting results in changes in the sensitivity of the associated emotional systems such that they are better attuned to the intensity of actual fighting in adulthood (K. MacDonald, 1988). The physical pain that would have occurred while playing the Swing-Kicking Game almost certainly resulted in more aggressive boys than would otherwise have been the case. More likely than not, these boys were also less sensitive to the distress of other people and better able to suppress their own fear and reactions to physical pain.

Compare the game of baseball played in modern America and the game of Throw at Each Other With Mud played by the Sioux 200 hundred years ago; similar games were common throughout Native American tribes (United States) and in many other parts of the world (Eibl-Eibesfeldt, 1989). Both games require many of the same physical, social, and cognitive competencies involved in coalitional warfare in traditional societies (Geary, 1995b). Both require the formation of ingroups and outgroups, the strategic coordination of the activities of ingroup members as related to competition with the outgroup, the throwing of projectiles at specific targets, and the tracking and reacting to the movement of these projectiles. The latter activities mesh well with the advantages of boys and men in throwing distance, velocity, and accuracy, and with their skill at intercepting thrown objects (Thomas & French, 1985; Watson & Kimura, 1991). These component skills and the male advantage in upper body strength and length of the forearm are the same competencies that are involved in the use and avoidance of being hit by projectile weapons.

In short, boys' rough-and-tumble play and fighting games provide the activities needed to fine tune the competencies associated with physical one-on-one and coalition-based male–male competition as it is often expressed during periods of conflict in traditional societies. Cultural factors are expected to influence the magnitude of any corresponding sex differences, but the early physical differences in the arms and later the upper body of boys and girls and the sex differences in the physical size of our ancestors (see Chapter 5, this volume) make it all but impossible to deny an evolutionary history of male–male competition. The point here is that these physical sex differences, the sex differences in children's self-organized play, and their openness to social influences on the intensity and form of this play are all interrelated. Their play provides a means to adapt biologically biased sex differences to the nuances of what it takes to achieve cultural success as adults, at least in traditional contexts.

Play Parenting

For primate species in which females provide more parenting than males, juvenile females are more attentive to and engage in more alloparenting (e.g., holding a younger sibling) than their brothers (Nicolson, 1987; see Chapter 4, this volume). When provided with the opportunity to play with a doll or other plush toys or with wheeled toys (e.g., a car), female vervet monkeys (*Cercopithecus aethiops sabaeus*) and female rhesus macaques (*Macaca mulatta*) carried and played with the dolls or similar plush toys more often than did their brothers (G. M. Alexander & Hines, 2002; Williams & Pleil, 2008). The male vervet monkeys interacted with all of the toys more often than did their sisters and so the sex difference emerged in terms of the proportion of all time spent with the toys (e.g., the percent of toy time that involved a doll). The testing for the rhesus monkeys was similar to that used with children and the sex difference emerged because of the indifference of males to the plush toys; 30% of the females but only 9% of the males showed a preference for the plush toys. In some species, play parenting increases the survival rate of first-born offspring (Pryce, 1993), in keeping with a skill development component of play.

The same sex difference is found in children, as would be expected on the basis of the sex difference in parental investment (see Chapter 6, this volume). Throughout the world, girls are assigned childcare roles, especially caring for infants, more frequently than are boys (Todd et al., 2018; Whiting & Edwards, 1988), although boys are expected to contribute in some hunter–gatherer societies (Hewlett, 2017). Independent of parental requests, girls seek out and engage in childcare, play parenting, and other domestic activities (e.g., playing house) with younger children or child substitutes (e.g., dolls) more frequently than do same-age boys (Pitcher & Schultz, 1983). Sandberg and Meyer-Bahlburg (1994) found that nearly 99% of 6-year-old girls frequently played with dolls, as compared with 17% of same-age boys (it was not clear if this included play with "action figures"). By 10 years old, 92% of girls frequently played with dolls compared with 12% of same-age boys. Similar differences were found 30 years earlier, despite significant changes in the social roles of men and women in the United States (Sutton-Smith et al., 1963). These sex differences have also been documented across many traditional societies, such as the Yanomamö, !Ko Bushman of the central Kalahari, the Himba of southwest Africa, and the Baka of the Congo Basin in central Africa (Eibl-Eibesfeldt, 1989; Kamei, 2005; Konner, 2010).

The magnitude of these differences varies across age and context (Berman, 1980; Whiting & Edwards, 1988). Girls and boys show some interest in infants from about 18 months old until about 6 years old, although girls often shown more positive emotions in the presence of infants than do boys (Nichols, Svetlova, & Brownell, 2015). After this age and continuing into adolescence and early adulthood, girls and women are (on average) more responsive to and interested in infants and younger children than are boys and men (Berman, Monda, & Myerscough, 1977; Cárdenas, Harris, & Becker, 2013; Maestripieri & Pelka, 2002; Whiting & Edwards, 1973). The emergence of this sex difference is due to a drop (or no change) in boys' interest in infants and younger children and an increase in girls' interest during adolescence (Goldberg, Blumberg, & Kriger, 1982). The latter is related in part to the increase in estradiol concentrations during puberty (Sprengelmeyer et al., 2009), as is the case with many other species of primate (Nicolson, 1987). In keeping with this argument, women's general attraction to infants appears to decline in middle and old age, as estradiol concentrations decline (Maestripieri & Pelka, 2002).

Women with higher testosterone concentrations are less attentive to infant faces than are other women (Holtfrerich, Schwarz, Sprenger, Reimers,

& Diekhof, 2016), and girls who were prenatally exposed to androgens and are affected by congenital adrenal hyperplasia (CAH) engage in less play parenting than do their sisters (Berenbaum & Snyder, 1995; Collaer & Hines, 1995). Direct observation of the play activities of 5- to 8-year-old girls affected with CAH and unaffected same-sex relatives revealed that unaffected girls played with dolls and kitchen supplies 2.5 times longer than did girls with CAH (Berenbaum & Hines, 1992). These girls, in turn, played with boys' toys (e.g., toy cars) nearly 2.5 times longer than did unaffected girls. The same pattern was found in a follow-up study 4 years later (Berenbaum & Snyder, 1995). With this latter study, the children were also allowed to choose a toy to take home after the assessment was complete. More than 1 out of 4 of the unaffected girls chose a doll to take home, as compared with less than 1 out of 15 of the girls with CAH.

In sum, a sex difference in play parenting, favoring girls, is found in developed and traditional societies and in fact in most other primates (Eibl-Eibesfeldt, 1989; Nicolson, 1987). These patterns do not rule out social influences on these sex differences but nonetheless provide strong support for the evolutionary prediction that play parenting will be more strongly expressed in the sex that provides the majority of the parental investment. Further support is provided by Tiger and Shepher's (1975) study of sex differences in the socially egalitarian kibbutzim. Their study revealed a change back to "traditional sex roles" after the first generation, and a stronger push by women than by men for a family centered rather than a communal centered social organization. It remains to be determined, however, if girls' play parenting contributes to their later child-rearing competencies.

Locomotor and Exploratory Play

As covered in Chapter 4 of this volume, locomotor play is found in a wide variety of species and often mirrors evolutionarily critical activities (e.g., running and frequently changing direction as a way to evade predators). Exploratory play is included in this section because it is sometimes coupled with locomotor play. The extent to which these activities fine tune motor and muscular systems to the nuances of the local ecology or maintains them while the animal is developing remains to be determined (Graham & Burghardt, 2010), although there is some evidence that these types of activities promote the development of motor skills (Berghänel et al., 2015). The same pattern of consistent sex differences found for rough-and-tumble play and play parenting is not seen across species (Power, 2000). For the most part, males and females appear to be more similar than different, probably because they encounter similar locomotor demands, such as catching prey, avoiding predators, and migrating.

On the basis of these patterns, girls and boys might be expected to be more similar than different with respect to locomotor and exploratory play, but nevertheless there are several reasons to expect more engagement by boys than by girls. Across traditional societies, men travel farther from the home village than do women for many reasons, including developing relationships with the kin of potential brides, developing alliances with the men of neighboring villages, hunting, and intergroup warfare (Chagnon, 1997; K. Hill & Hurtado, 1996; K. Hill & Kaplan, 1988; D. H. MacDonald & Hewlett, 1999). To engage in these activities, men have to be aware of and travel in larger and oftentimes more novel ecologies than do women, which will be more dependent on allocentric (i.e., "bird's-eye view") than egocentric navigation (see Chapter 9, this volume). Exploration is needed to construct an allocentric representation of the environment and early experiences might contribute to the later ability to do so. Moreover, there are additional ecological skills associated with hunting and intergroup warfare (e.g., learning how to track prey) that can take 10 to 20 years to master (Gurven, Kaplan, & Gutierrez, 2006). Unlike women's foraging for fruit or tubers, hunting requires an ability to track and predict the movements of evasive prey, human and nonhuman.

Developmental sex differences in locomotor and exploratory play are theoretically important because they provide the experiences in the local ecology that better prepare men for raiding, hunting, and so forth, and at the very least they help to physically prepare boys for these activities. Sex differences in exploration of the ecology might also contribute to some of the brain and cognitive sex differences that favor boys and men described in Chapter 13 of this volume.

Sex Differences

The greater activity level of infant boys continues into childhood and beyond and is expressed as a sex difference in frequency of engagement in vigorous physical play (Eibl-Eibesfeldt, 1989; Reimers, Schoeppe, Demetriou, & Knapp, 2018; Whiting & Edwards, 1988). The sex difference is related in part to the more frequent group-level competitive play of boys and to a greater engagement of boys in solitary running (Eaton & Enns, 1986; Lever, 1978). Engaging in these types of activities contributes to cardiovascular health and physical fitness (Poitras et al., 2016), which is typically more important for men than for women in traditional cultures (e.g., men often engage in more vigorous physical labor and hunting; Walker, Hill, Kaplan, & McMillan, 2002). At least for children in developed nations, it is not clear whether engaging in these types of activities improves any specific motor skills (e.g., balance; Poitras et al., 2016), but it is often described as an important component of learning how to hunt, fish, and engage in other adult-like activities in ethnographic descriptions of children in traditional contexts (Gosso, Resende, & Carvalho, 2018; Hewlett, 2017; Lancy, 2014, 2016; Lew-Levy, Reckin, Lavi, Cristóbal-Azkarate, & Ellis-Davies, 2017).

In addition to providing a way to practice culture-specific motor skills during development (e.g., shooting a bow and arrow), the sex difference in physical activity results in larger play ranges for boys than for girls. Exploration of large ranges is important for developing an allocentric representation or a cognitive map of the region in which they live and may also be important for the normal development of the brain system that supports these representations. Matthews (1987, 1992) found that boys and girls in suburban England played within close proximity of one or both of their parents during childhood (i.e., preschool years). During juvenility and beyond, boys had a larger play range than did girls. For 8- to 11-year-olds, boys' unrestricted (by parents) play range covered from 1.5 to 3 times the area of girls' unrestricted play range. Whiting and Edwards (1988) reported a similar sex difference for children in Peru and Guatemala, and for three separate groups in Kenya. For the Ache (Paraguay), who live in dense tropical rain forest, the size of boys' and girls' range does not typically diverge until adolescence (K. Hill & Hurtado, 1996). Whenever it emerges, boys not only engage in more locomotor activities in a larger range than do girls, they explore and manipulate (e.g., build things, such as forts) the ecology much more frequently (Matthews, 1992).

Skill Development

For nonhuman species, the development of an allocentric representation of the environment is dependent on active exploration (O'Keefe & Nadel, 1978). The same is true for children. Active exploration contributes to children's formation of allocentric representations or cognitive maps of the environment and the ease of forming these maps improves during the juvenile years (i.e., 7–12 years old; Bullens, Iglói, Berthoz, Postma, & Rondi-Reig, 2010; Lehnung et al., 2003). An example is provided by Matthews' (1987) study of the relationship between exposure to a novel environment and children's ability to later generate a map of this environment. Here, 8- to 11-year-olds were taken on a 1-hour tour of an unfamiliar area. In one condition, the children were given a map of the entire area and were then taken on the tour, with the guide pointing out various landmarks. In the second, more memory demanding condition, a group of children was given a map of half of the area and their tour was interrupted for 30 minutes at the halfway point, although the same landmarks were pointed out as in the first tour. At the end of the tour, the children were asked to draw a map of the entire area. The maps where analyzed in terms of the inclusion of key landmarks and the clustering and relative orientation of these landmarks, which is the basis for allocentric navigation. The maps of boys and girls did not differ in the overall amount of information provided but sex differences did emerge for other features.

For the group taken on the uninterrupted tour, girls included more landmarks in their maps and boys included more routes (e.g., roads), but there were no other sex differences. For the group taken on the memory-demanding tour, boys outperformed girls on a number of map features. At all ages but especially for the 10- and 11-year-olds, "boys showed a keener appreciation of the juxtaposition of places" (Matthews, 1987, p. 84). Boys were better at integrating clusters of landmarks in ways that reflected their actual positions and showed significantly fewer distortions of landmark positions than did girls. Moreover, "some of the older boys . . . managed to show a Euclidean grasp of space" (Matthews, 1987, p. 86). In other words, under conditions with fewer supports many boys but few girls were able to mentally reconstruct an accurate allocentric representation of the topography of an unfamiliar environment, retaining general orientation, clustering, and Euclidean relations (e.g., relative direction) among important landmarks. In short, many boys drew an accurate map of the environment.

The study, however, does not demonstrate that boys' exploratory experience enhanced their spatial abilities, but rather demonstrated that boys implicitly—without the intention to learn—develop cognitive maps of large-scale space during exploration. In an experimental study, J. F. Herman and Siegel (1978) constructed a replica of a small town and assessed kindergarten, 2nd- and 5th-grade children's ability to reconstruct this town after walking through it or watching someone else walk through it three times. When the "town" was placed in a large space (i.e., a gymnasium) boys were more accurate at reconstructing the town in 2nd and 5th grade, but not in kindergarten, where all of the children had difficulty with the task. Boys' advantage emerged after they walked through the town once or twice, but disappeared after the third walk. These findings are consistent with boys' automatic development of cognitive maps and suggest that girls can also develop cognitive maps but require additional experience and some supports. In a small-scale study of the Logoli (Kenya), Munroe, Munroe, and Brasher (1985) found that boys but not girls who traveled farther from home performed better on spatial tests.

These types of studies illustrate the importance of the exploration of large-scale space for the development of some types of spatial abilities. Furthermore, these and related studies suggest that boys may benefit more from these and other forms of spatial experiences than girls (Levine, Foley, Lourenco, Ehrlich, & Ratliff, 2016; Nazareth, Herrera, & Pruden, 2013). The overall pattern is also consistent with an evolved bias to engage in activities that will adapt folk abilities (folk physics in this case) to local conditions, as described in Chapter 9 of this volume. On this view, engagement in sex-typed activities creates experiences that interact with early sex differences in folk systems. The interaction between children's experiences and early biases eventually results in the larger sex differences that are found in adolescence and adulthood, as illustrated in Figure 10.3.

Object-Oriented Play

Object play is common in species that feed on a variety of foods and that have to manipulate different types of objects, including prey and tools, in different ways (see Chapter 4, this volume). Object play typically has an exploratory component and includes object manipulation that is similar to prey capture behaviors or behaviors that involve tool use. Whether or not object play provides practice and refinement of prey capture and tool use skills is not certain, although there is some evidence that it is indeed helpful for skill development (Caro, 1980; Montgomery, 2014; Power, 2000). The alternative is that these play activities maintain but do not refine evolved competencies that involve object manipulation. Either way, human sex differences in at least some aspects of children's object manipulation play are predicted to follow from the sex difference in complex tool construction that is found in traditional cultures.

In these cultures, men work with a wider range of objects than do women (Daly & Wilson, 1983; Murdock, 1981). The activities that are performed exclusively or primarily by men include metal work, weapon making, the manufacture of musical instruments, work with wood, stone, bone and shells, boat building, the manufacture of ceremonial objects, and net making (Daly & Wilson, 1983). Across cultures, nearly 92% of those activities that appear to be the most similar to the likely tool-making activities of *Homo habilis* and *Homo erectus* (e.g., weapon making; work with wood, stone, bone, and shells) are performed exclusively by men; just over 1% of these activities are performed exclusively by women and about 7% are performed by both sexes (Daly & Wilson, 1983; Gowlett, 1992). At the same time, there are no object-working activities that show the same degree of exclusivity for women, although across cultures women engage in pottery making, basket making, and weaving much more frequently than do men (Murdock, 1981). To the extent that some tools, such as stones used as projectile weapons or spears, provided an advantage in male-on-male aggression, their use and any associated play patterns that enhance the ability to make tools is a component of sexual selection.

In any case, the archaeological record indicates that miniature objects that likely served as toys and a way to introduce children to adult tools and activities date back tens of thousands of years (Riede, Johannsen, Högberg, Nowell, & Lombard, 2018). These types of toys are in fact common in many traditional societies today and allow even very young children to become familiar with and skilled at using sex-typical tools (Lancy, 2016, 2017). Young children are sometimes able to determine how objects can be used as tools, without observing others, but they are not skilled at constructing even simple tools (Chappell, Cutting, Apperly, & Beck, 2013). Tool construction is complicated and often not attempted until the later juvenile years or adolescence through a combination of observation, imitation, trial-and-error, and sometimes explicit instruction (Lancy, 2016). The following sections review sex differences in object play and in the development of the skilled use of objects as tools.

Sex Differences

In traditional cultures, children's play with objects, including miniature versions of adult tools, is very sex-typed and likely influenced in part by the observation of the sex-segregated activities of their parents (D. E. Brown, 1991; Lew-Levy et al., 2017). However, these sex differences are not completely influenced by social observation. In situations where children are free to engage with a variety of objects, boys and girls often but not always engage in different types of object-oriented play (Eibl-Eibesfeldt, 1989; Freedman, 1974; Pellegrini & Hou, 2011; Sandberg & Meyer-Bahlburg, 1994; Sutton-Smith et al., 1963). Girls on average tend to engage more frequently in the broad category of construction play that includes play with puzzles, markers, clay, and so on (J. F. Christie & Johnsen, 1987; Rubin, Fein, & Vandenberg, 1983). Boys engage in a more restricted category of play with inanimate mechanical objects (e.g., toy cars) and construction play that involves building (Garai & Scheinfeld, 1968). Boys also engage in the experimental manipulation of these objects, such as taking them apart and trying to put them back together, more frequently than do girls (Hutt, 1972).

The degree to which boys are interested in play with inanimate mechanical objects is illustrated by the earlier described Sandberg and Meyer-Bahlburg (1994) study. It was found that 97% of 6-year-old boys frequently played with toy vehicles (e.g., cars) as compared with 51% of same-age girls. At 10 years old, 94% of boys frequently played with toy vehicles but only 29% of girls did so. Sutton-Smith et al. (1963) found the same sex difference 30 years earlier and Eibl-Eibesfeldt (1989) described a similar pattern with !Ko children. Here, an analysis of 1,166 drawings revealed that boys drew technical objects, such as wagons and airplanes, 10 times more frequently than did girls (20% vs. 2%). An analysis of the drawings of 5- and 6-year-old Japanese children revealed that 94% of the boys but only 5% of the girls drew these types of objects, all of which could move (e.g., car, plane; Iijima, Arisaka, Minamoto, & Arai, 2001). The same pattern has been found in the drawings of children in China, Bali, Sri Lanka, India, and Kenya (Freedman, 1974).

In all, girls prefer toys that can be nurtured (e.g., stuffed animals) and boys prefer toys that can be put into motion or can be used to build (e.g., toy train, blocks; Eisenberg, Murray, & Hite, 1982). These differences are consistent with the earlier described sex differences in infants' orientation toward people or things and a corresponding bias to focus on information in the what (girls) or where and how (boys) visual streams (G. M. Alexander, 2003; Handa & McGivern, 2015). Overall, the key findings are that these sex differences in play are consistent with the infancy research, sex-typed behaviors in traditional contexts, and the sex differences in brain and cognition that are covered in Chapters 12 and 13 of this volume.

Skill Development

In traditional contexts, children's play with objects that resemble adult tools is thought to contribute to their ability to effectively use them when they become adults (Lancy, 2016, 2017; Riede et al., 2018). However, these studies do not typically measure the frequency of children's play with these objects as related to how quickly they become skilled at using them. Most studies of this type are conducted in developed nations and here the relationship between children's play with objects and their later abilities in various domains is not fully understood. As an example of one positive result, Jennings (1975) found that the free play activities of preschool children could be classified as largely people-oriented or largely object-oriented. Children whose play was object-oriented "performed better on tests of ability to organize and classify physical materials" (Jennings, 1975, p. 515), as assessed by tests of spatial cognition (e.g., the ability to mentally represent and manipulate geometric designs) and the ability to sort objects, for example, based on color and shape. There are other studies that also suggest benefits to this type of play (Pellegrini & Gustafson, 2005), but it is not currently known if children in developed nations experience long-term gains from object play (Lillard et al., 2013; Pellegrini, 2016).

In traditional contexts, girls and boys play with toy tools and eventually learn to use adult versions of them. Sex differences in the process of learning to use tools is not known, but there are suggestions of an early difference. Z. Chen and Siegler (2000) found that 18-month-old boys have small to moderate advantages over girls in several aspects of early tool use, such as in using a hooked stick to retrieve a desired toy. Boys were better at applying tool-related knowledge learned in one setting to another setting, were more consistent in the use of tools across settings, and were more successful in the use of tools in problem-solving. Without any hints from an adult, 79% of the boys and 31% of the girls were able to use such tools to retrieve a desired toy. Gredlein and Bjorklund (2005) found that 3-year-old boys but not girls who engaged in boy-typical forms of object-oriented play were better at using a tool to retrieve a desired object, as found by Z. Chen and Siegler. However, these sex differences may disappear in older children, at least for use of simple tools and simple mechanical reasoning tasks (Remigereau et al., 2016).

These results are in need of replication and further study but leave us with the hypotheses that young boys' have at least a skeletal understanding of how to use simple objects as tools and that boys' knowledge of tool use benefits more from object-oriented play than does girls' knowledge. The combination is consistent with the model shown in Figure 10.3, whereby early biases in folk domains (attention to objects) are enhanced during children's self-initiated social and play activities. In this case, sex differences in the mechanical reasoning abilities described in Chapter 13 of this volume may be preceded by early sex differences in attention to objects and implicitly framing them as potential tools.

Sociodramatic Play

Sociodramatic play involves groups of children enacting some social episode, often with great flair and emotion, that is centered on an everyday or imaginary theme, such as dinner, hunting, or dragon slaying (Rubin et al., 1983). This form of play is commonly reported in the ethnographic literature and is thought to support the development of skills (e.g., tracking and hunting) that will be needed in adulthood (Lew-Levy et al., 2017). Whether engagement in sociodramatic play has the additional benefit of improving social skills more generally or enhancing social-cognitive abilities (e.g., theory of mind) is less certain and any such effects are likely to be small (Lillard et al., 2013). The interesting question is the sex difference in the types of themes that emerge during this type of play. The fantasy themes emerge around 2 years old and peak around 6 to 7 years old (Pellegrini & Bjorklund, 2004). Boys and girls regularly engage in sociodramatic play, but differ in the associated themes and the roles they tend to adopt, as noted by Pitcher and Schultz (1983):

> Boys play more varied and global roles that are more characterized by fantasy and power. Boys' sex roles tend to be functional, defined by action plans. Characters are usually stereotyped and flat with habitual attitudes and personality features (cowboy, foreman, Batman, Superman). Girls prefer family roles,

> especially the more traditional roles of daughter and mother. Even at the youngest age, girls are quite knowledgeable about the details and subtleties in these roles. . . . From a very early age girls conceive of the family as a system of relationships and a complex of reciprocal actions and attitudes. (p. 79)

In other words, the sociodramatic play of boys focuses, more often than not, on themes associated with power, dominance, and aggression. The sociodramatic play of girls focuses, more often than not, on interpersonal relationships, including those among family members. These activities reflect the same sex differences found in rough-and-tumble play and play parenting, respectively. More broadly, the themes that emerge in sociodramatic play involve the enactment of roles and behaviors associated with intrasexual competition, such as imitating prestige-based activities for boys (e.g., hunting, fighting), and parenting.

Engagement in these fantasies is likely supported by the brain and cognitive systems for mentally representing the social dynamics described in Chapter 9 of this volume. Children's fantasies are mental representations of social scenarios organized by the evolutionarily salient motives to compete, which often involves cooperation, and to reproduce. Of course, children are not ready for these activities, but they need to prepare for them. Part of this preparation might involve learning how to mentally simulate and think about social situations. The fantasy component of sociodramatic play provides practice at using mental simulations to rehearse later social strategies and provides a vehicle for the expression of the motivational and emotional mechanisms associated with adult activities.

SEX HORMONES AND DEVELOPMENT OF SEX DIFFERENCES

It is clear that children in traditional contexts learn many aspects of sex-typical activities, such as hunting and food preparation, through the observation and imitation of their parents, other adults, and older peers (Lew-Levy et al., 2017). Children in these contexts generally have considerable freedom in determining for themselves what they find interesting and what to imitate and it is unlikely that the different activity patterns of boys and girls are largely imposed on them by adults (Lancy, 2016). Moreover, in many of these societies there are no explicit gender roles for boys and girls to follow, but nevertheless it is possible that children choose to imitate same-sex adults and peers on the basis of their identification as a boy or a girl, as proposed by gender-role theorists (Bem, 1981; W. Wood & Eagly, 2002). As described previously, there is not a strong relation between parental sex-typed beliefs or children's own sex-typed beliefs and their actual behavior, although there do appear to be some wider social influences on this behavior.

Whatever the contribution of these social influences, many of the sex differences described in this chapter are related to prenatal and early postnatal exposure to sex hormones, especially testosterone and other androgens. For infant boys, there is a postnatal surge in testosterone concentrations that peaks at about 2 months old and then declines to childhood (low) levels by about 7 months old; this is sometimes called a “mini puberty” (Forest, Cathiard, & Bertrand, 1973; Hines, Spencer, et al., 2016). The following sections review the relationship between exposure to these hormones and children’s sex-typed behavior.

Prenatal Hormones

The relationship between prenatal exposure to male hormones and later behavior and cognition is assessed by studying children who have been exposed to hormones taken by their mothers when pregnant, have genetic disorders that result in excess production of androgens, or through the assessment of hormone levels during the pregnancy (Hines, Constantinescu, & Spencer, 2015). The latter involves taking amniotic fluid from the mother about halfway through the pregnancy and assessing hormone concentrations; testosterone gets into the amniotic fluid by diffusion through the fetus’ skin and through the fetus’ urination into the amniotic fluid. CAH is the most commonly studied genetic disorder and results in excess production of adrenal androgens that have testosterone-like effects. The disorder is typically detected at birth and controlled through medication and the excess exposure to androgens is for the most part only during prenatal development.

In an early review of this literature, Collaer and Hines (1995) concluded that the “clearest evidence for hormonal influences on human behavioral development comes from studies of childhood play. Elevated androgen in genetic females . . . is associated with masculinized and defeminized play” (p. 92). Hormonal influences on these types of outcomes and others that emerge later in life are most consistently found for children with CAH, as mentioned previously for interest in dolls, and with maternal use of hormonal medications during pregnancy (e.g., Ehrhardt, Meyer-Bahlburg, Feldman, & Ince, 1984; Hines et al., 2015; Reinisch, Mortensen, & Sanders, 2017).

This is illustrated by studies of girls with CAH. These girls have object-oriented play, social play (e.g., enjoying rough-and-tumble play), and levels of aggression that are in-between that of typical boys and girls (Berenbaum & Hines, 1992; Berenbaum & Snyder, 1995; Pasterski et al., 2011; D. Spencer et al., 2017). In studies of younger children, girls with CAH played with boys’ toys—a helicopter, two cars, and a fire engine—nearly 2.5 times longer than did unaffected girls, and played with boys’ toys more than 3 times longer than they played with girls’ toys (e.g., a doll). When given an opportunity to take a toy home, 43% of the girls with CAH chose a toy car or airplane, but none of the unaffected girls chose these items; boys with CAH and unaffected boys chose these items 57% and 61% of the time, respectively. Iijima et al. (2001) found that the drawings of girls with CAH included a mix of boy-typical and girl-typical features, including many mobile vehicles that boys often draw. These girls also show less interest in infants than do other girls (Leveroni & Berenbaum, 1998), but at the same time identify as girls and typically play with other girls (Berenbaum, Beltz, Bryk, & McHale, 2018).

During the juvenile years, girls with CAH continue to engage in more boy-typical activities than do other girls. As an example, Berenbaum and Snyder (1995) showed that these girls engaged in many of the boy-typical activities reported by Sandberg and Meyer-Bahlburg (1994). On the basis of self and parental report, between 7 and 8 out of every 10 girls with CAH engaged in more group-level athletic competition than did their unaffected peers (often their sisters in these studies). A follow-up study revealed that these differences persist into adolescence (Berenbaum, 1999). Several studies have found that girls with CAH are more verbally and physically aggressive than their unaffected sisters (Pasterski et al., 2007; D. Spencer et al., 2017); Pasterski et al. (2007) found that 4 out of 5 girls with CAH were more aggressive than the average unaffected girl.

As adults, women with CAH continue (on average) to show an interest in male-typical activities (e.g., sports) and occupations (Frisén et al., 2009). Most of them identify as women and have heterosexual relationships, although a higher proportion report being homosexual or bisexual (about 30%) than is found in the general population (about 2%–3%; Frisén et al., 2009). Hines, Pasterski, et al. (2016) found that girls with CAH were less influenced than were other girls or were boys with and without CAH to the labeling of toys as for girls or for boys. The implication is that girls with CAH are less responsive to or resistant to some aspects of sex-typical socialization that in turn might contribute to these longer term differences between these girls and their unaffected peers.

The results from studies of the relationship between amniotic testosterone concentrations and later sex differences are not as clear cut. This is probably because these studies typically include only one assessment of testosterone concentrations which is not an ideal way of measuring overall exposure during prenatal development (Hines, Golombok, Rust, Johnston, & Golding, 2002; Knickmeyer et al., 2005; Lutchmaya, Baron-Cohen, & Raggatt, 2001, 2002; D. Spencer et al., 2017). In one of the largest studies of this kind, Auyeung et al. (2009) examined the relationship between prenatal amniotic testosterone concentrations and sex-typed play in 212 6- to 10-year-olds. For both sexes, higher prenatal testosterone concentrations were associated with more frequent boy-typical play, in keeping with the studies of children with CAH. However, in a similar study Hines et al. (2002) only found this relation for girls. It is possible that most boys receive sufficient exposure to prenatal testosterone to result in sex-typical play behaviors and having somewhat higher than average levels of exposure are not important. For girls, however, higher than average exposure to prenatal testosterone results in more male-typical play, as found with studies of girls with CAH.

There is also some evidence that prenatal exposure to testosterone is related to children's social interests and competencies (Knickmeyer, Baron-Cohen, Raggatt, Taylor, & Hackett, 2006) For instance, Lutchmaya et al. (2001) examined the relation between prenatal testosterone concentrations and the frequency with which 12-month-olds made eye contact with their mother. Girls made more eye contact than did boys, as is commonly found. Prenatal testosterone concentrations were related to the frequency of boys' eye contact but not in a straightforward way. Boys with the lowest and highest concentrations had the lowest frequency of eye contact. In a related study, Lutchmaya et al. (2002) assessed the vocabulary of boys and girls at 18 and 24 months old. At 18 months old, the vocabulary of girls was more than double that of boys. At 24 months old, the typical girl knew 40% more words than did the typical boy. At this age, higher prenatal testosterone concentrations were associated with lower vocabulary scores but only when both sexes were assessed together, and therefore these results need to be considered preliminary.

As noted, Collaer and Hines (1995) concluded that prenatal exposure to male hormones results in an increase in boy-typical play and social activities and a decrease in girl-typical play and social activities. The numerous studies conducted since this early review support these conclusions. These later studies also show that the influence of prenatal hormones continues through childhood into adolescence and adulthood. The effects are strongest for engagement in the sex-typical activities described in the earlier Play section and continue to result in a bias toward male-typical interests into adulthood. These effects are, however, weaker for other traits. The vast majority of girls and women with CAH identify as girls and women and this identification influences many aspects of their social behavior above and beyond the influence of prenatal hormones (Berenbaum et al., 2018). These social behaviors include activities with other girls which appears to have an important socializing influence (see Chapter 11, this volume).

Postnatal Hormones

The relationship between boys' postnatal surge in testosterone concentrations and their later behavior and cognition has only been systematically studied during the past decade. This postnatal surge is important for the maturation of boys' genitals (Main, Schmidt, & Skakkebæk, 2000), and contributes to the sex difference in sex-typed play behaviors (Lamminmäki et al., 2012), social development (G. M. Alexander, 2014), and perhaps to some of the sex differences in brain and cognition that are covered in Chapters 12 and 13 (Constantinescu, Moore, Johnson, & Hines, 2018).

Independent of prenatal exposure to hormones, boys who have larger postnatal surges in testosterone concentrations engage in more boy-typical play and less girl-typical play than do other boys (Lamminmäki et al., 2012; Pasterski et al., 2015; but see G. M. Alexander & Saenz, 2012). Larger postnatal surges in testosterone concentrations are also associated with delayed babbling in infancy (Quast, Hesse, Hain, Wermke, & Wermke, 2016), smaller vocabularies at 2 years old (Kung, Browne, Constantinescu, Noorderhaven, & Hines, 2016), and relatively poor language development at 4 years old (Schaadt, Hesse, & Friederici, 2015). Moreover, Constantinescu et al. (2018) found that boys with higher postnatal testosterone concentrations are more sensitive to the spatial orientation of objects 5 months later relative to boys with more typical concentrations.

Although it is typically less dramatic than that seen in boys, girls also go through a mini puberty whereby they experience elevated levels of estradiol and progesterone during the first 6 months of life (Winter, Hughes, Reyes, & Faiman, 1976). Girls with higher concentrations of estradiol during mini puberty have more advanced babbling during infancy (Quast et al., 2016; Wermke, Hain, Oehler, Wermke, & Hesse, 2014; Wermke, Quast, & Hesse, 2018) and better language comprehension at 4 years old than do other girls (Schaadt et al., 2015). In contrast, Kung et al. (2016) found that infant girls with higher testosterone concentrations during mini puberty had a smaller vocabulary at 2 years old than did girls with lower early testosterone concentrations. The relationship between early testosterone concentrations and girls' language development is basically the same as that found for boys, although girls of course have lower concentrations on average and still maintain advantages over boys in this area (see Chapter 12, this volume).

In all, these types of studies are intriguing but still in their infancy, so to speak, and we do not fully understand the influences of postnatal hormones on sex differences in children's behavioral and social development. Nevertheless, the overall findings indicate that the postnatal surge in testosterone and estradiol concentrations are important contributors to many of the sex differences described in this chapter and in later chapters.

CONCLUSION

The length of the developmental period has increased considerably during human evolution (Bogin, 1999), corresponding with an increase in the complexity of human social systems and the range of ecologies occupied by humans (Dunbar, 1993; Flinn, Geary, & Ward, 2005). The complexity of these systems is related, in part, to the dynamics of cooperation and competition that emerges in and among human groups and in reproductive dyads (Chagnon, 1988; Geary, 2002a; Symons, 1979). There are many ways in which sexual selection is an important part of this dynamic mix (see Chapters 6, 7, and 8, this volume). Folding these sex differences into those described in this chapter makes sense, if one important function of the developmental period is to provide the experiences needed to refine and adapt evolved folk competencies to the nuances of local conditions.

The experiences emerge, in part, through children's attentional biases, through their self-initiated play and social activities, and through wider cultural factors (e.g., Greenough et al., 1987; Scarr, 1992). The seeds of children's self-initiated activities appear to be found in the attentional biases of boy and girl infants. The question for us is the extent to which the magnitude of these sex differences reflects our evolutionary history or more proximate social learning mechanisms (e.g., selective imitation). These are not mutually exclusive mechanisms and almost certainly interact in many ways (Levine et al., 2016). Whatever the mix of factors, the sex differences described in this chapter (e.g., interest in dolls, spatial skill development) are consistent with many of the sex differences in parenting, competition, and mate choice described in previous chapters.

The delayed physical maturation of boys relative to girls and the sex difference in the timing, duration, and intensity of the pubertal growth spurt follow the same pattern found in other polygynous primates (Leigh, 1996). Across these species, sex differences in the pattern of physical maturation are more consistently related to the intensity of physical male–male competition than to alternative explanations, such as a sex difference in foraging strategy. Many of the human sex differences in physical traits and competencies (e.g., a longer forearm and greater upper body strength in men) are also readily explained in terms of male-on-male aggression using projectile and blunt force weapons (Keeley, 1996). Many of the sex differences in physical development and physical competencies have almost certainly been shaped by sexual selection.

The sex differences in rough-and-tumble play, exploratory behavior, size of the play range, and the tendency of boys to form competitive coalitions and within-coalition dominance hierarchies are also consistent with an evolutionary history of one-on-one and coalitional male–male competition. In this view, these features of boys' play and social behavior involve a preparation for later within-group dominance striving and coalition formation for intergroup aggression. Through parenting practices, such as degree of physical discipline, the selective imitation of competitive activities, gender schemas, and actual experiences within same-sex groups (see Chapter 11, this volume), boys learn how to best achieve within-group social dominance and practice the competencies associated with male–male competition in their particular culture. They learn how to achieve cultural success (e.g., by leading raids on other villages or becoming a star football player; Winegard, Winegard, & Geary, 2014).

The focus on boys and male–male competition is not to downplay the importance of our evolutionary history for understanding girls' development, but rather to make a point. Sexual selection is a powerful set of mechanisms that allows us to incorporate children's behavior and development into a wider evolutionary framework that simultaneously allows for social and other experiential influences on emerging sex differences. The dynamics of sexual selection are influenced by more fundamental differences in the potential rate of reproduction and in parental investment, and we find human sex differences here as well. Girls' more frequent engagement in play parenting follows readily from women's greater investment in children and is consistent with sex differences found in other species in which females invest more heavily in offspring than do males.

11

Sex Differences in Social Development

The journey into the world of boys and girls continues in this chapter, but attention is turned to the nuances of their social behavior and development as it is expressed in the contexts of peer groups and dyadic relationships. The sex differences that unfold in these contexts are a continuation of boys' and girls' self-directed preparation for engaging in the survival and reproductive activities described in previous chapters. Their preparation accelerates during the juvenile years (i.e., 7–12 years old) as they segregate into same-sex peer groups and create very different boy and girl cultures. This chapter begins with this segregation and the processes that underlie it. From there, an evolutionary framework is provided for conceptualizing differences in the peer relationships of boys and girls and men and women, and how these relationships are consistent with many of the sex differences described in previous chapters. The framework is followed by reviews of peer relationships in group and dyadic contexts and related sex differences in social motives and behaviors. These sections are tied together with a broader discussion of social development and evolution, and the chapter closes with a consideration of the potential influences of parents on the expression of social sex differences.

BOYS' AND GIRLS' CULTURES

The social and economic worlds (e.g., division of labor) of men and women tend to be segregated in many ways in traditional cultures (D. E. Brown, 1991; Pasternak, Ember, & Ember, 1997). One result is that women and men need a

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different mix of social, behavioral, cognitive, and physical skills to be successful in these different worlds. One evolved function of the juvenile and adolescent years is to refine and adapt these skills to the local group and culture. Much of this adaptation occurs in the context of same-sex social groups, where boys and girls learn to cope with same-sex social dynamics and engage in the sex-typical activities of the adults in their culture. Some of these differences were described in Chapter 10 of this volume. The following sections review boys' and girls' self-initiated segregation into same-sex groups and the different types of social relationships that form in the context of these groups.

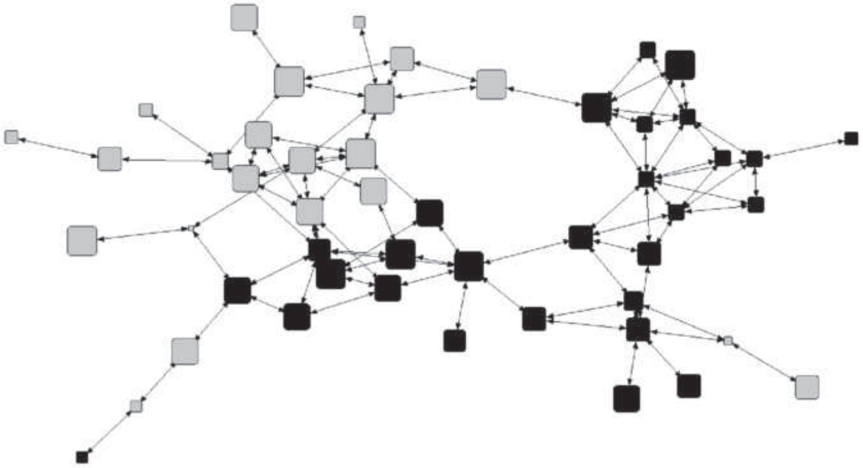
Segregation

When there are enough boys and girls in the local area, children segregate into boys' and girls' groups. The segregation occurs independent of adult interventions and even in societies in which women's and men's social and economic worlds overlap much more than they do in traditional contexts. In fact, the formation of same-sex play and social groups is one of the most consistently found features of children's behavior (Maccoby, 1988, 1998; Whiting & Edwards, 1988). Children begin to form these groups before they are 3 years old and do so with increasing frequency throughout the juvenile years. In a longitudinal study of children in the United States, Maccoby and Jacklin (1987) found that 4- to 5-year-olds spent 3 hours playing with same-sex peers for every 1 hour they spent playing in mixed-sex groups. By the time these children were 6- to 7-years-old, the ratio of time spent in same-sex versus mixed-sex groups was 11 to 1. The same pattern has been documented in Canada, China, England, Hungry, Kenya, Mexico, the Philippines, Japan, and India (Kwan et al., 2019; Strayer & Santos, 1996; P. J. Turner & Gervai, 1995; Whiting & Edwards, 1988), although the degree of segregation varies across these societies. In many traditional contexts where there are fewer potential playmates, children often play in mixed-age and mixed-sex groups, but Figure 11.1 shows that their core friendships are still segregated by sex (Ponzi, 2011).

The different play and social styles of girls and boys contribute to the segregation (Maccoby, 1988; Serbin, Powlishta, Gulko, Martin, & Lockheed, 1993). Girls and boys not only play differently (see Chapter 10, this volume), they use different social strategies to get what they want (e.g., toys) and to influence other children. In situations where access to a desired toy is limited (e.g., a movie-viewer that can be used by only one child at a time), boys and girls use different strategies (on average) for gaining access to this toy (W. R. Charlesworth & Dzur, 1987). More often than not, boys gain access by playfully shoving and pushing other boys out of the way, whereas girls gain access by means of verbal persuasion (e.g., polite suggestions to share) and sometimes verbal commands (e.g., "It's my turn now!").

Maccoby (1988, 1998) concluded that the sex differences in play and social styles contribute to segregated social groups because children are unresponsive to the styles of the opposite sex. Boys sometimes try to initiate

FIGURE 11.1. The Social Networks of Boys and Girls



Although children in traditional cultures often play in mixed-age and mixed-sex groups, their close friendships are still segregated. The gray squares are girls and the black squares are boys, and the lines connecting them indicate mutual friendships. Age is proportional to the size of the squares. In a small Caribbean village, most friendships among 5- to 11-year-olds are with children of the same sex. From *Social and Psychobiological Regulation of the Human Child's Hypothalamus-Pituitary-Axis: An Ontogenetic Perspective* (p. 110), by D. Ponzi, 2011, Doctoral dissertation, University of Missouri. Copyright 2011 by D. Ponzi. Reprinted with permission.

rough-and-tumble play with girls, but most girls withdraw from these initiations, whereas most other boys readily join the fray (Benenson, 2014). Girls often attempt to influence the behavior of boys through verbal requests and suggestions but boys, unlike other girls, are generally unresponsive (W. R. Charlesworth & La Freniere, 1983). Many readers may wonder whether boys ever become responsive—they do by adulthood, somewhat (Maccoby, 1990). There is also peer pressure to avoid the opposite sex, especially among boys. This includes things such as teasing about "cooties" (an early sexually transmitted infection, apparently) if a child interacts with a member of the opposite sex (Maccoby, 1988). In short, the differences in play and social styles result in children forming groups based on mutual interests and the ability to influence group activities, and one result is the formation of largely same-sex social networks.

The sex difference in play interests and social styles is influenced in part by prenatal and postnatal exposure to male hormones (see Chapter 10, this volume). There is also a role for gender schemas, which includes the explicit knowledge of one's sex, the categorization of other children as boys or girls, and the tendency to congregate with children in the same social category (Berenbaum & Snyder, 1995). For instance, Berenbaum, Beltz, Bryk, and McHale (2018) found that the boy-typical play of girls with congenital adrenal hyperplasia (CAH; excess prenatal exposure to male hormones) resulted in less time spent in girl-only groups, but they still spent most of their time with other girls (if less time than the average girl). The time spent with other girls in turn was related to their self-identification as a girl.

Even so, many girls with CAH prefer boys as playmates, consistent with Maccoby's (1988) position that children with boy-typical play, interests, and social styles (boy or girl) will congregate into play groups that differ from those formed by children with girl-typical play, interests, and social styles. As an example, Hines and Kaufman (1994) found that 44% of 3- to 8-year-old girls with CAH indicated that boys were their most frequent playmates. By comparison, only 11% of unaffected girls indicated that their most frequent playmates were boys. Of same-age boys, whether or not they had CAH, 80% indicated that other boys were their most frequent playmates. As with their play, girls with CAH show a more mixed pattern of social relationships as they develop (i.e., they are not as sex-segregated as other girls), in keeping with the joint contributions of hormones and social-identification. Hines, Pasterski, et al. (2016) found that girls with CAH were less influenced than were other girls or were boys with and without CAH to the labeling of toys as for girls or for boys. The implication is that girls with CAH are less responsive or resistant to some aspects of sex-typical socialization that in turn might contribute to the longer term differences between these girls and their peers without CAH.

The Cultural Divide

The net result of sex segregation is that boys and girls spend much of their childhood in distinct peer cultures (J. R. Harris, 1995; Maccoby, 1988). It is in the context of these cultures that differences in the social styles and preferences of girls and boys become larger and congeal into patterns that they will take into adolescence and adulthood (Martin & Fabes, 2001). This section begins with an evolutionary frame that places boys' and girls' cultures in the context of male–male competition and male philopatry (i.e., when males stay in their birth group) and situates women's relationships in these social groups. The discussion then moves to descriptions of peer relationships in the context of groups and dyads.

Evolution of Social Styles

Following Caporael (1997), Geary, Byrd-Craven, Hoard, Vigil, and Numtee (2003) proposed that children's attentional, behavioral, and social styles are inherently biased such that they will recreate the relationships (e.g., mother–infant attachment) and activities that enhanced the survival and reproductive prospects of our ancestors. As an example, the tendency of boys to form large and competitive social groups during their play automatically provides them with the experiences that will contribute to their ability to form competitive coalitions in adulthood. In other words, the coalitional competition described in Chapter 8 of this volume advantaged men who were able to develop and maintain large and competitive groups. The ability to coordinate the activities of and develop trust among the men that compose these groups would be facilitated by earlier engagement in group-level competitive play (essentially practice for later competition), creating an advantage for delayed maturation. Any advantage of a slower development would only be realized if children were biased to engage in activities that enhanced survival or reproductive prospects in adulthood, including forming the types of relationships that were important for our adult ancestors (see Chapter 9, this volume). This relationship between developmental activities and outcomes in adulthood necessarily means that children must be biased to create relationships that mirror those of our ancestors.

Many of these adult relationships are related in one way or another to the demands of raising children (Chapter 6, this volume), attracting and keeping mates (Chapter 7, this volume), and competing for preferred mates (Chapter 8, this volume). To provide an anchor for an evolutionary analysis of children's social development, Geary et al. (2003) decomposed male–male coalitional and one-on-one competition as they are expressed in traditional societies. These dynamics allowed us to make predictions about the nuances of these forms of competition and how they would be expressed during boys' social development, compared with that of girls. The details are provided in Table 11.1. Many of the features described in the table have been discussed previously, including men's coalition formation and dominance hierarchies (Chapter 8, this volume), muted expression of emotions (Chapter 9, this volume), and physical traits associated with male–male competition (Chapters 5 and 10, this volume), among others.

The goal here is to outline a theoretical perspective that places the process of group formation and the nuances of dyadic relationships in the context of the reproductive demands described in previous chapters. Specifically, Geary et al. (2003) proposed that girls and women and boys and men have different styles of social relationships in the context of groups and dyads, in part, because of the cost–benefit trade-offs associated with the formation of large, competitive coalitions compared with emotionally supportive dyads. When it comes to coalitional competition, size matters: Across species, larger coalitions have a competitive advantage over smaller ones (Wrangham, 1999). The coalitions are of course fluid because the gains of victory are distributed, often unequally according to dominance rank, among coalition members. The result is a balance between the benefits of having a large enough ingroup to be competitive and the costs of having to share gains with ingroup members. As noted in Chapter 5 of this volume, male philopatry and kinship will increase the likelihood that a bias toward coalition formation will evolve in men and will mitigate (because of the genetics of kinship) the costs of sharing valuable resources among coalitionary confederates (W. D. Hamilton, 1964; Packer, Gilbert, Pusey, & O'Brieni, 1991).

The features of girls' and women's dyadic relationships are described later in this chapter. The time commitment, emotional support, and social risks associated with these relationships are high, and they limit the number that can be developed and maintained. The trade-offs are shown Figure 11.2, where the *x*-axis represents the number of same-sex friendships and the *y*-axis the costs of maintaining each of them. The many benefits of girls' and

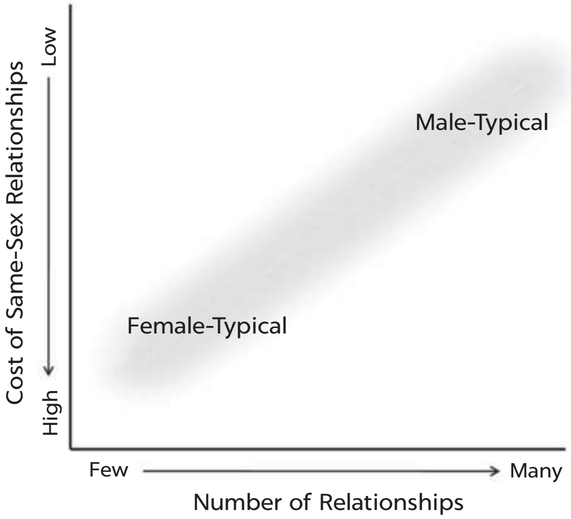
TABLE 11.1. Social Dynamics and Supporting Mechanisms of Boys' and Men's Social Behavior

Group formation and maintenance	
Ultimate selection pressures	Proximate selected forms
Group-level dynamics	
1. Male–male competition for A. control of local ecology and resources contained therein, and B. control of reproductive dynamics.	1. Coalition formation: A. Warfare over control of ecologies (e.g., land) and reproductive opportunity (e.g., raiding). B. Hunting for individual survival and provisioning of kin and family, and to enhance cultural success and through this mating prospects. C. Protection of kin and family from other male coalitions. 2. Intragroup dynamics: A. Dominance hierarchy to facilitate coordinated activity. B. Low threshold to form emotional and social bonds with group members, to facilitate group size. C. Role specialization and differentiation. D. Shared goals and attentional, behavioral focus on ecological problems (e.g., building a fort) or group competition.
One-on-one dynamics	
1. Male–male competition for A. dominance and influence within the coalition.	1. Focus on dominance indicators: A. Physical: size, musculature, skill. B. Social and cognitive: leadership and other competencies that facilitate group performance. C. Emotional: aggression, lack of fear. 2. Individual relationships: A. Easily formed with shared activities, especially cooperative competition against another group of boys. B. Formed more strongly among individuals of similar status (to facilitate greater reciprocity). C. Dominance contests are constrained. D. Tolerance of interpersonal conflict to allow for dominance contests while maintaining coalition cohesion.

Note. From "Evolution and Development of Boys' Social Behavior," by D. C. Geary, J. Byrd-Craven, M. K. Hoard, J. Vigil, and C. Numtee, 2003, *Developmental Review, 23,* p. 453. Copyright 2003 by Elsevier. Adapted with permission.

women's friendships (e.g., intense social and emotional support) are traded for fewer of them (Benenson, 2014, 2019; Rose & Asher, 1999; Rose & Rudolph, 2006; S. E. Taylor et al., 2000), as represented by the lower left area of Figure 11.2. The upper right area represents the formation of larger social networks that are common among boys and men and that could only be developed and maintained by relatively low-cost activities, such as coordinated efforts to achieve a common goal (e.g., winning a sporting competition). As described in Chapter 10 of this volume, boys often engage in these types of games and

FIGURE 11.2. The Cost–Benefit Trade-Offs in Same-Sex Relationships



The diagonal haze represents a continuum of trade-offs between the costs associated with the development and maintenance of same-sex friendships and their number. The white areas are combinations that are unusual or difficult to maintain. The lower left darkened area represents the maintenance of a few very intense relationships with high levels of emotional and social support, which are common among girls and women. The upper right darkened area represents a larger network of social relationships that can be maintained at lower costs (e.g., through shared activities), which are common among boys and men.

enjoy the team-based competition, even with some risk of injury (Hassrick, 1964; Scalise Sugiyama, Mendoza, White, & Sugiyama, 2018). The cost–benefit trade-offs associated with interpersonal intimacy does not mean that boys and men do not form dyadic friendships, as many of them do (J. G. Parker & Asher, 1993). What it means is that the cost of maintaining the same style of interpersonal relationship as is common in girls' and women's friendships would place severe constraints on the ability of boys and men to form large, well-functioning and competitive coalitions (Geary & Flinn, 2002).

To achieve these coalitions, boys and men must have a lower threshold for forming and maintaining same-sex social friendships (e.g., with less time-intensive interpersonal disclosure) and must be more tolerant of interpersonal conflict in the context of these relationships. Tolerance for conflict is necessary to maintain the coalition and at the same time compete for within-coalition status. Dominance striving must, at the same time, be balanced against the cost of potentially losing the coalitional support of other boys and men, and therefore social and psychological mechanisms that restrict dominance-related differentials between ingroup members are an important feature of these relationships, as argued by Boehm (2009, 2012; Boehm et al., 1993). In other words, the capacity to form high-quality relationships among nonkin exists in both sexes (Dunbar, 2018b), but the mechanisms that support the development and maintenance of these relationships and the social contexts, especially group-level competition, in which they are most likely to be expressed differ (Geary & Flinn, 2002; S. E. Taylor et al., 2000).

If male philopatry facilitated an evolved bias to form male coalitions in our ancestors (see Chapter 5, this volume), then females' friendships would have been more dependent on the social and emotional mechanisms that evolved to support relationships among nonkin (Geary, 2002b), because females would have often migrated to the group of their mates and emigrated away from kin. These mechanisms are captured by Trivers' (1971) reciprocal altruism, the psychological mechanisms (e.g., warmth, guilt) that promote long-term friendships on the basis of a strict equality of the give-and-take in a relationship. Girls and women still develop close relationships with their parents, children, and other kin, but male philopatry and the need to maintain relatively large male coalitions created different social ecologies for our male and female ancestors and different patterns of cost–benefit trade-offs in their same-sex relationships.

If girls' and women's relationships are more heavily dependent on reciprocal altruism than those of boys and men, then the former will involve more monitoring of the give-and-take of the relationship and a lower threshold for dissolving the relationship when strict reciprocity is not achieved, and this is the case. This does not mean that boys and men are not reciprocal in many of their friendships, but rather that girls and women are less tolerant of non-reciprocal relationships and that the maintenance of any such relationship is more strongly dependent on equalitarian reciprocity among girls and women than among boys and men.

The principle benefit for girls and women is a core set of relationships that provide social, emotional, and interpersonal stability, particularly support during times of interpersonal conflict with other individuals, such as a spouse or a spouse's other wives (S. E. Taylor et al., 2000). At the same time, the high investment of time, disclosure of personal information and near constant availability for social support place severe constraints on the number of these relationships that can be simultaneously maintained. Relative to boys and men, it appears that the emotional closeness in girls' and women's friendships evaporates more quickly without frequent contact and interpersonal engagement (S. B. Roberts & Dunbar, 2015). The level of personal disclosure that is common in them can also leave the girl or woman vulnerable to social manipulation and other forms of relational aggression by their friends, should the relationship dissolve (Bond, Carlin, Thomas, Rubin, & Patton, 2001; Murray-Close, Ostrov, & Crick, 2007). The risk of relational aggression and girls' and women's sensitivity to this form of aggression place further constraints on the number of such friendships (see Chapter 8, this volume).

Peer Relationships

Peer relationships typically refer to dyadic friendships (among nonkin) and most of the research in this area has focused on the dynamics of these friendships (e.g., amount of personal disclosure; Hartup & Stevens, 1997), including sex differences (J. A. Hall, 2011; Rose & Asher, 2017). The dynamics of girls' dyadic friendships are well understood, and boys' dyadic friendships are sometimes seen as deficient (e.g., less interpersonal disclosure) in comparison. Boys' are not in fact deficient, they simply form and maintain friendships in different ways than do girls, including through engagement in group-level activities (e.g., team sports) and competitive play. As noted previously, these different ways of forming friendships allow boys to integrate into a larger social network than is typically found with girls, a pattern that is even reflected in the pictures posted on social media by women (more dyadic photos) and men (more group photos; David-Barrett et al., 2015). The following discussion first provides details on these dynamics and then turns to the formation and maintenance of dyadic friendships.

Forming groups. The sex difference in coalition formation and engagement in between-group competition was mentioned in Chapter 10 of this volume. This brief overview did not provide insights into the process of group formation, contrast this process with that of girls' relationship formation, or detail the strategies used to gain social influence and dominance in the context of these groups. In the context of these groups, status striving is expressed as a mix of physically coercive behaviors (e.g., bullying), prosocial behaviors (e.g., helping), and relational aggression, and the achievement of status is associated with enhanced control of desired resources and enhanced social influence (Hawley, 1999, 2003; Hawley, Little, & Card, 2008). Girls and boys can use any or some combination of these social strategies but often put them into practice in different frequencies and in different ways.

The process of group formation and the social strategies used during this process are nicely illustrated by Savin-Williams' (1987) ethological study of adolescents. Social relationships that developed during the course of a 5-week summer camp were documented for groups of 12- to 16-year-old boys and girls who were assigned to the same cabin. Within these same-sex groups, boys and girls formed dominance hierarchies and frequently used relational aggression to establish social dominance, including name calling ("homo," "perverted groin") and gossiping. For both sexes, this form of aggression often occurs when there is an audience and sends a broader message regarding dominant–submissive relationships (Benenson et al., 2002).

At the same time, there were important differences in boys' and girls' groups. The key differences included the stability and integration of social hierarchies (i.e., the degree to which all group members became friends), the degree to which dominance displays were direct or indirect, the coercive use of physical strength and skills to establish dominance, and the benefits of achieving dominance (Hawley, 2003; J. G. Parker & Seal, 1996; Rose & Rudolph, 2006). In some groups, boys began their bid for dominance within hours of arriving in the cabin, whereas most of the girls were superficially polite for the first week and then began to exhibit dominance-related behaviors. Boys' dominance-related behaviors included ridicule as well as directives ("Get my dessert for me"), counter dominance statements ("Eat me"), and physical assertion (e.g., play wrestling, pillow fights, and sometimes actual physical fights). More than 90% of the time these behaviors were visible to all group members, were clearly directed at one boy, and were attempts to establish dominance over this individual.

Girls used ridicule, recognition, and verbal directives to establish social dominance, but used physical assertion only 33% as frequently as did boys. In contrast to boys' blatant behaviors, more than 50% of the girls' dominance behaviors were indirect, involving relational aggression. One girl might suggest to another girl that she "take her napkin and clean a piece of food off of her face," whereas under the same conditions a boy would simply call his less-kept peer a "pig" and then try to enlist other boys in a group-wide ridicule session of this boy. Once the target of this attack was "down," lower status boys would typically use the opportunity to attempt to establish individual dominance over this peer. Girls, in contrast, often overtly recognized the leadership of another girl. Recognition was the second most common form of dominance-related behavior with girls but occurred infrequently with boys (23% vs. 6%). In these cases, less-dominant girls would approach their more dominant peer for advice, social support, grooming (e.g., having her hair combed), and so on.

As documented in other studies (J. G. Parker & Seal, 1996), Savin-Williams (1987) found that by the end of summer camp boys' groups showed greater stability and cohesiveness relative to the first week of camp. Most of the girls' groups, in contrast, were on the verge of splintering or had already split into "status cliques based on popularity, beauty, athletics, and sociability" (Savin-Williams, 1987, p. 124). Some of the dominant girls disengaged from the cabin-group and spent most of their free time with one or two friends. Dominant boys never disengaged and spent most of their free time directing the group in competitive athletic activities against other groups. In short, dominant boys more actively and more successfully controlled group activities than did dominant girls, as illustrated by the following flag-making exercise:

> Andy [the alpha male] immediately grabbed the flag cloth and penciled a design; he turned to Gar for advice, but none was given. Otto [low ranking] shouted several moments later, "I didn't say you could do it!" Ignoring this interference, Andy wrote the tribal name at the top of the flag. Meanwhile, Delvin and Otto were throwing sticks at each other with Gar watching and giggling. SW [the counselor] suggested that all should participate by drawing a design proposal on paper and the winning one, as determined by group vote, would be drawn on the flag. . . . Andy, who had not participated in the "contest," now drew a bicentennial sunset; it was readily accepted by the others. Without consultation, Andy drew his design as Gar and Delvin watched. Gar suggested an alteration, but Andy told him "stupid idea," and continued drawing. Otto, who had been playing in the fireplace, came over and screamed, "I didn't tell ya to draw that you Bastard Andy!" Andy's reply was almost predictable, "Tough shit, boy!" (Savin-Williams, 1987, p. 79)

Andy's mode of domination was more physically assertive and verbally aggressive than that of the dominant boys in other cabins. The result was the same, however. The dominant boys got first choice of what to eat (e.g., they almost always got the largest desserts), where to sleep, and what to do during free time. Across cabins, dominant girls also differed in their social styles. Although some girls were physically assertive and direct in their attempts to dominate other girls, the most influential girls (over the course of the 5 weeks) were subtle, as exemplified by Ann:

> [Her] style of authority [was] subtle and manipulative, she became the cabin's "mother." She instructed the others on cleanup jobs, corrected Opal's table manners ("Dottie, pass Opal a napkin so she can wipe the jelly off her face"), and woke up the group in the morning. . . . Ann became powerful in the cabin by first blocking Becky's [the beta female] dominance initiations through refusing and shunning and then through ignoring her during the next 3 weeks. By the 5th week of camp Ann effectively controlled Becky by physical assertion, ridicule, and directive behaviors. (Savin-Williams, 1987, p. 92)

For boys and girls, the achievement of social dominance was related to athletic ability, physical maturity, and leadership. Dominant girls were more socially popular than were many of the dominant boys (e.g., Andy was not well liked by his cabin mates, but they followed his directives) and physical attractiveness was more important for achieving social dominance within boys' groups than within girls' groups. In all, the boys described the ideal leader as someone who is

> determined and tries hard at what he does, considerate in tolerating underlings, organizes activities, and knows what to do and makes the right decisions. The [girls'] groups emphasized expressive attributes: relates to my problems, friendly, outgoing, patient, considerate in respecting the needs and feelings of others. (Savin-Williams, 1987, p. 127)

Ethological and other studies indicate that these social patterns congeal as adolescence merges into adulthood (Ahlgren & Johnson, 1979; Savin-Williams, 1987). Ahlgren and Johnson (1979) found that at about the time of puberty, girls' social motives become more cooperative and less competitive than those of their younger peers. Savin-Williams (1987) found that by the end of adolescence, there was a significant reduction in ridicule, "backbiting, bickering, and cattiness" (p. 150) in girls' interpersonal relationships, compared with early adolescence. By late adolescence, girls' dyadic relationships also showed greater stability (e.g., less changing of "best friends"), more recognition, greater sensitivity to the needs and emotions of their friends, more helping behavior, and fewer attempts at establishing dominance than was found during early adolescence.

Boys' relationships changed as well. By late adolescence, boys' group-level games were characterized by greater focus and organization, with fewer negative criticisms and more encouragement directed toward ingroup peers than was found with younger boys (Savin-Williams, 1987). During their dominance-related encounters, older boys used physical assertion less frequently and recognition more frequently than did their younger peers. In early adulthood, higher status men are more generous with coalition partners than are higher status women, suggesting the men are engaging in more coalition building than women (Markovits, Gauthier, Gagnon-St-Pierre, & Benenson, 2017). Men also show more postconflict affiliation and reconciliation behaviors with their opponents than do women, again suggesting a stronger emphasis on relationship maintenance following conflict in men (Benenson et al., 2009; Benenson, White, et al., 2018; Benenson & Wrangham, 2016; S. Y. Lee, Kesebir, & Pillutla, 2016; Pham, Barbaro, Mogilski, Shackelford, & Zeigler-Hill, 2017).

Dyads. Although the typical boy engages in some form of activity that involves groups of his friends, the typical girl talks with only one of her friends (Eder & Hallinan, 1978; Lever, 1978; Rose & Rudolph, 2006). Boys, of course, have one-on-one friendships but spend less of their social time with peers in exclusive, dyadic encounters than do girls. In fact, boys' dyadic relationships tend to be embedded within the network of friends described above. Over time, all of the boys in the ingroup are likely to become friends with one another to varying degrees, but girls' friendships are more likely to be exclusive (Eder & Hallinan, 1978). J. G. Parker and Seal's (1996) study of peer relationships during a 4-week summer camp illustrates the process of embedding dyadic friendships into larger social networks termed *network density*. During the first week of camp, there were no sex differences in network density. Three to 4 weeks later, nearly 9 out of 10 boys were embedded in a more cohesive social network—all network members knew and liked each other—than was the average girl.

There are also important qualitative differences in the nature of girls' and boys' dyadic friendships (J. A. Hall, 2011). As they move into the juvenile years (i.e., 7–12 years old), girls' relationships become more exclusively focused on one or two best friends. Compared with boys' friendships, girls' friendships are characterized by higher levels of emotional support, more frequent intimate exchanges (e.g., talking about their problems), and they are a more central source of help and guidance in solving social and other problems (J. A. Hall, 2011; Maccoby, 1990; J. G. Parker & Asher, 1993; Rose & Asher, 1999; Savin-Williams, 1987). Girls are more interpersonally engaged in the relationship and as a result they know more about their best friend than do boys (Markovits, Benenson, & Dolenszky, 2001). During discussions, girls are more sensitive to the social–emotional cues of their partner (Buck, Savin, Miller, & Caul, 1972), and work harder to minimize perceived inequalities in the give-and-take of the relationship and in outcomes (e.g., having a boyfriend) that are important to both girls (Ahlgren & Johnson, 1979; Benenson, Durosky, et al., 2018; Winstead, 1986).

For both sexes, conflicts of interest are common among friends. When this happens, girls invest more than boys in resolving these conflicts through accommodation, compromise, and other socially constructive means, whereas boys tend to use a more direct and confrontational approach (J. G. Parker & Asher, 1993; Rose & Asher, 1999). Despite the subtle approach to managing conflicts, girls are more sensitive to personal slights on the part of their best friend and respond with more initial and lingering negative affect than do boys (e.g., sadness, anger; Rose & Asher, 2017; Whitesell & Harter, 1996), a pattern that continues into adulthood and into work settings (S. Y. Lee et al., 2016). Their friendships are also more fragile; girls' relationships are much more likely to permanently dissolve as a result of conflict, betrayal, or other stressors on the relationship (Benenson, 2019; Benenson & Christakos, 2003; Lever, 1978).

Social Motivations and Personality

In addition to the tendency of boys and girls to organize their peer relationships into larger-scale social networks and intimate dyadic friendships, respectively, there are broader sex differences in social motives, behaviors, and personality. These are sex differences that can manifest in many different types of relationships, not just those with same-sex peers. The most consistently found differences are boys' and men's stronger concerns about social dominance and their relative hierarchical position and girls' and women's social agreeableness and tendency to nurture. These sex differences are found across traditional, developing, and developed societies (e.g., Feingold, 1994; Whiting & Edwards, 1988). In their study of the social development of children in Liberia, Kenya, India, Mexico, the Philippines, Japan, and the United States (with less extensive observations in Peru and Guatemala), Whiting and Edwards (1988) concluded,

> Of the five major categories of interpersonal behavior explored in [these studies]—nurturance, dependency, prosocial dominance, egoistic dominance, and sociability—two emerge as associated with sex differences. Across the three older age groups (knee, yard, and school-age children) girls on average are more nurturant than boys in all dyad types . . . while boys are more egoistically dominant than girls. (p. 270)

These findings are consistent with Eagly's (1987) description of men and women as being agentic and communal, respectively, and are consistent with many other studies of adolescents and adults. Feingold (1994), for instance, examined sex differences on personality tests normed in the United States; analyses of test norms are especially informative because they are based on large (105,742 people in this study) and typically nationally representative samples. Feingold found moderate to large sex differences for "tender-mindedness" (i.e., nurturance and empathy), which favored women, and assertiveness (e.g., dominance-related activities), which favored men. Overall, about 6 out of 7 women scored higher than did the average man on measures of tender mindedness and about 7 out of 10 men scored higher than the average woman on measures of assertiveness. The magnitude of these differences did not vary much for samples assessed from the 1940s to the 1990s and varied little across groups of adolescents and younger and older adults (see also Lueptow, Garovich-Szabo, & Lueptow, 2001).

Multiple studies of sex differences in personality were also available for adults from Canada, Finland, Germany, and Poland and confirmed the pattern found in the United States, although the magnitude of the differences varied across cultures (Feingold, 1994). These sex differences were confirmed in two large-scale studies that spanned 57 nations and included 40,668 people. Critically, the sex differences are larger in cultures that are more socially and politically gender-equal and with the fewest social restrictions on personal expression (Costa, Terracciano, & McCrae, 2001; Schmitt, Realo, Voracek, & Allik, 2008). In other words, social changes that result in more personal freedoms and that promote the political and economic advancement of women are associated with larger sex differences in these domains and in fact, in many others (Schmitt et al., 2017; Stoet, Bailey, Moore, & Geary, 2016; Stoet & Geary, 2018). Overall, the sex differences tend to be small to moderate on individual aspects of personality (e.g., agreeableness; Kajonius & Johnson, 2018). However, when the combination of personality traits is considered, the sex differences are quite large and yield a male-typical (e.g., high dominance and emotional stability) and female-typical (e.g., high social sensitivity and warmth) mix of traits (Del Giudice, Booth, & Irwing, 2012; T. Kaiser, 2019).

Ahlgren and Johnson (1979) found a similar pattern in the social motivations of second to 12th graders. The social motives of children and adolescents were captured by two salient themes: cooperation (e.g., "I like to learn by working with other students") and competition (e.g., "I like to do better work than my friends"). At all grade levels, girls endorsed cooperative social behaviors more frequently did than boys, whereas boys endorsed competitive social behaviors more frequently than did girls. A study of 250 14-year-olds revealed the same pattern: boys' social goals were relatively more focused on the achievement of dominance and leadership, whereas girls' social goals were relatively more focused on the establishment of intimate and nurturing relationships (Jarvinen & Nicholls, 1996). The largest sex differences were for the establishment of intimacy. More than 4 out of 5 girls rated this goal as being more important than did the average boy, whereas 3 out of 4 boys rated achieving dominance as being more important than did the average girl.

Knight and Chao (1989) found the same pattern in the rules that 3- to 12-year-olds used to distribute a valuable resource (i.e., money) amongst themselves and their social group. These studies were designed to determine whether the children had preferences for *equality* (minimizing differences between oneself and others), *group enhancement* (enhancing the overall resources of the group, regardless of how this effects one's own resources), *superiority* (trying to maximize one's resource relative to other group members), or *individualism* (enhancing one's resources independent of peer resources). Self-interest was evident in the resource distributions of younger boys and girls, as about 50% of them showed an individualism preference. At the same time, 1 out of 4 girls but none of the boys showed an equality preference, whereas 1 out of 5 boys but only 1 out of 20 girls showed a superiority preference. By 6 years old, the majority of boys showed a superiority preference, whereas the girls were largely split between the individualism and equality preferences. For 9- to 12-year-olds, 3 out of 4 boys showed a superiority preference, compared with 1 out of 5 girls. The remaining girls were split evenly (40% each) between the individualism and equality preferences; only 7% of the boys showed an equality preference (see also Benenson, Durosky, et al., 2018).

In all, these patterns are consistent with the argument that women and men, as part of their motivation to control, are biased such that they will attempt to organize their social worlds in ways that contributed to survival and reproductive prospects in our ancestors (see Chapter 9, this volume). The mix of girls' and women's personality traits (on average) that fosters cooperation and a social motive of equality contributes to the development and maintenance of the intimate dyadic relationships that are important sources of social and emotional support. A focus on leveling social inequalities in wealth and power might also reduce male-on-male conflict that often spills over into the lives of women and children (Keeley, 1996; Machel, 1996; M. White, 2012), and provides a social safety net. Boys' and men's personality and motivational focus on dominance, superiority, and competition follows in a very straightforward way from the relationship between status and reproductive outcomes across traditional, developing, and developed nations (see Chapter 8, this volume).

SOCIAL DEVELOPMENT AND EVOLUTION

This section integrates the just described sex differences into the framework laid out earlier and with the life history approach described in Chapter 9 of this volume. In theory, children's self-generated niche seeking and the nature of their peer relationships provide the experiences needed to elaborate and adapt the individual- and group-level folk-psychological cognitive modules and corresponding motivational and emotional components to their community's social structure and customs (see Chapter 9, this volume). Peer relationships within girls' and boys' cultures also allow them to practice and refine the specific social and other skills they will later use in the contexts of adult relationships. During development, among other things, they learn which social strategies work well for them and which do not (e.g., social persuasion vs. attempts to dominate; K. MacDonald, 1996).

Boys' play fighting is readily understood in terms of an evolutionary history of one-on-one male–male competition (see Chapter 10, this volume). The process of coalition formation during boys' social development and the embedding of their friendships into the wider ingroup network are readily understood in terms of an evolutionary history of coalitional competition (see Geary et al., 2003). In this view, the social culture that emerges within boys' groups provides a context for refining individual-level dominance-related competencies and an opportunity to develop the competencies necessary to form and maintain cohesive and effective large-scale coalitions. Particularly telling is the speed and ease with which boys form these ingroups and the social support and role differentiation that emerges as they congeal into an integrated coalition (J. G. Parker & Seal, 1996; Savin-Williams, 1987). In cultures with male philopatry, the boys and adolescents that compose these play groups will become the leaders and warriors of their generation. By adulthood, they will have spent 10 to 15 years engaging each other in play fighting and coalitional games and in doing so will have had ample opportunity to prepare for the rigors of male–male competition in traditional contexts (Scalise Sugiyama et al., 2018; see Chapter 8, this volume).

In contrast to boys and men, girls and women do not routinely form coalitions to compete against groups of other girls and women nor are they as concerned about establishing social dominance. This does not mean that girls and women are not concerned about their relative status; they are and they should be: Status results in more social influence and greater access to important resources and through this has survival and reproductive consequences (see Chapter 6, this volume). Relational and sometimes physical aggression over romantic partners is common and clearly illustrates that girls and women can be very competitive with one another (see Chapter 8, this volume). In work or other settings in which girls and women are in frequent contact, they do develop subtle dominance relationships (Björkqvist et al., 1994; Campbell, 2002; Stockley & Campbell, 2013). These dominance struggles are relatively subtle in comparison to those of men, because the reproductive gains for men are many times higher than they are for women in many traditional societies and almost certainly throughout human evolution (see Chapter 8, this volume).

With the exception of research on relational aggression, much of the peer relationship literature has focused on the positive characteristics and benefits of girls' and women's relationships with their close friends. The depictions of these relationships are correct but leave unaddressed the deeper questions as to why girls and women form these intense friendships and why they differ from the friendship styles of boys and men (Rose & Asher, 2017). The question of why girls and women are more superficially friendly and socially outgoing in many social contexts also remains to be answered. These aspects of girls' and women's relationships and social behaviors reflect the social ecology that would emerge in the context of an evolutionary history of male philopatry (Geary, 2002b). Again, this does not mean that our female ancestors always emigrated into the group of their mate, but it appears to have been a common pattern, as was described in Chapter 8 of this volume.

In these circumstances, our female ancestors likely found themselves in a social world in which they were more isolated from close kin than were their mates. In this view, the greater attentiveness of girls and women to social cues (e.g., facial expressions), their more frequent and positive social signaling (e.g., smiling), their skill at strategically using emotion cues (Chapter 9, this volume), and their general motivation to develop a few intimate social relationships as an end in itself are adaptations to these social conditions. These sex differences are discussed in more detail in the next chapter, but as an example, about out 7 out of 10 women smile more frequently in noncompetitive social situations than does the average man and they direct these smiles more frequently to other women than to men (J. A. Hall, 1984). S. E. Taylor and colleagues (2000) provided a tend-and-befriend explanation for these and related social sex differences:

> Specifically, we propose that women's responses to stress are characterized by patterns that involve caring for offspring under stressful circumstances, joining social groups to reduce vulnerability, and contributing to the development of social groupings, especially those involving female networks, for the exchange of resources and responsibilities. We maintain that aspects of these responses, both maternal and affiliative, may have built on the biobehavioral attachment–caregiving system. (pp. 421–422)

Their conclusion is consistent with Christov-Moore et al.'s (2014) review showing greater empathy and sensitivity to social and emotional cues in female than male primates as related to the sex difference in care of infants. In this view, girls' and women's friendships evolved from this maternal system. However, this cannot be a simple replication of the mother–infant attachment system because girls' friendships develop with same-age peers and not younger children, as might be expected if these friendships are engaging parenting and parent–child attachment systems. Girls' social motives and behaviors with their friends differ from their play parenting described in Chapter 10 of this volume and women's friendships differ from their relationships with their children. These differences suggest girls' and women's friendships are not simply engaging the attachment-caregiving system, even if it initially evolved from it. Some other later evolving mechanisms must be involved.

Geary and Flinn (2002) and Geary (2002b) suggested these other mechanisms are Trivers' (1971) social and emotional processes that underlie reciprocal altruism, which creates long-term relationships with nonkin. They suggested these processes became more elaborated in the context of women's than men's friendships because of the different social ecologies that result from male philopatry. If we approach the issue from another direction, being embedded in a network of male kin would more or less automatically provide males with a system of social support that does not need to be repeatedly confirmed, but no such extensive kin-based support system would be available for immigrant females. In this situation, intimate relationships would provide an important resource in a potentially hostile social environment but relationships that would be based more on reciprocal altruism than on kin-based attachment systems. There are several core aspects of girls' and women's friendships that are consistent with reciprocal altruism. Compared with that of boys' and men's, girls' and women's friendships are more fragile and more heavily dependent on equality. The high investment needed to develop and maintain these relationships is also consistent with this view, as the closeness of relationships with nonkin fades quickly without frequent contact and emotional engagement (Dunbar, 2018b).

In all, when boys and girls have the opportunity to form relationships without interference from parents and other adults, they do so in ways that are consistent across cultures. They create social worlds that are centered around same-sex friendships. Boys find group activities to be rewarding and exciting and these emotions fuel further engagement in these activities. It is not a coincidence that boys' groups and group-level play mimic many aspects of between-group warfare in traditional societies, and that years of engaging in this type of play leads to the development of well-integrated, role differentiated, and effective coalitions. Similarly, girls find the intimacy and social support afforded by close dyadic relationships to be rewarding. They form many of these relationships while growing up and in the process, they become very skilled in the development and maintenance of these relationships by the time they reach adolescence and adulthood. These relationships are an important source of social and emotional support for coping with the stressors of childrearing and competition from other women (sometimes cowives) and their husbands.

PARENTING

There is no question that children's survival and development is critically dependent on the care provided by their parents and kin (see Chapter 6, this volume). Our concern here is about more subtle effects of parenting on children's emerging social and cognitive competencies. As described in Chapter 6 of this volume, similarities between parental characteristics and those of their children can be due to overlapping genes, child-evocative effects (i.e., parents react to the heritable characteristics of the child), or to parental treatment of children independent of evocative effects (Klahr & Burt, 2014; Scarr & McCartney, 1983). As described in Chapter 10 of this volume, there is a widespread belief that parents and other adults are socializing children in ways that result in sex-typed behaviors and cognition (e.g., Dinella & Weisgram, 2018), but any such effects are weaker than many people believe (J. R. Harris, 1995; Rowe, 1994).

As a complement to children's niche seeking (see Chapter 9, this volume), most parents provide an evolutionarily expectant rearing environment (Greenough, Black, & Wallace, 1987), such as synchronized mother–infant interactions and exposure to language. The resulting experiences begin to flesh out the skeletal competencies of folk modules (e.g., Kuhl et al., 1997). In cultures with sufficient resources, experiences that go above and beyond the evolutionarily expectant ones do not appear to have a strong long-lasting influence on the developing child (Scarr, 1992). Of course, behaviors outside of the range that naturally occurs in parent–child relationships (e.g., severe neglect), can compromise children's development. Most parents, however, provide a level of investment that allows for normal development, and variations in parental behaviors within this normal range do not appear to be systematically related to variations in most child outcomes. Regardless, an overview of some of the proposed explanations of how parents and other socializing agents might create or exaggerate developmental sex differences is provided next. The bottom line is that the importance of many of these explanations is greatly overstated.

Parental Treatment of Boys and Girls

Lytton and Romney (1991) provided an exceptionally comprehensive assessment of the parental treatment of boys and girls involving 172 studies and 27,836 participants. In this meta-analysis, parental treatment was assessed across eight broad socialization areas, including amount of interaction, achievement encouragement, warmth and nurturance, encouragement of dependency, restrictiveness, disciplinary strictness, encouragement of sex-typed activities, and clarity of communication directed toward the child.

For studies conducted in North America, there were very few differences in the ways in which parents treated their daughters and sons, as assessed by observation, parental report, and child report. One exception was for encouragement of sex-typed activities, although the difference was small. For about 2 out of 3 boys, parents encouraged sex-typed activities more frequently than they did with the average girl. This result appears to largely reflect an active discouragement of sons, especially by fathers, from playing with girls' toys (e.g., dolls); sex atypical play is often associated with later nonheterosexuality which is a concern for some parents (J. M. Bailey et al., 2016). The only other notable difference was for studies conducted in Western nations outside of North America. Here, sons received more physical discipline than did daughters. A related meta-analysis revealed that mothers talked more and provided more encouraging speech to their daughters than to their sons (Leaper, Anderson, & Sanders, 1998), but this may be related to the greater social responsiveness of daughters than sons and to more mutual concern between mothers and daughters than between mothers and sons (R. Butler & Shalit-Naggar, 2008). In other words, Leaper et al.'s (1998) findings for differences in the maternal treatment of sons and daughters might be due to child-evocative effects, as might Lytton and Romney's (1991) results for harsher parental treatment of boys.

A more recent meta-analysis that included information from more than 15,000 families, controlled for children's behavior (these were all observational studies) and confirmed that parents' treatment of their sons and daughters is very similar (Endendijk, Groeneveld, Bakermans-Kranenburg, & Mesman, 2016). They focused on parents' strategies for influencing the behavior of their children, ranging from praise to harsh physical punishment. Overall, both parents "were slightly more controlling with boys than with girls, but the effect size can be considered negligible" (Endendijk et al., 2016, p. 20).

Selective Imitation

It is clear that observation and imitation of parents and older peers contributes to children's learning of culturally important skills in traditional contexts (Gosso, Resende, & Carvalho, 2018; Hewlett, 2017; Lancy, 2014; Lew-Levy, Reckin, Lavi, Cristóbal-Azkarate, & Ellis-Davies, 2017). Nevertheless, it is not likely that the sex differences described in this chapter and the previous chapter are simply due to children's selective imitation of the same-sex parent or same-sex peers. On the basis of a review of 23 studies of children's imitative behavior, Maccoby and Jacklin (1974) tentatively concluded "that early sex typing is not a function of a child's having selectively observed, and selectively learned, the behavior of same-sex, rather than opposite-sex, models" (p. 299). Barkley, Ullman, Otto, and Brecht (1977) reached the same conclusion after reviewing 81 relevant studies. In an empirical study of their own, they found that girls tended to imitate traditionally feminine behavior (e.g., playing house) and boys tended to imitate traditionally masculine behavior (e.g., play fighting) whether these behaviors were enacted by a man or by a woman. It is not likely that these findings result from children only imitating behavior that is considered to be sex appropriate, at least not in any straightforward way.

Children's explicit knowledge of gender roles is only weakly related to the actual behavioral sex differences described in this chapter and the previous chapter (P. J. Turner & Gervai, 1995; Weisner & Wilson-Mitchell, 1990). This does not rule out more subtle influences of social learning and knowledge of gender roles on the expression of developmental sex differences (Bussey & Bandura, 1999; Leaper & Brown, 2018; Martin, Ruble, & Szkrybalo, 2002). This knowledge may be one social–cultural mechanism that provides information to children on how to be successful in their particular culture, including the selective imitation of the same-sex parent or same-sex peers (see Chapter 10, this volume). Slaby and Frey (1975), for instance, found that young boys who labeled themselves as boys and who understood that they will someday be men attended to men more frequently than did boys who did not yet understand that one's biological sex is constant through time.

Even so, Barkley et al.'s (1977) review and results suggest that different activities capture the attention of boys and girls and that this is what they are most likely to imitate. Indeed, girls and boys selectively attend to and find more attractive and engaging behaviors that are traditionally defined as sex-typed (see Chapter 10, this volume). For instance, Frick, Clément, and Gruber (2017) found that boys were more likely to imitate behavior related to tool use than were girls. Endicott provides another illustration with her description of the play of Batek children in Malaysia. The Batek are a relatively egalitarian hunter–gatherer society in which "no gender distinctions are made in the terms for children, siblings, cousins, and grandchildren" (Endicott, 1992, p. 282):

> Playgroup activities range from pretending to move camp to imitating monkeys to play-practicing economic skills such as blowpipe-hunting, digging tubers, collecting rattan, and fishing. Fathers sometimes intervene in the activities of children to offer advice about how to perform these skills. For example, when several children were pretending that they were harvesting honey by smoking bees out of a hive high in a tree in the middle of camp, a father who often participated in honey collecting showed the children how to properly construct rattan ladders to use for climbing up to the hive. It was the older boys, in the 10- to 12-year-old range, *who paid closest attention to this informal lesson*. (Endicott, 1992, p. 288; italics added for emphasis)

The bottom line is that children pay attention to and imitate adults and older children and in this way learn how to engage in culturally important, and often sex-typed, activities. It is not the case, however, that they imitate same-sex others simply based on a shared social identify of being a male or a female. They often imitate same-sex others because these adults and older children are engaging in activities that boys and girls find interesting and rewarding.

Parenting Across Cultures

The vast majority of research cited in the previous two sections was conducted in Western, educated, industrialized, rich, and democratic societies (WEIRD; Henrich, Heine, & Norenzayan, 2010). Although studies conducted in these nations suggest that parents do not strongly influence individual differences in children's personality and social behavior, cross-culture comparisons do find a relation between parenting and at least some child outcomes (Barry, Josephson, Lauer, & Marshall, 1976; Low, 1989; K. MacDonald, 1992; Sosis, Kress, & Boster, 2007). These seemingly contradictory findings are due, in part, to differences in how the relationship between parenting and child outcomes are measured. For within-culture studies, like those reviewed by Lytton and Romney (1991), individual differences in children's behavior are related to individual differences in parenting style, whereas cross-cultural studies involve comparisons of average differences across groups of people from different societies. On top of this methodological difference, within- and cross-culture studies may yield different results because the range of parenting behaviors is larger when assessed across rather than within cultures (K. MacDonald, 1992).

To illustrate, in societies characterized by high levels of intergroup aggression, parenting practices for boys and girls tend to be harsher, including more physical discipline and less responsiveness to the child's emotional state relative to parenting practices found in more peaceful societies (Barry et al., 1976). One apparent result is a cross-cultural difference in the average level of aggression found in societies with relatively harsh as opposed to relatively warm parenting (Ember & Ember, 1994; K. MacDonald, 1992). At the same time, the pattern of sex differences remains within cultures, even when girls or women from one culture might be described as more aggressive, on average, than boys and men from another culture. The cross-cultural pattern suggests that parenting can accentuate or attenuate the expression of certain social behaviors (e.g., frequency of physical aggression), but these effects largely result in cross-cultural differences in the behavior of same-sex children and not the creation of sex differences in one culture but not another.

Low (1989) analyzed child-rearing practices across 93 cultures as they were related to social structure (i.e., stratified vs. nonstratified societies and group size) and marriage system (i.e., polygynous vs. monogamous). In nonstratified polygynous societies where men can improve their social status and increase the number of women they can marry, the socialization of boys focuses on fortitude, aggression, and industriousness. These are traits that will likely influence cultural and reproductive success in these contexts (see Chapter 8, this volume). For these nonstratified societies, there was a very strong linear relation between the socialization of competitiveness in boys and the maximum number of wives allowed within the society. The more women a man can marry, the more competitiveness was emphasized in parental socialization of sons.

In stratified societies where men cannot improve their social status, boys are not strongly socialized to exhibit aggression and fortitude, although industriousness is still important. For girls, there is a relation between the amount of economic and political power held by women in the society and socialization practices. In societies where women can inherit property and hold political office (largely WEIRD societies), girls are socialized to be less obedient, more aggressive, and more achievement oriented compared with girls who live in other societies. Low (1989) concluded that "there is thus some evidence that patterns of child training across cultures vary in ways predictable from evolutionary theory, differing in specifiable ways between the sexes, and varying with group size, marriage system, and stratification" (p. 318). In other words, these cross-cultural studies suggest that parents can enhance or reduce many of the sex differences described in this chapter and the previous chapter and do so in ways related to the social and reproductive competition that the children will encounter in adulthood.

CONCLUSION

The length of the developmental period has nearly doubled during the course of hominin evolution (C. Dean et al., 2001; see Chapter 10, this volume). Changes in the pattern of development can result from changes in social (e.g., intrasexual competitors), ecological (e.g., food availability), and other demands (e.g., risk from predators) that influence survival during each developmental period and that influence later survival and reproductive prospects (see Chapter 4, this volume). The mechanisms that resulted in the change in the human developmental period are not yet fully understood, but much of this change likely resulted from increasing complexity of social dynamics (R. D. Alexander, 1989; D. H. Bailey & Geary, 2009; Flinn, Geary, & Ward, 2005; Geary, 2005). Many of the social sex differences described in this chapter stem from changes in human life history development and specifically evolved to allow boys and girls to learn the nuances of their local culture and to prepare for the forms of reproductive demands described in Chapter 6 (i.e., parental investment), Chapter 7 (i.e., intersexual choice), and Chapter 8 (i.e., intrasexual competition) of this volume.

Sex differences in interests, play patterns, and styles of social influence result in the segregation of boys and girls into different cultures (Maccoby, 1988, 1998), especially during the juvenile years but continuing into adolescence. The culture that girls and boys create for themselves amplifies and congeals sex differences that begin to emerge by 3 years old, and some of them in infancy. The sex differences in rough-and-tumble play, the process of friendship formation among boys, and the embedding of these dyadic relationships into a larger ingroup flow easily with an evolutionary history of coalitional male–male competition and the formation of dominance hierarchies within the coalition. From a life history perspective, these features of boys' play and social behavior involve a preparation for later within-group dominance striving and coalition formation for intergroup aggression (Geary et al., 2003). Through a combination of parenting practices, like the degree of physical discipline, the selective imitation of competitive activities, and actual experiences within same-sex peer groups, boys learn how to best achieve within-group social dominance and congeal into a role-differentiated and effective coalition by early adulthood.

Girls' peer relationships are a critical part of their social development and form the core of their social support network from the juvenile years onward (S. E. Taylor et al., 2000). Girls' friendships differ in many ways from boys' friendships (Rose & Asher, 2017). Girls spend more of their peer time in dyadic interactions with their best friend, they disclose more about themselves, and rely more on this friend for help with social and other problems (J. G. Parker & Asher, 1993; Rose & Asher, 1999). These relationships are much more socially demanding and time intensive than those of boys, and girls usually only maintain one or two of them at a time (J. G. Parker & Seal, 1996). Ironically, despite high levels of intimacy, personal disclosure, and support from their friends, girls' relationships are more fragile than are boys' and are more strongly dependent on equality in the give-and-take of the relationship and equality of outcomes that are important to them (Benenson, 2014; Benenson & Christakos, 2003; Rose & Rudolph, 2006; Whitesell & Harter, 1996). These relationship dynamics are, in part, a reflection of an evolutionary history of male philopatry and our female ancestors emigrating to the group of their mate. In this circumstance, distantly related or unrelated women are a potential source of social support, but the establishment of such relationships is predicted to be based more strongly on reciprocal altruism (Trivers, 1971) than on kin-based systems (cf. S. E. Taylor et al., 2000).

12

Sex Differences in Folk Psychology

Throughout the 20th century and continuing into the 21st, the issue of human sex differences in brain and in cognition has captured the attention of the general public and that of many scientists (Baron-Cohen, 2003; Blum, 1997; L. Ellis et al., 2008; D. F. Halpern, 2000; Kimura, 1999). Among serious scholars, it is no longer a question of whether men and women differ in the pattern of cognitive abilities or in aspects of brain organization, but rather their magnitude, practical importance, and origin. The next two chapters focus on these differences and use the taxonomy of folk domains introduced in Chapter 9 of this volume to do so. The discussion focuses on the origin of sex differences in brain and cognition from the clarifying light of sexual selection. There are many examples of sex differences in reproductive behaviors, cognition, and brain organization that are influenced by hormonal mechanisms and that can be placed within the broader framework of sexual selection (see Chapter 4, this volume). Humans are no different. This chapter begins with a brief introduction to sex differences in brain size and organization followed by a consideration of sex differences in folk psychology. Differences in folk biology and in folk physics are covered in Chapter 13 of this volume.

BRAIN SIZE AND ORGANIZATION

Sexual selection can result in sex differences in brain size, organization, and function, in the same way that intrasexual competition and intersexual choice have resulted in the evolution of sex differences in physical size,

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coloration patterns, and behavioral biases in the many species that were discussed in previous chapters. There have been substantive changes in brain size and likely brain organization over the course of human evolution (see Chapter 5, this volume), but the contributions of sexual selection to these changes are only understood at a very basic level. There is some evidence that intense male–male competition is associated with a larger neocortex (the most recently evolved areas of the brain) in males than in females (Pawłowskil, Lowen, & Dunbar, 1998; Sawaguchi, 1997), but much remains to be determined regarding specific areas of the brain related to this competition (Lindenfors, Nunn, & Barton, 2007).

Still, in many ways, much more is known about human sex differences in brain and cognition than about sex differences in nonhuman primates. In the following sections, general findings on human sex differences in brain size, organization, and function are reviewed, but any potential relations to sexual selection are not mentioned until specific folk psychology domains are discussed in later sections. The goal here is to provide a brief taste of what is currently known about sex differences in the human brain.

Relative Size and Organization

This section begins with a brief overview of basic sex differences in the brain and its development. Cognitive sex differences and associated brain systems following the folk domains framework (see Chapter 9, this volume) are the focus of later sections and the following chapter. However, there is a long evolutionary history of physical male–male competition in our species and this section closes with a description of sex differences in the brain systems associated with such competition.

General Pattern of Sex Differences

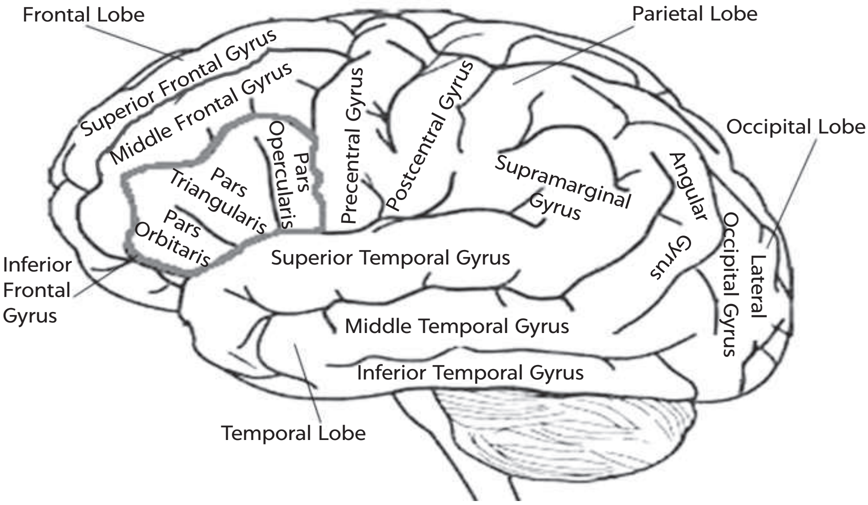
Chapter 5 of this volume described how the sex difference in physical size (e.g., height) decreased since *Australopithecus* (about 4 million years ago) and noted a corresponding reduction in the size of the gap between the smallest and largest brain volumes in our more recent ancestors. The combination suggests that the average brain size of our male and female ancestors likely converged since the emergence of *Homo* (about 2 million years ago). Sex differences in overall brain size persist, nevertheless.

In a detailed analysis of autopsied brains, Pakkenberg and Gundersen (1997) found that compared with women's brains, men's brains are (on average) 13% heavier, occupy 15% more volume, and contain 16% more neurons, among other differences. Brain imaging studies confirm these sex differences (Ruigrok et al., 2014). In an early study of young adults, C. M. Leonard et al. (2008) found that the overall brain volume of more than 9 out of 10 men is larger than that of the average woman. In the largest study of this type conducted to date (including 5,216 people), Ritchie et al. (2018) found the same sex difference for overall brain volume for middle-age and older adults, as well as similar sex differences, which favor men, in gray matter (neurons) and white matter (axons that connect neurons) volumes.

These sex differences are consistent across the four major lobes of the neocortex—frontal, temporal, parietal, and occipital (see Figure 12.1)—but are reduced to about a 10% male advantage once the sex difference in body size is controlled (D. Falk, Froese, Sade, & Dudek, 1999). The sex differences are somewhat smaller at birth (about a 6% male advantage) but quickly reach adult levels, although sex differences in the pace with which many specific brain regions develop continues through early adulthood (Gao, Alcauter, Smith, Gilmore, & Lin, 2015; Giedd et al., 1999; Knickmeyer et al., 2013; Lenroot & Giedd, 2006; Satterthwaite, Vandekar, et al., 2014; Satterthwaite et al., 2015). In a brain-imaging study of 1-month-old infants, D. C. Dean et al. (2018) found that boys had 8% more brain volume than did girls and found numerous sex differences in gray and white matter in various brain regions, some favoring girls and others favoring boys. There are in fact even earlier sex differences. Wheelock et al.'s (2019) brain-imaging study of 4- to 6-month-old fetuses indicated sex differences in the pattern of prenatal brain development. They found that boys and girls had different patterns in the ways in which many regions of the brain were connected as well as sex differences in developmental changes in the pattern of these connections. Findings such as these indicate that later sex differences in brain organization might have their roots in prenatal brain development.

In any case, the most interesting sex differences are found when total brain volume is considered (L. Cahill, 2006; Goldstein et al., 2001; Gur et al., 1999; Sowell et al., 2007). Once brain size is adjusted, women have a thicker cortex

FIGURE 12.1. Major Lobes (Frontal, Parietal, Occipital, and Temporal) and Gyri (Ridges Between Folds or Sulci in the Brain) of the Human Neocortex



From Creative Commons Zero. Available from https://upload.wikimedia.org/wikipedia/commons/b/bf/Brain-en.png. In the public domain.

than do men, and in fact women's advantage here exists in a few areas without adjusting for brain size (Luders et al., 2006; Ritchie et al., 2018; Sowell et al., 2007). Moreover, women typically have proportionally more gray matter than do men in many of the areas within the frontal lobe as well as in areas of the superior temporal lobe, among others. Men have proportionally more gray matter in parts of the parietal and visual (occipital) lobes and in areas associated with some aspects of sexuality, emotion (amygdala), and spatial abilities (hippocampus), among others (Fish et al., 2020; Gur et al., 1999; Lotze et al., 2019; Ruigrok et al., 2014; J. L. Wood, Murko, & Nopoulos, 2008).

There are also sex differences in the organization of white matter tracts (called the connectome), suggesting differences in the extent to which individual brain regions are interconnected in women and men (Ingalhalikar et al., 2014; Ritchie et al., 2018). Ingalhalikar et al. (2014) constructed a map of key white matter tracts that run through and across each hemisphere (side of the brain) for boys and girls and men and women and found substantive differences. They concluded that "male brains are optimized for communicating within the hemispheres, whereas female brains are optimized for interhemispheric communication" (Ingalhalikar et al., 2014, p. 825). These differences are related in part to the larger brain of men than women, because larger brains have more connections within hemispheres independent of sex (Hänggi, Fövenyi, Liem, Meyer, & Jäncke, 2014). Even with control of brain size, women's brains are more interconnected across hemispheres than are men's brains (Szalkai, Varga, & Grolmusz, 2018).

The study of sex differences in white matter tracts includes a long-standing and vigorously debated question regarding the corpus callosum. This is a bundle of 200 million axons that allow communication across the left- and right-hemispheres. DeLacoste-Utamsing and Holloway (1982) reported that the back portion of the callosum was shaped differently in men and women and, relative to overall brain weight, was larger in women. They speculated "that the female brain is less well lateralized—that is, manifests less hemispheric specialization—than the male brain for visuospatial functions" (DeLacoste-Utamsing & Holloway, 1982, p. 216), in keeping with Ingalhalikar et al.'s (2014) findings. However, this finding has been debated, refuted, and revived ever since (e.g., Bishop & Wahlsten, 1997). More recent studies have found subtle differences, including more axons in some areas of the corpus callosum for men and more axons in other areas for women (e.g., Björnholm et al., 2017; Dubb, Gur, Avants, & Gee, 2003), including in the areas originally identified by DeLacoste-Utamsing and Holloway.

The faster development of girls than boys described in Chapter 10 of this volume is mirrored in many aspects of brain maturation. There are some inconsistencies in the literature, but longitudinal studies that assess the same individual multiple times indicate faster development of gray matter and white matter tracts in girls than in boys (Gennatas et al., 2017; Giedd et al., 1999; Lebel & Deoni, 2018; Mills et al., 2016). Gray matter volumes peak earlier in girls than boys in several brain regions (e.g., frontal lobe) and earlier in boys than girls in other regions. The overall development of girls' white matter tracts appears to be largely complete by about 16 years old but some of these tracts continue to develop into the early 20s for boys (Simmonds, Hallquist, Asato, & Luna, 2014). It could be that these overall patterns are simply due to the general sex difference in the pace of development, but this does not seem to be the entire story. Different areas of the brain mature at different rates for boys and girls suggesting that there are important region-specific growth rates above and beyond the faster overall growth of girls (Gennatas et al., 2017; Giedd et al., 1999; cf. Mills et al., 2016).

There are many sex differences in the brain, but this does not tell us whether these differences are substantive relative to the many similarities in the brains of boys and girls and men and women (Joel et al., 2015). Joel et al. (2015) examined sex differences in gray matter and white matter across multiple brain regions and found considerable overlap for all of them. On the basis of these findings they concluded that "most brains are comprised of unique 'mosaics' of features, some more common in females compared with males, some more common in males compared with females, and some common in both females and males" (Joel et al., 2015, p. 15468). In other words, these mosaics imply that there is not a male-typical or a female-typical brain. By analogy, the human face is also a mosaic and there will be overlap in the size of core features (e.g., eyes) but the sex of the individual is easily determined by most people (Bruce et al., 1993). The same is true for the human brain, although it takes sophisticated technology to do so (N. E. Anderson et al., 2019; Chekroud, Ward, Rosenberg, & Holmes, 2016; Del Giudice et al., 2016; O. R. Phillips et al., 2019). Chekroud et al. (2016) were able to correctly classify the sex of 93% to 95% of adults on the basis of brain mosaics, including 92% when head size was not included. N. E. Anderson et al. (2019) also found that 93% to 94% of adults could be classified as a man or a woman based on the organization of the gray matter in their brains.

The evolutionary significance of these and other neural sex differences remains to be determined and must be approached with caution. As an example, the sex difference in the proportion of gray matter and white matter might be a reflection of the overall difference in the average size of women's and men's brains and not evolved traits per se. Larger brains tend to have proportionally more white matter than smaller ones because of the necessity of transmitting information across farther distances (D. Falk, 2001). The absolutely and proportionally higher white matter in men's brains might be due to the larger overall size and not a direct result of sexual selection or other evolutionary pressures. The best candidates for brain regions that have been shaped by sexual selection are those that not only exhibit sex differences but are disproportionally large and better interconnected relative to other brain regions within the same sex. These differences are also expected to be functionally linked to cognitive sex differences that may contribute to intrasexual competition or intersexual choice, as is discussed in following sections.

A Brain for Fighting

Among primates with intense physical male–male competition, males have larger cortical and subcortical regions associated with sensorimotor integration and aggression (e.g., amygdala) than do females (Lindenfors et al., 2007; Lindenfors & Tullberg, 2011; Stanyon & Bigoni, 2014). Across primate species, the size of the amygdala—associated with sexual and aggressive reactivity, among other things—increases as the intensity of physical male–male competition increases. The same is true for the sensorimotor systems involved in quickly reacting to changes in the environment, as would occur during male-on-male fighting. Given that male–male competition is often physical in traditional contexts and almost certainly throughout hominin evolution, it is not surprising that the same pattern is found in humans.

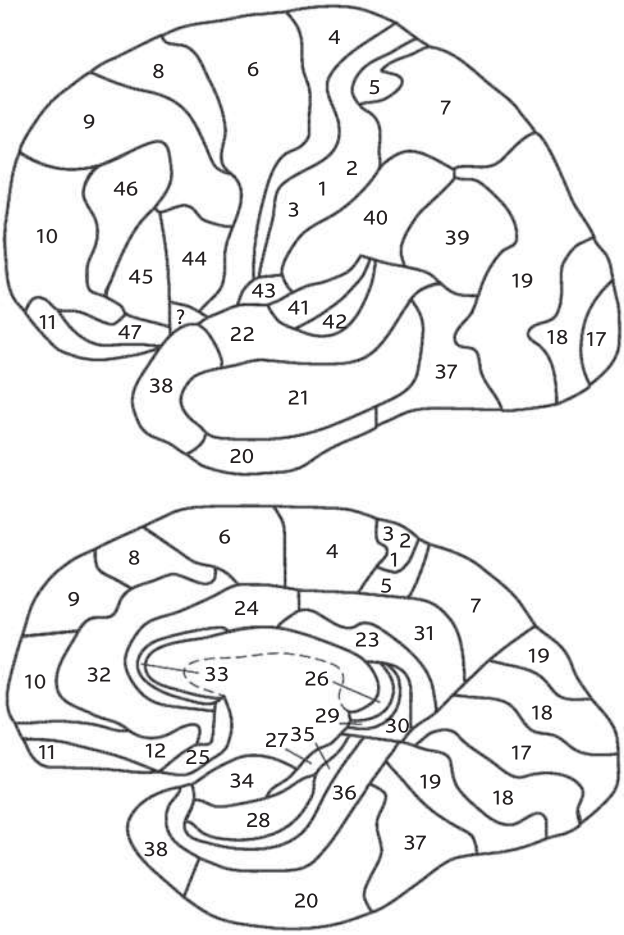
As with other primates with intense physical male–male competition, the amygdala is larger in men than in women but due in part to the sex difference in overall brain size (Marwha, Halari, & Eliot, 2017). Even with control of overall brain size, men have larger gray matter volumes (more neurons) in some regions of the amygdala than do women (Lotze et al., 2019; Ritchie et al., 2018). Brain regions involved in motor control (e.g., Brodmann Area 6 in Figure 12.2) and sensorimotor integration are also larger in men than women, controlling for the sex difference in brain size (de Lacy, McCauley, Kutz, & Calhoun, 2019a, 2019b; Lotze et al., 2019; Ritchie et al., 2018). There appear to be testosterone-driven changes in at least some regions of the amygdala and sensorimotor areas as children move through puberty (Bramen et al., 2012; Fish et al., 2020; Giedd et al., 1996; Hu, Pruessner, Coupé, & Collins, 2013; Neufang et al., 2009). Moreover, white matter connections between areas associated with the ability to quickly react to the environment are also enhanced by increases in testosterone concentrations during puberty (Goddings et al., 2014; Herting, Maxwell, Irvine, & Nagel, 2011). Nguyen et al. (2016) found that higher testosterone concentrations during adolescence were associated with lower connectivity between the amygdala and areas of the prefrontal cortex (e.g., Brodmann Area 10, Figure 12.2) that would normally contribute to the ability to suppress aggressive and other emotional impulses. Lower connectivity between these two regions in turn was associated with more frequent engagement in aggressive behaviors.

These of course are not the only sex differences related to sexual selection but meld nicely with the sex differences in various physical competencies, which favor boys, that are evident early in life and that become exaggerated during adolescence (see Chapter 10, this volume). In other words, men's bodies are built for physical competition and so are their underlying brain systems. These include systems that respond to aggressive challenges and integrate the accompanying emotions with the physical skills that enable men to quickly react to the physical aggression of other men.

Hormones and Gene Expression

This section provides a general overview of the relation between sex hormones and sex differences in brain development and organization; more detailed

FIGURE 12.2. Maps of Brodmann's Areas of the Human Neocortex



The top section is the lateral (outer) view of the cortex, whereas the bottom section is the medial (center) view. Many of these areas can be subdivided into specialized subregions that may process different forms of information. Very generally, Areas 1, 2, 3, 5, 31, and 43 are part of the parietal cortex and support a variety of functions including sense of body position, attention, and spatial competencies. Areas 17, 18, and 19 are part of the occipital cortex and support simple and complex visual perception. Areas 22, 41, 42, and subregions of Areas 40 and 38 are part of the temporal cortex and support simple and complex auditory and speech perception. Areas 20, 21, 26–28, 34–37, and 52 are also part of the temporal lobe, but support a variety of complex visual competencies. Areas 4, 6, and 8 are involved in complex motor movements and are part of the frontal cortex. Area 44 and subregions of Area 45 are involved in speech generation and gesture and are part of the frontal cortex. Areas 9, 10, 11, 25, 46, 47, and subregions of Area 45 are part of the prefrontal cortex and support behavioral control, executive function, and many complex social competencies. Areas 23, 24, 30, (parts of 31), 32, and 33 are part of the cingulate cortex and support attentional and emotional functions. Illustration by Mark Dubin. Reprinted with permission.

information is provided in following sections on the specific folk-psychological abilities. A glimpse at research that examines the pattern of gene expression associated with sex differences in brain development and function is also provided. This level of detail is beyond the general scope of this book, and so this section will simply serve as an introduction to this type of research. It is included nevertheless, because in the coming decades these types of studies will likely become common and increasingly important for fully understanding sex differences in the human brain.

Hormones

Recall, prenatal exposure to sex hormones can organize (e.g., enlarge or shrink) areas of the brain that support sexually selected behaviors and cognition and postnatal exposure to these hormones can activate them (A. P. Arnold & Gorski, 1984; Ball & Balthazart, 2004; see Chapter 4, this volume), although these relations are nuanced and not yet fully understood (Adkins-Regan, 2005). To further complicate matters, there are direct genetic influences on sex differences in brain organization and function that are independent of hormones and these too remain to be fully explored (A. P. Arnold, 1996, 2017; Lentini, Kasahara, Arver, & Savic, 2013). Nevertheless, the basic relations between prenatal, early postnatal, and later exposure to sex hormones and brain and cognition are well understood in many nonhuman species and there have been consistent advances in our understanding of their influences in our own species (L. Cahill, 2006; McCarthy, 2016).

There are a few studies of the relation between amniotic testosterone concentrations and the organization of later brain structures (Chura et al., 2010; Lombardo et al., 2012). Lombardo et al. (2012), for instance, found that boys' fetal testosterone concentrations were associated with their later (at 8–11 years old) gray matter volumes in several areas associated with folk psychology. These included areas that support some aspects of language, such as Wernicke's area (Brodmann Area 22, Figure 12.2), social decision making (e.g., Brodmann Area 11), and theory of mind (parts of Brodmann Areas 22 and 40); these are discussed in more detail in later sections of this chapter. These are preliminary results, and differences prior to adolescence might not be the same as those found in adulthood because of the substantial pruning of gray matter and development of white matter tracts that occur during adolescence. Nevertheless, these types of studies compliment Wheelock et al.'s (2019) brain-imaging finding of different patterns of brain connectivity in girls and boys during prenatal development.

Hormonal influences on brain development during adolescence are easier to study and better understood (Bramen et al., 2011, 2012; De Bellis et al., 2001; Herting et al., 2011; Neufang et al., 2009; Raznahan et al., 2010), although much remains to be determined (Herting & Sowell, 2017). These hormonal changes can result in the activation of areas that were organized prenatally or early postnatally and can also result in further organizational changes. Among the more consistent findings are hormonal influences on the earlier noted sex differences in gray matter pruning and white matter connectivity. In addition to the relationship between testosterone and connectivity of the amygdala, there are sex differences in the development of some regions of the hippocampus (e.g., as related to memory) during pubertal development (Fish et al., 2020; Giedd et al., 1996; Hu et al., 2013; Neufang et al., 2009; Satterthwaite, Vandekar, et al., 2014). Although a sex difference in overall size is not always found once total brain volume is taken into account (Tan, Ma, Vira, Marwha, & Eliot, 2016), the overall size of the hippocampus is larger in boys and men than in girls and women (Fish et al., 2020). Many of the changes that occur during adolescence may be dependent on prenatal exposure to male hormones (Ernst et al., 2007); development occurs with the combination of sex-typical prenatal and pubertal hormone exposures.

Developmental changes in the amygdala and hippocampus are important because they contribute to sex differences in sensitivity to threats and sexual opportunity and to sex differences in memories for personal experiences. The sex differences in the organization of these brain systems combine with circulating hormone concentrations in adulthood to influence behavioral and cognitive biases. For instance, circulating testosterone concentrations appear to influence the sensitivity of the amygdala and other brain regions associated with emotion regulation to threat and to other social cues (Stanton, Wirth, Waugh, & Schultheiss, 2009; van Wingen et al., 2010).

For nonhuman species, circulating estradiol influences gray matter volume in areas of the hippocampus (Woolley & McEwen, 1992). The increase in estradiol concentrations that precede ovulation is associated with the generation of new neurons within the hippocampus and better integration of neurons with one another. These and more molecular changes are associated with improvements in learning and memory (e.g., of personal experiences or episodic memory; Fortress & Frick, 2014). The same is true across women's ovulatory cycle (Goldstein et al., 2005; Lisofsky et al., 2015; Pletzer, Harris, & Hidalgo-Lopez, 2018; Protopopescu et al., 2008). These studies have consistently found that increases in estradiol concentrations are associated with increases in gray matter volume in several areas of the hippocampus and with improvement in verbal memory. There may also be cycle-related gray matter changes in a few other brain regions and changes in the functional connectivity (increased coherence) of the hippocampus to other brain areas, but these are not found as consistently.

These types of studies illustrate how exposure to various sex hormones can influence sex differences in the organization and the function of key areas of the brain that are associated with behavioral (e.g., aggression) and cognitive (e.g., verbal memory) sex differences. In the following sections, studies of this type are integrated with sex differences in folk abilities and placed in a broader evolutionary context.

Gene Expression

Sex differences in the pattern of brain organization and function must be related to deeper sex differences in the pattern of gene expression. These often include epigenetic changes or the turning of specific genes on or off without affecting the underlying DNA (Forger, 2016; McCarthy, 2016). These types of epigenetic changes have been thoroughly studied as related to the estrogen related changes in the hippocampus in nonhuman animals (Fortress & Frick, 2014). Differential gene expression is also found in men and women, although the same gene may be differentially expressed under many conditions (M. Crow, Lim, Ballouz, Pavlidis, & Gillis, 2019; Trabzuni et al., 2013). The pattern of differential expression within the human brain involves thousands of genes, including different sets of genes at different life history stages (Shi, Zhang, & Su, 2016). The sex differences in gene expression within the brain are largest at puberty but extend back to prenatal brain development (O'Brien et al., 2019; Shi et al., 2016).

Shi et al. (2016) compared the pattern of human sex differences in gene expression with those found in chimpanzees (*Pan troglodytes*). This comparative approach indicated that male-biased genes (i.e., those more strongly expressed in males than in females) showed more evidence for recent evolutionary selection than did female-biased genes, consistent with more intense sexual selection on males than females during human evolution (see Chapter 8, this volume). Indeed, there is consistent evidence that sexual selection contributes to sex-biased gene expression across species (e.g., Harrison et al., 2015; Pointer, Harrison, Wright, & Mank, 2013; Reinius et al., 2008; A. E. Wright & Mank, 2013). For instance, Reinius et al. (2008) found large sex differences in the pattern of gene expression in the visual cortex of two polygynous primates, humans and a species of macaque (*Macaca fascicularis*) and little difference for the monogamous marmoset (*Callithrix jacchus*). The pattern is interesting because sexual selection is more intense in polygynous than in monogamous species.

Many of the hormone-influenced sex differences are associated with sex differences in the underlying patterns of gene expression. The sex-biased expression patterns of at least some of these genes will have been influenced by sexual selection and are likely related to the development and expression of sexually selected traits described in this book.

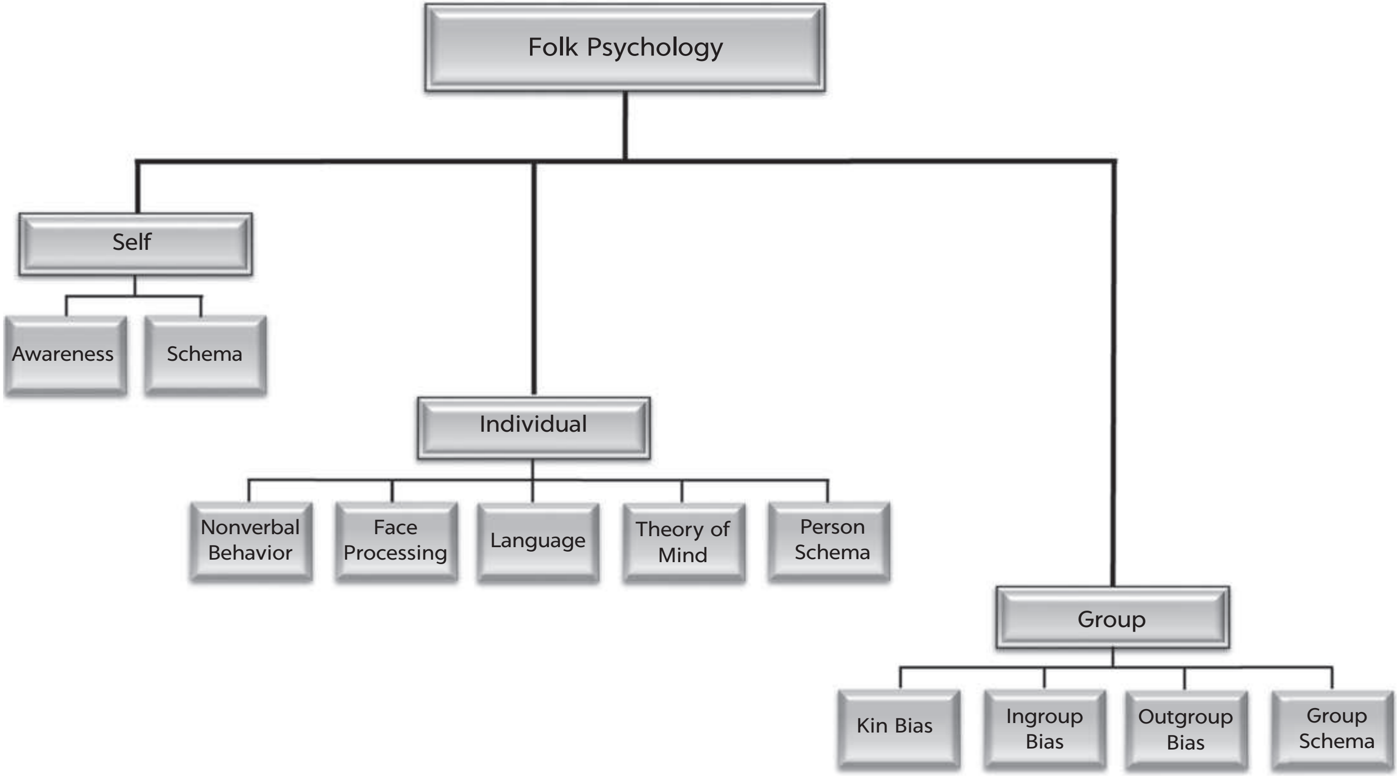
FOLK PSYCHOLOGY

This section returns to the folk domains that were outlined in Chapter 9 of this volume and focuses specifically on folk psychology. Figure 12.3 reproduces the folk psychology domains and organizes the reviews presented in the following sections. In each section, there is a focus on cognitive sex differences (e.g., in language) and when there are relevant studies available, differences in the supporting brain systems and any hormonal influences on these systems are discussed. Before turning to specific folk abilities, sex differences in biases in visual perception are reviewed.

Biases in Visual Perception

Sex differences in visual-perceptual biases mean that boys and men often focus on different things in world than do girls and women. These biases also

FIGURE 12.3. Core Evolutionarily Salient Abilities, Knowledge Domains, and Cognitive Biases Associated With Folk Psychology



provide a bridge between small sex differences in the attentional focus of girls and boys in infancy and the widening of these differences as children develop and move into adulthood. These early biases in the "what," "where," and "how" visual pathways are related to prenatal hormone exposure and link these early sex differences to those covered in this chapter and Chapter 13 of this volume (G. M. Alexander, 2003; Handa & McGivern, 2015). These differences are consistent with the earlier described sex differences in infants' orientation toward people or things and a corresponding bias to focus on information in the what (girls) or where and how (boys) visual streams (see Chapter 10, this volume). These biases appear to result, at least in part, from sex differences in the organization of the dorsal (top) and ventral (bottom) visual streams and appear to influence which aspects of the environment are more likely to capture an individual's attention from the bottom-up, automatically (McGivern, Mosso, Freudenberg, & Handa, 2019). Handa and McGivern (2015) noted the following:

> The visual system is the dominant sense in primates on which the brain relies for information about the world. Thus, small biases during development toward processing movement or objects can have long-term effects on the acquisition of higher cognitive skills . . . differential development of dorsal/ventral processing can be expected to have a broad influence on cognitive style related to bottom-up and top-down processing [of social and ecological information]. (pp. 111–112)

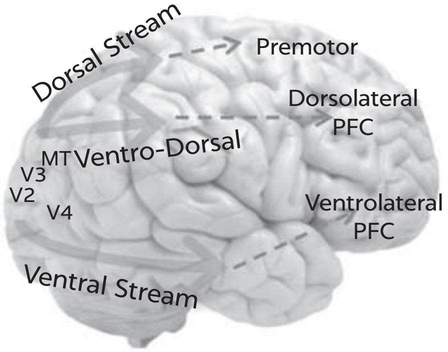
As shown in Figure 12.4, many of the sex differences in folk physics are dependent on the where and how organization of the dorsal visual stream, whereas many of the sex differences in folk psychology are dependent on the what organization of the ventral visual stream. Both sexes use both visual streams and both streams work simultaneously, but a bias to attend more to dorsal stream information will result in greater sensitivity to large-scale space, movement in space, acting on the environment, and an implicit understanding of how objects can be used as tools. In contrast, a bias to attend more to ventral stream information will result in greater sensitivity to features of individual objects, including faces, and will likely facilitate other forms of social information processing (e.g., theory of mind). As outlined in Figure 10.3 (see Chapter 10, this volume), any early biases in these areas provide continuity with the sex differences found in infants and may result in different ways in which boys and girls experience the world that, in turn, will exaggerate early sex differences and contribute to the differences in folk psychology and folk physics found in adulthood.

Self

As shown in Figure 12.3, folk psychology includes brain systems and knowledge organized around the self, including self-awareness (e.g., awareness of one's self as a social being) and self-schema (e.g., knowledge of one's traits). These are core features of the brain's default mode network (see Chapter 9, this volume; Raichle, 2015; Rugg & Vilberg, 2013), especially areas in the prefrontal cortex (e.g., Brodmann Areas 10, 11, and 12 in Figure 12.2; LeDoux & Brown, 2017).

FIGURE 12.4. Sex Differences in the Dorsal and Ventral Visual Stream

Dorsal Stream Skills Related to Folk Physics
Targeting – Visuomotor Guidance
Mental Rotations – Abstract Visualization
Navigation – Cardinal Directions
Tool Use



Ventral Stream Skills Related to Folk Psychology
Language Fluency – Semantic Encoding
Face Processing
Episodic/Autobiographical Memory

Sex differences in folk domains are related in part to biases in the tendency to focus more on dorsal visual stream information (males) or ventral visual stream information (females). Many of the sex differences in folk physics (Chapter 13, this volume) are dependent on dorsal visual stream information, whereas those in folk psychology are dependent on ventral visual stream information. MT = visual area MT (medial temporal); PFC = prefrontal cortex; V = visual. From “Steroid Hormones, Receptors, and Perceptual and Cognitive Sex Differences in the Visual System,” by R. J. Handa and R. F. McGivern, 2015, *Current Eye Research*, *40*, p. 114. Copyright 2015 by Taylor and Francis. Adapted with permission.

There are also pubertal changes in many of these and related regions (e.g., Brodmann Areas 24 and 32) that are associated with self-evaluations and social comparisons as well as increased integration of these with the brain’s reward centers (not shown in Figure 12.2; Pfeifer et al., 2013). Developmental change is similar in boys and girls during the early stages of puberty but diverge thereafter (Satterthwaite, Shinohara, et al., 2014). In other words, the brain systems that support folk psychology undergo an important enhancement and reorientation during puberty, including many sex-specific changes.

Psychologically, self-awareness anchors the mental models that people generate as part of their social problem-solving, their rehearsal of strategies to help them improve their social status and their access to culturally important resources (Geary, 2005; see Chapter 9, this volume). In the context of these mental simulations, self-knowledge will be particularly important for traits that an individual can use to better achieve these outcomes or traits that might influence the corresponding social dynamics. These include traits like physical attractiveness and social status that influence how an individual is perceived by others and his or her relative influence.

The associated studies show that the self-focus of women and men and many of the traits that are central to this focus are related to mate choices, competition for mates, or social relationships related to parenting and investment in children. In other words, people often have an explicit awareness of many of the sex differences described in previous chapters, even if they do not understand the contexts in which these biases evolved. For instance, when reflecting on or describing themselves (e.g., "I am . . ."), women are more likely to view themselves in terms of close relationships with family members or friends, whereas men are more likely to view themselves as members of a group or team (Gabriel & Gardner, 1999; Grysman & Hudson, 2013). These sex differences follow the developmental patterns described in Chapter 11 of this volume and are consistent with the sex differences described in a later section of this chapter.

In keeping with the sex differences in emotional expressivity and intensity, about 7 out of 10 women are more self-aware of nuances in their feelings and have better memories for the details of emotionally charged personal experiences than does the average man (Barrett, Lane, Sechrest, & Schwartz, 2000; Cahill et al., 2001; Cahill, Uncapher, Kilpatrick, Alkire, & Turner, 2004; Grysman & Hudson, 2013; R. Wright, Riedel, Sechrest, Lane, & Smith, 2018). McRae, Reiman, Fort, Chen, and Lane (2008) found that women's awareness of their feelings is related in part to activation of the anterior cingulate cortex (Brodmann Area 24, Figure 12.2), an area of the brain that triggers explicit representations of the current context when a decision or choice needs to be made (Botvinick, Braver, Barch, Carter, & Cohen, 2001). Girls and women are more sensitive to emotion-eliciting change in social and other conditions and their emotional state automatically "pops" into their awareness. In this way, they are better able to use awareness of their feelings as a barometer that is highly sensitive to change in social conditions, including the emotional state of other people (R. Wright et al., 2018). The triggering of these feelings and awareness of them facilitates the use of mental models for determining the source of the change and for strategizing about dealing with it. Sensitivity to change in emotions melds nicely with women's use of relational aggression and the corresponding need to detect subtle cues associated with social competition and devising a plan to cope with this competition (see Chapter 8, this volume).

The relationship between sexual selection (e.g., mate choices) and sex differences in self-awareness and self-reflection are more straightforward for physical traits than for psychological ones. This is because physical traits are more easily measured than feelings and because we know which physical traits have likely evolved under the influence of competition and mate choices. The usefulness of this approach is illustrated by several corresponding predictions. The first is that boys and men will show greater awareness and valuation of the physical strength and athletic ability that is related to male–male competition, as well as traits that influence female choice (e.g., relative cultural success). The second prediction is that women will show greater awareness and valuation of facial features, weight, and breasts, traits that influence men's mate choices and are thereby a focus of female–female competition. Women's evaluation of their physical traits has in fact been the subject of numerous sociological and social–psychological debates and studies, including the study of the sexual objectification of women:

> Sexual objectification occurs whenever people's bodies, body parts, or sexual functions are separated out from their identity, reduced to the status of mere instruments, or regarded as if they were capable of representing them . . . when objectified, individuals are treated as bodies and, in particular, as bodies that exist for the use and pleasure of others. (Fredrickson, Roberts, Noll, Quinn, & Twenge, 1998, p. 269)

The issue here is the emphasis on women's bodies as sexual objects that in turn follows from the stronger preference of men than women for casual sex, as well as men's focus on women's physical traits when making mate choices (see Chapter 7, this volume). The dynamic has, however, become exaggerated in many cultures because girls and women can now compare themselves with images of attractive women presented in mass media (Betz, Sabik, & Ramsey, 2019; Grabe, Ward, & Hyde, 2008) and because of the heightened female–female competition in societies with socially imposed monogamy; the latter makes desirable men more choosy.

In general, girls and women tend to reflect on their behavior and traits more frequently than do boys and men across many domains (Fejfar & Hoyle, 2000), and their body is a common area of reflection and appraisal (K. A. Phillips, Menard, & Fay, 2006). Compared with young men, young women in the Unites States are more concerned about their relative thinness, are more aware of and monitor their weight more frequently, and feel shame if they do not meet their internalized standard for thinness (Mintz & Betz, 1986). In a study of body dysmorphic disorder—a psychiatric disorder that involves preoccupation with an imagined bodily defect (American Psychiatric Association, 2013)—K. A. Phillips et al. (2006) found many similarities in the symptoms of women and men but also found a sex difference in the areas of preoccupation: "Women were more likely to obsess about the appearance of their skin, stomach, weight, breast/chest, buttocks, thighs, legs, hips, and toes" (p. 83). Similar concerns are found in women with subclinical body dysmorphic disorder or eating disorders (Dolan, Birtchnell, & Lacey, 1987; S. C. Schneider, Mond, Turner, & Hudson, 2019). Brain imaging studies reveal activation of the anterior cingulate cortex and amygdala when women process body-image information, consistent with an attentional focus on and more intense negative feelings about unfavorable social comparisons (Kurosaki, Shirao, Yamashita, Okamoto, & Yamawaki, 2006; C. Preston & Ehrsson, 2016).

There is less research on the physical traits that are the focus of boys' and men's self-reflections, but what is known is also in line with predictions. Men are more likely to consider themselves to be underweight and to explicitly focus on and sometimes obsess about their muscularity (Mintz & Betz, 1986; K. A. Phillips et al., 2006; S. C. Schneider et al., 2019). Men's concern about muscularity is as great and may be slightly greater than women's concern about thinness. Among young adults, Smolak and Murnen (2008) found that more than 9 out of 10 men were more focused on their muscularity than was the average woman, whereas 4 out of 5 women were more focused on their thinness than was the average man. T. J. Wade (2000) found that young men with higher self-rated physical fitness and competence (e.g., strength, reflexes) and with facial features associated with social dominance had a higher self-esteem and considered themselves to be more sexually and physically attractive than did other men. These self-evaluations are consistent with women's preferences for mates (see Chapter 7, this volume) and with the traits associated with male–male competition.

The key point of this section is that adolescent girls and women self-focus more than do boys and men on the physical traits that influence male choice and female–female competition, and adolescent boys and men self-focus more on the physical traits that influence female choice and physical male–male competition. These patterns are not at all surprising, if self-awareness and social comparison processes evolved at least in part as a consequence of social competition (R. D. Alexander, 1989; Flinn, Geary, & Ward, 2005; Geary, 2005), with sexual selection being an important component of this competition.

Individual

As shown in Figure 12.3, the individual-level components of folk psychology support one-on-one dyadic interactions and relationships. Sex differences in sensitivity to nonverbal behavior and in nuances in the reading of facial expressions are discussed next, followed by reviews of sex differences in language competencies and in theory of mind and person schemas. In each section, the reviews are organized in terms of cognition, brain, and hormones. Most of these systems will be more highly elaborated in women than in men, because of female–female competition and the reliance on relational aggression in the context of this competition (Geary, Winegard, & Winegard, 2014) and because of the importance of developing and maintaining same-sex dyadic relationships that are part of women's social support network (Geary, 2002b; S. E. Taylor et al., 2000). Same-sex relationships, however, need not be the only source of sex differences in individual-level folk-psychological competencies. The sex differences in parental investment and in the need to monitor potentially predatory men may have also resulted in more sensitive competencies in women than in men (Garver-Apgar, Gangestad, & Simpson, 2007; Hampson, van Anders, & Mullin, 2006).

If the evolutionary importance of same-sex relationships, whether they are competitive or supportive, is critical, then girls and women should be more sensitive to same-sex than to opposite-sex social cues. If the monitoring of potentially predatory men or managing relationships with their husband has been relatively more important, then women should be more sensitive to men's than to women's social cues. Women are sensitive to the nonverbal communication (e.g., facial expressions) of men, but the bulk of the evidence indicates that they are generally more sensitive to the social cues of women. Men in contrast appear to be especially sensitive to the dominance-based cues (e.g., angry facial expression) of other men.

Nonverbal Behavior and Facial Expressions

As noted previously, each review of sex differences in the folk domains is organized in terms of cognition, brain, and hormones. Links to sexual selection are made in each section, as warranted.

Cognition. Girls and women are better than boys and men at interpreting and sending nonverbal social messages, including skill at reading emotional states conveyed in facial expressions, gesture, and body language and in generating nuance in the social use of these forms of communication (Buck, Savin, Miller, & Caul, 1972; J. A. Hall, 1978, 1984; J. A. Hall & Matsumoto, 2004; McClure, 2000; Proverbio, 2017; Rosenthal, Hall, DiMatteo, Rogers, & Archer, 1979; van Beek & Dubas, 2008; H. L. Wagner, Buck, & Winterbotham, 1993). Rosenthal et al. (1979) conducted one of the most ambitious and comprehensive assessments of sex differences in this area, with the development of a standardized test—the Profile of Nonverbal Sensitivity—for the assessment of sensitivity to nonverbal emotion cues. These cues are visual (e.g., facial expressions, body posture), auditory (e.g., emotional tone conveyed in utterances), and a combination of both. The test involves watching a film of 220 short segments of a woman's nonverbal behavior, including facial expressions, body posture, and content-filtered speech (i.e., speech in which the individual words cannot be identified but the emotional tone can), as well as segments that include combinations of cues. The test was initially administered to 492 adolescents and in follow-up studies to more than 4,000 children and adults. Assessments were done on three or more samples from Australia, Canada, the United States, Israel, and New Guinea and smaller samples from Northern Ireland, Mexico, New Zealand, Hong Kong, West Germany, and Singapore.

Girls and women were more accurate than were boys and men when judging emotion cues on the basis of facial expressions, body posture, and vocal intonation (Rosenthal et al., 1979). These sex differences were found in all nations in which 3 or more samples were obtained (J. A. Hall, 1984). J. A. Hall (1984) concluded that the advantage of girls and women in the decoding of nonverbal messages "is most pronounced for facial cues, less pronounced for body cues, and least pronounced for vocal cues" (p. 27). When all nonverbal cues are provided, which is a more accurate assessment of these skills in the real world, about 17 out of 20 girls and women are more accurate at decoding the emotion cues of another individual than is the average same-age boy or man (J. A. Hall, 1978).

Overall, women appear to be better at recognizing the facial expressions of men than those of women, especially when they convey negative emotions (Thompson & Voyer, 2014), but they are better at emotionally communicating with other women. Buck et al. (1972) found that dyads of women are more effective in expressing and reading the emotion cues of the other woman than are dyads of men, and Wagner et al. (1993) found that women are more accurate in judging the subtle emotion cues of other women (e.g., inferring their emotional state) than the emotion cues of men. Girls and women also have a better memory for faces than do men, especially same-sex faces (Asperholm, Högman, Rafi, & Herlitz, 2019; Cortes, Laukka, Lindahl, & Fischer, 2017; Herlitz & Lovén, 2013). Almost 3 out of 4 girls and women have a better memory for the faces of other girls and women than does the average boy or man for the faces of other boys and men.

Girls' and women's advantage in reading the emotion cues of same-sex others appears to emerge from a combination of allocating more attention than boys and men to the processing of same-sex faces, especially the eyes; the greater sensitivity of girls and women to subtle emotion cues signaled by facial expressions and other nonverbal behaviors; and the greater expressiveness of women than men (J. K. Hall, Hutton, & Morgan, 2010; Herlitz & Rehnman, 2008; H. Hoffmann, Kessler, Eppel, Rukavina, & Traue, 2010; Sasson et al., 2010). For the latter, roughly 17 out of 20 women convey more information in their facial expressions than does the average man and nearly 3 out of 4 women engage in social smiling and maintain eye contact more consistently than does the average man (J. A. Hall, 1984), as is found in infancy (see Chapter 10, this volume). Men on average are poor at reading the nonverbal cues of women, and often misperceive sexual interest as friendliness (Farris, Treat, Viken, & McFall, 2008) or misperceive friendliness as sexual interest (Haselton & Buss, 2000).

One area in which these sex differences are typically smaller or reversed is men's processing of threat cues from other men. Men, for instance, are generally better at detecting the angry facial expressions of other men than they are the angry expressions of women (Rotter & Rotter, 1988; Wagner et al., 1993; M. A. Williams & Mattingley, 2006). In two large-scale studies involving more than 1,100 people, Rotter and Rotter (1988) found that women are more accurate than men in judging disgust, fear, or sadness in the facial expressions of both sexes, and an angry expression on the face of other women. Men, in contrast, are more accurate in detecting an angry expression on the face of other men. Dimberg and Öhman (1996) concluded that men are more sensitive to the angry expressions of other men than they are to the angry expressions of women, especially when these anger-signaling cues are expressed in adult men as contrasted with adolescents and when the expressions are directed toward the individual (e.g., with eye contact). The finding that men might be especially sensitive to the angry expressions of other men is consistent with Rosenthal and colleagues' (1979) finding that men are particularly sensitive to negative dominance-related cues (e.g., being disrespected).

Brain. Many of the brain regions that support the processing of facial expressions, body posture, and other nonverbal social cues are part of the visual ventral stream shown in Figure 12.4. This what stream focuses the individual on details of the people or objects he or she is engaged with and goes from primary visual cortex through temporal cortex, with reciprocal connections to the amygdala (for emotion processing, not shown in Figure 12.3) and parts of the ventrolateral prefrontal cortex (e.g., Brodmann Areas 11 and 47, Figure 12.3; Handa & McGivern, 2015; Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013; Milner & Goodale, 1995). Among other things, the ventral pathway includes systems for face and body processing and for integrating these with emotions, prior memories, and knowledge about others (i.e., person schema). Similar pathways are found in the macaque (*Macaca mulatta*) where they contribute to the recognition of others, sensitivity to others' behavioral focus, and generation of behavioral plans (e.g., Kravitz et al., 2013). This is an evolutionarily ancient system of brain regions that supports dyadic interactions and relationships. Catani and Bambini (2014) proposed that this system has been elaborated during human evolution, including its integration with the language system and medial prefrontal areas (e.g., Brodmann Areas 11 and 12) involved in social inference (i.e., theory of mind) and decision making.

Among other things, this network of brain regions is important for the evaluation of social situations and for generating plans to react to them and is often engaged differently in men and women. After correcting for the sex difference in brain size, the social–emotional processing areas of the prefrontal cortex (e.g., Brodmann Area 11) that are important for social decision making are relatively larger (more gray matter) in women than in men (Goldstein et al., 2001; Gur, Gunning-Dixon, Bilker, & Gur, 2002; Lotze et al., 2019; J. L. Wood, Heitmiller, Andreasen, & Nopoulos, 2008). The amygdala and these areas of the prefrontal cortex, along with the anterior cingulate cortex (e.g., Brodmann Area 24, Figure 12.2), are richly interconnected and operate to balance the emotional and rational components of social decision making and behavioral responding in social contexts (Adolphs, 1999). As noted in Chapter 9 of this volume, women and men show different patterns of engagement of these regions when viewing emotion-eliciting images, with men engaging in more top-down management of their emotional responses than women (Filkowski, Olsen, Duda, Wanger, & Sabatinelli, 2017).

In addition to the sex differences in proportional size of the amygdala (more gray matter in men) and ventromedial prefrontal cortex (more gray matter in women), these regions are interconnected differently in men and women (Lotze et al., 2019; Ritchie et al., 2018; Tranel, Damasio, Denburg, & Bechara, 2005). There are more functional connections between these regions in the right-hemisphere for men and the left hemisphere for women. The combination of differences in proportional size and connectivity appears to contribute to women's advantage in inhibiting behavioral responses, especially aggression, in emotionally charged situations (Gur et al., 2002), and may contribute to women's better memory for the details of emotional episodes. Vivid memory for these details is associated with activation of the left amygdala (stronger in women), whereas memory for the overall gist of the episode is associated with activation of the right amygdala (stronger in men; L. Cahill, 2006). The left amygdala, along with the face processing part of the brain (i.e., the fusiform gyrus, Brodmann Area 37), also contributes to women's better memory for same-sex faces (Armony & Sergerie, 2007; Lovén, Svärd, Ebner, Herlitz, & Fischer, 2014). In short, the brain systems that contribute to these aspects of folk psychology are reasonably well understood, and there is now consistent evidence for sex differences in the size, connectivity, and reactivity of these systems in social contexts.

There are also several brain-imaging studies of sex differences in these regions as related to competition and mate choices (e.g., Rupp et al., 2009; Zhuang, Ji, Zhao, Fan, & Li, 2017). One such study was covered in Chapter 7 of this volume: Cloutier et al. (2008) found that women and men showed activation of the nucleus accumbens—associated with feelings of pleasure and reward—when viewing attractive faces of the opposite sex, but only men showed activation of areas of the ventromedial cortex that are associated with reward-driven social behaviors and motivations. Women and men find viewing attractive faces of the opposite sex pleasurable, but men appear to be more ready to consider how they might act on these feelings. While viewing visually erotic pictures, men show stronger activation of the amygdala than do women, consistent with the sex differences in interest in casual sex and the role of visual cues in male choice (Hamann, Herman, Nolan, & Wallen, 2004).

Aleman and Swart (2008) found sex differences in the brain responses to facial expressions of disgust and contempt. Both signal disapproval and negative emotions, but the latter signals social superiority and dominance. In response to contemptuous as well as to angry facial expressions, men show stronger brain activation in the amygdala and prefrontal areas involved in social evaluations and aggression than do women (Kret & De Gelder, 2012). Women, in contrast, show stronger responses to facial expressions that signal disgust. The results are consistent with men's greater emphasis on dominance relations than women, and women's greater risk aversion than men (i.e., disgust prompts an avoidance response).

Hormones. As might be expected for evolved systems that show sex differences, prenatal and pubertal exposure to sex hormones influence some aspects of the development and function of the above described brain systems, as do circulating hormones (e.g., testosterone). Early exposure to sex hormones appears to influence later functioning of some of these regions, such as the amygdala (Ernst et al., 2007), and the entire network undergoes changes during pubertal development (Bramen et al., 2011; Fish et al., 2020; Neufang et al., 2009; Swartz, Carrasco, Wiggins, Thomason, & Monk, 2014; Vijayakumar, Pfeifer, Flournoy, Hernandez, & Dapretto, 2019). The sex differences in these areas are not consistently related to circulating hormone concentrations assessed at any one time point during adolescence, but they are related to markers of pubertal stage (e.g., pubic hair development) that reflect longer term changes in hormone concentrations (Vijayakumar, Op de Macks, Shirtcliff, & Pfeifer, 2018). During childhood, boys' and girls' amygdala shows similar rates of growth but adolescent boys' amygdala continues rapid growth until they are about 20 years old and then growth slows, whereas the growth of adolescent girls' amygdala slows when they are about 13 years old (Fish et al., 2020). Other social information processing regions of the brain diverge in girls and boys during the middle and later stages of puberty (Satterthwaite, Vandekar, et al., 2014), although the relationship between these changes and the sex differences in the processing of nonverbal social cues is not yet fully understood.

As described in Chapter 8 of this volume, there is a modest relationship between men's circulating testosterone concentrations and their status striving and reactions to provocation and challenge (Archer, 2006; Carré et al., 2017; Geniole et al., 2019; Mehta, DesJardins, van Vugt, & Josephs, 2017; Schultheiss, Wirth, & Stanton, 2004), as is found in nonhuman primates (M. N. Muller, 2017). It is not surprising that higher circulating testosterone concentrations are associated with heightened sensitivity to social threat and stronger reactivity of the amygdala when men detect potential threats (e.g., angry facial expressions; Derntl et al., 2009; Goetz et al., 2014; Radke et al., 2015; van Honk et al., 1999; Wirth & Schultheiss, 2007). High testosterone concentrations simultaneously reduce fear and disrupt the functional connectivity between the amygdala and areas of the prefrontal cortex (e.g., Brodmann Areas 10 and 12) involved in the top-down control of emotions (Bos, Hermans, Ramsey, & van Honk, 2012; Heany et al., 2018; Volman, Toni, Verhagen, & Roelofs, 2011). The combination increases the potential for reacting aggressively during confrontations and increases engagement in status-oriented risk taking, both of which are related to male–male competition.

Estradiol concentrations also influence the sensitivity of these and other social brain systems (Sacher, Okon-Singer, & Villringer, 2013; Toffoletto, Lanzenberger, Gingnell, Sundström-Poromaa, & Comasco, 2014). The earlier described relationship between estradiol and gray matter in the hippocampus contributes to women's better memory for emotional experiences, a memory advantage that peaks around the time of ovulation (Goldstein et al., 2005; Lisofsky et al., 2015; Pletzer et al., 2018). Goldstein et al. (2005) demonstrated that the influence of stressors on sensitivity of the amygdala, areas of the prefrontal cortex (e.g., Brodmann Areas 10 and 11), and the anterior cingulate cortex (Brodmann Area 24), among other brain regions, varies across women's ovulatory cycle. Specifically, exposure to stress when estrogen levels are rising and fertility is high is associated with heightened responsiveness of these brain regions to exposure to unpleasant nonverbal social cues, such as a photo of a threatening person, but dampened responsiveness during menstruation. Women are also faster at processing men's facial features when estradiol concentrations are high (Macrae, Alnwick, Milne, & Schloerscheidt, 2002). Progesterone concentrations, in contrast, may disrupt women's ability to discriminate angry and fearful facial expressions from facial expressions signaling other negative emotions, such as disgust (Derntl, Kryspin-Exner, Fernbach, Moser, & Habel, 2008).

The overall pattern is consistent with behavioral studies showing that around the time of ovulation women are generally more cautious around men they do not know (Chavanne & Gallup, 1998; Garver-Apgar et al., 2007; M. M. McDonald, Coleman, & Brindley, 2019). The increased sensitivity of these brain regions does not simply result in an increase in cautiousness, it depends on context. The increasing estradiol concentrations prior to ovulation can in fact reduce women's reactivity to some social stressors and enhance their mood and sensitivity to reward, as well as improve their top-down control of emotional reactions (Albert, Pruessner, & Newhouse, 2015; E. G. Jacobs et al., 2015; Sacher et al., 2013). Changes in the sensitivity of and connectivity among the underlying brain systems also contribute to the increase in sexual motivation that occurs during this time (see Chapter 7, this volume). The improved sensitivity to nonverbal social cues (e.g., facial expressions) and the enhanced top-down control of sexual interest and emotional state in turn are important features of women's ability to exercise their mate choices, including the avoidance of potentially predatory men.

Language

As with the previous section, the discussion of sex differences in language begins with cognition and then moves to the underlying brain systems and hormonal influences on their function.

Cognition. Girls and women have advantages in many language areas, but they do not have an advantage on all tests of verbal ability (D. F. Halpern, 2000), like the verbal section of the SAT (Hyde & Linn, 1988). This is because these types of tests are not good measures of evolved language abilities (see Chapter 14, this volume). Nor do girls and women necessarily talk more: A large-scale study of the conversations of college students revealed no sex difference in the number of words spoken throughout the day, although there was more variation among the men than among the women because some men talked quite a bit and others not so often (Mehl, Vazire, Ramírez-Esparza, Slatcher, & Pennebaker, 2007). Girls do talk more than boys during the first 2 years of life and up through adolescence, but boys (at least some of them) may talk more during adolescence (Leaper & Smith, 2004). However much they talk, men and women often talk about different things. In a study of 319 conversations across various contexts, Dahmardeh and Dunbar (2017) found that groups of Iranian women talked about personal issues (60% of conversational words) about twice as often as did groups of Iranian men (32% of words), whereas men talked about factual topics (e.g., sports, politics; 28% of words) more often than did women (17% of words). Independent of the sex differences in conversation and across most ages, sex differences are consistently found in aspects of language production, language comprehension, and the pragmatics of language (K. J. Anderson & Leaper, 1998; D. F. Halpern, 2000; Hyde & Linn, 1988; Kimura, 1999; Majeres, 2007).

Pragmatics refers to the use of language in social contexts. Here, boys and men tend to use language to attempt to assert their social dominance, a form of status display, in their interactions with other males as was illustrated by Andy in Chapter 11 of this volume:

> Boys in their groups are more likely than girls in all-girl groups to interrupt one another; use commands, threats, or boasts of authority; refuse to comply with another child's command; give information; heckle a speaker; . . . top someone else's story; or call another child names. (Maccoby, 1990, p. 516)

The magnitude of the sex difference in this social style varies with age and social context (K. J. Anderson & Leaper, 1998; Leaper & Smith, 2004). During development, the largest differences emerge when boys are in one-on-one interactions with an unfamiliar peer. In these contexts, 3 out of 5 boys use more directives ("Go do this . . .") than does the average girl, but there are no sex differences for other aspects of assertive language (e.g., making generally negative comments; Leaper & Smith, 2004). In adulthood, men use intrusive, dominance-oriented interruptions somewhat more frequently than do women, except in group settings. These are contexts in which dominance displays convey information to a wide audience (Vigil, 2009), and here almost 3 out of 4 men intrusively interrupt others more often than does the average woman as a means of displaying dominance (e.g., superior knowledge).

Language is more central to the development and maintenance of intimate and reciprocal dyadic relationships for girls and women than it is for boys and men (see Chapter 11, this volume), and this is reflected in their dialogues. Girls and women more frequently show socially enabling language, which provides equal time to all members of the group and allows other girls and women to express their thoughts and feelings. In all-girl groups, they

> are more likely than boys to express agreement with what another speaker has just said, pause to give another girl a chance to speak, or when starting a speaking turn, acknowledge a point previously made by another speaker. . . . Among girls, conversation is a more socially binding process [than among boys]. (Maccoby, 1990, p. 516)

Again, the magnitude of these differences varies with age and context (Leaper & Smith, 2004).

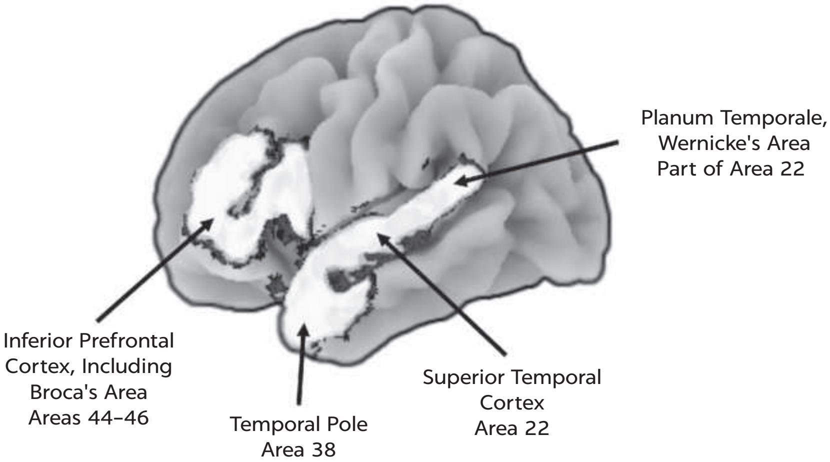
Language is also a relatively more central feature of female–female competition than it is of male–male competition. Girls' and women's aggression and social competitiveness is more likely to be expressed relationally than physically through the manipulation and disruption of the social relationships of their competitors. As described in Chapter 8 of this volume, relational aggression is conveyed in part through language, specifically gossiping about other girls, spreading lies and rumors about their sexual behavior, telling secrets, and attempting to control other girls' social behavior. The use of language in relational aggression combined with the importance of language for the development and maintenance of reciprocal same-sex relationships sets the stage for evolutionary selection to elaborate basic language competencies more in women than in men, in much the same way that physical male–male competition has resulted in larger and physically stronger men.

The cognitive and brain evidence supports this evolutionary prediction. Relative to boys and men, girls and women have advantages for many basic language-related skills, including the length and quality of utterances (e.g., in their utterances women show standard grammatical structure and a correct pronunciation of language-sounds more frequently than do men), the ease and speed of articulating complex words, the ability to generate strings of words, the ease of word learning and speed of retrieving individual words from long-term memory, and skill at remembering and discriminating basic language sounds (Asperholm, Nagar, Dekhtyar, & Herlitz, 2019; Cavaco et al., 2015; D. F. Halpern, 2000; Hampson, 1990a; Hyde & Linn, 1988; Majeres, 2007; Pauls, Petermann, & Lepach, 2013). Girls and women also show fewer pauses (e.g., "uhh" breaks) in their utterances than do boys and men (J. A. Hall, 1984) and are less likely to show language delays (Norbury et al., 2016). There are small or no sex differences in some language disorders but others affect as many as 2 to 4 times more boys (e.g., stuttering; Norbury et al., 2016; Tallal, 1991). Women also process the prosody (e.g., speech rhythm, emotional tone) of language more quickly and with less allocation of attention than do men (Schirmer & Kotz, 2003; Schirmer, Kotz, & Friederici, 2005).

The relative advantage of girls and women in these areas ranges from small to very large, depending on age and the competence being assessed. Girls' language development proceeds more quickly than that of boys, such that more than 3 out of 5 girls have more advanced language skills at 3 years old than does the average same-age boy. Many of these differences disappear over the next 2 years, although there are 40% more boys than girls among children with the poorest language skills and 40% more girls than boys among those with the best skills (Lange, Euler, & Zaretsky, 2016). For simple speech tasks, as in speed of producing or remembering related words (e.g., different types of furniture), about 2 out 3 women outperform the average man (Hyde & Linn, 1988; Pauls et al., 2013). Similarly, about 3 out of 4 women commit fewer speech errors (e.g., retrieving the wrong word) than does the average man (J. A. Hall, 1984). One study found that 9 out of 10 women outperformed the average man in the ability to discriminate basic language sounds (R. A. Block, Arnott, Quigley, & Lynch, 1989), and an analysis of sex differences across many different studies indicated that nearly 9 out of 10 men have more pauses in their utterances than does the average woman (J. A. Hall, 1984). These latter findings represent some of the largest cognitive sex differences ever documented.

Brain. The core regions associated with language comprehension and production are in the left hemisphere of the brain and are shown in Figure 12.5 (Gernsbacher & Kaschak, 2003; Geschwind & Levitsky, 1968). Other brain regions, including several in the right hemisphere, are also engaged during conversations, but these core areas are enough to illustrate sex differences in the language system. The highlighted regions include the classic Broca's area and surrounding regions that support language production and comprehension, Wernicke's area that is important for processing speech sounds, and other areas of the temporal lobe that contribute to word retrieval and language comprehension (e.g., temporal pole; Gernsbacher & Kaschak, 2003; Hurley, Bonakdarpour, Wang, & Mesulam, 2015). The basic architecture of the language system (and most other brain systems) forms prenatally (Keunen, Counsell, & Benders, 2017), and brain imaging studies confirm its specialization for processing language in the first months of life (Dehaene-Lambertz et al., 2010). As noted, Catani and Bambini (2014) proposed that the language system is integrated with brain areas in the ventral visual stream and is more broadly

FIGURE 12.5. Classic Language Areas in the Human Neocortex



The numbers next to the labels are Brodmann area map coordinates, as elaborated in Figure 12.2.

integrated with the other folk psychology systems shown in Figure 12.3. The result is the integration of language with the other folk-psychological abilities during social interactions, as part of a functional system for interacting and developing relationships with other people.

Early studies of sex differences in the language system were based on autopsied brains or people with language deficits following brain injury (e.g., aphasia; Harasty, Double, Halliday, Kril, & McRitchie, 1997). In a now classic study, Geschwind and Levitsky (1968) demonstrated that the planum temporale (which processes speech sounds) is physically larger in the left temporal cortex than the comparable area in the right cortex for about 2 out of 3 people. This asymmetry (i.e., left larger than right) is more pronounced in men than in women (Guadalupe et al., 2015; Wada, Clarke, & Hamm, 1975), and the same is found in infant boys and girls (G. Li et al., 2014). These findings and other factors, including fewer language disorders associated with damage to the left-hemisphere in women than in men (Kimura, 1987, 1999), led McGlone (1980) to conclude that language functions are differentially represented in the left- and the right-hemisphere (i.e., left and right cortex) for women and men. Specifically, many basic language skills are represented in both hemispheres for many women but are disproportionately represented in the left hemisphere for most men; these sex differences are most evident with comparisons of right-handed men and women (Annett, 1985; Hampson, 1990a).

On the basis of an analysis of autopsied brains, Harasty et al. (1997) concluded that Broca's area and the homologous area (mirror image) in the right hemisphere are 20% larger in women than men, and 30% larger for Wernicke's area (i.e., planum temporale); regions corresponding to the planum temporale and those nearby are important for identifying specific people on the basis of their voice (Formisano, De Martino, Bonte, & Goebel, 2008). In another autopsy study, Witelson, Glezer, and Kigar (1995) found that women have a higher density of neurons in the input layers of the planum temporale but not for the output layers. It cannot be known with certainty from this study, but the sex difference in the input layers might provide women with an advantage in discriminating nuances in language sounds. With control of overall brain size, C. M. Leonard et al.'s (2008) brain imaging study also revealed that the planum temporale is disproportionately larger in women than in men. In fact, women's planum temporale was large independent of overall brain size. A related study that matched men and women on brain size found that women had more gray matter along the superior temporal sulcus, including the planum temporale, than did men (Luders, Gaser, Narr, & Toga, 2009). Lotze et al. (2019) found the same for overall gray matter in the superior temporal sulcus as well as more gray matter in women's Broca's area (see also Kurth, Jancke, & Luders, 2017), but no specific differences in the planum temporale.

There may also be sex differences in the subcortical areas that support language fluency (e.g., basal ganglia) and in the architecture and volume of the white matter tracts that integrate Broca's and Wernicke's area within the left hemisphere and with the right-hemisphere homologues (Hagmann et al., 2006; Herting et al., 2014; Szeszko et al., 2003). Gong et al. (2009) found tighter clustering of brain networks in several regions of the left hemisphere in women than in men, including two regions that support language comprehension. Brain imaging studies suggest that women and men do not differ in the basic regions that support the processing of simple language sounds and words (Sommer, Aleman, Bouma, & Kahn, 2004). However, more women than men show parallel activation of the homologues of Broca's and Wernicke's areas in the right hemisphere during some more complex aspects of language processing (Kansaku, Yamaura, & Kitazawa, 2000) and possibly with the integration of speech with the prosody and emotional tone of what is being said (Schirmer & Kotz, 2006).

Although much remains to be determined about sex differences in the language system, especially during development (Etchell et al., 2018), the overall results are consistent with the greater evolutionary elaboration of this system in women than in men. The finding that some of these areas are as large or larger in women than those in men, even without control of the sex difference in brain size, indicates significant advantages to women with enhanced language competencies. The dynamics of female–female relational aggression and the use of language to maintain same-sex relationships are strong candidates for the corresponding selection pressures.

Hormones. As with nonverbal social abilities, sex differences in language competencies are influenced by a combination of early and pubertal exposure to sex hormones, as well as by circulating hormones (e.g., O'Connor, Archer, Hair, & Wu, 2001; Thilers, Macdonald, & Herlitz, 2006). It has been hypothesized that prenatal exposure to testosterone modifies the development of the brain systems that will later support language competencies (Geschwind &

Galaburda, 1987; Witelson, 1991), and this might be the case. The basic architecture of the language network forms prenatally and exposure to high prenatal and early postnatal testosterone concentrations may slow boys' language development (see Chapter 10, this volume; Hines, Spencer, et al., 2016; Lutchmaya, Baron-Cohen, & Raggatt, 2001). Early exposure to testosterone may also adversely influence a wider range of social-cognitive (folk psychology) competencies (Baron-Cohen, Knickmeyer, & Belmonte, 2005).

Prenatal testosterone exposure and circulating testosterone concentrations in adulthood may result in less interaction (through the corpus callosum) between the two hemispheres during language processing, which is more typical among boys and men than girls and women (Grimshaw, Bryden, & Finegan, 1995; Hampson, 2016; Papadatou-Pastou & Martin, 2017). Moreover, Lombardo et al. (2012) found that higher prenatal testosterone concentrations were associated with lower gray matter volumes for boys' Broca's, Wernicke's, and other language areas. There are also sex differences in the rate of maturation of the brain systems that support language during puberty, and these appear to contribute to girls' advantage in some areas of language during early adolescence (Porter, Collins, Muetzel, Lim, & Luciana, 2011). These areas remain sensitive to circulating testosterone concentrations into adulthood (Hahn et al., 2016; A. V. Witte, Savli, Holik, Kasper, & Lanzenberger, 2010). Hahn et al. (2016), for instance, found that testosterone treatment of female-to-male transsexuals resulted in gray matter reductions in Broca's and Wernicke's areas and enhanced white matter connectivity between them.

The latter might be due to a general effect of testosterone on white matter development (Bielecki et al., 2016), but testosterone treatments are sometimes associated with reductions in language competencies in female-to-male transsexuals (Van Goozen, Cohen-Kettenis, Gooren, Frijda, & Van de Poll, 1994, 1995). Following 3 months of hormonal treatments, Van Goozen and colleagues (1994, 1995) found that female-to-male transsexuals scored 30% to 34% lower on two measures of verbal fluency, one assessing the ability to generate words and the other the ability to generate sentences. Male-to-female transsexuals in contrast take estrogens and drugs that suppress the release of male hormones. Their performance on the word fluency test decreased slightly (6%) but improved significantly (22%) for the sentence fluency test. These results are intriguing and consistent with a hormonal influence on language competencies, but need to be considered preliminary because much remains to be determined regarding the influence of hormonal treatments on the brain and cognition of transsexual individuals (Gómez-Gil et al., 2009; Guillamon, Junque, & Gómez-Gil, 2016; E. S. Smith, Junger, Derntl, & Habel, 2015).

In any case, there are also studies of the relation between language competencies and hormonal fluctuations across the ovulatory cycle. Returning to Figure 7.3 (see Chapter 7, this volume), estradiol concentrations are at their lowest during menstruation, increase rapidly, peak a few days prior to ovulation, and then decline rapidly. Following ovulation, estradiol and progesterone concentrations increase and then decline just prior to the onset of menstruation. Despite these well-documented hormonal changes, documenting a relationship between these changes and language competencies is not straightforward. This is because estradiol can have general effects on attentional control and working memory that provide women with an advantage on some language-based memory tasks but may not be specifically related to the language system. This advantage will fluctuate across the ovulatory cycle, making comparisons of women's and men's competencies a moving target (Hjelmervik et al., 2012).

Despite these complications, there is evidence that hormonal changes across the ovulatory cycle can influence aspects of women's language competencies (Hampson, 1990a; Hodgetts, Weis, & Hausmann, 2015). For instance, Hampson (1990a, 1990b) found that the speed of articulating words is at its highest when estradiol and progesterone concentrations are relatively high, and Hodgetts et al. (2015) found that high estradiol concentrations are associated with enhanced bilateral (engaging both hemispheres) processing of language sounds. Compared with these hormones, women's circulating testosterone concentrations are less variable across the ovulatory cycle but also appear to influence their fluency with language. Thilers et al. (2006) found that higher concentrations of circulating testosterone are associated with lower verbal fluency (speed of generating words) in women, and Schattmann and Sherwin (2007) found that reducing women's testosterone concentrations improved their verbal fluency. However, a relationship between hormone concentrations and women's language abilities is not always found (Mordecai, Rubin, & Maki, 2008), possibly because these tend to be small-scale studies and the overall effects are generally small when they are found.

Prenatal and pubertal development of at least some aspects of the language system are influenced by exposure to testosterone (e.g., suppressing development in boys' language system), and these in turn contribute to girls' and women's advantages in many associated competencies (e.g., verbal fluency, discrimination of language sounds). Sex differences in these competencies also appear to be influenced by circulating testosterone and estradiol (and perhaps progesterone) concentrations in adulthood, but these effects appear to be smaller than those associated with prenatal and pubertal exposure to these same hormones.

Theory of Mind and Person Schema

Theory of mind and person schema are covered together, because person schema is the store of knowledge (e.g., personality, warmth) about familiar others that is built, in part, through theory of mind and because this knowledge will influence an individual's inferences about familiar others' thoughts and feelings in specific contexts. This section begins with a review of sex differences in these domains followed by a combined brain and hormones section.

Cognition. Recall that girls typically express more empathy for the distress of other people than do boys. The previous section Nonverbal Behavior and Facial Expressions focused on girl's and women's advantage in the ability to "read" corresponding social cues including a sensitivity to the emotions signaled by others' facial expressions. The empathetic responses may or may not indicate an understanding of the internal state of the distressed individual, and certainly does not for infant girls who cry when hearing the distress of other infants (Simner, 1971). Likewise, many responses to facial expressions and other social cues occur rapidly and without a conscious awareness of the internal state of the person sending the signals (Öhman, 2002).

Many of these automatic responses to others' social signals are components of an evolutionarily old empathy system that is found in social primates and especially in females of these species (Christov-Moore et al., 2014). Theory of mind goes at least one step beyond these sex differences and represents the critical ability to make conscious inferences about the intentions and beliefs of other people and to infer whether the emotions signaled by facial expressions or other cues are an accurate reflection of the actual feelings of the individual (Baron-Cohen, 1995; Leslie, Friedman, & German, 2004).

Girls and women have advantages in most other individual-level social competencies, and we might then expect them to have an advantage for least some aspects of theory of mind (Baron-Cohen, 2003). Moreover, girls and women might be particularly skilled when it comes to understanding other girls and women and especially as this relates to these others' thoughts, intentions, and feelings about significant relationships. This expectation follows from their use of relational aggression in the context of female–female competition and the importance of close dyadic relationships as a source of social support. Boys and especially men, in contrast, might be more focused on competitors' thoughts and intentions as they relate to larger-scale groups and politics. Rather than a focus on what the competitor is intending with respect to a few specific relationships, the focus is on how a potential competitor intends to organize larger, competitive groups or convince many others to vote for them in an election, for instance. These predictions follow from the discussion of sex differences in how men and women prefer to organize their social worlds (see Chapter 9, this volume).

Another way to think about this is in terms of whether theory of mind is being used in the context of specific relationships or the behavior of a specific individual, or in terms of more abstract chess-like social strategizing. The latter might involve making inferences about how multiple individuals in a competing group might interpret a potential threat or opportunity and how they might organize themselves in response, or how groups of unrelated individuals might organize themselves in mutually beneficial ways. These types of coordinated actions often require inferences about the intentions and likely behaviors of groups of interacting people (e.g., level of cooperation) and are assessed by behavioral economists using social strategy games. There is much to be learned about how people interpret these situations, but men often (although not always) do better than women in this type of social strategizing (Colman, Pulford, & Krockow, 2018; Cubel & Sanchez-Pages, 2017; Dittrich & Leipold, 2014; Herbst, Dotan, & Stöhr, 2017).

Most psychological studies of theory of mind, in contrast, have largely focused on individuals' ability to make inferences about the thoughts and feelings of one other person (e.g., a friend). Early studies in this area suggested a small advantage for girls and women or no sex differences (Bosacki, 2000; Bosacki & Astington, 1999; Charman, Ruffman, & Clements, 2002; Lucariello, Durand, & Yarnell, 2007; S. Walker, 2005) and occasionally an advantage for men (Russell, Tchanturia, Rahman, & Schmidt, 2007). More recent studies using more complex tasks indicate an advantage for girls and women in many contexts (Benenson et al., 2013; Kirkland, Peterson, Baker, Miller, & Pulos, 2013). In one of the more comprehensive of the developmental studies, Banerjee (1997) administered two theory-of-mind tests to 3- to 5-year-olds. The first assessed how well the children understood that the expression of social cues (e.g., facial expressions) could differ from the individual's actual feelings; children who do not understand this distinction believe that if another individual looks happy then he or she must feel happy. The second test assessed their understanding of social display rules, which included emotion signals that should be suppressed in certain situations so as not to hurt another person's feelings. Both of these competencies were assessed by presenting the child with a series of stories in which the character was motivated to hide his or her emotional state, as illustrated by the following:

> [Diana has a brother named Bill. Bill was not very nice today, so Diana] wants to hide his favorite toy. That's what she does—she hides his favorite toy. When Bill comes home, he can't find his toy anywhere. Diana is really happy because Bill can't find his toy anywhere. But Diana doesn't want Bill to see how she feels, because then Bill will shout at her. So Diana tries to hide how she feels. (Banerjee, 1997, p. 115)

After hearing each story, the children were presented with a series of facial drawings depicting happy, sad, and neutral expressions and were asked "Show me the picture for how Diana really feels. How does Diana really feel when Bill can't find his favorite toy?" (Banerjee, 1997, p. 116). After this, they were asked to point to the picture for how Diana was trying to look. A similar procedure was used to assess their understanding of display rules. The overall results revealed that relative to boys, young girls better understand that others' social cues can differ from their actual feelings. In terms of display rules girls "seem more attuned to the social context" (Banerjee, 1997, p. 127) than boys. Charman et al. (2002) replicated Banerjee's findings of an advantage for young girls but also found that boys caught up by the time they were 6 years old, at least for basic theory of mind skills. Using a more complex task, Bosacki (2000; Bosacki & Astington, 1999) found that 3 out of 4 12-year-old girls were more skilled than the average same-age boy at making inferences about the thoughts, feelings, and social perspective of their peers.

Other studies suggest that girls and boys use their theory of mind skills in different ways in the context of their peer relationships (Bosacki & Astington, 1999; Dunn, Cutting, & Demetriou, 2000). S. Walker (2005) found that young girls with good theory of mind skills engaged in more prosocial behavior (e.g., cooperating, sharing) than did less competent girls or boys in general. Boys with good theory of mind skills engaged in more aggressive, disruptive, and attention seeking behaviors than did less competent boys or girls in general.

Dunn et al. (2000) found that girls were more likely than boys to focus on the internal feelings of friends during potential conflicts of interest, whereas boys were more likely to focus on emotionally neutral mental states (e.g., what the friend was thinking). In other words, it seems that girls use of their theory of mind and general social skills to form cooperative relationships, and boys use it to bring attention to themselves and in doing so gain in peer-group status. These sex differences mirror the adult sex differences in social and political orientation described in Chapter 9 of this volume.

Theory of mind has not been directly studied in the context of relational aggression but Benenson et al.'s (2013) studies get close. In one study associated with cooperative behavior among a group of people, they found that women are more sensitive to social cues that signaled risk of social exclusion than are men. The result suggested that women are quicker than men to assume that others who are not being fully cooperative intend to exclude them. In a follow-up study, they found that women had higher heart rate increases, indicating a stronger stress response, when reading scenarios of social exclusion, in keeping with higher risks and costs of social exclusion for women than for men (Benenson, Markovits, Thompson, & Wrangham, 2011). Recall that boys' and men's groups are larger than those of girls and women and more easily incorporate other members (see Chapter 11, this volume). Girls' and women's dyadic relationships are an important source of social support and are more exclusive than those of boys and men, and there is more competition for relationships with best friends among girls and women. One feature of relational aggression is the exclusion of potential competitors from the social group. In other words, women's competition for mates and best friends involves excluding potential competitors from access to these relationships and creates pressures for the evolution of biases that reduce this risk.

The person schema is focused on knowledge about specific others, rather than the more general ability to make inferences about the internal states of others. As described in Chapter 12 of this volume, girls' friendships involve more frequent discussions of social and personal problems than do boys' friendships (J. Parker & Asher, 1993; Rose & Asher, 2017), and thus girls often know more personal information about their friends than do boys (Markovits, Benenson, & Dolenszky, 2001; Swenson & Rose, 2003). This store of personal knowledge contributes to girls' and women's ability to maintain these intimate relationships to better infer the sources of their friends' interpersonal stressors and provide better support to them. Should the relationship turn sour, this personal information is often used in the context of relational aggression. Knowledge about the feelings and vulnerability of one's friend is less central to boys' relationships, because this is not information that is directly relevant to male–male competition in the same way as are readily observable physical, athletic, and leadership traits.

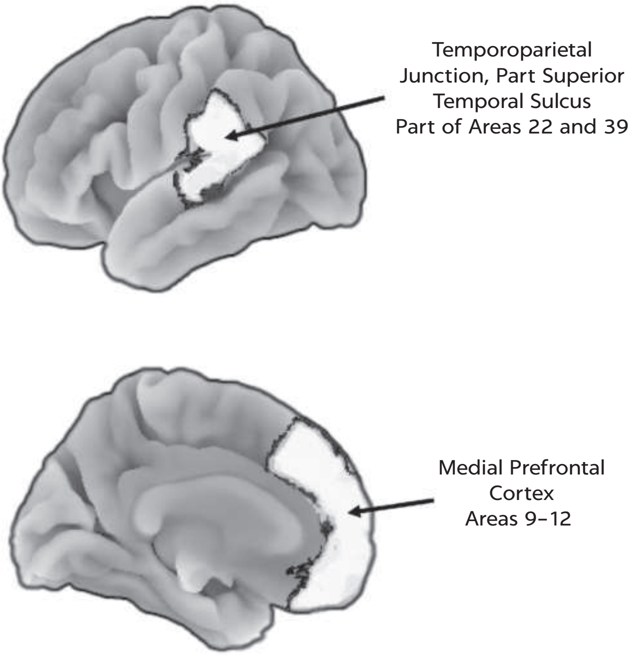
Brain and hormones. The empathy system that supports sensitivity to the social cues of others (e.g., for vocalizations) is likely at least part of the evolutionary foundation for theory of mind (Christov-Moore et al., 2014). The empathy system includes mirror neurons that have the intriguing property of firing when an individual engages in a specific behavior, such as making a facial expression and firing in much the same way when observing that same behavior in others. So, observing someone with a sad facial expression triggers brain regions that overlap with those associated with feeling sad. The result is "feeling their pain," which is critical for emotional empathy. These neurons also respond to the body movements of others and help to predict their behavioral intentions (Van Overwalle & Baetens, 2009). Theory of mind involves additional cognitive competencies and brain regions that often interact with but are separate from those that support the mirror neuron system. The theory of mind system enables an explicit representation (e.g., "She looks sad") and interpretation of the emotion or other social cues of others (LeDoux & Brown, 2017), as well as more complex social judgments (e.g., regarding the morality of others' actions; Van Overwalle & Baetens, 2009).

As with other complex folk abilities, there is much to be resolved about the details of the brain and cognitive systems that support theory of mind, but for our purposes they refer to the formation of mental representations of others' minds, especially their thoughts and feelings (Gallagher & Frith, 2003; Leslie et al., 2004; Schaafsma, Pfaff, Spunt, & Adolphs, 2015). The specific brain regions that are engaged when thinking about others' minds can vary from one goal (e.g., understanding others' thoughts) to another (e.g., understanding others' emotions; Schaafsma et al., 2015), but nevertheless there are some regions that are common across these goals (Carrington & Bailey, 2009; Van Overwalle & Baetens, 2009).

The most commonly engaged regions are shown in Figure 12.6 and include the temporoparietal junction and medial (toward center) prefrontal cortex in both hemispheres. The temporoparietal junction is sensitive to spatial orientation, including the tracking of others' eye gaze, and overlaps with part of the language cortex in the left hemisphere. The integration may be important for verbally stating others' intentions. The temporoparietal junction in the right hemisphere supports a more intuitive or "gut reaction" sense of others' intentions (Filmer, Fox, & Dux, 2019). The medial prefrontal areas are important for thinking about and interpreting others' intentions and making any associated decisions. Other areas, like parts of the default mode network, are sometimes also engaged in theory of mind and may be important for integrating others' intentions with one's best interest.

Functional and anatomical sex differences in the brain regions supporting the mirror neuron and theory of mind systems have not been extensively studied, but there is evidence for such differences (Y. Cheng et al., 2009; Chou, Cheng, Chen, Lin, & Chu, 2011; de Lacy, McCauley, Kutz, & Calhoun, 2019b; Schulte-Rüther, Markowitsch, Shah, Fink, & Piefke, 2008; Takeuchi et al., 2013). R. Wright et al. (2018) found that women are more sensitive to nuances in their own emotional states than are men. Their enhanced self-awareness contributes to their better understanding of the emotional state of others, consistent with mirror neurons that would engage similar brain regions for evaluations of the self and others. Controlling for overall brain

FIGURE 12.6. Key Brain Areas Engaged in Theory of Mind



The top figure is the lateral (outer side surface) view of the brain and the bottom is the medial (center) view of the brain. The numbers next to the labels are Brodmann area map coordinates, as elaborated in Figure 12.2.

volume, women have more gray matter volumes than do men in several core areas of the mirror neuron and theory of mind systems (Y. Cheng et al., 2009; Feis, Brodersen, von Cramon, Luders, & Tittgemeyer, 2013). These include portions of the temporoparietal junction and the medial prefrontal cortex of the right hemisphere. Takeuchi et al. (2013) found that women with higher white matter volume in the right temporoparietal junction had better theory of mind skills than did other women, but there was no such relation among men (see also Yamasue et al., 2008).

When processing emotion-laden facial expressions, Schulte-Rüther et al. (2008) found stronger activation in women than men in the right prefrontal cortex, whereas men showed stronger activation in the left temporoparietal junction. The latter is associated with separation of self from others (among other things), suggesting more emotional distancing in men than in women, which would be helpful for abstract social strategizing. In other situations, like trying to understand others' beliefs rather than feelings, women also show more medial prefrontal activation and more engagement of the left temporoparietal region than do men (C. K. Frank, Baron-Cohen, & Ganzel, 2015). In addition, women have proportionally (controlling for overall brain volume) more gray matter in the medial prefrontal areas associated with theory of mind and social decision making (Goldstein et al., 2001; Gur et al., 2002; J. L. Wood, Heitmiller, et al., 2008), more white matter integration among areas involved in social-emotional processing (Tunç et al., 2016), and mild electrical stimulation of these areas enhances women's but not men's theory of mind (Adenzato et al., 2017). These areas in the left hemisphere appear to be more critical than those in the right hemisphere for women's social-emotional functioning, whereas men's functioning is more dependent on the right hemisphere (Tranel et al., 2005).

Although much remains to be learned, there is evidence for early and pubertal hormonal influences on the development and function of the mirror neuron and theory of mind systems, as well as an influence of circulating hormones (DeSoto, Bumgardner, Close, & Geary, 2007; van Honk et al., 2011). Prenatal exposure to testosterone appears to delay boys' development of theory of mind (Chapman et al., 2006) and is associated with less sensitive theory of mind competencies in adulthood (Khorashad et al., 2018; see Chapter 10, this volume). Administering testosterone to women results in lower empathy and reduced theory of mind competencies, especially if they had higher than typical prenatal exposure to testosterone (Hermans, Putman, & van Honk, 2006; van Honk et al., 2011). These effects might be due to a testosterone-related suppression of the mirror neuron system and less functional connectivity within the theory of mind system (Bos et al., 2016; Hermans et al., 2006). There is also intriguing but preliminary evidence that some aspects of theory of mind might be directly influenced by X-chromosome genes, independent of sex hormones (Strandqvist et al., 2018).

In all, these studies provide an early but intriguing glimpse into the brain and hormonal systems that contribute to girls' and women's greater sensitivity to the emotional states of others and the ability to consciously think about these states. These abilities provide girls and women with advantages in the use of relational aggression and the formation of intimate same-sex relationships. The associated sex differences, however, are not simply due to elaborations of girls' and women's abilities in these areas. Exposure to testosterone appears to actively suppress the development and functioning of these same brain systems in adolescent boys and men, at least in the context of one-on-one relationships, in keeping with the idea that a lack of empathy provides some advantages in the context of male–male competition. The latter might have also contributed to men's apparent advantage in abstract social strategizing (e.g., strategy for raiding another village), but the hormonal and brain systems that contribute to this sex difference are not currently known.

Group

Compared with individual-level social competencies, much less is known about sex differences in the cognitive and brain systems that underlie the parsing of the social world into kin, ingroup and outgroups, and ideology.

Kin

Preferential treatment of kin is ubiquitous across species and the same is expected of women and men (Hames, 2016; W. D. Hamilton, 1964). The important question is whether there are sex differences in the pattern of kin preferences. When viewed from the perspective of the sex differences in the potential rate of reproduction and the cost–benefit trade-offs of focusing on mating or on parenting (see Chapter 3, this volume), it is not surprising that women invest more in their children than do men. A less obvious prediction is that men will show a bias for male kin, especially when their group is engaged in frequent intergroup conflict.

In societies characterized by intense physical male–male competition and frequent intergroup conflict, the activities of men tend to be relatively more centered on relationships among adult-male kin than on relationships with their wives and children (Draper & Harpending, 1988; Pasternak, Ember, & Ember, 1997). In fact, relatively cohesive male kin-groups are often found in traditional societies that are frequently engaged in intergroup conflict, although this pattern is most common in economically mid-level societies, such as agricultural ones without a central government (Pasternak et al., 1997). The reader will recall that the population genetics research touched on in Chapter 8 of this volume provides further evidence for intense competition among male kin-groups during our evolutionary history (e.g., Zeng, Aw, & Feldman, 2018; Zerjal et al., 2003).

Of course, as coalition size increases men have to cooperate with more distantly related kin and often with male kin through marriage (Macfarlan et al., 2018; Mathew & Boyd, 2011). In societies with ecologically or socially imposed monogamy, in contrast, men tend to focus more on their wives and children than on the larger network of male kin (Flinn & Low, 1986). This is because central governments and professional police forces suppress male-on-male violence (Daly & Wilson, 1988b) and disrupt kin-based coalitional competition, and because the reproductive benefits of violent competition are reduced when men's opportunity for polygyny is suppressed (Henrich, Boyd, & Richerson, 2012).

The perceptual and cognitive systems that enable people to discriminate kin from nonkin are not well understood but appear to be influenced by experiences during development and by physical similarity (Kurland & Gaulin, 2005). People avoid marrying others with whom they grow up and thus avoid inbreeding risks (Tal & Lieberman, 2007). When processing the faces of unfamiliar others (e.g., different race), the amygdala and fear are often quickly and automatically triggered, resulting in caution with or avoidance of these others (Wheeler & Fiske, 2005). In other words, we have brain systems and emotional states that alert us when we see people that differ from those who are familiar to us. During human evolution, the most familiar people would have been kin. The preferential treatment of kin may also be influenced by feelings of emotional closeness (Korchmaros & Kenny, 2001) and the expectation that kin are likely to help during times of need (Kruger, 2003). In any case, the most consistent sex difference is in terms of investment in children, with the strength of men's bias toward male relatives varying with risk of group-level conflict in the local area.

Ingroups and Outgroups

When it comes to the cognitive and behavioral processes that support ingroup and outgroup dynamics, there are probably more similarities than differences between boys and girls and men and women (L. E. Davis, Cheng, & Strube, 1996; Rogers, Hennigan, Bowman, & Miller, 1984; Towson, Lerner, & de Carufel, 1981). Individuals of both sexes readily form ingroups and outgroups and make judgments about ingroup members that are more favorable than those about members of outgroups. Sex differences in some aspects of these dynamics follow from an evolutionary history of coalitional male–male competition (see Chapter 8, this volume) and are predicted to become exaggerated during periods of intergroup conflict. The more theoretically important findings are sex differences in the level of bias against and desire to dominate outgroups (Sidanius & Ekehammar, 1983; Sidanius, Pratto, & Mitchell, 1994) and the level of intragroup cooperation during competitive situations (Balliet, Li, Macfarlan, & Van Vugt, 2011; Gaertner & Insko, 2000; Van Vugt, De Cremer, & Janssen, 2007).

In the context of between-group competition (e.g., competitive sports), boys form larger same-sex groups than do girls (see Chapter 11, this volume). One dynamic is that boys' groups are better integrated than are girls' groups (J. G. Parker & Seal, 1996) and are more accessible to boys who might otherwise be considered as members of an outgroup (Benenson, 2014). Rogers et al. (1984) showed that under some conditions Black boys and White boys are more likely to play together than are Black girls and White girls, who showed a strong tendency to self-segregate into same-race groups. The greater integration of boys' groups was largely due to competitive play, "because Black and White boys need each other to form complete sports teams" (Rogers et al., 1984, p. 215). Even so, the formation of mixed-race teams is to compete against another group of boys, who, by definition, form an outgroup. The mixed-race permeability of boys' groups in the service of outgroup competition should be considered against the backdrop of stronger racism—when mixed-race cooperation is not necessary—among men than among women (Sidanius & Ekehammar, 1983).

Once competitive groups have formed, boys and men show higher levels of ingroup reciprocal cooperation than do girls and women (Gaertner & Insko, 2000; Savin-Williams, 1987; Van Vugt et al., 2007) and exert more social pressure on ingroup members to conform to group-sanctioned activities. Boys and girls exert this pressure on their same-sex peers, but it is relatively stronger within boys' groups than within girls' groups. Boys, for instance, show a greater concern for and teasing about "cooties" than do girls (Maccoby, 1988). Adults' attitudes toward homosexuals show the same sex difference. Men and women have similar attitudes toward lesbians, but "men's attitudes toward homosexuality are particularly negative when the target is a gay man rather than a lesbian" (Whitley & Kite, 1995, p. 147); about 7 out of 10 men had more negative attitudes toward gay men than did the average woman. A similar pattern is found with the Ache (Paraguay; K. Hill & Hurtado, 1996). In this society, men who take on a feminine role and behaviors are called *panegi* (*pane* means unlucky in hunting):

> Men who are *panegi* generally do not hunt, but instead collect plant resources and insect larvae. They weave baskets, mats . . . and other female handicrafts. [These men] were low status and not always treated well. They were forced to do menial chores . . . and were also often the butt of jokes and off-color sexual humor. (K. Hill & Hurtado, 1996, pp. 276–277)

Gay men who are feminine in their behaviors may be discriminated against by other men because of an implicit assumption that these gay men's contributions to male–male coalitional competition will be limited, and recent evidence suggests that this is indeed the case (Winegard, Reynolds, Baumeister, & Plant, 2016). These results further suggest that the decline in physical male–male competition and the creation of social and economic niches that do not require physical prowess should result in the gradual decline of this bias. Historical changes in attitudes toward homosexuality in wealthy and highly developed nations show just such a decline (T. W. Smith, Son, & Kim, 2014).

The results from several experimental studies also reveal sex differences in the dynamics of ingroup and outgroup relationships, particularly when these dynamics involve direct competition or the distribution of resources (L. E. Davis et al., 1996; Van Vugt et al., 2007; Van Vugt & Spisak, 2008). In one study, fifth and sixth graders watched videos of boys and girls working in low- and high-competition settings (Towson et al., 1981). In the high-competition setting, the workers were described as being members of a boys' team or a girls' team, thus creating a same-sex ingroup and an opposite-sex outgroup. The task was to determine each worker's pay. In the low-competition setting, boys and girls paid the more productive worker more than her or his less productive peer (60% vs. 40%), regardless of the workers' sex. When the more productive worker was a girl in the high-competition setting, boys paid her significantly less than when she was the more productive worker in the low-competition setting. Girls, in contrast, showed the opposite pattern. Girls paid productive boys the same amount in the high- and low-competition settings, but substantially favored productive girls in the high-competition setting. In short, during periods of competition, boys discriminated against the outgroup, whereas girls boosted the ingroup.

L. E. Davis et al. (1996) studied the behavior of same-sex groups that differed in racial composition, thus implicitly creating a same-race ingroup and other-race outgroup. Each group was composed of four individuals (two White and two Black, or three of one race and one of the other). Each group was provided with a brief description of 10 people (no information was provided on race) and were then "given the hypothetical scenario that war had been declared and that an existing fallout shelter could support only six individuals. Thus, four individuals must be excluded from the shelter so that six could live to rebuild a new society" (L. E. Davis et al., 1996, p. 159). The task was to reach a consensus about which four people would be excluded from the shelter. The contentiousness allowed for the testing of several hypotheses about group dynamics. One of which is that intergroup tensions increase when ingroups and outgroups are of equal size, and this was the case. Men and women rated the group atmosphere as relatively cold and unpleasant for groups that contained two individuals of each race. For women, however, the racial composition of the group did not influence their overall satisfaction with the final decision, as most women were satisfied. Men's highest levels of satisfaction were found for groups where one race was the majority, and their lowest levels of satisfaction were found when the group consisted of two individuals from each race. The pattern suggests that women were able to reach a consensus that was supported by all of the group members, regardless of group composition. Men reached a consensus in groups where the ingroup had a numerical majority but did not when the ingroup and outgroup were equal in size.

Sidanius and his colleagues (Sidanius, Pratto, & Bobo, 1994; Sidanius, Pratto, & Mitchell, 1994) have repeatedly demonstrated that men—across ethnic group, social class, education level, religion, nationality, and political party—have a stronger group-related social dominance orientation than do women (Ho et al., 2015; I. C. Lee, Pratto, & Johnson, 2011). Men are more likely than women to view groups, however defined (e.g., nationality, ethnically, or arbitrarily), as hierarchically arranged in terms of social status and distribution of resources and to endorse policies (e.g., military spending) that will strengthen the ingroup vis-à-vis the competitive abilities of other groups. Across these studies, about 2 out of 3 men endorsed group-based inequality more strongly than did the average woman. Moreover, individual differences in men's social dominance orientation are weakly related to their desire for ingroup dominance (Pratto, Sidanius, Stallworth, & Malle, 1994). Even men who are low on the ingroup status hierarchy can have a strong identification with their ingroup and strong attitudes about the hierarchical position of their group relative to other groups.

In sum, individuals of both sexes form ingroups and outgroups and generally favor ingroup members over outgroup members. However, relative to girls and women, boys and men form larger ingroups, exert more intense social pressures on ingroup members to adhere to group ideologies, are more cooperative within the ingroup during times of intergroup competition, and regardless of their ingroup status have more hierarchical and prejudicial attitudes about intergroup relationships. All of these sex differences result in cohesive all-male groups and groups that are easily provoked into coalition-based competition, in keeping with the pattern of male–male competition found in traditional societies and early empires.

Brain and hormones. There are numerous studies of the brain regions that are engaged when people process information about members of ingroups and outgroups (L. T. Harris & Fiske, 2006; Krautheim et al., 2019; Lin, Qu, & Telzer, 2018; Van Bavel, Packer, & Cunningham, 2008; Wheeler & Fiske, 2005). Depending on the dynamic, these include aspects of the mirror neuron system that supports emotional empathy—it is more sensitive when engaging with the ingroup—as well as the theory of mind and emotion-processing regions (e.g., amygdala, insula), with positive emotions and engagement of theory of mind regions associated with identification with the ingroup. The processing of information (e.g., faces) about outgroup members in contrast is associated with a dampening of the sensitivity of the mirror neuron system (reduced empathy) and increased sensitivity of the brain regions associated with fear and disgust. When these responses are combined with little or no activation of the prefrontal cortex or activation of areas associated with status judgments (low for outgroup members), the result can be an emotional dehumanization of the outgroup (Bruneau, Jacoby, Kteily, & Saxe, 2018; L. T. Harris & Fiske, 2006).

Based on the history of male-on-male violence described in Chapter 8, this volume, it would be expected that these dehumanization mechanisms are more easily engaged in men than women, at least in contexts with ongoing and intense intergroup rivalries. Unfortunately, we do not know if there are sex differences in the pattern of brain activation when processing outgroup information, or whether any such differences are moderated by levels of intergroup competition. However, we do know that the dehumanization of competitors seems to occur more readily for individuals who are high in social dominance orientation (Haslam & Stratemeyer, 2016), and these are typically men. This does not mean that women are immune to the process. Arnocky et al. (2019) found that women and especially competitive women tended to dehumanize and act aggressively toward other women who dressed in a sexually provocative manner. Still, it is very likely that the threshold for dehumanizing others is lower for men than for women.

Men's testosterone concentrations can influence and be influenced by group-level competition (Diekhof, Wittmer, & Reimers, 2014; Flinn, Ponzi, & Muehlenbein, 2012; Oxford, Ponzi, & Geary, 2010; see Chapter 8, this volume). These hormonal responses are related to the intensity of men's identification with their group, defense of their "home field," their contributions to the groups' competitiveness, and competitive outcomes (P. C. Bernhardt, Dabbs, Fielden, & Lutter, 1998; P. B. Gray, McHale, & Carré, 2017; Trumble et al., 2012). In other words, the hormonal mechanisms that have evolved to support one-on-one male–male competition in primates and other species (M. N. Muller, 2017; Wingfield, Hegner, Dufty, & Ball, 1990) are well integrated with the cognitive and behavioral aspects of men's coalitional competition. We also know that high concentrations of circulating testosterone can change the sensitivity of many of the brain regions associated with the formation of ingroups and outgroups and involved in dehumanization (Bos et al., 2016; Hermans et al., 2006). However, these and other potential hormonal influences on sex differences in the brain systems that are engaged during ingroup and outgroup dynamics are not well understood.

Group Schema

As described for the Turkana (East Africa) in Chapter 8 of this volume, kinship influences the formation of coalitions for small-scale raids on other groups but larger-scale raids require the cooperation of more distantly related or unrelated men (Mathew & Boyd, 2011). As described in Chapter 9 of this volume, larger groups have a competitive advantage over smaller ones and this in turn almost certainly contributed to the evolution of the human bias to form ingroups and outgroups on the basis of social identification, which is represented by Group Schema in Figure 12.3. This section elaborates on these issues with additional discussion of the processes involved in social identification and any associated sex differences.

Social–psychological studies have yielded a wealth of information on the processes that contribute to group and social identification (Fiske, 2002; Hewstone, Rubin, & Willis, 2002). Social identification theory refers to the categorizing of one's self and others on the basis of a personal identification with a socially defined category (e.g., nationality, religion; Atran & Ginges, 2012; Tajfel & Turner, 1979). Self-evaluations and evaluation of others, as well as the ingroup and outgroup biases described previously, are influenced by the social groups (e.g., sex, race, nationality) that contribute to one's identity. Some scholars have argued that the sex differences in social dominance orientation actually reflect social identification processes. More precisely, the extent to which men and women identify with the social groups of male and female, respectively, and their attitudes toward perceived inequalities and social privileges of these two groups (e.g., M. S. Wilson & Liu, 2003). In this view, the sex difference in social dominance is due to identification with one's sex, the sex differences in cultural success (see Chapter 14, this volume), and men's wish to maintain this advantage rather than an evolutionary history of coalitional competition.

From an evolutionary perspective, social dominance orientation and social identity theory are not competing but rather complementary processes. In contexts with ongoing intergroup tensions and overt conflict, men are predicted to identify with male-based social-competitive groups and to organize these groups hierarchically. If this hypothesis is correct, then social identification with competitive groups (e.g., a sports team or nationality) should be more easily instantiated in men than women, and men should show a stronger tendency to organize themselves around these social-competitive identities than women. Nevertheless, there are probably more similarities than differences in women's and men's social identification processes.

Under conditions that implicitly or explicitly provide a reminder of one's mortality (e.g., being exposed to issues associated with death), women and men show a marked increase in their endorsement of the ingroup's social ideology and more negative attitudes toward people who question this ideology (Arndt, Greenberg, Pyszczynski, & Solomon, 1997). These findings, however, were confounded by the use of the ingroup category (e.g., *America*) along with the mortality cue manipulation. In a series of experiments in which mortality risk was explicitly (e.g., writing about one's death) or implicitly (e.g., saying words like *funeral*) presented without reference to an ingroup social category, Arndt, Greenberg, and Cook (2002) found that men and women differ in their subsequent thoughts. Men thought more about group-related ideologies (e.g., nationality), whereas women thought more about romantic relationships. Men's cognition under threat is certainly consistent with a bias to rally around an ideology-base group, but many questions remain to be answered.

CONCLUSION

There is no question that men and women differ in terms of brain size and organization and in terms of the corresponding pattern of cognitive competencies. Serious debate is now focused on the origins of these differences, in particular the contributions of biology and culture. As is discussed throughout this book, an exclusive focus on one type of explanation or the other creates a false dichotomy, because evolved biases emerge in cultural contexts that can exaggerate, suppress, or distort the expression of the corresponding behaviors or cognitive competencies. The real debate is with regard to the relative contributions of biology and culture and the extent to which the former is modifiable by the latter. The debate will no doubt continue for some time to come. My goal for this chapter was to consider if existing sex differences in brain and folk psychology are consistent with what we have learned about intrasexual competition and intersexual choice in previous chapters.

It is more difficult to make these connections to the sex differences in brain size and organization than to the cognitive sex differences, because few of the associated studies were specifically designed to test predictions related to sexual selection. As an example, the finding that men have a larger brain, on average, than women, even after controlling for body size, is consistent with findings for other species of primate (Sawaguchi, 1997); specifically, more intense male–male competition is associated with larger brain size in males than females. However, the relation between gross size differences and male–male competition or female choice remains to be determined. A more definitive case for the importance of sexual selection comes from sex differences in brain regions that support cognitive and behavioral competencies directly related to intrasexual competition or intersexual choice, after controlling for the sex difference in brain size.

Strong candidates for such brain regions include the planum temporale and other language-supporting areas. Here, women's advantages in the size and organization of these areas (C. M. Leonard et al., 2008; Lotze et al., 2019) fits well with their advantage on many dimensions of language competence (R. A. Block et al., 1989; Cavaco et al., 2015). If language is more central to female–female competition than it is to male–male competition, then these regions have been elaborated in women, at least in part, as a result of women's intrasexual competition. Other strong candidates include the amygdala and ventromedial areas of the prefrontal cortex and the interconnects between them (Gur et al., 2002; Ritchie et al., 2018), as related to the processing of nonverbal social information (e.g., facial expressions) and reacting to social dynamics. As noted earlier, men's larger amygdala is related to hormonal changes during puberty (Bramen et al., 2012) and may result in lower thresholds for behaviorally reacting in sexual and aggressive contexts. The latter would contribute to men's disproportionate use of physical aggression to resolve conflicts, especially as directed toward other men (Daly & Wilson, 1988b). The latter is of course a common feature of male–male competition in people, as is a relatively large male amygdala (among other things) in other primates with intense male–male competition.

In any case, there are sex differences in all three core areas of folk psychology with respect to the processing of information related to the self, other individuals, and with respect to group dynamics. The combination of sexual selection and cultural influences provides a vantage point for understanding these differences that cannot be captured by either process alone. Social–psychological theories regarding the sexual objectification of women have captured a real phenomenon (e.g., Fredrickson et al., 1998), but leave unanswered the more basic question as to why women would be sexually objectified more than men. The answer can be found with the sex differences in parental investment and the cost–benefit trade-offs associated with casual sex. It is not a coincidence that many of the physical traits that are objectified in women are the same ones that men use in their mate choices and the same traits that are cues to women's reproductive potential (see Chapter 7, this volume). The combination of male choice and female–female competition will make some traits (e.g., facial features, breasts) more central to women's sense of self than others, but cultural factors can exaggerate this focus and has in Western mass media (see Chapter 14, this volume).

The sex differences in the individual-level cognitive competencies (e.g., reading body language and facial expressions) indicate that girls and women have a much more nuanced approach to relationship dynamics than do boys and men. Female–female competition often involves subtle manipulation, at least compared with male–male competition, of social relationships, especially when the competition is over a romantic partner (T. Reynolds, Baumeister, & Maner, 2018; Vaillancourt & Sharma, 2011; see Chapter 8, this volume). These individual-level competencies are also more critical to women's than to men's formation of dyadic friendships that are a source of social support, including alloparenting in traditional contexts. A key domain in which men are predicted to have an advantage is in the formation of ideologically based ingroups. This follows from an evolutionary history of male–male competition and the competitive advantage of large coalitions over smaller ones. There is much to be learned, but boys and men do show a different pattern of ingroup and outgroup dynamics than do girls and women, especially during intergroup competitions (e.g., Van Vugt et al., 2007), and they think more in terms of group ideologies than girls and women in threatening circumstances (Arndt et al., 2002).

In all, our understanding of social-cognitive (i.e., folk psychology) sex differences and in the underlying brain systems only makes sense in terms of the evolutionary selection pressures related to competition over mates, mate choices, and investment in children described in previous chapters. As described in Chapters 10 and 11 of this volume (see also Figure 10.3), our evolutionary history resulted in a protracted developmental period and the ability to adapt these systems to the nuances of the local social group. This plasticity opens these systems to broader social influences and a way to integrate these influences within an evolutionary perspective.

13

Sex Differences in Folk Biology and Folk Physics

This chapter continues the discussion of sex differences in brain and cognition, but now turns the attention to the folk biology and folk physics systems described in Chapter 9 of this volume. Most people living in highly developed and economically diverse nations are far removed from the day-to-day demands on people living in traditional societies, and they may not fully appreciate the importance of folk biological and folk physical competencies. The combination is critical for survival in traditional contexts and provided our ancestors with the ability to modify and control the ecology in ways that are uniquely human. Without the corresponding ability to dominate the ecology (R. D. Alexander, 1989), the modern world as we know it would not exist and would not be maintainable. R. D. Alexander's (1989) concept of ecological dominance and the evolution of the associated brain and cognitive systems was addressed previously (Geary, 2005; see also Flinn, Geary, & Ward, 2005), but sex differences in these systems have not been discussed. The following sections address these sex differences, beginning with folk biology and then folk physics.

FOLK BIOLOGY

The fundamentals of folk biology were introduced in Chapter 9 of this volume, and Chapter 5 argued that the sexual division of labor and its evolution is not the primary source of human sex differences. However, this does not mean

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that the sexual division of labor, in particular hunting and gathering, did not result in the evolution of sex differences in some forms of folk biological and folk physical competence (Silverman & Eals, 1992), but rather some of these followed from sex differences that emerged earlier in our evolutionary history. For instance, coalitional male–male competition likely preceded cooperative hunting, but hunting in and of itself is now an important prestige-based component of male–male competition and female choice in many traditional societies. Likewise, women's competence at foraging and food preparation can influence men's mate choices in these same societies (Betzig, 1989). The evolution of folk biological knowledge is influenced, at least in part, by sexual selection, in addition to its importance for survival and natural selection. Folk biological knowledge is also important for the preparation of traditional medicines, including use of animal parts and native plants for the treatment of a wide array of common ailments (Mahawar & Jaroli, 2008).

To the extent that folk biological knowledge influenced skill at gathering, hunting, and treating illness, and to the extent that women and men differed in these activities, sex differences will evolve in the cognitive and brain systems that support ease of learning about and interest in other species (Barbarotto, Laiacona, Macchi, & Capitani, 2002; Caramazza & Shelton, 1998). Any such sex difference should be expressed in children's play activities (see Chapter 10, this volume) that flesh out folk biological knowledge and adapt it to the local ecology (see Chapter 9, this volume). On the basis of the traditional division of labor, boys are likely to show greater interest in potentially hunted species and to engage in early play activities (e.g., selective imitation of men's and older boys' hunting) that will prepare them to become hunters in adulthood. Girls are likely to show a relative bias toward plants and interest in their potential uses as foods and medicines.

Compared with folk psychology and folk physics, sex differences in folk biological knowledge have not been as systematically assessed, but there are some sex-specific differences in knowledge of local plants (flora) and animals (fauna) and differences in the use of some plants (e.g., Roulette, Njau, Quinlan, Quinlan, & Call, 2018; van Andel, de Boer, Barnes, & Vandebroek, 2014). The latter includes women's avoidance of certain plants (usually bitter tasting) when pregnant or breastfeeding or use of others to promote lactation, as well as men's use of stimulants before embarking on potentially lethal raids (Lehmann & Mihalyi, 1982; Roulette et al., 2018). The focus here, however, is on sex differences in the overall knowledge of plants and animals, not culture-specific uses of them.

Folk Biological Knowledge

At its most basic level, folk biology includes peoples' knowledge of local plants and animals, but their knowledge is more nuanced than this and can include distinctions between closely related species. The ability to classify various species of plant and animal often comes with an understanding of their essence, which is species-specific knowledge about the stable physical and behavioral characteristics of the species, including its use of the ecology (e.g., where and when they can be found; Atran, 1994; Malt, 1995; see Chapter 9, this volume).

Flora

Berlin, Boster, and O'Neill (1981; see also Boster, 1985) conducted one of the more extensive assessments of sex differences in folk biological knowledge with their study of the Aguaruna, a forest-dwelling tribe in northern Peru. Their subsistence activities include gardening, fishing, hunting, and collecting foods in the forest. Among other assessments, women and men were asked to name and classify (i.e., put related species together) species of plant grown in local gardens and were interviewed to determine their depth of knowledge about these different species (Boster, 1985). As a group, women showed more agreement among themselves about the classification of these species, greater complexity in the overall classification system, and more nuanced knowledge about individual species than did men. In a study of the Paniya and Kuruma tribes in India, Cruz García (2006) found that mothers were more knowledgeable of local plants than fathers and passed this folk biological knowledge to their children more often than did fathers; children also learn from other adults and from peers (Setalaphruk & Price, 2007). Nahua (Mexico) women are more efficient foragers and appear to be more knowledgeable about a wider variety of species (e.g., fungi) than their male counterparts (Pacheco-Cobos, Rosetti, Cuatianquiz, & Hudson, 2010).

Women and men act as healers in traditional cultures (e.g., Ankli, Sticher, & Heinrich, 1999), and men know more about medicinal plants in some cultures, whereas women know more in others (Torres-Avilez et al., 2016). Advantages for men are typically found in sub-Saharan Africa (e.g., Teklehaymanot & Giday, 2007), with women knowing as much and typically more about medicinal plants than men in other parts of the world (Begossi, Hanazaki, & Tamashiro, 2002; Monteiro, Albuquerque, Lins-Neto, Araújo, & de Amorim, 2006; J. M. Nolan & Robbins, 1999). Figueiredo, Leitão-Filho, and Begossi (1993, 1997) found that for groups of South Amerindians residing at the Sepetiba Bay region of Brazil, women showed greater knowledge of medicinal plants than did men. J. M. Nolan and Robbins (1999) described women healers in the rural Ozark Mountains (Arkansas and Missouri, United States):

> In Ozark communities, women play pivotal roles in the delivery of health care. For example, it is mostly women who gather wild plants from forests and herbs from garden patches to prepare medicinal concoctions, provide treatment to the sick, and assist in natal events. . . . Known among the hill folks as *granny women*, these practitioners are especially experienced in childbirth management . . . yet are knowledgeable in using plant-based medicines for treating illnesses. (p. 68)

The potential usefulness of this folk biological knowledge was demonstrated in a study of the Tsimané, a horticultural and foraging society in the Amazon (Bolivia; McDade et al., 2007). The activity of the immune system—indicating current infection—and indices of adequate nutrition and growth were assessed for 330 children across 13 Tsimané villages. Mothers' and fathers' folk biological knowledge was assessed and used to predict their children's health. After controlling for multiple other factors (e.g., age, years of formal education), these researchers found that mothers with more diverse folk biological knowledge had children with fewer infections and who were at lower risk for poor nutrition and stunted growth. Mothers in the bottom 15% to 20% of folk biological knowledge had children who were 50% more likely to be in poor health compared with children whose mothers had average folk biological knowledge. Fathers' folk biological knowledge was also considerable but did not contribute to their children's health above and beyond the contributions of their wives' knowledge. McDade et al. (2007) suggested "women may be experts in using plants to prevent and treat infectious disease, whereas men may possess more knowledge relevant to construction or habitat management" (p. 6137).

Fauna

Given men's greater participation in hunting in traditional societies, it is not surprising that they typically have more complex knowledge of local animals than do women. Berlin et al. (1981) asked groups of Aguaruna men and women to name and classify more than 150 specimens of local species of bird, some of which men hunt with blowguns. The classification system of men was more highly differentiated and showed more consistency across raters than did the classification system of women. For many species, the men's classification system was very similar to the corresponding taxonomy developed by Western biologists. Atran (1994) found a similar sex difference in the folk biological knowledge of the Itza-Maya (Guatemala). Men and women showed similar taxonomies for local animals but differed considerably in their level of expertise. In their classifications, women were more likely to rely on static morphological features of the animal, such as color or body shape, than were men, whereas men relied "more on complexly related features of behavior, habitat, diet, and functional relationship to people" (Atran, 1994, p. 331) than did women. Among the Mayangna and Miskito (Nicaragua), men have more diverse knowledge of local fish species, which they hunt with bow-and-arrow, than do women, and more knowledgeable men have better fishing returns than their less-knowledgeable peers (Koster, Bruno, & Burns, 2016).

In support of the predicted developmental sex difference, there is some indication that boys attend to potentially dangerous and wild animals more often than do girls and know more about these animals (Blurton Jones, Hawkes, & O'Connell, 1997; DeLoache, Simcock, & Macari, 2007; Eibl-Eibesfeldt, 1989; Setalaphruk & Price, 2007). For instance, Eibl-Eibesfeldt (1989) noted that boys growing up in a kibbutz (Israel) "often identified in their symbolic games with animals, such as horses, dogs, snakes, frogs, and wolves, and not with those surrounding them, like cows, lambs, sheep or chickens" (p. 282). He also found that the drawings of !Ko boys (central Kalahari) depicted domestic and wild animals about 3 times more frequently than did girls' drawings. Blurton Jones et al. (1997) documented a related sex difference in the self-initiated activities of Hadza (Tanzania) children older than 10 years. Before this age, boys and girls forage; after this age, boys generally restrict their activities to hunting, despite the fact that their hunting returns—in terms of calories—are much lower than would be the case if they continued to forage.

Brain and Hormones

The next section provides a brief discussion of the brain systems that support folk biological knowledge and touch on some potential hormonal influences.

Brain

Our understanding of the brain systems that support folk biological knowledge largely comes from studies of brain injury (e.g., stroke) or disease (e.g., encephalitis), as these affect the ability to categorize, discriminate, and describe plants, animals, and man-made objects (Farah, 1996; Laws & Neve, 1999; Löw et al., 2003). In these studies, an individual who suffered from a stroke might be asked to point to the carrots or airplane in Figure 13.1. The results of these types of studies suggest distinct perceptual, cognitive, and brain mechanisms for the categorization of living and man-made things (Capitani, Laiacona, Mahon, & Caramazza, 2003; Farah, 1996) and some evidence for distinct systems for the categorization of and knowledge about plants and animals (Hart & Gordon, 1992). Because injury and disease typically result in damage to multiple brain regions, these studies have not allowed for the localization of this knowledge to specific regions. These studies do suggest, at the very least, involvement of the left temporal cortex (e.g., part of Brodmann Area 22; see Figure 12.2, Chapter 12, this volume; Schmidt et al., 2019), as do some brain imaging studies. Löw et al. (2003) found evidence that different but adjacent regions of the left temporal cortex supported knowledge about plants, animals, and man-made objects.

A more interesting pattern is that men are overrepresented—by a factor of 3—among patients with difficulties identifying and describing fruits and vegetables following some forms of brain damage (Gainotti, 2005; Laiacona, Barbarotto, & Capitani, 2006; Moreno-Martínez, Quaranta, & Gainotti, 2019). These findings do not appear to be related to women's advantage in verbal fluency (see Chapter 12, this volume), which would provide them with an advantage on some of these assessments (e.g., number of vegetables that can be named in 1 minute), or their greater familiarity with fruits and vegetables. In fact, despite their advantages in verbal fluency, women are more likely to have deficits identifying and describing animals than are men following certain types of brain injury (Gainotti, 2005; Moreno-Martínez et al., 2019). For adults with no brain damage, P. McKenna and Parry (1994) found that women were better at naming fruits and vegetables and men were better at naming animals, but other studies have not found this sex difference (Barbarotto et al., 2002; Gerlach & Gainotti, 2016). Unfortunately, the key

FIGURE 13.1. Assessment of People's Ability to Discriminate Plants, Animals, and Man-Made Objects

Certain forms of brain injury can make it difficult for individuals to point to items in one category (e.g., man-made) but not others (e.g., fruits).

prediction that men will be more attuned to wild animals compared with domestic animals has not been assessed in these studies.

Hormones

A strong link between fluctuating hormone levels and sex differences in folk biological knowledge is not expected, because fruits and vegetables must be gathered daily and animals hunted regularly in traditional societies. Prenatal exposure to testosterone and hormonal changes associated with puberty may bias boys and girls and men and women to focus on different features of the biological world and to have different interests (e.g., wild animals vs. flowers), but this remains to be demonstrated.

There may be less direct influences of sex hormones on folk biological competencies. Silverman and Eals (1992) hypothesized that women's advantage in object location memory is the result of the sexual division of labor (i.e., women's gathering). The sex difference does not emerge until puberty, suggesting a potential influence of sex hormones on this form of memory (Voyer, Postma, Brake, & Imperato-McGinley, 2007). Pacheco-Cobos et al. (2010) confirmed that relative to men, women have more efficient foraging strategies, a better memory for good foraging locations, and more nuanced knowledge about the species that are likely to be found in these locations.

As described in Chapter 10 of this volume, some hunting competencies (e.g., use of bow-and-arrow) improve as a result of physical growth during puberty but it is not known if there is a corresponding improvement in folk biological knowledge and related interests and cognitive competencies. One possibility, for instance, is that these hormonal changes also result in improved detection of movement in large scale space, as would be important for the detection of potential prey at long distances.

Origin

In all, boys and men show a greater interest in and are more knowledgeable about local animals than are girls and women, whereas girls and women are more knowledgeable about local plants. At this point, we do not know enough to draw firm conclusions about the origin of the sex differences in these folk biological competencies. The differences found in traditional societies could result from the different subsistence activities of men and women. These activities could result in a sex difference in knowledge of local plants and animals without any inherent differences in the ways in which women and men organize or learn about the biological world (e.g., Boster, 1985). This explanation is less likely for sex differences (e.g., women knowing more about plants) that have emerged in modern societies (Laiacona et al., 2006), although these differences are often smaller than those found in traditional contexts (Gerlach & Gainotti, 2016). I suspect the differences arise from the combination of sex differences in inherent attentional and interest biases and corresponding sex differences in engagement with the biological world. The tendency of boys to attend to wild and potentially dangerous animals more frequently than girls might reflect such an attentional bias, and associated activities (e.g., play hunting) would eventually result in a sex difference in knowledge of local plants and animals (Blurton Jones et al., 1997; Eibl-Eibesfeldt, 1989).

FOLK PHYSICS

The following discussion of sex differences in folk physics is focused on movement, representation, and tool use (see Figure 9.5, Chapter 9, this volume). *Movement* refers to our ability to act on and respond to the physical world, and *representation* refers to our ability to remember and mentally reconstruct this world. *Tool use* is our ability to modify objects and use them to gain control of biological resources (e.g., weapons used in hunting), change the physical world or our exposure to it (e.g., build shelters, dams), and influence human social dynamics (e.g., weapons used in warfare).

Movement

The discussion of sex differences in movement is divided into sections on cognition, brain, and hormones.

Cognition

As discussed in Chapter 12 of this volume, G. M. Alexander (2003) and Handa and McGivern (2015) proposed as model of the development of the "where" and "how" dorsal stream and the "what" ventral stream of the visual system and how these systems contribute to many cognitive sex differences. More precisely, they proposed that prenatal and early postnatal exposure to testosterone may enhance aspects of the development and function of the where and how systems and result in a sex difference favoring boys for interest in and memory of object motion (Voyer, Voyer, & Saint-Aubin, 2017; see Chapter 10, this volume). This framework and the early sex difference in focus on object motion may provide the seeds for later sex differences in the detection of objects obscured in a complex visual scene, detecting and tracking the movement of objects in physical space, and skill at behaviorally reacting to these moving objects (Law, Pellegrino, Mitchell, et al., 1993; Peters, 1997; Schiff & Oldak, 1990). The following sections detail how sex differences in these areas are consistent with an evolutionarily elaboration of the cognitive abilities that support men's use of and protection from projectile weapons.

Detecting objects. Men have several perceptual and cognitive advantages stemming from the visual system (Abramov, Gordon, Feldman, & Chavarga, 2012a; McGuinness, 1976; Vanston & Strother, 2017), even though women have more sensitive sensory systems in the areas of touch, smell, taste, and some aspects of hearing (Velle, 1987). Men have sharper vision than women, are better at detecting the orientation of objects relative to a background, and are better at seeing individual objects embedded in a complex montage of objects. Before puberty, about 3 out of 5 boys show better skills in these areas than does the average girl, whereas in adulthood about 7 out of 10 men outperform the average woman (Linn & Petersen, 1985; Velle, 1987; Voyer, Voyer, & Bryden, 1995). Boys' and men's advantages here are related to sex differences in aspects of the where dorsal visual stream and a heightened sensitivity of some of the most basic features of the visual cortex. The latter includes sharper distance vision and heightened sensitivity to colors in the yellow–blue spectrum, which is often accompanied by low sensitivity to color variation in the red–green spectrum (Abramov, Gordon, Feldman, & Chavarga, 2012b; G. M. Alexander, 2003).

About 8% of men have varying degrees of color blindness, in which they are poor at discriminating colors in the red–green spectrum; about 2% of men cannot discriminate red from green at all (Nathans, Piantanida, Eddy, Shows, & Hogness, 1986). Discrimination of red from green appears to be an evolved feature of the primate visual system that supports the detection of fruit and other colorful foods (Shyue et al., 1995), and these men should be at an evolutionary disadvantage. However, sensitivity to variation in color in the red–green spectrum comes with a cost, or rather insensitivity with an advantage. Men who are color blind have an advantage in detecting camouflaged objects, especially objects in dappled light (Morgan, Adam, & Mollon, 1992). In other words, the evolution and expression of systems that enable the detection of red objects against a green background comes at a cost to the ability to detect camouflaged objects embedded in a varied background and vice versa.

Boys and men have advantages over girls and women in the ability to visually discriminate one object from another when they are both partially hidden and especially so when the objects are at a distance. Boys and men also have an advantage in detecting the location of sounds and in identifying a specific sound against background noise (McFadden, 1998). These sex differences will give men an advantage in detecting the movement of animals or other people in a forest or at a distance against a natural background, as would be important when ambushing rivals from neighboring groups or when hunting.

Tracking objects. Men also show advantages in the ability to judge the velocity and trajectory of a moving object, in the ability to generate visual images of a moving object, in the ability to estimate when a moving object will hit them, and in accuracy at hitting a moving object with a thrown projectile (Paivio & Clark, 1991; Schiff & Oldak, 1990). In a set of experiments, Law, Pellegrino, and Hunt (1993) asked men and women to judge the relative distance traveled by two objects and their relative velocity. No sex differences were found in the ability to judge which object had traveled farther, although men are better than women in estimating distances longer than those assessed by Law et al. (Deregowski, Sheperd, & Slaven, 1997). In any case, Law et al. found that men have moderate to large advantages in the ability to judge object velocity. In one of the studies, more than 4 out of 5 men were more sensitive to relative velocity (i.e., which object was moving faster than the other) than was the average woman. Practice and feedback improved the performance of men and women, but the magnitude of men's advantage did not change; practice does, however, reduce or eliminate men's advantage on some less complex tracking tasks and for some visual attention tasks (Feng, Spence, & Pratt, 2007; Joseph & Willingham, 2000).

In another series of experiments, Schiff and Oldak (1990) demonstrated that men were more accurate than women in judging time-to-arrival (i.e., whether an object moving toward them would either hit or pass by them). For objects that only could be seen, about 3 out of 4 men were more accurate at judging time-of-arrival than was the average woman. Men were also more accurate at judging time-of-arrival for objects that only could be heard. Judging time-of-arrival may have a practical function; Watson and Kimura (1991) found that about 3 out of 4 men could block targets that were thrown at them (i.e., tennis balls shot from launching devices) with their right and left hand with greater skill than could the average woman. As a group, men successfully blocked an average of 26 of the 30 tennis balls shot at them (the number blocked by women was not reported), suggesting that the task was too easy for men and likely underestimated the magnitude of the sex difference in blocking skill.

Overall, men's advantages in these areas are consistent with the evolution of perceptual and motor abilities that are defenses against projectile weapons. This ability is critical given the high male mortality from male–male competition in traditional contexts (see Chapter 8, this volume), most of which is due to the use of blunt force (e.g., clubs) and projectile (e.g., bow-and-arrow) weapons. The refinement of these perceptual and motor abilities requires practice, as was illustrated in Chapter 10 of this volume with the Throw at Each Other With Mud game of the Sioux (North America):

> Teams of boys attacked [each other] with mud balls which they threw from the tips of short springy sticks. Each boy carried several sticks and an arsenal of mud as he advanced. "It certainly hurt when you got hit, so you must duck and throw as you attack." Sometimes live coals were embedded in the mud balls to add zest to the game. (Hassrick, 1964, p. 130)

All of this was no doubt great fun for these boys but at the same time refined the perceptual, cognitive, and motor systems that would support skill at offensively using projectile weapons and defending oneself against them.

Intercepting objects. Whether hunting or ambushing rivals, success depends on the ability to hit a target with a projectile, often a thrown one (e.g., rock, spear). Chapter 10 of this volume described boys' and men's substantial advantage over same-age girls and women in throwing distance, velocity, and accuracy (Thomas & French, 1985). Jardine and Martin (1983) found that about 7 out of 8 adolescent boys threw more accurately at a nonmoving object than did the average same-age girl, whereas 9 out of 10 of their fathers threw more accurately than their mothers. The same sex difference is found in the Hadza, a traditional hunter-gatherer society in Tanzania (Cashdan, Marlowe, Crittenden, Porter, & Wood, 2012). To control for men's greater experience in the use of bows, Cashdan and colleagues (2012) asked women and men to throw beanbags underhanded at targets that were 4 meters to 9 meters away. This is a very easy task compared with actual combat with projectile weapons or their use in hunting. Depending on distance, 8 to more than 9 out of 10 men were more accurate in their throws than was the average woman.

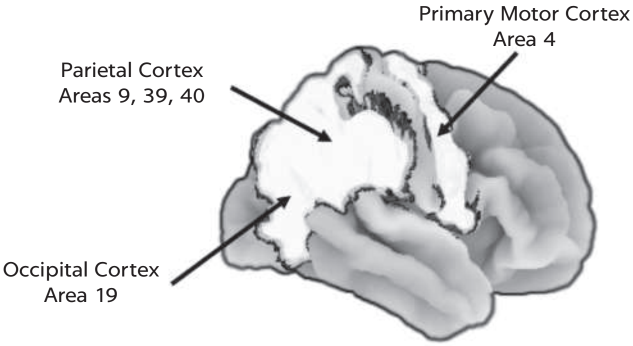
More typically, the target is at a farther distance and is often moving, as illustrated by the Throw at Each Other With Mud game. Accordingly, Peters (1997) assessed men's and women's accuracy at hitting a moving target with a thrown object. Three out of 4 men were more accurate than the average woman at hitting a close and slow-moving target, but this gap widened as the speed of the target increased. Men's accuracy was related to their better estimation of the velocity of the moving target and better timing of the release of the thrown object vis-à-vis the velocity of the target (Crozier, Zhang, Park, & Sternad, 2019); men's advantage on this task was not related to their reported participation in sports that involved throwing objects. On top of advantages in these component competencies (e.g., estimating target velocity), Peters hypothesized that men's overall advantage in throwing accuracy was related to the coordination of the where and when systems that are part of the dorsal visual stream (Handa & McGivern, 2015).

Brain

Detecting and behaviorally reacting to objects moving in space involves coordination of the where and spatial attention regions of the parietal cortex (e.g., Brodmann Areas 7, 39, and 40; see Figure 12.2, Chapter 12, this volume) with areas of the visual (e.g., Brodmann Area 19) and motor cortices (e.g., Brodmann Area 4), along with contributions from several subcortical areas (Milner & Goodale, 1995; Posner, 1994; Scott, 2004). A few, but not all, of these areas are illustrated in Figure 13.2. There are subtle sex differences in the architecture of most of these brain regions (Amunts et al., 2007; de Lacy, McCauley, Kutz, & Calhoun, 2019a, 2019b; Goldstein et al., 2001; Kong et al., 2018; Lotze et al., 2019; Ritchie et al., 2018; Sowell et al., 2007). For instance, Salinas et al. (2012) found sex differences, especially during adolescence, in the development of the parietal cortex involved in visuospatial attention and in more complex spatial abilities. By adulthood, men have more surface area in these regions of the brain than do women, controlling for overall brain size. So, if the brain were to be unfolded and laid flat, men would have proportionately (controlling brain size) more area in the parietal cortex than would women.

In an autopsy study, Amunts et al. (2007) found that men had absolutely and proportionately more volume and surface area in the motion-detection region of the right hemisphere (parts of Brodmann Areas 19, 37, and 39; see Figure 12.2, Chapter 12, this volume) than did women. The elaboration of men's motion-detection brain regions is specific to the right hemisphere and is contrasted with more uniform (because of the sex difference in overall brain size) sex differences in adjacent areas of the visual cortex. The right motion-detection region is part of the dorsal visual stream and might also have more connections to other brain regions in men than in women, including the spatial attention areas of the right parietal cortex and other regions that support behaviorally responding to and acting on the external world (Milner & Goodale, 1995; Posner, 1994). These regions are important for tracking the movement of objects in space and behaviorally reacting to them

FIGURE 13.2. Key Brain Areas for Visuospatial and Visuomotor Abilities



Different mixes of subsections of the highlighted areas will be engaged for different visuomotor activities, as will areas of the prefrontal cortex (not highlighted). The numbers next to the labels are Brodmann area map coordinates (see Figure 12.2, Chapter 12, this volume).

(e.g., catching a ball). These sex differences are potentially analogous to the sex-specific enlargement of the planum temporale in women as related to language processing (C. M. Leonard et al., 2008; see Chapter 12, this volume), but their contribution to the sex differences described above (e.g., motion detection) are not fully understood.

Hormones

Prenatal exposure to male hormones contributes to some of these sex differences (J. A. Y. Hall & Kimura, 1995; Hines et al., 2003; Van Goozen, Slabbekoorn, Gooren, Sanders, & Cohen-Kettenis, 2002). Hines et al. (2003) found that about 3 out of 4 women affected by congenital adrenal hyperplasia (CAH; excess prenatal exposure to male hormones) were more accurate than the average woman at hitting targets about 3 meters away. For one of these throwing tasks, the accuracy of these women was comparable to that of men, and on the other task their accuracy was in-between that of unaffected women and men. Another way to assess these influences is to compare individuals who are homosexual with those who are heterosexual. These types of comparisons are informative, because sexual orientation is likely to be influenced in part by prenatal exposure to sex hormones (e.g., J. M. Bailey et al., 2016). To control for the sex difference in the structure of the arms and shoulders, which will influence throwing competence, J. A. Y. Hall and Kimura (1995) compared the throwing accuracy of homosexual men with that of heterosexual men and women. Heterosexual men were more accurate than heterosexual women, as is typically found, and the targeting accuracy of homosexual men did not differ from that of heterosexual women (see also Van Goozen et al., 2002).

Men's advantages in locating objects on the basis of sound and in identifying specific sounds against background noise also appears to be related to prenatal exposure to testosterone (McFadden, 1998), as does their advantage in detecting the orientation of objects (Collaer, Reimers, & Manning, 2007; Van Goozen et al., 2002). Moreover, higher circulating testosterone concentrations enhance men's top-down control of their visuospatial attention (Hansen, McAuliffe, Goldfarb, & Carré, 2017; Schutter, Peper, Koppeschaar, Kahn, & van Honk, 2005), whereas increases in progesterone levels in the second half of women's ovulatory cycle may disrupt it (Hausmann & Güntürkün, 2000; Pletzer, Harris, & Ortner, 2017). Other studies of the relationship between circulating hormones and the visuospatial abilities assessed in this section are more mixed. Some studies find a relationship (Hampson, 1990a; Hampson & Kimura, 1988), whereas others do not (Liben et al., 2002; Van Goozen et al., 2002). The inconsistent results may be due to larger prenatal than postnatal effects, or because identifying a relationship between circulating hormone concentrations and perception and cognition is like trying to hit a moving target. This is because men's testosterone levels vary across the day (highest in the morning) and women's sex hormones vary across their ovulatory cycle.

Representation

The previous section focused on sex differences in the ability to act on and respond to change in the physical environment. This section focuses on sex differences in the ability to form mental representations of the environment (e.g., images of the local ecology) and to remember this environment. Sex differences in these representational and memory skills have been studied for many decades and the pattern is complex. Men typically outperform women in navigating in the environment and on tests that involve the representation and mental rotation of images in three-dimensional space (see Figure 13.3), whereas women have an advantage in remembering the location of objects (Herlitz, Nilsson, & Bäckman, 1997; Linn & Petersen, 1985; Pauls, Petermann, & Lepach, 2013; Silverman & Eals, 1992; Voyer et al., 2007). Moreover, tasks of the same name can produce different results from one study to the next because of differences in task complexity. Men typically outperform women on complex versions of the task (e.g., three-dimensional virtual mazes), with smaller or no sex differences on less complex versions (e.g., two-dimensional mazes; Coluccia & Louse, 2004).

Despite these complications, a consistent pattern of sex differences has emerged for spatial abilities that are related to the different reproductive and foraging activities of men and women in traditional societies. These competencies include the ability to generate mental representations of the large-scale physical environment, which is related to skill at navigating within this environment (Cashdan et al., 2012; Vashro, Padilla, & Cashdan, 2016); the ability to mentally manipulate or transform three-dimensional representations, which may engage the same cognitive systems used to represent and navigate in three-dimensional space (Just & Carpenter, 1985; Shepard, 1994) or which may be useful for tool construction (Hegarty, 2004); and the ability to remember the location of specific objects in the environment (Pacheco-Cobos et al., 2010; Silverman & Eals, 1992).

Navigation

Boys have larger home ranges than girls (Matthews, 1987, 1992; see Chapter 10, this volume). The same sex difference is found in adults in traditional

FIGURE 13.3. An Example of How Three-Dimensional Mental Rotation Abilities Are Assessed

The goal is to determine which of the figures on the right (first and third) are rotations of the figure on the left and which (second) is a rotation of the mirror image of the figure on the left.

and modern societies. Men travel farther than women in traditional societies because of differences in hunting compared with foraging, to find mates, and sometimes simply to explore. Across five traditional societies, D. H. MacDonald and Hewlett (1999) reported that men traveled roughly 2 to 4 times farther than women during their typical ranging activities. Ecuyer-Dab and Robert (2004) asked women and men in Montreal to record their daily personal and professional travel in a diary. Men ranged farther than women for personal and professional travel in and around Montreal, and men's personal travel range was 1.8 times larger than women's range.

In many traditional contexts, men with enhanced spatial abilities have larger travel ranges than do other men, and in at least some of these societies, they also have more wives and children (Cashdan et al., 2012; Vashro & Cashdan, 2015; Vashro et al., 2016). These sex differences, however, only appear to emerge where men have significantly larger travel ranges than women (Trumble, Gaulin, Dunbar, Kaplan, & Gurven, 2016). Trumble and colleagues (2016) did not find a sex difference in navigation abilities among the Tsimané, but here men's mobility is restricted by their ecology (dense forest with no distal cues like mountains) which limits the opportunity for spatial abilities to fully develop. The same is true for children (Levine, Vasilyeva, Lourenco, Newcombe, & Huttenlocher, 2005). Reduced ability to explore the environment appears to compromise the development of boys', but not girls', spatial abilities, consistent with the importance of engagement in sex-typical activities for the full emergence of many sex differences (see Chapter 9, this volume).

When boys and girls have the opportunity to explore the environment in sex-typical ways (e.g., play some distance away from their home), sex differences emerge. When asked to generate a map after exploring a novel environment, boys' maps show more accurate clustering of environmental features and more accurate representations of the geometric relations (i.e., cardinal direction) among these features (e.g., building A is northwest of building B; Matthews, 1992). Boys and girls also differ in the extent to which they focus on landmarks (e.g., specific buildings) or routes (e.g., roadways) in their maps. In this study and others, girls have been found to attend more to landmarks and relative direction (e.g., building A is left of building B) and boys to routes and cardinal direction, although this sex difference is more common in adolescence than in childhood (Choi & Silverman, 2003).

The same pattern is again found in adults (Holding & Holding, 1989). As an example, Galea and Kimura (1993) asked men and women to study a map of an unfamiliar, fictitious town, and then tested their ability to learn a route within this town. Men learned the route in less time, with fewer practice trials, and made fewer errors during learning. A follow-up task revealed that women remembered more street names and the locations of landmarks, whereas men had a better recall of the geometric relations among the landmarks. Men also show advantages in route learning and navigation when drawing maps (Coluccia, Iosue, & Brandimonte, 2007), show advantage in navigating virtual mazes (Moffat, Hampson, & Hatzipantelis, 1998), have a better memory for routes (Asperholm, Högman, et al., 2019), and show an advantage during wayfinding (Nazareth, Huang, Voyer, & Newcombe, 2019; Silverman et al., 2000). In the latter study, women and men were led on a circuitous 410-meter walk through an unfamiliar wooded area that did not have obvious external landmarks to aid in navigation. The participants were stopped at four locations, and their sense of cardinal direction was assessed by asking them to place an arrow pointing in the direction of the start location. At a fifth location, they were asked to lead the experimenter back to the start location as quickly and directly as possible. Men's arrow placements and their return walk indicated they had a better sense of cardinal direction than did the women.

Saucier, Bowman, and Elias (2003) found that women tend to use verbal labels for remembering landmarks and relative direction when navigating, whereas men are more likely to rely on a nonverbal visuospatial strategy, consistent with Silverman et al.'s (2000) findings for sense of cardinal direction (see also Nazareth et al., 2019). With a little experience, men generate a "bird's-eye view" or allocentric representation of large-scale space, and once they have done this, they can better use short-cuts to get from one place to another (A. P. Boone, Gong, & Hegarty, 2018; Munion, Stefanucci, Rovira, Squire, & Hendricks, 2019; see Figure 9.6, Chapter 9, this volume). This is not to say that women cannot form allocentric representations of space, just that men do so more easily (with less experience) and more frequently than do most women (Ferguson, Livingstone-Lee, & Skelton, 2019; Gagnon et al., 2018). Men's enhanced sense of large-scale space and geometric relations among landmarks is expressed in other ways. Beatty and Tröster (1987) found that young college men in all regions of the United States have more geographic knowledge (e.g., location of U.S. cities on a map) than do women of the same age and region. Basically, men's navigational advantage is associated with greater interest in maps and as a result they tend to know more about geography than do women.

Boys and men also have advantages over girls and women in the ability to generate and mentally manipulate three-dimensional images. In fact, this is one of the larger sex differences in spatial cognition (Linn & Petersen, 1985; Peters et al., 1995; Vandenberg & Kuse, 1978; Voyer et al., 1995). These sex differences are found at the earliest age at which the test can be reliably administered (i.e., early adolescence) and is found at every age thereafter (Linn & Petersen, 1985; Neuburger, Jansen, Heil, & Quaiser-Pohl, 2011; Voyer et al., 1995). Between 15 and 20 years old, about 4 out of 5 boys and men are better able to generate and mentally manipulate three-dimensional images than is the average girl or woman, and between 20 and 35 years old, about 6 out of 7 men outperform the average woman (Linn & Petersen, 1985). Men's advantage is related in part to their ability to mentally rotate the whole image, whereas women are more likely to compare parts of the images (Hegarty, 2018).

Whatever they are doing, the sex difference is universal. In a study of more than 200,000 people, Lippa, Collaer, and Peters (2010) showed that men's advantage here and in a related spatial ability was found in all 53 nations in which people were assessed and was largest in Western, educated, industrialized, rich, and democratic nations (Henrich, Heine, & Norenzayan, 2010). In other words, the sex difference is largest for people living in wealthy, healthy, and egalitarian nations, consistent with the sex- and trait-specific sensitivities to social and environmental stressors that are covered in the following chapter (Geary, 2015, 2016). Although the ability to generate mental representations of images and manipulate them is related to the spatial abilities and underlying brain systems that support navigation, they are not entirely the same (Galea & Kimura, 1993; Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006; Hegarty, Richardson, Montello, Lovelace, & Subbiah, 2002). The details are not important here other than to highlight that there are different types of spatial abilities that share some common features but are also distinct in other ways.

Object Location Memory

One of these distinct abilities is memory for the location of objects in different places in the ecology. In this case, girls and women have advantages over boys and men which is consistent with the sexual division of labor (Eals & Silverman, 1994; T. W. James & Kimura, 1997):

> Spatial specializations associated with foraging should have . . . evolved in females. Food plants are immobile, but they are embedded within complex arrays of vegetation. Successful foraging, then, would require locating food sources within such arrays and finding them in ensuing growing seasons. (Silverman & Eals, 1992, p. 535)

To test this hypothesis, women and men were given 1 minute to examine the objects in an array similar to that shown in Figure 13.4 and were then presented with two additional sheets of objects (Silverman & Eals, 1992). The first included the same objects shown in the original array and several additional items, whereas the second showed the same items but with some of them moved to a different location. The first test assessed object memory by asking participants to circle all of the items that were on the original sheet and crossing out the new ones, and the second test assessed object location memory by asking participants to circle the objects that were in the same location and crossing out objects that had moved. Women outperformed men on both tests. Three additional studies confirmed this pattern and found that 8- to 13-year-old girls outperformed same-age boys on object memory tests, but not on location memory tests.

Follow-up studies confirmed these basic sex differences, with some nuance for object location memory (Eals & Silverman, 1994; Ecuyer-Dab & Robert, 2007; T. W. James & Kimura, 1997). Overall, about 6 to 7 out of 10 adolescent girls and women have a better memory for viewed objects and their location than does the average same-age boy or man (Voyer et al., 2017). In the same meta-analysis, Voyer and colleagues (2017) confirmed that there is not a sex difference in object location memory before the onset of puberty. Once the pubertal changes are under way, girls' and women's advantage on object location tests varies with test and item type. Their most consistent advantages are

FIGURE 13.4. An Example of a Stimulus Array Used in Tests of Object Memory and Location Memory

for familiar items, under incidental learning conditions, and when asked to recall rather than recognize item location. With incidental learning, the participants are exposed to an array of objects (e.g., randomly placed on a desk) but are not explicitly asked to attend to them and then later asked to recall where each object was located. Under these conditions, at least 7 out of 10 girls and women recall more locations than does the average boy or man. There are no sex differences, however, when participants are explicitly asked to learn the location of each object for later testing. So, when just casually sitting in a room for a few minutes, women have a better memory than men for the objects that were in the room and a better memory for where they were located in the room.

Women's memory advantages here fit well with the demands of foraging, because some edible foods, such as tubers (roots), can only be located on the basis of their position relative to local landmarks and might only be edible at certain times of the year (Ecuyer-Dab & Robert, 2007). The ability to remember where these foods are when they are ready to be harvested will provide an important advantage in traditional contexts, as was demonstrated by Pacheco-Cobos et al. (2010) for the Nahua. Additional support for the foraging hypothesis is provided by the enhanced ability of many women to discriminate subtle variation in natural colors (Jameson, Highnote, & Wasserman, 2001), which appears to have evolved in primates to aid in the detection of fruits and other types of foraged food (Shyue et al., 1995).

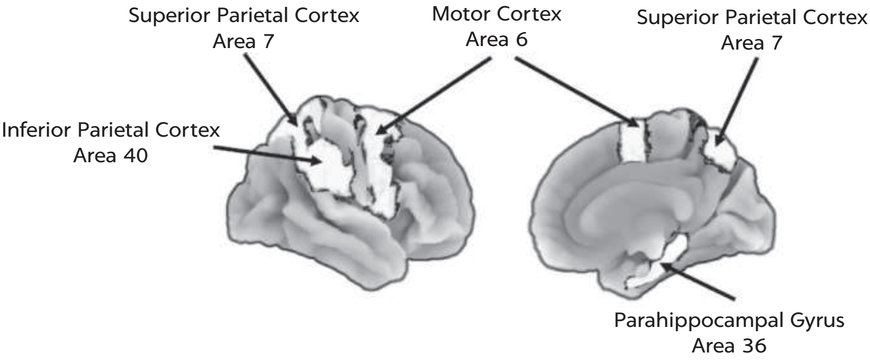
For most domains, women have a better memory for personal experiences than do men (Herlitz et al., 1997), and this could provide an alternative explanation for their advantage on object memory and object location tasks. In other words, women's superior episodic memory (memory for personal experiences) might account for the just-described sex differences, not an evolved advantage for foraging per se. However, women's advantage is not found on all episodic memory tasks and in fact men have a considerable advantage on tasks that require incidental recall of routes (Herlitz & Rehnman, 2008). The latter is of course consistent with the sex differences reviewed previously, but also suggests that women's advantage in episodic memory is not found for all visual arrays, suggesting specific enhancements related to foraging. Any such enhancement and men's better memory for routes could easily emerge from a sex difference in a bias to attend to different things in the environment, a bias that is likely influenced in part by the sex difference in attention to dorsal and ventral visual stream information (G. M. Alexander, 2003; Handa & McGivern, 2015).

Brain

Chapter 9 of this volume touched on the brain systems involved in navigation and object location memory. Areas of the right hippocampus and right parietal cortex (e.g., Brodmann Areas 7 and 40; see Figure 12.2, Chapter 12, this volume) are particularly important for the allocentric representations of large-scale space and for navigating in this space (Maguire, Frackowiak, & Frith, 1996; O'Keefe & Nadel, 1978; Whitlock, 2017). Locating and remembering the location of objects in space also engages parts of the parietal cortex as well as the left and right parahippocampal areas (areas surrounding the hippocampus; e.g., Brodmann Area 36) and part of the fusiform gyrus that supports object identification and naming (Brodmann Area 37; Ekstrom et al., 2003; Epstein & Higgins, 2007). Several of these key areas are shown in Figure 13.5 and are important for the generation and mental manipulation of images (e.g., rotation; Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Cona & Scarpazza, 2019; Just, Carpenter, Maguire, Diwadkar, & McMains, 2001; Zacks, 2008). Regions in the left and the right parietal areas are engaged, especially when thinking about and manipulating complex images.

There are sex differences in the anatomy and development of some of these regions and in their engagement during complex spatial activities (Fish et al., 2020; Goldstein et al., 2001; Sowell et al., 2007). Across brain regions, men generally have more surface area than do women (Ritchie et al., 2018), but as described previously there are sex differences in the development of the parietal cortex that appear to result in relatively (controlling overall brain size) more surface area in some parts of the parietal cortex of men than of women (Koscik, O'Leary, Moser, Andreasen, & Nopoulos, 2009; Salinas et al., 2012). At the same time, there are other parietal areas in which women have relatively more surface area or proportionately more gray matter than do men, but these appear to be more important for social-cognitive competencies

FIGURE 13.5. The Key Brain Areas for Spatial Attention, Memory, and Generating Mental Images



Different mixes of subsections of the highlighted areas are engaged for these different forms of spatial ability, as are areas of the prefrontal cortex (not highlighted). The lateral (outer side surface) of the brain is shown on the left and the medial (center) on the right. The numbers next to the labels are Brodmann area map coordinates (see Figure 12.2, Chapter 12, this volume).

(e.g., theory of mind) than for spatial abilities (Feis, Brodersen, von Cramon, Luders, & Tittgemeyer, 2013; Lotze et al., 2019).

Several studies have found that the size and structure of the hippocampus is related to ease of generating maps of large-scale space, spatial reasoning, and mentally rotating objects within men but not within women (Colom et al., 2013; Schinazi, Nardi, Newcombe, Shipley, & Epstein, 2013). This sex difference might reflect strategic differences in how women and men tackle spatial problems, as was described with women's use of verbal labels and landmarks to navigate and men's use of a cognitive map (Galea & Kimura, 1993). In other words, men's enhanced spatial abilities, supported in part by the hippocampus, makes the use of spatial problem-solving strategies easier than is the case for women, who use different strategies (e.g., partially based on their language advantage). There are also sex differences in the volume (favoring men) and thickness (favoring women) of the parahippocampal gyrus (see Figure 13.5), which is important for recognizing and remembering familiar scenes, retrieving cognitive maps of a traveled area, and remembering the location of objects in the area, among other things (Cona & Scarpazza, 2019; Huntgeburth, Chen, Ptito, & Petrides, 2017; Lotze et al., 2019). At this time, however, it is not known how these anatomical differences contribute to these cognitive sex differences.

There are also differences in the system of brain regions that women and men engage during spatial activities (de Lacy et al., 2019a, 2019b; Grön, Wunderlich, Spitzer, Tomczak, & Riepe, 2000; Hoppe et al., 2012; S. Kaiser et al., 2008; Schöning et al., 2007). For instance, Grön and colleagues (2000) examined brain activity while women and men navigated through a virtual maze. Although there were many similarities, there were several important differences. Men showed greater activation of the left hippocampus whereas women showed greater activation of the right prefrontal-parietal network. Men's activation patterns suggested an automatic, bottom-up processing of geometric coordinates of the maze to aid in navigation, whereas women's patterns suggested the use of a more explicit and effortful, top-down strategy. In other words, men seemed to cruise through the maze with less cognitive effort than did women, as would be expected if the brain and cognitive systems that support navigation have been more highly elaborated during human evolution for men than for women.

Women also appear to engage in more cognitive effort during the mental rotation of three-dimensional images, such as those shown in Figure 13.3 (T. Butler et al., 2006; Jordan, Wüstenberg, Heinze, Peters, & Jäncke, 2002). During the mental rotation of these types of images, T. Butler et al. (2006) found that women showed greater activation of prefrontal areas associated with cognitive effort than did men, whereas men showed greater activation in areas of the parietal cortex (Brodmann Area 7; see Figure 12.2, Chapter 12, this volume) associated with the generation and manipulation of images (Cona & Scarpazza, 2019). Koscik et al. (2009) found that men have disproportionately more surface area (controlling overall brain surface area) in these regions, especially in the left hemisphere, than do women. Men's parietal surface area predicted competence at mentally rotating images but was unrelated to other cognitive abilities. The results here are similar to those found for the hippocampus and navigation and suggest a sex difference in the brain regions engaged and strategies used to solve spatial problems.

There are anatomical sex differences in several of the brain regions that support navigation, object location memory, and the generation and mental manipulation of complex images, as well as sex differences in the mix of brain regions that are engaged during spatial activities (e.g., Hegarty, 2018). These differences are consistent with the earlier described sex differences in navigational ability and strategies and object location memory and may contribute to the sex differences in the implicit understanding of tools.

Hormones

The relationship between exposure to sex hormones and the sex differences in complex spatial abilities has been extensively studied and is detailed next for prenatal and early postnatal exposure and for circulating hormone concentrations. Prenatal, early postnatal, and pubertal exposure to sex hormones likely contributes to the sex differences in spatial abilities, but circulating hormone concentrations in adulthood have small or no influence on these sex differences.

Prenatal. The study of individuals with CAH and individuals who are homosexuals allows us to understand how prenatal exposure to sex hormones can influence later sex differences. A relatively large analysis of 128 girls and women with CAH and 61 boys and men with CAH revealed significant relationships between prenatal exposure to male hormones and later spatial abilities (Puts, McDaniel, Jordan, & Breedlove, 2008). Almost 7 out of 10 women affected by CAH outperformed their unaffected peers on the types of mental rotation tasks shown in Figure 13.3, whereas nearly 3 out of 4 affected men performed more poorly than their unaffected peers. Collaer and Hines (2020) confirmed this pattern for men but did not find a consistent spatial advantage for women with CAH, suggesting that the postnatal surge in testosterone might be more important than prenatal exposure for the development of spatial abilities. The results for men with CAH are consistent with some studies of nonhuman species showing that excess prenatal exposure to the hormones that normally enhance male-typical traits can sometimes undermine their development (e.g., Jašarević et al., 2011), although these deficits might also be related to a suppressed postnatal surge in testosterone.

Mueller et al. (2008) constructed a virtual water maze in which individuals had to "swim" to an underwater platform when placed in random locations in the maze. The participants included individuals with CAH who varied in terms of the severity of the disease and thus in the level of prenatal exposure to male hormones. The men swam faster and more directly to the platform and had significantly fewer trials in which they failed to find the platform than did women in all groups except the group of women with the severest form of CAH (i.e., those with the highest prenatal exposure to androgens). These women swam as quickly to the platform as the men. Although CAH is typically detected at birth and treated, the treatments do not always completely suppress the excess production of hormones. The result can be higher than normal exposure to male hormones before puberty, which results in faster bone maturation. Individuals with indications of premature bone maturation swam to the platform more quickly and with fewer failures than did individuals with CAH and normal bone maturation. These results indicate that prepubertal, postnatal exposure to androgens can also affect the development of spatial competence. Indeed, infant boys with a strong postnatal surge in testosterone concentrations have better spatial abilities several months later than do boys with a less robust surge (Constantinescu et al., 2018).

It is also the case that homosexual women score higher on many tests of spatial abilities, including three-dimensional mental rotation, than do heterosexual women (Rahman & Wilson, 2003b; van Anders & Hampson, 2005), whereas homosexual men score lower than heterosexual men (Hassan & Rahman, 2007; Rahman, Andersson, & Govier, 2005; Rahman & Koerting, 2008; Rahman & Wilson, 2003b). Overall, these effects are larger and more consistent for homosexual men than women (Xu, Norton, & Rahman, 2017). Using the previously described water maze task, Rahman and Koerting (2008) found that homosexual men had longer swim times than did heterosexual men and swim times similar to that of heterosexual women. As found for heterosexual women, homosexual men also use more landmarks during navigation (Rahman et al., 2005) and have better object location memories than do heterosexual men (Hassan & Rahman, 2007). Van Goozen et al. (2002) administered a battery of spatial ability measures to homosexual female-to-male transsexuals and male-to-female transsexuals and to heterosexual men and women. Heterosexual women had the lowest scores on three mental rotation tasks, followed by the homosexual female-to-male transsexuals, the homosexual male-to-female transsexuals, and the heterosexual men, respectively. In other words, the performance across groups tracked the likely levels of prenatal exposure to androgens or sensitivity to androgens.

Further support comes from the study of genetic males who are insensitive to testosterone at the cellular level and develop as females (without prenatal exposure to male hormones individuals develop as females). Strandqvist et al. (2018) found that individuals with insensitivity to male hormones had female-typical spatial abilities and these were, as is typically found, substantially lower than those of typical men of the same age and education level. van Hemmen et al. (2016) found the same pattern, and that genetic males who were insensitive to testosterone had brain-activation patterns that were similar to those of women when mentally rotating images. These activation patterns were significantly different from those found in men with sex-typical sensitivity to testosterone.

Circulating. As mentioned previously, the study of the relationship between circulating hormones and cognition is like trying to hit a moving target. There are some potential relations to spatial abilities, but these results are not as consistent as those found for prenatal exposure. One idea is that women's performance on spatial tests that typically favor men varies across the ovulatory cycle (see Figure 7.3, Chapter 7, this volume) and will be highest when their estradiol and progesterone levels are low. There have been several of studies that have found just this pattern (e.g., Hampson, 1990a; Hampson, Levy-Cooperman, & Korman, 2014), but overall any relationship between fluctuations in these hormones and women's spatial abilities is likely to be small and may not exist at all (Sundström Poromaa & Gingnell, 2014).

Similarly, a relationship between spatial abilities and circulating testosterone concentrations in young men and women has been found in some studies (Aleman, Bronk, Kessels, Koppeschaar, & van Honk, 2004; Driscoll, Hamilton, Yeo, Brooks, & Sutherland, 2005), but many other studies find a small relationship or no relationship at all (Guerrieri et al., 2016; Puts et al., 2010). In the largest study of this type conducted to date, Puts and colleagues (2010) assessed 160 women and 177 men twice, once when sex hormone levels are generally high (e.g., testosterone in the morning) and once when they are generally low (e.g., testosterone in the evening). There was no consistent relationship between testosterone concentrations and mental rotation abilities for men or women. For any individual, spatial abilities did not vary with changes in their testosterone concentrations, and men or women with higher testosterone concentrations did not have better spatial abilities than their same-sex peers with lower concentrations.

In an experimental study, Guerrieri et al. (2016) assessed men's and women's spatial abilities and then medically suppressed the release of sex hormones for several months. The suppression of testosterone had no effect on men's spatial abilities or their advantages over women. For a few tests, men performed better when their testosterone concentrations were low but this was likely due to practice effects, because scores often are better the second time a test is taken, which in this study was when hormone concentrations were low. Suppression of estradiol was associated with an improvement in women's performance on some spatial tests but not others, and again the improvements were likely due to practice effects.

The majority of these types of studies have assessed young adults and do not address the question of whether the pubertal surge in sex hormone concentrations contributes to the sex differences in spatial abilities. As mentioned previously, there are sex differences in the maturation of several of the brain regions that support spatial abilities (Fish et al., 2020; Salinas et al., 2012; Satterthwaite, Vandekar, et al., 2014). During this time, boys' modest advantage in abilities supported by these areas becomes substantially larger as they move through puberty, especially for more complex spatial abilities (e.g., mentally manipulating complex images; Lauer, Yhang, & Lourenco, 2019; Voyer et al., 1995). Lauer et al.'s (2019) meta-analysis indicated that boys' advantage for more complex spatial abilities more than doubles from 7 to 16 years old.

However, it is not known at this time whether these cognitive sex differences are linked to the pubertal changes in the brain regions that support spatial abilities, although there is some indication that this might be the case (Foland-Ross, Ross, & Reiss, 2019; Modroño et al., 2019). Foland-Ross and colleagues (2019) administered a testosterone-like hormone to boys with a genetic disorder that is associated with low testosterone concentrations during puberty. After 2 years of treatment, and compared with boys with the same disorder who were administered a nonhormonal placebo, the treated boys showed substantial development of the hippocampus and enhanced spatial memory. For the treated boys, larger gains in hippocampal volume were associated with better spatial memory.

Tool Use

Tool construction is much more common among men than among women across traditional societies (Daly & Wilson, 1983; Murdock, 1981); boys appear to develop an intuitive sense of how to use objects as tools at a younger age than girls (Z. Chen & Siegler, 2000; Gredlein & Bjorklund, 2005), and prenatal exposure to androgens results in more frequent engagement in the object-oriented play that appears to facilitate learning how to use objects as tools (Berenbaum, Bryk, & Beltz, 2012; J. T. Davis & Hines, 2020; see Chapter 10, this volume). Moreover, men have more knowledge about tools than do women (Capitani, Laiacona, & Barbarotto, 1999). The brain systems that support tool use in humans are part of the dorsal visual stream that is enhanced in boys and men (G. M. Alexander, 2003; Handa & McGivern, 2015), and include areas of the parietal cortex that are involved in mental rotation and mental imagery and the coordination of these regions with those that support object grasping and manipulation (Johnson-Frey, 2004). Indeed, mechanical reasoning is facilitated by the ability to generate and mentally manipulate images (Hegarty, 2004). The left inferior parietal lobe in particular might be especially important for reasoning about tools and mechanical reasoning more generally (Reynaud, Lesourd, Navarro, & Osiurak, 2016), although actual tool use is also related to brain areas associated with procedural (motor movements) and explicit memories for prior use of tools, among other areas (see Osiurak & Heinke, 2018).

On the basis of these factors, sex differences favoring boys and men in the ability to reason about and effectively use tools, especially in novel contexts, might be expected. Boys and men do report greater interest in mechanical objects and how they work (e.g., Greenberg, Warrier, Allison, & Baron-Cohen, 2018), and there are large sex differences on mechanical reasoning tasks in adolescence and adulthood (Hedges & Nowell, 1995). About 4 out 5 boys and men score higher on complex mechanical reasoning tasks than do same-age girls and women. At the same time, sex differences are not always found for simple mechanical reasoning tasks for older children or adults (Osiurak et al., 2009; Remigereau et al., 2016). The differences across studies are likely due to the complexity of the tasks, as sex differences are often small or nonexistent for easier tasks (e.g., two-dimensional spatial rotation) but are much larger for similar-sounding but more complex ones (e.g., three-dimensional spatial rotation; Lauer et al., 2019). Although much remains to be learned, especially with respect to sex differences, the existing studies are consistent with a stronger evolutionary elaboration of the brain and cognitive systems that support mechanical reasoning and tool use in men than in women.

CONCLUSION

As with our discussion of sex differences in folk psychology, our inferences about the natural history of sex differences in folk biology and folk physics need to be made with some caution, with an eye on sex differences in intrasexual competition, intersexual choice, and the division of labor. Compared with our knowledge of sex differences in folk psychology, we know little about sex differences in folk biology. What we do know, however, is consistent with the division of labor found in traditional societies (i.e., women's foraging, men's hunting; Murdock, 1981).

When differences are found in these societies, women know more about local plants than do men and they use this knowledge for food gathering and preparation and for folk medicines, although in some cultures the men are more knowledgeable about folk medicines than are women (Torres-Avilez, de Medeiros, & Albuquerque, 2016). McDade et al.'s (2007) finding that Tsimané women's, but not men's, knowledge of folk medicines is associated with better health and development for their children is an important one. This is the type of reproductive outcome (offspring survival) that would result in the evolution of folk biological cognitive domains (see Chapter 9, this volume), and in this case, a sex difference for knowledge of local plants. An evolved cognitive module does not necessarily mean a fixed, hard-wired brain system, but rather soft constraints that result in early attentional biases and ease of learning in the domain. We do not yet know if girls and women learn about local plants more easily than do boys and men. While awaiting such studies, we gather additional evidence from the advantage of women in the detection of subtle variation in color in the red–green spectrum (vision that evolved in fruit-eating primates; Shyue et al., 1995) and from Silverman and Eals' (1992) hypothesis and corresponding results (Voyer et al., 2007) that adolescent girls and women have better object location memories than do same-age boys and men. All of these findings are what would be expected if the benefits of foraging were higher for women than for men during our evolutionary history.

Evidence for a corresponding specialization for men's hunting is also found in the folk biological literature (e.g., their greater knowledge of local animals) and in the sex differences in detection of camouflaged objects, tracking object motion at a distance, skill at hitting these moving objects with projectiles, and for navigating in and mentally representing novel large-scale environments (Atran, 1994; M. J. Morgan et al., 1992; Peters, 1997). Whether these sex differences initially emerged from hunting or male–male competition that involved the use of projectiles is debated, although I favor the latter. Evidence that men are also better than women at judging when an object thrown at them will hit them and at blocking such objects indicates male–male competition is a core selective pressure (Schiff & Oldak, 1990; Watson & Kimura, 1991). This is because these are defensive competencies that would not be necessary for hunting. Even if male–male competition was the initial selection pressure for the evolution of these competencies, once they evolved, their use in hunting would reinforce and perhaps further exaggerate the corresponding sex differences, especially given that women prefer successful hunters as mates (see Chapter 7, this volume).

14

Sex Differences in the Modern World

This final chapter offers some thoughts on how the many sex differences in evolved biases that were covered throughout this book might be expressed in the modern world. Of course, much of what we observe day-to-day is expressed in a cultural and historical context that often differs in important ways from the evolutionary contexts of our ancestors. Nevertheless, our evolutionary past echoes forward and influences the expression of sex differences in many areas of modern life. These influences are illustrated with respect to sex differences in school (e.g., reading achievement), at work (e.g., occupational choices), and in the pattern of behavioral and psychological disorders or psychopathology (e.g., risk of depression). A brief discussion of sexual orientation and variation in sexual relationships is also included, and the chapter closes with discussion of sex-specific vulnerabilities related to exposure to certain types of stressors (e.g., the Horsemen of the Apocalypse, man-made toxins; see Chapter 4, this volume).

SEX DIFFERENCES IN SCHOOL

In every nation in which it has been assessed, girls report liking school more than boys do (L. Ellis et al., 2008). Given this, it is not too surprising that girls generally get better grades than boys do from elementary school through college. This is nothing new, as the earliest study of this kind was published more than 100 years ago (Miles, 1910). These differences emerge because the

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social organization of schools is better suited to girls than to boys, and because in relation to boys, girls are more compliant with teacher requests, miss fewer school days, and turn in their assignments with greater frequency. At the same time, there is no sex difference in overall academic achievement, as measured by standardized tests, but there are consistent differences in some specific academic areas, including reading, writing, mathematics, and some of the sciences (Hedges & Nowell, 1995; Stoet & Geary, 2013; Willingham & Cole, 1997). These differences are found during the early elementary school years (sometimes earlier) and grow larger as children progress through school (Reilly, Neumann, & Andrews, 2019).

The largest differences favoring girls are for components of writing, including spelling and the correct use of grammar, with about 7 out of 10 girls outperforming the average boy in overall writing performance (J. Petersen, 2018; Reilly et al., 2019). Girls also have a small but cross-nationally consistent advantage in reading achievement, with about 3 out of 5 girls outperforming the average boy (Reilly et al., 2019; Stoet & Geary, 2013). Overall, there are about twice as many boys as girls in the lowest levels of reading and writing performance and twice as many girls as boys at the highest levels of performance.

The largest differences favoring boys are for the physical sciences, mechanics, and technology (Dekhtyar, Weber, Helgertz, & Herlitz, 2018; Hedges & Nowell, 1995; H. Stumpf & Stanley, 1998). In some of these areas, more than 9 out of 10 boys outscore the average girl, and there are 10 boys to every girl among top performers (e.g., mechanical reasoning, knowledge of electronics; Hedges & Nowell, 1995). Boys' advantage in mathematics is small and varies from one nation to the next for the average student. Nevertheless, there are more consistent sex differences in some areas of mathematics (D. Halpern et al., 2007), and there are about two or three boys (sometimes more) to every girl among the top performers (Makel, Wai, Peairs, & Putallaz, 2016). The sex differences in the pattern of academic achievement are interesting and important, but at first blush they appear to be far removed from the cognitive domains covered in Chapters 12 and 13 of this volume.

It has been argued that these folk abilities provide the foundation for the construction of culturally specific abilities and knowledge (Geary, 1995a; see also Chapter 9, this volume). I call the latter *biologically secondary abilities* to distinguish them from the biologically primary folk abilities discussed in previous chapters. There is not always a sharp distinction between these forms of ability, especially in the very early years of schooling (Geary & Berch, 2016). Still, acknowledging that some abilities are universal (e.g., language) and that others (e.g., reading) can be built from them but only as a result of cultural practices, especially formal schooling, is essential for an understanding of modern education (Geary, 2005, 2007, 2008).

The distinction is important because it allows for a framing of sex differences in achievement outcomes as they might relate to differences described in Chapters 12 and 13 of this volume. I cannot detail the mechanisms needed to construct secondary abilities from primary ones (see Geary, 2007, 2008), but note that intelligence is among them. After a brief tour of sex differences in intelligence, reading and mathematics are used to illustrate how this approach can be used to link evolved sex differences in folk abilities to sex differences in academic abilities.

General Intelligence

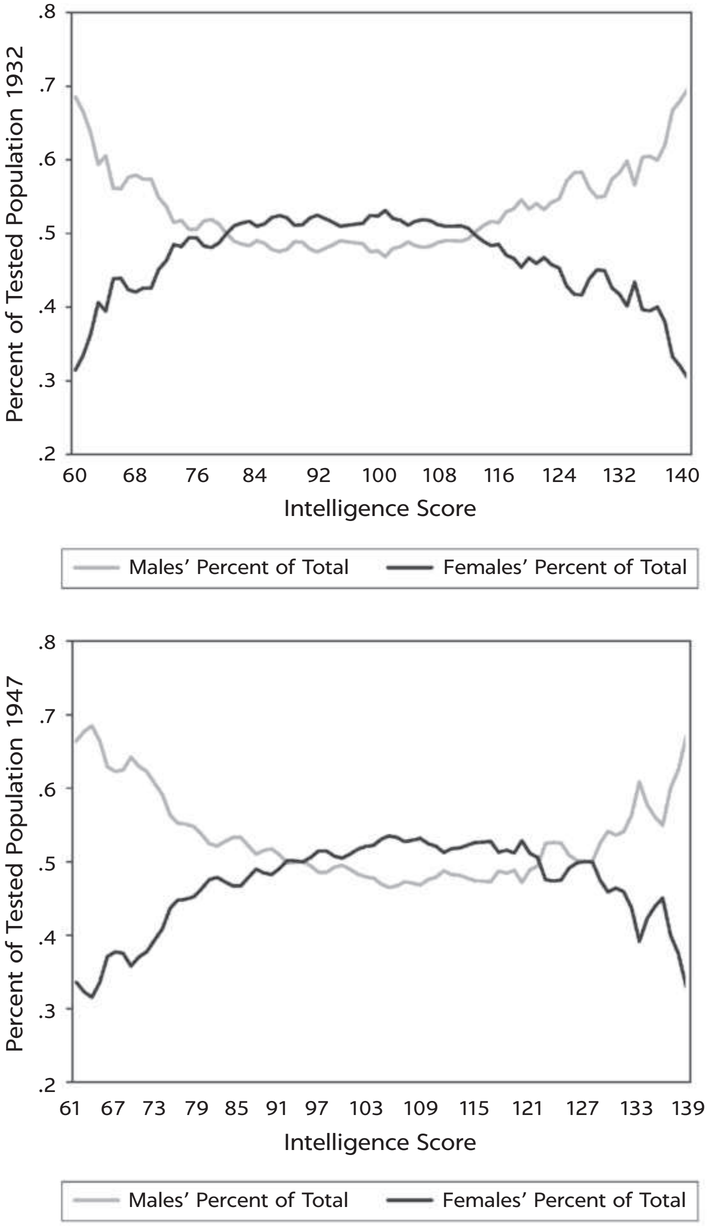
General intelligence is typically measured using IQ tests and is composed of the ability to focus attention on the matter at hand and to use working memory resources to reason and problem solve about this matter (see Chapter 9, this volume; Geary, 2005). General intelligence is important for our discussion because it influences the ease of learning in school and the outcomes on academic achievement tests. Critically, the combination of intelligence and academic abilities contribute to occupational outcomes in the modern world (Gottfredson, 1997; Kell, Lubinski, & Benbow, 2013).

The issue of whether there are sex differences in intelligence is a long-standing one that often generates considerable rancor and debate (Blinkhorn, 2005; Irwing & Lynn, 2005). In a meta-analysis of sex differences in the intelligence of young adults, Irwing and Lynn (2005) found a 3- to 5-point advantage for men, as did Jackson and Rushton (2006). However, other studies have found small to no sex differences for children or adults (Dykiert, Gale, & Deary, 2009; van der Sluis et al., 2006, 2008). One of the largest and most representative of these studies included more than 150,000 11-year-olds and found no average sex difference in intelligence (W. Johnson, Carothers, & Deary, 2008). The mixed results may be related in part to the different tests that were used and ages assessed across studies (Arribas-Aguila, Abad, & Colom, 2019; Buczyłowska, Ronniger, Melzer, & Petermann, 2019; W. Johnson & Bouchard, 2007). These differences are potentially important because any sex differences in intelligence may vary across development.

Buczyłowska et al. (2019) found that 2-year-old girls had an advantage over same-age boys in nonverbal reasoning that was equivalent to about 2 IQ points, but this sex difference disappeared over the next several years. In a study of more than 10,000 adolescents and using seven different types of tests (many tests provide a better estimate of intelligence), Arribas-Aguila et al. (2019) found no sex difference in intelligence in early adolescence, as found by W. Johnson et al. (2008), but a modest advantage of about 4 IQ points emerged for boys by the end of adolescence, consistent with at least some findings for adults (Irwing & Lynn, 2005). These developmental sex differences may be related to the sex differences in the timing and pattern of brain maturation (R. Lynn, 1994), but this remains to be directly assessed.

In any case, a more consistent finding is that there are more boys and men at the high and low ends of intelligence (Deary, Irwing, Der, & Bates, 2007; Feingold, 1992b; Lubinski & Humphreys, 1990; Wai, Cacchio, Putallaz, & Makel, 2010). One of the best examples of this is again provided by W. Johnson et al.'s (2008) assessment of more than 150,000 11-year-olds. The distributions of the intelligence scores of these children are shown in Figure 14.1

FIGURE 14.1. Sex Differences in the Distribution of Intelligence Scores



The proportion of 11-year-old boys and girls with different intelligence scores assessed in the 1932 (top) and 1947 (bottom) Scottish Mental Surveys; proportions are 3-point moving averages. From "Sex Differences in Variability in General Intelligence: A New Look at the Old Question," by W. Johnson, A. Carothers, and I. J. Deary, 2008, *Perspectives on Psychological Science*, *3*, p. 525. Copyright 2008 by Sage. Reprinted with permission.

for the 1932 (top) and 1947 (bottom) Scottish Mental Surveys. Both surveys show that there were two boys to every girl at both extremes, as well as an over representation of boys in the lower range of the distributions (intelligence < ~80). Of the most extreme scores in the top distributions, about 70% of the children with scores of 60 and 140 are boys and 30% are girls. Scores at these extremes represent roughly the bottom and top 1% of intelligence, respectively. In a unique study that controls for many aspects of the prenatal and postnatal environments, Deary et al. (2007) compared the intelligence of 1,296 pairs of opposite-sex twins. There was only a small male advantage for average intelligence, but again there were more brothers than sisters at the high and low ends. For the top 2% of scores, brothers outnumbered sisters 2 to 1.

The biological factors that contribute to this variation are debated and not fully understood (see Craig, Haworth, & Plomin, 2009; Geary, 2018; W. Johnson et al., 2008). Traits that have evolved through intrasexual competition or intersexual choice are often more sensitive to ecological and social conditions than are other traits, and one consequence is a sex difference in the variability of these traits (Geary, 2015). If intelligence has contributed more to competition among males than among females or influenced female choice more than male choice (Arden, Gottfredson, Miller, & Pierce, 2009; G. F. Miller, 2000), then the variability among boys and men and the sex difference in average intelligence may vary from one culture to the next and historically. Whatever the case, consideration of this variation is practically important because these differences can contribute to sex differences in the extremes of academic and occupational achievement. With respect to more typical performance in school, the average boy and girl are more or less equal in intelligence and so for these children sex differences in academic abilities (e.g., reading) must be related to something other than IQ.

Academic Patterns

It has been argued elsewhere that the working memory and attentional components of intelligence, along with the ability to systematically reason, problem solve, and form abstract concepts, contribute to the ability of people to modify evolved folk systems to learn how to read, write, do geometry, and other culturally specific academic competencies (Geary, 2005, 2007). Even with similar average levels of intelligence, sex differences can emerge in academic domains to the extent that there are sex differences in the primary folk systems on which the academic competences are built. This is illustrated using the sex differences in reading and some aspects of mathematics.

Reading

Girls and women have a modest but consistent advantage on reading tests across historical periods and nations (L. Ellis et al., 2008; Hedges & Nowell, 1995; Reilly et al., 2019; Stoet & Geary, 2013, 2015; Willingham & Cole, 1997). Some of the sex differences we reviewed in Chapter 12 may be the source of their advantage. In particular, the advantage of girls and women in the mechanics of language production and in language comprehension, along with theory of mind, appear to provide them with a head start over boys and men when learning how to read and in comprehending text that involves nuanced social relationships.

The critical link is that reading is built on the evolved language system (Mann, 1984; Rozin, 1976), such that there is a substantive overlap with the brain regions that support the acquisition of language and many aspects of reading, including basic phonological decoding (i.e., sounding out written words), reading fluency, and text comprehension (Paulesu et al., 2001; C. J. Price & Mechelli, 2005; Pugh et al., 1997; Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003). In a review of brain imaging and related research on language processing, C. J. Price (2000) concluded that the passive processing of language sounds occurs in the traditional Wernicke's area, speech production involves Broca's area and areas that support word articulation, and the representations of the meaning of spoken and heard utterances is distributed across the temporal and parietal cortices (see also Chapter 12, this volume). One of the first steps in learning how to read is phonological awareness, an explicit understanding of the language sounds associated with specific letters and letter combinations (e.g., "ba," "pa"), and Wernicke's and Broca's areas are involved in this learning, in the reading of individual words, and in aspects of text comprehension (e.g., Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Paulesu et al., 2001).

There are also nonlanguage brain regions that support reading (McCandliss, Cohen, & Dehaene, 2003), but the basic point should be clear. Children with advanced language skills learn how to read more easily and read more fluently than do other children. As described in Chapter 12 of this volume, girls and women have advantages over boys and men in the brain and cognitive systems that support language acquisition and use, and they should also have advantages in reading (and writing), in theory. The previously noted sex differences in reading achievement in school-age children and adults are consistent with this expectation. In keeping with more rapid language development in girls than boys (Lange, Euler, & Zaretsky, 2016), young girls learn the basics of reading at an earlier age and with less difficulty than do same-age boys (Chipere, 2014; Sigmundsson, Eriksen, Ofteland, & Haga, 2017). In a study of nearly 500 children at the beginning of their schooling, Sigmundsson et al. (2017) found that girls had advantages over boys in the recognition of letters and in knowledge of the corresponding sounds. These are essential skills during the initial stages of learning how to read, and girls' early advantage here almost certainly contributes to the later sex differences in reading achievement.

Independent of brain and cognition, sex differences in reading interests contribute to the sex differences on reading comprehension tests (Asher & Markell, 1974). Girls and women read more than boys and men, independent of actual reading ability (M. C. McKenna, Kear, & Ellsworth, 1995), and read more about romance and other interpersonal relationships than do boys and men. Girls and women are more interested in the details and nuance of their actual social relationships than are boys and men, and this interest is expressed in their leisure reading and often assessed in reading comprehension tests.

When boys and men read, they read more about politics, competition (e.g., sports), and technical matters (e.g., Benton, 1995; Willingham & Cole, 1997). These sex differences mirror some of the sex differences described in Chapter 11 of this volume, as well as many of the other sex differences covered throughout the book, including those related to male–male competition, tool use, and mechanical knowledge. In short, I am proposing that the sex differences in reading interests reflect deeper sex differences that reflect our evolutionary history.

Mathematics

Mathematics is considered a gateway to employment in well-paying and prestigious science, technology, engineering, and mathematics professions (STEM), and because of this the issue of sex differences in mathematical competence is a continuing source of review, conjecture, and heated debate (Ceci & Williams, 2007; Ceci, Williams, & Barnett, 2009; D. Halpern et al., 2007; Stoet & Geary, 2018). Across grades and nations, the overall sex difference in mathematics achievement is small (Hyde, Fennema, & Lamon, 1990; Lindberg, Hyde, Petersen, & Linn, 2010; Stoet, Bailey, Moore, & Geary, 2016), but practically important differences emerge for high school (or secondary) mathematics (Lindberg et al., 2010) and at the high end of performance (D. Halpern et al., 2007; Harnisch, Steinkamp, Tsai, & Walberg, 1986; Penner, 2003; Wai et al., 2010). Most of the associated assessments of sex differences were based on overall mathematics achievement or for general performance in particular domains (e.g., algebra, geometry).

When differences are assessed within domains, girls often outperform boys on school-taught algorithmic or computational problems and boys tend to outperform girls on more novel, spatial-related problems (M. B. Casey, Nuttall, Pezaris, & Benbow, 1995; E. S. Johnson, 1984; Lindberg et al., 2010; Marshall & Smith, 1987). Sex differences also tend to increase with increases in the complexity of the mathematics. For high school algebra, boys have a small advantage overall (Harnisch et al., 1986; Lindberg et al., 2010), but this gap becomes about 4 times larger for more complex aspects of algebra (Harnisch et al., 1986).

Geary (1996) argued that these differences are related, at least in part, to the advantage of boys and men in the spatial abilities described in Chapter 13 of this volume, the sex difference in interest in people (stronger in women) versus things (stronger in men), and to the higher numbers of men than women at higher levels of mathematics achievement. The solving of multistep mathematical word problems illustrates the relation between spatial abilities and the sex differences in some areas of mathematics. The solving of these problems is easier if the relationships among the variables or quantities in the problem statements are diagramed or spatially represented (A. B. Lewis, 1989). Boys and men typically outperform girls and women on these types of problems and their advantages are explained in part by their spontaneous use of spatial representations during problem-solving (M. B. Casey et al., 2015;

Geary, Saults, Liu, & Hoard, 2000; E. S. Johnson, 1984). Of course, the evolutionary elaboration of men's spatial abilities was not driven by skill at solving word problems, but these abilities can nevertheless be used to solve such problems, as well as problems in many other evolutionarily novel domains.

There are multiple influences on the development of mathematical and other STEM competencies and multiple biological and social influences on the sex differences in these domains (Ceci et al., 2009). Important social influences are suggested by recent changes in the ratio of boys and men to girls and women at the very high end of performance on mathematical tests. The ratio has dropped from about 13 to 1 in 1983 to roughly 3 to 1 today (Benbow & Stanley, 1983; Ceci et al., 2009; Wai et al., 2010). Girls and women also have more anxiety about mathematics than do boys and men above and beyond the sex difference in mathematics achievement, and this too likely contributes to sex differences in long-term interests in mathematics and mathematics-related careers (Geary et al., 2019; Stoet et al., 2016). Even so, boys' and men's advantages in spatial abilities and their greater interest in things (vs. people) contribute to the sex differences in some mathematical domains.

SEX DIFFERENCES AT WORK

In the modern world, occupational success means cultural success, and cultural success means reproductive success for men but not typically for women (see Chapter 8, this volume). In traditional societies, men are much more focused than women on attaining social and cultural status, because success in these spheres often means the difference between reproducing or not. To be sure, social status is important to women and their children, but the consequences of not directly achieving some modicum of success are not as severe as they are for low-status men. It follows from these patterns that men will have an inherent motivational bias to devote time and effort into achieving success in their cultural niche. On the basis of the sex difference in parental effort, women in turn are predicted to trade time and effort that would otherwise be focused on attaining cultural success for time and effort to devote to their families. Women who do not make this trade-off often pay the cost of having fewer children, on average (see Chapter 8, this volume).

All of these predicted patterns are found in the modern workplace (K. R. Browne, 2002). Across occupations "evidence consistently suggests that despite comparable educational qualifications, tenure, and occupational attitudes, women have not achieved occupational status comparable to that of men" (S. D. Phillips & Imhoff, 1997, p. 46). I am not arguing that bias does not sometimes contribute to these differences, but I am saying that bias is not a sufficient explanation for all of them. In addition to motivational differences, there are cognitive and social factors that contribute to the sex differences in occupational attainment as well as differences in occupational interests.

These differences are illustrated for STEM fields, as these are often a source of social and political contention (National Academy of Sciences, 2006). The differences here are largely for fields that focus on inorganic topics (e.g., physics, engineering, computer science) and not the life sciences and related fields (e.g., medicine, veterinary medicine), where women often outnumber men (e.g., Lofstedt, 2003). In addition to cognitive and social influences on sex differences in the pursuit of and accomplishment in STEM fields, men and women who enter these fields or have the capacity to do so make different work–life trade-offs. Men work longer hours and are relatively more career-focused than are women and achieve more on average (Aguinis, Ji, & Joo, 2018; McCabe, Lubinski, & Benbow, 2019), whereas more women than men prioritize relationships with family and friends over occupational accomplishment (Ferriman, Lubinski, & Benbow, 2009). The sex differences in these trade-offs are not restricted to STEM fields; they are broadly evident in modern nations (Hakim, 2002) and are evident in one form or another in all human cultures (see Chapters 6 and 8, this volume).

Cognitive Influences

More men than women enter high-paying mathematics-intensive STEM occupations, and this pattern contributes to the overall wage advantage enjoyed by men (Chevalier, 2007; Paglin & Rufolo, 1990). The attainment of the educational credentials that allow access to certain high-paying STEM careers, such as engineering, is made easier by a number of cognitive factors; specifically, above average intelligence and above average spatial, mathematical, and mechanical competencies (Bernstein, Lubinski, & Benbow, 2019; Gottfredson, 1997; Humphreys, Lubinski, & Yao, 1993). Boys' and men's advantages in spatial abilities and mechanical reasoning were discussed in the previous chapter, and sex differences at the high end of mathematics achievement were discussed in the Mathematics section of this chapter.

Sex differences in the latter contribute to the sex difference in the proportion of men and women entering mathematics-intensive STEM fields. Individuals who enter these fields tend to have SAT-Mathematics and Graduate Record Examination-Quantitative scores that are in the 600 to 800 range on the old scale (500 was average, 800 was the top) and the ratio of men to women with scores in this range is between 2 to 1 to more than 5 to 1 (Paglin & Rufolo, 1990). The ratio of top-scoring men to women on physics tests is nearly 3 to 1 and about 5 to 2 on chemistry tests (Stanley, 1993). A similar pattern is found for many other advanced placement tests, including tests in all areas of physics and chemistry (Stanley, Benbow, Brody, Dauber, & Lupkowski, 1992). In other words, many more men than women have the minimal spatial, mathematical, and mechanical competencies needed to succeed in many inorganic STEM fields.

This is not the whole story, however, as it is not simply the absolute level of performance in mathematics or other areas that influences college course taking and career choices. Each individual's best academic and cognitive competence also influences these choices (Dekhtyar et al., 2018; Stoet & Geary, 2018). Individuals who are better in language-based than mathematics-based areas are more likely to obtain college degrees (e.g., in the humanities) and pursue careers that capitalize on this comparative advantage, even if they have exceptionally high mathematical abilities (Bernstein et al., 2019). Throughout the world, adolescent girls are on average relatively better in language-based than mathematics- or science-based areas, whereas adolescent boys show the opposite pattern, and this in turn at least partially explains the sex difference in STEM career choices (Stoet & Geary, 2018).

Nevertheless, in a longitudinal study of more than 165,000 people, Dekhtyar et al. (2018) found that this comparative advantage was more strongly expressed in the occupational choices of men than women; fewer women went into technology and mathematics when they had strengths in these fields than did men with similar cognitive profiles. Several potential reasons for this are discussed next. Whatever the reasons, women who enter STEM careers in inorganic areas are very similar to their male colleagues in many ways (Lubinski, Benbow, Shea, Eftekhari-Sanjani, & Halvorson, 2001), there just are not as many of these women as men.

Social Influences

I suspect that social sex differences may be relatively more important than the cognitive ones for understanding why more men than women enter and stay in inorganic STEM fields. When women and men are free to choose their own careers, their occupational interests and choices consistently differ (Quadlin, 2020). On interest tests, "young women [score] higher than young men on domestic, artistic, writing, social service, and office service vocational interests and young men [score] higher than young women on business, law, politics, mathematics, science, agriculture, athletics, and mechanical interests" (Willingham & Cole, 1997, p. 178). The sex difference in vocational interests is especially striking among the mathematically gifted. When they are in their 20s, for every mathematically gifted woman who is working toward or who aspires to earn an advanced degree in a mathematics-intensive STEM field, there are 8 equally talented men (Lubinski & Benbow, 1994).

For these gifted individuals, the sex difference in the pursuit of an advanced education in STEM areas cannot be attributed to cognitive factors, because all of these women have the mathematical and intellectual competencies necessary to succeed in these careers. Nor can the difference be attributed solely to a bias against women; gifted women as a group do not view mathematics as a "male occupation" and are not discouraged from pursuing mathematics-intensive careers (e.g., Raymond & Benbow, 1986). Rather, the sex difference in the pursuit of inorganic STEM careers is driven in part by the occupational and social interests of these gifted men and women.

People who enter STEM fields, especially inorganic ones, tend have a relatively "low need for people contact" (Lubinski, Benbow, & Sanders, 1993,

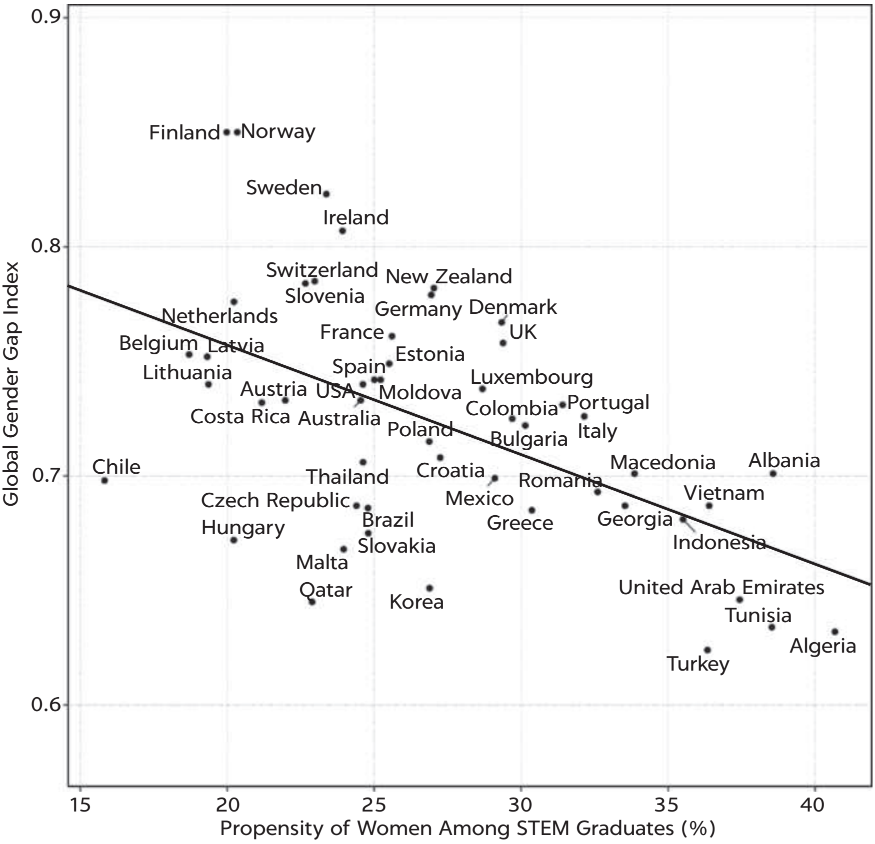
p. 701) and tend to prefer work environments that provide many theoretical and investigative activities. Mathematically gifted men who enter these fields do indeed show this pattern of occupational and social interests. As a group, mathematically gifted women "are more socially and esthetically oriented [than their male peers] and have interests that are more evenly divided among investigative, social and artistic pursuits" (Lubinski et al., 1993, p. 702). In short, proportionally fewer of these women enter STEM fields because they have broader social and occupational interests than their male peers. The gifted women who do enter these fields are very successful in them, but as they move from graduate school to their mid-30s, more of these women than their male counterparts make trade-offs that will likely affect their career development. More precisely, more women than men who have children shift their priorities so they can devote more time to their families and to the wider community (Ferriman et al., 2009; see also Pinker, 2008); the shift from a career- to family-focus makes sense in terms of the sex differences in life-histories trajectories (i.e., women have a sharper decline in fertility than men beginning in their 30s).

The same pattern of sex differences applies to less-gifted men and women and to non-STEM careers (Chevalier, 2007; Lauermann, Tsai, & Eccles, 2017; Su & Rounds, 2015; Su, Rounds, & Armstrong, 2009), although there are many career-focused women. Women are actually more heterogeneous than are men when it comes to career focus (Hakim, 2002). Hakim theorized that about 20% of women in modern societies are work-focused (>50% of men are work-focused), 20% are home-focused, and the remainder prefer some combination of work and home activities. A nationally representative survey of adults in the United Kingdom confirmed this general pattern, with 14% of women indicating a work-focused preference, 16% a home-focused preference, and the remainder a mixed home- and work-preference (Hakim, 2002). Most women were able to achieve these preferences (see also Eccles & Wang, 2016). The vast majority (82%) of well-educated and work-focused women had full-time careers, whether or not they had children; "patriarchal values have very little impact, and child care responsibilities have no impact at all on work rates among work-centered women" (Hakim, 2002, p. 446). If anything, the home-focused women were less able to realize their preferences, as many of them had to work to contribute to family finances (e.g., to help pay a home mortgage).

There are, in addition, social influences on occupational choices but these are not the influences that many people believe. Stereotype threat is one of the latter and a popular explanation of the sex differences in pursuit of mathematics-intensive college majors and careers (S. J. Spencer, Logel, & Davies, 2016; S. J. Spencer, Steele, & Quinn, 1999). The argument is that the stereotype that "women are not as skilled in mathematics as men" undermines women's performance in situations that involve mathematics. One way in which this could occur is through a preoccupation with the stereotype when solving mathematics problems, with the preoccupation distracting women from mathematical problem-solving and thereby undermining their performance. The concept is a favored explanation for the sex differences in mathematics-intensive areas, but the actual effect of this stereotype on girls' and women's mathematical performance is small and possibly nonexistent (Flore & Wicherts, 2015; Ganley et al., 2013; Stoet & Geary, 2012).

Paradoxically, the sex differences for many psychological and behavioral traits are larger in Western, educated, industrialized, rich, and democratic (WEIRD) nations (Henrich, Heine, & Norenzayan, 2010) than they are in developing nations or in traditional cultures (Schmitt et al., 2017). These are nations in which women and men are more free to pursue their interests, which often increases the magnitude of any associated sex differences. Stoet and Geary (2018) found that this is also the case for the sex difference in inorganic STEM fields, as shown in Figure 14.2. They found that the propensity of women to pursue college degrees in these fields (based on the percentage of

FIGURE 14.2. National Gender Equality and the Propensity of Women to Obtain College Degrees in Inorganic Science, Technology, Engineering, and Mathematics Fields



As equality within nations increases, as measured by the Global Gender Gap Index, the propensity of women (based on percentage of all women enrolled in college) to obtain college degrees in inorganic science, technology, engineering, and mathematics (STEM) fields decreases. Figure by Gijsbert Stoet. Reprinted with permission.

women in college) declines as nations become wealthier and more egalitarian. One reason is that most of these nations have social safety nets that make the pursuit of high-paying occupations less critical than in other nations. The safety net in turn frees women to pursue occupations that are more consistent with their interests in people (vs. inorganic things) and social relationships (Su & Rounds, 2015).

SEX DIFFERENCES IN PSYCHOPATHOLOGY

Numerous behavioral and psychological sex differences have been covered throughout this book. The following section touches on behavioral and psychological issues that are considered to be pathological in modern societies. Del Giudice (2018) provides an extensive evolutionary framing of psychopathology, and the next sections illustrate the usefulness of this approach by examining sex differences in externalizing (e.g., different forms of behavioral aggression, substance abuse) and internalizing (e.g., anxiety, depression) disorders, respectively (see also Martel, 2013).

The focus here is on externalizing and internalizing disorders because these, along with thought disorders (e.g., paranoid delusions), appear to capture the core issues that underlie many more specific disorders (Caspi et al., 2014), and because there are sex differences in these core areas. In a large-scale study of more than 1,000 individuals who were followed from childhood to adulthood, Caspi et al. (2014) did not find a sex difference in risk of thought disorders but they did find that boys and men were more likely to show some form of externalizing symptoms or be diagnosed with an externalizing disorder, and adolescent girls and women were more likely to show some form of internalizing symptoms or be diagnosed with an internalizing disorder. Once other factors were taken into consideration, about 4 out of 5 boys or men showed more externalizing behaviors than did the average girl or woman, whereas more that 4 out of 5 girls or women showed more indications of internalizing symptoms than did the average boy or man. More generally, the sex differences in externalizing behaviors are evident in young children and continue into adolescence and adulthood, whereas the sex differences in internalizing symptoms and behaviors do not typically emerge until adolescence and continue into adulthood (Martel, 2013).

Some details on these sex differences are provided next and include accidental injury with the discussion of externalizing disorders, because the behaviors that result in these mishaps are also more common in boys and men than in girls and women and likely have a similar evolutionary root.

Externalizing Disorders and Accidents

On the basis of sex differences in physical intrasexual competition and risk taking, it is not surprising that boys and men outnumber girls and women when it comes to externalizing disorders and accidental injuries (L. Evans, 2006; Martel, 2013; B. N. Rosen & Peterson, 1990; Rushton, 1996; see Chapter 8, this volume). A few of these sex differences are described next.

Externalizing Disorders and Violence

Consistent with an evolutionary history of physical one-on-one and coalitional male–male competition, there "is no known human society in which the level of lethal violence among women even approaches that among men" (Daly & Wilson, 1988b, p. 146). As discussed in Chapter 8 of this volume, during much of human history, dominance-based status striving was a common feature of men's reproductive strategies and often included the murder of ingroup or outgroup rivals. Perpetrators of violence often enjoyed an increase in social status and marriage prospects (Betzig, 1986, 2012; Chagnon, 1988). This form of status striving is suppressed in developed nations today and directed into prestige-based competition (i.e., acquiring culturally valued skills; Henrich & Gil-White, 2001). Despite the suppression of this way of achieving one's goals, these behaviors or precursors to them are still expressed in the modern world.

In an analysis of same-sex homicide rates across developing and developed nations, including homicide records dating from more than 700 years ago, Daly and Wilson (1988b) found that male-on-male homicide occurs between 30 and 40 times more frequently than does female-on-female homicide. Male-on-male homicide occurs most frequently during the initial mate-finding stage of the lifespan (i.e., late teens through mid-20s) and more frequently among unmarried than married men (M. Wilson & Daly, 1985). Moreover, roughly 2 out of 3 male-on-male homicides occur as a result of social conflict rather than being crime-specific (e.g., during the course of a robbery), and more than half of the homicides are associated with "matters of status competition and the maintenance of face" (Daly & Wilson, 1988b, p. 175). In an extensive analysis of more than 290,000 homicides in the United States, T. Allen, Salari, and Buckner (2020) found that 87% of them were perpetrated by men and that the largest cluster was male-on-male homicides among acquaintances in their 20s. In contrast, about 2% of homicides across all ages involved a woman killing another woman.

Men not only kill each other much more frequently than do women, they also kill women more frequently than women kill men, but the difference here is smaller than the difference between male-on-male homicide and female-on-female homicide. In T. Allen et al.'s (2020) analysis, 23% of homicides involved men killing women and 10% involved women killing men. This form of male-on-female violence, as well as serious nonlethal assaults, often stems from mate guarding and sexual jealousy (see Chapter 7, this volume). I am not excusing these forms of violence, but rather noting that they can be better understood and addressed by placing these social dynamics within an evolutionary context. Even if male violence was once effective and adaptive as a reproductive strategy, it is no longer nor should it be in the modern world.

The sex differences in homicide rates are mirrored by sex differences in nonlethal forms of behavioral aggression (Piquero, Jennings, Diamond, & Reingle, 2015), and in externalizing forms of psychopathology among children and adolescents (Martel, 2013). These are not simply antisocial behaviors, but from an evolutionary perspective involve conflicts of interest and often dominant–submissive relationships between the victim and perpetrator. Among children these include conduct disorder, which involves a persistent pattern of violating social rules and the rights of others, as well as aspects of attention-deficit/hyperactivity disorder, which includes excess physical activity and at times aggressive behaviors. Many of these children also exhibit a tendency toward callousness and emotional indifference to the well-being of others; a subset of these children and adolescents lack empathy and guilt.

This is not to say that children with externalizing disorders will become violent offenders, but they are at higher risk of engaging in various forms of antisocial behavior, including physical aggression, as they move into adolescence and adulthood (Eme, 2020; Moffitt, 2018; Moffitt & Caspi, 2001; Pardini & Fite, 2010; Quinsey, Skilling, Lalumiere, & Craig, 2004). Erskine et al.'s (2013) meta-analysis indicated that children with conduct disorder are 3.5 times more likely to commit a violent crime in adulthood than are other children. Many of these individuals have a host of other problems (e.g., poor educational outcomes, substance abuse) that undermine their cultural success in the modern world, but at least some of these same traits (e.g., callousness) might have been more functional in traditional contexts with frequent male–male physical competition. In other words, many of the key symptoms of these disorders might be traced back to an evolutionary history of male–male physical competition, but their full expression will also be influenced by developmental experiences and social factors (Martel, 2013).

In cultures with intense male–male warfare, child rearing practices (e.g., the Swing-Kicking Game of the Sioux, Chapter 10, this volume) and the initiation rites for boys tend to be harsh (Sosis, Kress, & Boster, 2007), and likely increased callousness and emotional indifference to the suffering of others, as well as encouraged behavioral aggressiveness. Individuals who are prone to physical aggression and with high levels of callousness and emotional indifference have lower levels of fear and anxiety, are less concerned about the wellbeing of others, discount the potential consequences (e.g., punishment) of their behavior, and engage in more predatory aggression than do other individuals (P. J. Frick, Ray, Thornton, & Kahn, 2014). This is a constellation of traits that seems to be well suited for violent male-on-male physical aggression, especially when directed toward people in an outgroup. Many of these individuals thrive in highly competitive and risky professions these days, if they have sufficient intelligence and the ability to control their physical aggressiveness (Del Giudice, 2018).

In any event, the finding that there are more boys and men than girls and women with externalizing disorders is generally consistent with a link to an evolutionary history of male–male competition but externalizing disorders are broader than this (e.g., including substance abuse) and the most direct link is to the subset of disorders that involve predatory aggression. These would include conduct disorder in children and antisocial personality disorder in adults. Overall and across time and nations, there are about two to four boys for every one girl with common externalizing disorders, including conduct disorder (Erskine et al., 2013; Wittchen et al., 2011). The most severe and persistent form of conduct disorder begins in early childhood, continues into adulthood, and is manifested as a repeated use of aggression and intimidation to achieve one's goals. Among these individuals, there are 10 or more boys and men for every one girl or woman (Moffitt & Caspi, 2001; Moffitt, Caspi, Rutter, & Silva, 2001). The latter conclusion is based on Moffitt and colleagues' (2001) seminal longitudinal study of more than 1,000 New Zealanders who were followed from childhood to adulthood. They found that 10% of the boys and 1% of the girls had a persistent pattern of externalizing behaviors, including poor attentional control and frequent physical fights with peers. As was described in Chapter 11 of this volume, Andy's use of physical and verbal intimidation to gain leadership of his cabin illustrated how these types of behaviors might be socially effective, although it does not work when adults are around and intervene to disrupt the dynamic.

Many of these children also experienced harsh parenting and other early stressors that are often associated with more frequent externalizing behaviors (Moffitt & Caspi, 2001; Moffitt et al., 2001), although it is not known whether these experiences exacerbate externalizing problems, are parental reactions to them (i.e., child evocative effects), or most likely some combination. Other studies suggest that children with typical levels of callousness and emotional indifference are affected by harsh treatment; their rates of violating the rights of others increases, whereas many children and adolescents who are very callous and unemotional violate the rights of others regardless of early background (P. J. Frick et al., 2014; Mealey, 1995). In other words, most boys can be socialized to be more (or less) callous and aggressive (see Chapter 11, this volume), whereas others are callous, aggressive, and self-serving for largely inherent reasons. Whatever the cause, there are more boys and men than girls and women at the extremes of these traits. Even in more typical samples, between 7 and 8 out of 10 boys and men score higher on callousness-unemotional traits than does the average girl and woman (Essau, Sasagawa, & Frick, 2006; Ueno, Ackermann, Freitag, & Schwenck, 2019). These patterns seem to follow from an evolutionary history of more intense and deadlier male–male than female–female competition and of women's higher level of investment in children and their need to develop intense and socially supportive friendships that mitigate callousness.

Accidents

Engagement in risky behaviors is an aspect of boys' and men's status striving (see Chapter 8, this volume), which in turn is a component of male–male competition. When successfully executed, a risky behavior can result in fame and sometimes fortune, but more typically it results in a boost in status within the daredevil's peer group. When unsuccessful, risky behavior often leads to accidental injuries and sometimes death. In a comprehensive assessment of childhood injuries and deaths in the United States, B. N. Rosen and Peterson (1990) documented a much higher frequency of accidental death and injury in boys than in girls. Boys experience nearly drowning about twice as frequently as girls and die as a result of drowning almost 4 times as frequently as girls. Boys are injured and killed more frequently than are girls while riding bicycles, playing on recreational equipment, and during unorganized (i.e., not supervised by adults) sports activities. For every girl that is injured on a playground, four boys are injured. For every girl who sustains a serious burn, three boys sustain an equally serious burn (e.g., while playing with fireworks). These patterns are not unique to the United States (e.g., A. Kim, Song, Park, Choi, & Cho, 2018).

B. N. Rosen and Peterson (1990) concluded that the sex differences in accidental injury and death rates are related to the sex differences in activity levels, risk taking, and the frequency of engagement in rough-and-tumble and competitive play. The same is found in adulthood, as illustrated by L. Evans' (2006) analysis of traffic fatalities in the United States, which "favor" adolescent boys and men by about a 4 to 1 ratio. As with male-on-male violence, the sex difference in traffic accident fatalities per capita peaks in the late teens and early 20s—again, the sex difference is not restricted to the United States (Rathi, 2018). In some cases, the reasons for the self-inflicted injury and death elude rational explanation and merit a posthumous "Darwin Award," an award for self-removal from the gene pool because of ill-advised behaviors. For every woman who has received this award, there are nine men (Lendrem, Lendrem, Gray, & Isaacs, 2014). The following provides some examples of individuals who received a Darwin Award:

> The man stealing a ride home by hitching a shopping [cart] to the back of a train, only to be dragged two miles to his death before the train was able to stop; and the terrorist who posted a letter bomb with insufficient postage stamps and who, on its return, unthinkingly opened his own letter. (Lendrem et al., 2014, p. 1)

Internalizing Disorders

Adolescent girls and women experience higher levels of fear and anxiety—common components of internalizing disorders—than do boys and men (Caspi et al., 2014). This is one of the reasons that girls and women suffer from fewer accidental injuries and deaths than boys and men and are much less likely to escalate interpersonal conflicts to extreme physical violence. From an evolutionary perspective, fear and anxiety have been honed by natural selection to prompt the individual to avoid circumstances that could result in injury or death. Boys' and men's greater risk taking, including escalated violence, can only be explained by sexual selection, because it is necessary in many contexts to achieve status. In the absence of these status and reproductive-related benefits, modest levels of fear and anxiety are protective but extreme levels can disrupt daily life and be considered a psychopathology (Del Giudice, 2018). The following sections illustrate a few ways in which these can manifest in the modern world.

Anxiety and Depression

Anxiety disorders (e.g., generalized anxiety, social phobia) often occur together and co-occur with some form of mood disorder, especially major depression (Ruscio et al., 2017), in part because the same genes contribute to susceptibility to these disorders (Kendler, 2004). Beginning in adolescence and continuing through adulthood, there are almost twice as many girls and women who suffer from socially important levels of anxiety and depression as same-age boys and men (Bandelow & Michaelis, 2015; Nolen-Hoeksema, 1987). Just as risk of injury and death are a frequent and unwanted consequence of boys' and men's higher levels of risk taking and physical competitiveness, anxiety and depression are a frequent and unwanted consequence of the protective effects of fear and anxiety. The sex difference in risk of depression may simply result from the expression of the genes that contribute to anxiety, or in some cases depression might be functional. Functional means the depressed person withdraws from important social relationships (e.g., husband, kin) and this prompts greater investment by these significant others in the depressed person (Hagen & Rosenström, 2016).

As reviewed in Chapter 12 of this volume, girls and women are more sensitive to nuance in social relationships than are boys and men. Aspects of the associated cost–benefit trade-offs were discussed in Chapter 8 of this volume with a discussion of girls' and women's use of relational aggression to socially maneuver for access to desired resources, including romantic partners (Benenson, 2013, 2014; T. Reynolds, Baumeister, & Maner, 2018). Sensitivity to the nuance of this maneuvering provides advantages to adolescent girls and women, but also greater sensitivity to the hostile behaviors and social manipulations of rivals that in turn result in heightened risk of anxiety and depression (e.g., Bond, Carlin, Thomas, Rubin, & Patton, 2001).

Likewise, the stronger intimacy and disclosure in girls' and women's friendships than in boys' and men's friendships make them more vulnerable should the relationship end, as it often does (see Chapter 11, this volume). In this circumstance, former friends might now be rivals with enough personal and potentially embarrassing information to disrupt their former friends' other social relationships. In other words, the benefits of heightened sensitivity to social dynamics and the benefits of intimate relationships with their best friends result in heightened risk of anxiety and depression when conflict occurs. It is not that boys and men are completely clueless when it comes to this form of competition (i.e., relational aggression), but rather it does not have the same degree of social and emotional potency as it does for girls and women.

Even when the relationship with a best friend is going well, the discussion of personal relationships and other stressors can be overdone. Girls and women who coruminate too often—repeatedly discuss unsolvable and emotional personal issues—are at risk for later depression (Rose, Carlson, & Waller, 2007; Rose, Glick, Smith, Schwartz-Mette, & Borowski, 2017) and increases in stress hormone levels (Byrd-Craven, Geary, Rose, & Ponzi, 2008). Girls and women also react more strongly—they are more likely to become depressed—to conflict with important people in their life, not just their best friend, especially "threats to intimacy and closeness in relationships" (Leadbeater, Blatt, & Quinlan, 1995, p. 12). Adolescent girls, for instance, are 4 times more likely than same-age boys to experience anxiety and depression following a lost relationship. On top if this, girls and women often experience symptoms of depression when negative life events affect their family or friends, whereas boys and men typically do not.

Relational female–female aggression and the risks involved in establishing and maintaining close interpersonal relationships with family members and a few friends are not the only sources of the sex difference in risk for anxiety and depression; other risks include childhood trauma and poor parent–child attachment, among other factors (e.g., Zahn-Waxler, Shirtcliff, & Marceau, 2008). They are the focus here, because they are understandable in terms of the sex differences covered in previous chapters. If adolescent girls are at risk for anxiety and depression in part because of a spike in female–female relational aggression during puberty, then we should be aware of the potency of this form of aggression on girls and take measures to reduce it. Socially isolated girls (and women) are particularly vulnerable and in need of additional social and psychological support.

Eating Disorders

Eating disorders, including anorexia nervosa (i.e., restricted food intake) and bulimia nervosa (i.e., binging and purging), are another form of internalizing disorder that disproportionately affects adolescent girls and women (Nagl et al., 2016; Smink, van Hoeken, Oldehinkel, & Hoek, 2014). Depending on severity, persistence, and form of the disorder, there are anywhere from three to more than 10 adolescent girls or women with an eating disorder for every adolescent boy or man with the same disorder. Worldwide, these disorders are the most common among adolescent girls and young women who live in affluent societies with socially imposed monogamy (Hoek, 2016).

As was discussed in Chapter 7 of this volume, anthropological and historical research indicated that "plump" women were considered more attractive than slender women in 44% of human cultures (J. L. Anderson, Crawford, Nadeau, & Lindberg, 1992), and today higher status individuals of both sexes tend to be heavier than their lower status peers in countries with low levels of economic development (Dinsa, Goryakin, Fumagalli, & Suhrcke, 2012). As countries become wealthier, higher status women are generally thinner than their lower status peers. These thinner women are more likely to marry higher income men, because in these contexts they are more desirable as marriage partners than are heavier women (Sorokowski, Kościński, Sorokowska, & Huanca, 2014; Tovée, Swami, Furnham, & Mangalparsad, 2006). When this preference is combined with socially imposed monogamy, female–female competition for the most desirable marriage partners will be more strongly influenced by relative thinness than it will in other contexts.

In the former contexts, men's focus on women's physical traits when choosing mates, women's self-focus on these same traits (see Chapter 12, this volume), and mass media representations of increasingly thin fashion models create a deadly mix for some women. Women's motivation to compete for romantic partners is based, in part, on enhancing the traits that men find attractive (see Chapter 8, this volume). Although most men do not find the ultrathin models often shown in women's magazines to be especially attractive, many women believe that this is what high-status men prefer in a spouse (Rozin & Fallon, 1988).

For some women, this competitive motivation is being expressed in unchecked and unhealthy ways, especially in perfectionistic and competitive women (Bardone-Cone et al., 2007; Dahlenburg, Gleaves, & Hutchinson, 2019). When these women are exposed to unusually thin fashion models (many of whom probably do not ovulate), there appears to be modest increases in their dissatisfaction with their body and distortions of their beliefs about eating (e.g., Bardone-Cone & Cass, 2007; Grabe, Ward, & Hyde, 2008). The combination can result in a run-away female–female competition and develop into anorexia nervosa or result in purging to maintain a desirable weight, if the woman views thin models as symbolic competitors, as many of them do. The inherent motivational bias is the same as other women but has spun out of control because of some combination of personality, media portrayals of "attractive" women, and other factors (Vaillancourt, 2013).

VARIATION IN SEXUAL ORIENTATION, GENDER IDENTITY, AND RELATIONSHIPS

This section provides brief reviews of homosexuality, transgender people, and consensual nonmonogamous relationships. The goal is to provide a glimpse at sexual behaviors and relationships that differ from the monogamous norm in WEIRD nations, and when information is available, integrate these with research in traditional cultures and from an evolutionary perspective.

Homosexuality

In nonhuman species, sexual attraction is termed sexual partner preference, and in mammals it is influenced by prenatal and early postnatal (depending on the species) exposure to testosterone. This exposure results in the masculinization of genitalia early in prenatal development and typically the masculinization and defeminization (i.e., suppression of female-typical sexual behaviors) of later sexual behavior, given sex-typical hormone levels during pubertal development (Balthazart, 2016; Phoenix, Goy, Gerall, & Young, 1959). There also appear to be direct genetic influences on sexual behavior

(A. P. Arnold et al., 2016; Bonthuis, Cox, & Rissman, 2012), as well as epigenetic (changes in gene expression without changing the underlying genes) influences on the masculinization or feminization of the underlying brain regions (Nugent et al., 2015).

In most cases, these processes result in a sexual preference for the opposite sex. However, subtle changes in the timing or magnitude of prenatal or early postnatal sex hormone exposure can result in a preference for the same sex (Balthazart, 2016). Most of the associated studies have been conducted in laboratory settings but homosexual behavior, including courtship displays, mounting (assuming a sexual position), and sometimes sexual activity, have been documented in a wide range of species in wild settings, often (but not always) when opposite-sex partners are not available (Bagemihl, 1999). Spontaneous same-sex preference and behaviors have been observed and extensively studied in some groups of Rocky Mountain bighorn sheep (*Ovis canadensis*), where as many as 8% of the males show a same-sex preference (Roselli, Reddy, & Kaufman, 2011). For this species and many others, there is an area of the brain, the sexually dimorphic nucleus in the hypothalamus, that contributes to sexual preference, and this is larger in males that prefer females and smaller in females that prefer males. For the rams with a same-sex preference, this area of the brain is in-between that typically found in males and females and likely contributes to their same-sex preference, although the reason for this anatomic difference is not fully understood.

Same-sex preference or homosexuality and bisexuality is found in all or nearly all human cultures in which it has been assessed and across historical time (J. M. Bailey et al., 2016). Overall about 2% to 3% of men and 1% to 2% of women are exclusively homosexual, which can refer to same-sex attraction and sexual fantasies but does not always result in same-sex sexual behavior (M. Diamond, 1993; A. L. Norris, Marcus, & Green, 2015; Savin-Williams, Joyner, & Rieger, 2012). A large-scale and nationally representative sample of adults in the United States indicated that about 97% identified as heterosexual, 2% identified as gay or lesbian, and 1% identified as bisexual (Ward, Dahlhamer, Galinsky, & Joestl, 2014). Men are generally strongly heterosexual or homosexual, whereas nonheterosexual women are more fluid in their sexual behavior and are more likely than men to be bisexual (Baumeister, 2000); Savin-Williams et al. (2012) found that about 2% of women reported equal attraction to women and men (i.e., bisexual). The latter relationships can form in the context of close affectionate friendships and may be short-lived (J. M. Bailey et al., 2016) or can express itself as the formation of heterosexual or homosexual relationships at different points in their life.

Many of the same processes that contribute to a same-sex preference in nonhuman species appear to contribute to sexual orientation in humans (see J. M. Bailey et al., 2016; Balthazart, 2016; Camperio Ciani, Battaglia, & Zanzotto, 2015; Rahman & Wilson, 2003a). As an example, individuals with congenital adrenal hyperplasia (CAH) have been prenatally exposed to excess levels of male hormones; as children, many girls with CAH show male-typical play behaviors and as adults, they show male-typical social and occupational interests (e.g., Berenbaum, Beltz, Bryk, & McHale, 2018; Pasterski et al., 2011). These women are also much more likely to be lesbian or bisexual than are women without CAH, although this is more often expressed in terms of sexual fantasies than sexual behavior (Meyer-Bahlburg, Dolezal, Baker, & New, 2008). The same pattern is found for women who have been prenatally exposed to medications (given to their mother) that mimic the effects of testosterone on brain development (Meyer-Bahlburg et al., 1995). However, as noted by Balthazart (2016),

> changes in sexual orientation as a result of endocrine [hormone] embryonic disruption always concern a fraction of affected individuals (usually a maximum of 30–40%) so that at least 60–70% of subjects in these conditions still display a heterosexual orientation. Other factors must therefore be involved. (p. 7)

The other influences include genetics (Rahman & Wilson, 2003a). There have been several studies suggesting that genes on the X chromosome and at least one other chromosome are associated with an increased frequency of homosexuality in men (Hamer, Hu, Magnuson, Hu, & Pattatucci, 1993; Sanders et al., 2015), but these studies are not conclusive. This is because the identified genes are not always replicated and even when they are, the effects of any single gene are likely to have only a small effect on sexual orientation. Twin studies also indicate that sexual orientation runs in families for both sexes and is partly inherited, but with some contributions of experiences unique to each individual (J. M. Bailey, Dunne, & Martin, 2000). At this time, the experiences that contribute to sexual orientation are not well understood.

Birth order is also important for men but not for women, with the rate of homosexuality increasing with each additional older brother. Blanchard and Bogaert (2004) found that about 2% of men who had no older brothers were gay, as compared with nearly 5% of men who had one or more older brothers. Overall, it appears that between 15% to 30% of male homosexuality is due to this fraternal birth order effect (Blanchard, 2018; Blanchard & Bogaert, 2004; Cantor, Blanchard, Paterson, & Bogaert, 2002). One potential contributing factor is mothers' development of antibodies to a protein (or proteins) expressed by a gene on the Y chromosome that contributes to aspects of sexual differentiation (Blanchard, 2001). In this view, mothers develop antibodies to this protein that then pass to the fetus and disrupt the mechanisms that result in some aspects of sex-typical development, including sexual orientation. The chance of this happening increases with each successive son, because later-born sons are more likely to be exposed to these antibodies than are earlier-born sons. Indeed, a recent study confirmed that mothers with gays sons who had older brothers had more antibodies than other men to at least one Y-linked protein involved in fetal brain development (Bogaert et al., 2018).

In these cases, homosexuality is not due to any direct genetic effects, but simply a consequence of an inadvertent immune response developed by the man's mother. This mechanism does not explain all of male homosexuality or female homosexuality or bisexuality. These other forms of nonheterosexual behavior are an evolutionary riddle, especially for men. This is because homosexual men, on average, have fewer children than do heterosexual men, and in some traditional contexts they have very few children (Iemmola & Camperio Ciani, 2009; Vasey, Parker, & VanderLaan, 2014). In adulthood, lesbian and bisexual women also have fewer children than do heterosexual women, but they have higher pregnancy rates during adolescence (Hodson, Meads, & Bewley, 2017). The latter might be due to more male-typical levels of sexual behavior and because their initial sexual experiences are often heterosexual (Bártová, Štěrbová, Varella, & Valentova, 2020; Rahman & Wilson, 2003a). The result in natural contexts would be a reduction in the gap between the reproductive success of lesbian and bisexual women and their heterosexual peers. As noted in Chapter 7 of this volume, arranged marriages in these contexts would also reduce the gap for women but less so for men. This is because most women will marry in these contexts but only the more competitive men will marry.

As reviewed by Rahman and Wilson (2003a), there are a number of evolutionary explanations for the maintenance of male homosexuality. One proposal is that gay men are "helpers at the nest," they invest their time and resources in the well-being of kin, especially nieces and nephews and in this way contribute the overlapping genes to the next generation. There is little support for this theory in WEIRD nations, but there is support in at least a few traditional cultures, including those in Samoa and Java (Indonesia; Nila, Barthes, Crochet, Suryobroto, & Raymond, 2018; VanderLaan & Vasey, 2012). However, for the helper strategy to be evolutionarily neutral, gay men would have to provide enough additional support to their kin to result in the survival of four additional nieces or nephews. Nila et al. (2018) assessed this for homosexual men in Java and found that these men provided more support to their nieces and nephews than did heterosexual men and had about one additional niece or nephew as a result of this support by the time they were 40 years old. Although consistent with the helper hypothesis, the increase in the number of nieces or nephews did not fully compensate for not having children themselves and was "insufficient to explain the maintenance of male homosexuality" (Nila et al., 2018, p. 2455).

Another theory that has received some support is based on sexually antagonistic pleiotropy, which means that the genes that benefit the reproduction of one sex can potentially undermine the reproductive prospects of the other (Camperio Ciani et al., 2015; Camperio Ciani, Cermelli, & Zanzotto, 2008). Genes and corresponding behaviors that are associated with higher reproductive success in women (e.g., higher femininity) are associated with lower reproductive success in male relatives, including brothers and sons. If true, then the female but not male relatives of gay men should have more children, on average, than women who have few or no gay close relatives. Indeed, Camperio Ciani, Corna, and Capiluppi (2004) found that the mothers and maternal aunts of gay men in Italy had more children on average than did the same relatives of heterosexual men, with no differences for paternal relatives. Iemmola and Camperio Ciani (2009) confirmed this pattern in a follow-up study, but maternal relatives (e.g., the mother's sister) of gay men do not always have more children than their paternal relatives (e.g., the father's sister) in other populations (M. King et al., 2005; Semenyna, Petterson, VanderLaan, & Vasey, 2017). At this point, sexually antagonistic pleiotropy may explain some proportion of male homosexuality but is not the only factor.

Overall, homosexual and bisexual behavior occur at low but consistent levels across species and human societies. Exclusive homosexuality is more common among men than women and, as a result, is better studied. It is very likely that different men are homosexual for different reasons, as was just described. In traditional and likely ancestral environments, men's homosexuality results in a reproductive disadvantage that appears to be only partially compensated for by the increased reproduction of their relatives and its maintenance remains to be fully understood. These reproductive costs were less likely in traditional contexts for women, given arranged marriages, but the fluidity of women's sexuality remains an interesting phenomenon. L. M. Diamond (2003) proposed that the biological systems that underlie sexual desire and emotional bonding are more distinct in men than in women, and as a result, intense friendships are more likely to result in sexual intimacy among women than among men. The latter are in fact common among women who identify as bisexual. Such bonding might be beneficial in traditional contexts, in terms of maintaining the social support of their partner. It is also possible that bisexuality might simply reflect the stronger bidirectional relations between the systems that support sexual desire and bonding in women than men that in some cases result in same-sex attraction and bisexuality, without any underlying evolutionary selection for bisexual relationships.

Transgender People

Gender identity refers to a person's psychological sense of their gender, typically whether they identify as female or male, with more than 99% of people identifying with the sex of their birth. A transgender person is someone whose natal sex (also referred to as their sex assigned at birth) does not match their gender identity. In some cases, a person's gender identity may fall into a category other than "man" or "woman" (e.g., nonbinary, gender fluid, gender queer, etc.).

Being transgender does not imply any specific sexual orientation. Therefore, transgender people may be heterosexual, homosexual, or bisexual. Natal males and natal females can be transgender and have been described in a variety of traditional contexts. Examples include the *fa'afafine* of Samoa (natal males; Vasey & VanderLaan, 2014) and the *mahu* of Tahiti (natal males and females; Elliston, 1999). The common feature is engagement in sex-atypical behavior (also referred to as gender-nonconforming behavior), usually beginning in childhood. The *fa'afafine*, for instance, are natal males who are attracted to men, are behaviorally effeminate, and are often in female-typical occupations or cultural niches.

In some cases, this manifests as gender dysphoria or an intense desire to be accepted as and often look like the opposite sex (e.g., natal males identifying as and wanting to be seen as women; American Psychiatric Association, 2013). Among children, cross-sex behavior, especially among girls (e.g., girls engaging in rough and tumble play), is not uncommon (3% of boys, 5% of girls), but this is not the same as a natal boy identifying as a girl or a natal girl identifying as a boy. About 1% to 2% of children who have not been referred for clinical assessments report a desire to be the opposite sex at some point during childhood, but this is not necessarily an indication that they have gender dysphoria (Ristori & Steensma, 2016; K. J. Zucker, 2017; K. J. Zucker & Lawrence, 2009). Gender dysphoria requires persistence in this desire and intense distress over one's natal sex, but about 85% of these children do not persist in the desire to change their sex in adolescence or adulthood (Ristori & Steensma, 2016; K. J. Zucker, 2005). Rather, many identify with their natal sex and are homosexual or bisexual as adults.

Children and adolescents who persist are often described as having early-onset gender dysphoria in adulthood (K. J. Zucker, Lawrence, & Kreukels, 2016). They have a history of fantasizing about or explicitly stating they want to be the opposite sex, often engaged in sex-atypical behavior as children, and tend to be homosexual. Individuals with late-onset gender dysphoria are overwhelmingly natal males, do not have a history of gender dysphoria, and are often heterosexual and live as heterosexuals for a large part of their adult life (Blanchard, 1988, 1989). Blanchard (1988, 1989) proposed that the later involved sexual arousal associated with imagining oneself as a woman, called *autogynephilia*, which has resulted in considerable controversy (Dreger, 2015).

Whatever the case, gender dysphoria is much less common in adulthood than in childhood (K. J. Zucker, 2017). Arcelus et al.'s (2015) large meta-analysis indicated that 1 in every 14,705 individuals were transwomen (i.e., natal males who identified as women), and 1 in every 38,461 individuals were transmen (i.e., natal women who identified as men). These may be underestimates because they are largely based on the numbers of people in the population who were receiving clinical services for gender dysphoria and even in these populations the prevalence has been higher in more recent studies, although it is still uncommon. At this time, it is unknown to what extent the recent increases in gender dysphoria reflect greater recognition and acceptance of these issues or other factors. It is possible that adolescents today feel more comfortable revealing their gender dysphoria to their peers. At the same time, it is possible that adolescents who have not experienced gender dysphoria may begin to experience it after hearing their peers disclose it. In these cases, it is not clear whether this is gender dysphoria as it has been traditionally understood. Littman (2018) states that this phenomenon

> is distinctively different than what is described in previous research about gender dysphoria because of the distribution of cases occurring in friendship groups with multiple individuals identifying as transgender, the preponderance of adolescent (natal) females, the absence of childhood gender dysphoria, and the perceived suddenness of onset. (p. 32)

Consensual Nonmonogamous Relationships

As was described in Table 7.2 of Chapter 7 of this volume, there are many different types of reproductive relationships across and within human cultures, including polygyny (one husband, several wives), polyandry (one wife, several husbands), and long-term and serial monogamy. Polygynous relationships are common across traditional cultures, although only 10% to 20% of men engage in them, with the remaining men monogamously married, or unmarried (Marlowe, 2003; Murdock, 1981). Polyandry is much less common overall (E. A. Smith, 1998), but occurs even in societies that anthropologists classify as polygynous (Scelza & Prall, 2018; Starkweather & Hames, 2012). In these situations, polygyny is common, especially among high-status men, but polyandrous relationships are still found, often among lower status men. Here, women often maintain several simultaneous relationships with several men and obtain social or material resources from each of them (Borgerhoff Mulder & Ross, 2019; Lancaster, 1989). Socially imposed monogamy is the norm in WEIRD cultures, although polygynous and polyandrous relationships occur in these cultures along with serial marriages.

The latter, however, do not involve simultaneous relationships with multiple spouses. In WEIRD nations, about 4% to 5% of people currently engage in consensual nonmonogamous relationships (Conley, Ziegler, Moors, Matsick, & Valentine, 2013; E. C. Levine, Herbenick, Martinez, Fu, & Dodge, 2018). These relationships vary from swapping sex partners ("swinging") to open relationships (each partner is free to pursue alternative sex partners) to longer term simultaneous romantic (polyamorous) relationships (Conley, Matsick, Moors, & Ziegler, 2017). E. C. Levine et al.'s (2018) nationally representative sample of adults in the United States revealed that 4% of couples were in some form of consensual nonmonogamous relationship, but this varied by sexual orientation. About 2% of heterosexual adults (of both sexes) and 5% of lesbian women were in such relationships, compared with 22% of bisexual adults (of both sexes) and 32% of gay men. Gay men are more likely to engage in swinging or be in an open relationship, in keeping with the higher desire for sexual variety among men than women (see Chapter 7, this volume). Polyamorous relationships are more common among bisexual people of both sexes. In addition to differences in sexual orientation, people who engage in consensual nonmonogamous relationships tend differ from monogamous individuals in terms of higher Openness to Experience (a dimension of personality) and lower Conscientiousness (e.g., adherence to norms, another dimension of personality; Moors, Selterman, & Conley, 2017).

Given these figures, it is not surprising that these types of nonmonogamous relationships are viewed more positively by gay couples than by lesbian or heterosexual ones (Solomon, Rothblum, & Balsam, 2005). Solomon and colleagues (2005) found that 40% to 50% of gay men who were married or in a noncivil relationship had agreed with their partner that extra-pair relationships were sometimes acceptable, compared with 5% of lesbian couples and 3.5% of heterosexual couples. The same is true among single adults (United States) who reported on past relationships (Haupert, Gesselman, Moors, Fisher, & Garcia, 2017). Overall, about 1 in 5 adults reported a consensual nonmonogamous relationship at some point in their life, although these are not always in the context of long-term relationships. These relationships were more common among gay and bisexual people, but the majority of people in these relationships were heterosexual. In other words, nonheterosexual people (especially men) are more likely to engage in these relationships than are heterosexuals, but because there are more heterosexual than nonheterosexual people overall, most consensual nonmonogamous relationships were among heterosexuals.

Studies suggest that some of these relationships can be as satisfactory as monogamous ones, but this depends on the type of nonmonogamous relationship (Balzarini et al., 2019; Conley et al., 2017; Conley, Piemonte, Gusakova, & Rubin, 2018; M. E. Mitchell, Bartholomew, & Cobb, 2014). Couples in polyamorous relationships are just as satisfied as monogamous couples, at least with respect to the primary polyamorous relationship. These relationships are often among married or cohabitating individuals, with the secondary partner living elsewhere and often receiving less investment (e.g., attention) and being less satisfied than the primary partner. The primary couple in polyamorous relationships often have explicit agreements and restrictions (e.g., not spending the night) regarding the secondary relationships and adherence to these is an important part of maintaining these relationships (Wosick-Correa, 2010). In contrast, people in open relationships often report greater overall sexual satisfaction than people in monogamous relationships, but with lower overall relationship quality.

In societies with socially imposed monogamy, many people have concerns about consensual nonmonogamous relationships (Conley et al., 2017), and many of these concerns can be understood in terms of the benefits that drove the social evolution of monogamy in these cultures. As was described in Chapter 8 of this volume, higher rates of male-on-male violence, as well as more crime generally, are associated with polygyny or the presence of many men with little prospect of marriage (Henrich, Boyd, & Richerson, 2012). In large populations, socially imposed monogamy will reduce the spread of sexually transmitted infections (STIs; Bauch & McElreath, 2016), and promote cooperation among men that in turn increases group size and competitiveness vis-à-vis potential outgroups. Within the core relationship, monogamy helps to control potentially disruptive levels of sexual and emotional jealousy, which requires additional effort (e.g., open communication and trust) among people in nonmonogamous relationships (Mogilski et al., 2019). Although many of the issues (e.g., STIs) that were controlled by socially imposed monogamy can now be addressed in other ways (e.g., medical treatment), the sexual orientation and personality of those engaging in consensual nonmonogamous relationships suggests that these are not likely to become wider spread.

SEX DIFFERENCES IN VULNERABILITY

This chapter closes with a brief discussion of how sexual selection can be used to predict age-, sex-, and trait-specific vulnerabilities to the Horsemen of the Apocalypse (i.e., nutritional deficits, disease, social conflict) and potentially to man-made toxins, summarizing more detailed discussions presented elsewhere (Geary, 2015, 2016, 2017, 2019). Traits that have been elaborated through sexual selection (intrasexual competition or intersexual choice) have evolved such that they are honest indicators of the individual's condition and are often social signals of this condition (Cotton, Fowler, & Pomiankowski, 2004; Johnstone, 1995; Zahavi, 1975; see Chapter 4, this volume). The peacock's (*Pavo cristatus*) train is one example, whereby the number and size of eye-spots on the train signal the male's health and possibly the health of his offspring. As a result, females benefit by having more robust offspring if they make mate choices on the basis of these traits (Loyau, Saint Jalme, Cagniant, & Sorci, 2005; Petrie, 1994; Petrie, Cotgreave, & Pike, 2009). As described in Chapter 4 of this volume, the efficiency of mitochondrial energy production might be the most fundamental process underlying the development, maintenance, and expression of all energy-demanding traits (G. E. Hill, 2014; Koch, Josefson, & Hill, 2017). Sexually selected traits (e.g., the peacock's train) would be particularly vulnerable because they are generally larger and more complex than other traits and therefore need more cellular energy for their full development and expression.

The details are not important here. The key idea is that the sex that is advantaged for the various traits discussed throughout this book (e.g., men's advantage in height, Tanner, 1990; women's advantage in language competencies, Cavaco et al., 2015; Pauls, Petermann, & Lepach, 2013) may have heightened vulnerabilities for these same traits—with advantage comes vulnerability. One consequence is that sex differences will be largest under favorable conditions and will shrink or even disappear for populations that grow up or are currently living in difficult circumstances, especially if these involve chronic poor nutrition, chronic disease, or exposure to intense social stressors or man-made toxins.

This model readily explains why women's advantages in verbal memory and men's advantages in various forms of spatial ability increase as general living conditions improve (i.e., in WEIRD nations; Asperholm, Nagar, Dekhtyar, & Herlitz, 2019; Lippa et al., 2010). Moreover, the sex differences in physical size are even larger in these nations because of better nutrition and health care. The reduction in the magnitude of the sex differences in physical traits (e.g., height) is most evident when the individual is chronically ill or poorly nourished during adolescence, the time when males show the most rapid and prolonged physical growth. Adolescent girls in these circumstances are compromised as well, but not as severely as same-age boys (e.g., Jardim-Botelho et al., 2008; McGarvey et al., 1992). One result is the magnitude of adolescent boys' and men's advantage on these traits (e.g., height, lean muscle mass) becomes smaller.

The bottom line is that an understanding of sexual selection and associated sex differences can provide a framework for understanding how exposure to various types of stressors can affects girls and women differently than they affect boys and men. In the following sections, the utility of this approach is further illustrated by detailing a few sex-specific vulnerabilities in folk psychology and folk physics.

Vulnerability in Folk Psychology

One way in which the vulnerability model might be useful is for better understanding potential sex-specific deficits associated with exposure to man-made toxins. A number of studies of nonhuman species have indicated that toxin exposure can affect males and females in different ways and that sexually selected traits (e.g., plumage color, spatial ability) are more severely compromised than are other traits (Bortolotti, Fernie, & Smits, 2003; Jašarević et al., 2011). Intoxicants, like cocaine, are a common form of toxin exposure for people, and can disrupt mitochondrial functioning (Caito & Aschner, 2015) and thereby reduce the energy available to the brain systems that support cognition (Geary, 2017). As a result, cognitive abilities that are more complex and require more underlying brain tissue or more intricate brain systems should be the most severely compromised. The basic result is that sex differences found in healthy individuals should be reduced in magnitude or disappear in toxin-exposed individuals.

Girls and women have advantages in many of the basic features of language comprehension and production (see Chapter 12, this volume), and early language development proceeds at a brisker pace for girls than boys. The latter is analogous to the more robust physical growth for boys than girls during pubertal development, and in this example should result in a heightened vulnerability of young girls' relative to young boys' language development. The heightened vulnerability of girls' language is illustrated by the effects of prenatal cocaine exposure (Bandstra et al., 2011; B. A. Lewis et al., 2011; Malakoff, Mayes, Schottenfeld, & Howell, 1999). Malakoff et al. (1999) examined natural language development in 2-year-olds who were prenatally exposed to cocaine and found a developmental lag on several language measures (e.g., mean length utterance) relative to unexposed children. Critically, the gap between exposed children and their same-sex peers was 3 to 6 times larger for girls than for boys. The authors concluded that "the effect of cocaine-exposure is qualified by gender and is stronger for girls than for boys" (Malakoff et al., 1999, p. 173). A similar pattern is found with studies of older children, especially for their expressive language (Bandstra et al., 2011; Beeghly et al., 2005; B. A. Lewis et al., 2004, 2011).

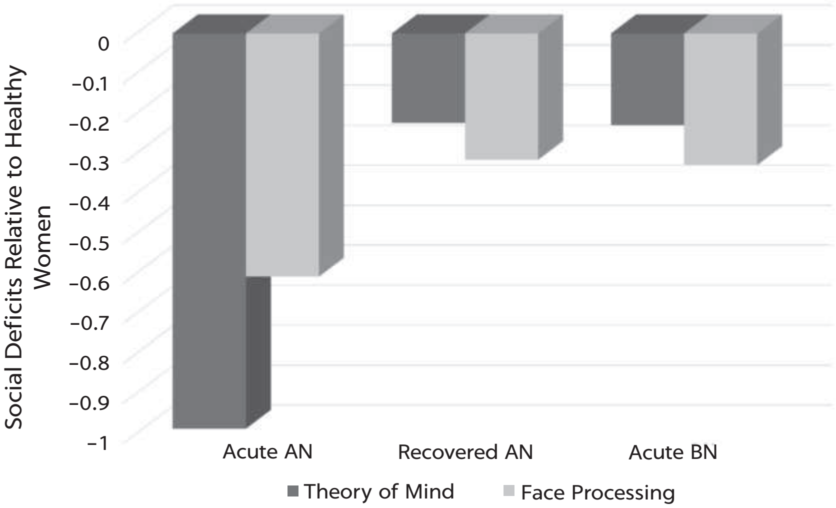
As another example, the treatment of acute lymphocytic leukemia (a form of cancer involving blood cells) involves cranial irradiation, chemotherapy, or their combination, and appears to result in sex-specific cognitive deficits. Cranial irradiation in combination with chemotherapy and especially before 4 years old can severely compromise girls' but not boys' developing language and verbal abilities (D. Christie, Leiper, Chessells, & Vargha-Khadem, 1995; Mulhern, Fairclough, & Ochs, 1991; Précourt et al., 2002; Robison et al., 1984). In one such study, Christie et al. (1995) found that girls who received cranial irradiation before they were 4 years old showed deficits on a composite measure of verbal comprehension. The magnitude of these deficits was such that 4 out of 5 of the girls who were treated before they were 4 years old had verbal competencies that were below that of boys who were treated at the same age or girls who were treated later in childhood. They concluded that their result "suggests that the developmental mechanism that contributes to superior female verbal ability is particularly vulnerable to cranial irradiation" (Christie et al., 1995, p. 139).

These sex-specific vulnerabilities are not restricted to young girls and language. Broader deficits in folk psychology (e.g., theory of mind) are found for women with anorexia nervosa. One of the Horsemen of the Apocalypse is famine or extreme nutritional stress as is found for women in the active stage of anorexia nervosa, and there is evidence that these women experience broad deficits in folk psychology. Women who eventually develop anorexia tend to have premorbid social-cognitive deficits (N. L. Zucker et al., 2007) and because of this, contrasts of women in acute and recovered stages of the disease are important. Women with bulimia nervosa have similar psychological issues that manifest in eating behavior but do not have the severe weight loss that is associated with anorexia, and these women also provide a useful contrast to the effects of acute anorexia on folk psychological abilities.

As shown in Figure 14.3, the weight loss accompanying anorexia is associated with large deficits in women's theory of mind, including their ability to make inferences about the thoughts and feelings of other people and deficits in reading facial expressions (Bora & Köse, 2016). The figure shows the deficits of women with anorexia or bulimia relative to healthy women of the same age. During the acute phase of anorexia, which is associated with severe weight loss and malnutrition, more than 4 out of 5 of these women have deficits in theory of mind relative to the average healthy woman, and almost 3 out of 4 have deficits in reading facial expressions. As can be seen in Figure 14.3, women with bulimia have much more modest deficits in these areas, and women with anorexia recover some of these competences once they regain a normal weight.

During the acute phase of anorexia, women also experience deficits in reading the emotions of others on the basis of voice and body posture (Oldershaw, Hambrook, Tchanturia, Treasure, & Schmidt, 2010), consistent with broad deficits in folk psychology. Women's deficits in these areas appear to be larger than those found for intelligence or academic abilities (Russell, Schmidt, Doherty, Young, & Tchanturia, 2009; Tapajóz Pereira de Sampaio, Soneira, Aulicino, & Allegri, 2013), suggesting the deficits are more evident in social-cognitive than in other cognitive domains. In one of the few studies of men with eating disorders (largely anorexia), there were no folk psychology deficits but these men did have a deficit in an area of folk physics, specifically,

FIGURE 14.3. Women's Folk Psychology Deficits Associated With Anorexia Nervosa



Deficits are in standard deviation units (*d*) and compared with healthy women. Women with acute anorexia nervosa (AN) have substantive deficits in theory of mind (making inferences about the beliefs and feelings of others) and face processing (inferring emotional state based on eyes). The deficits of women who have recovered from AN or with bulimia nervosa (BN) are more modest. Data from Bora and Köse's (2016) meta-analysis.

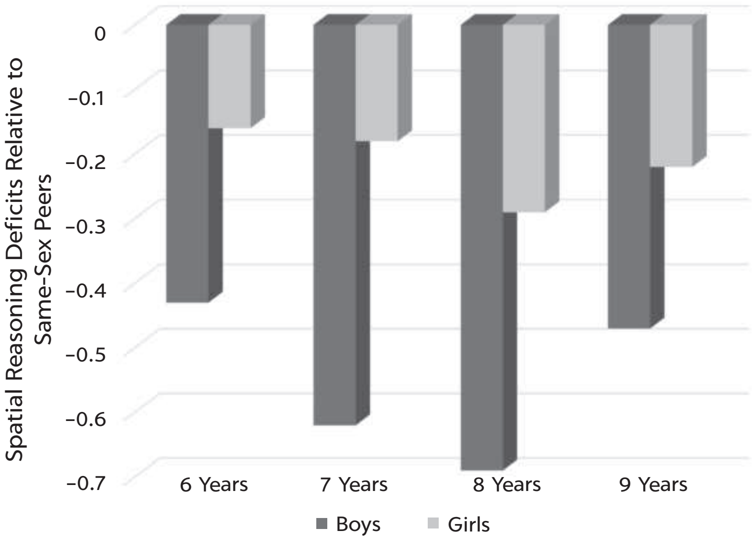
deficits in detecting objects embedded in a cluster of other objects (Goddard, Carral-Fernández, Denneny, Campbell, & Treasure, 2014).

Vulnerability in Folk Physics

On the basis of the vulnerability model, boys' and men's folk physics abilities should be more susceptible to stressors than those of girls and women. Most of the studies that could have assessed this hypothesis did not report sex differences or statistically removed any such differences and were not useful in determining if there were sex-specific vulnerabilities (e.g., Ribas-Fitó, Sala, Kogevinas, & Sunyer, 2001). Nevertheless, there are some indications that boys and men do indeed have a heightened vulnerability in the visuospatial components of folk physics domains.

An example is provided by the accidental exposure of thousands of people in Taiwan to PCB-contaminated cooking oil, including 74 women who were pregnant at the time or became pregnant soon thereafter (Rogan et al., 1988). Their children's health and aspects of their cognitive development were followed for years. A longitudinal assessment of these children from 6- to 9-years of age, inclusive, and relative to a group of demographically matched peers revealed that exposed boys' but not girls' spatial reasoning abilities were compromised (Guo, Lai, Chen, & Hsu, 1995), as shown in Figure 14.4. For unexposed children, boys scored higher on this measure than did girls

FIGURE 14.4. Boys' Folk Physics Deficits Associated With Toxin Exposure



Deficits are in standard deviation units (*d*) and compared with unexposed and demographically matched same-sex peers. Boys who were prenatally exposed to polychlorinated biphenyls (PCBs) showed more substantive deficits in spatial reasoning than did girls exposed to PCBs. The effects are statistically significant for boys but not for girls. Data from Guo, Lai, Chen, and Hsu (1995).

in most years, as is typically found (see Chapter 13, this volume), whereas exposed girls outperformed exposed boys in most years. Although boys who were prenatally exposed to cocaine did not show deficits in their early language development, deficits in visuospatial abilities may emerge later in childhood (Bennett, Bendersky, & Lewis, 2008), but this finding needs follow-up studies.

Studies of adults that have included appropriate folk physics measures have largely focused on occupational exposure to pesticides, solvents, and a variety of metals, such as aluminum and arsenic (Kishi et al., 1994; Nilson, Sällsten, Hagberg, Bäckman, & Barregård, 2002). Most of these toxins compromise mitochondrial energy production, among other things, and should disproportionately compromise the most elaborated cognitive abilities, which would include visuospatial abilities in men. The majority of studies have focused on men, because they are disproportionately represented in the occupations in which these exposures occur. Overall, the findings are mixed but generally show that exposure to one or more toxins can compromise men's memory for images, ability to detect objects hidden in arrays, and performance on more complex spatial cognition tests (Farahat et al., 2003; C. M. Ryan, Morrow, & Hodgson, 1988; Schwartz et al., 2000).

An example is provided by a study of Finnish factory workers' (men) level of aluminum exposure (through welding) and performance on a variety of cognitive measures (Akila, Stollery, & Riihimäki, 1999). With control of demographic and other factors, the primary deficits associated with aluminum exposure were "in tasks requiring working memory, particularly that relating to processing of visuospatial information" (Akila et al., 1999, p. 632). Men's occupational exposure to lead has also been well studied, with mixed or weak evidence for exposure-related declines in visual memory and object detection (C. M. Ryan, Morrow, Parkinson, & Bromet, 1987; Weisskopf et al., 2007).

The evidence is more consistent for exposure-related declines in more complex spatial abilities (Haenninen, Hernberg, Mantere, Vesanto, & Jalkanen, 1978; Schwartz et al., 2000). Haenninen et al. (1978) found that higher than normal lead levels in serum (blood) were associated with deficits in men's spatial cognition, visual memory, and psychomotor dexterity, but not in verbal abilities. These authors concluded the "performances that were most affected by lead were dependent on visual intelligence and visual-motor functions" (Haenninen et al., 1978, p. 688). Stewart et al. (2006) found that chronic lead exposure in men is associated with decreases in overall brain volume and specific deficits in white matter tracks in the parietal cortex, which will compromise visuospatial abilities (see Chapter 13, this volume).

CONCLUSION

I hope to have convinced many readers that C. Darwin's (1871) sexual selection represents a powerful set of processes that has shaped and will continue to shape the evolution of all sexually reproducing species, including our own. To be sure, there is much to be learned, especially how the expression of evolved biases is influenced by developmental experience and by cultural context. We will never fully understand developmental and cultural influences on the many sex differences covered in this book, and the many differences that were not covered, without placing them in the context of evolution in general and sexual selection in particular. This final chapter outlined a few ways in which sexual selection or evolutionary processes more broadly can be used to better understand sex differences that emerge in modern contexts, as well as variation in sexual orientation, gender identity, and relationships. Many cases, such as the sex difference in ease of learning how to read (Reilly et al., 2019; Stoet & Geary, 2013), are not directly related to an evolutionary history of intrasexual competition or intersexual choice but are an indirect result of these evolutionary processes. I proposed that these indirect (and sometimes direct) contributions inform our understanding of sex differences in school, at work, in psychopathology, and in vulnerability to the Horsemen of the Apocalypse and to other stressors.

In closing, I ask readers who remain unconvinced to reflect on the theory of evolution, of which sexual selection is one set of pressures. Evolution is not just another psychological, sociological, or anthropological theory; it has proven to be the unifying meta-theory for all of the life sciences. Eventually, all psychological, sociological, and anthropological models will need to be reconciled with the principles of natural and sexual selection. This endeavor promises to be an eye-opening journey that will inform and refine our understanding of sex differences for years to come.

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