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Sexual Selection in Homo sapiens

Parental Control over Mating and the Opportunity Cost of Free Mate Choice

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The book is dedicated to the memory
of my father Dimitrios Apostolou

Preface

Sexual selection is an evolutionary force which gives rise and shape to adaptations that enable reproductive access to the opposite sex (Andersson, 1994). There has been intensive research in this domain, which is based predominantly on nonhuman sexually reproducing species (Andersson, 1994; Dixson 2009, 2016; Hoquet, 2015), with some of these findings extrapolated to the human species (Miller, 2000). However, there are certain unique aspects in the mating patterns of our species, which turn such endeavors largely insufficient for understanding the workings of sexual selection in humans. The most striking difference with other nonhuman sexually reproducing species is the regulation of mating. In particular, the anthropological and historical records indicate that in the pre-industrial context, which characterized all human societies until approximately 300 years ago, access to the reproductive capacity of the opposite sex goes through parents who choose spouses for their children (Apostolou, 2014). Parental control over mating gives rise to a sexual selection force, namely, parental choice (Apostolou, 2007). The purpose of this book is to attempt to understand how this sexual selection force in particular and how sexual selection in general work in our species.

Sexual Selection in Humans

In post-industrial societies like the USA and the UK, people exercise mate choice relatively freely. It is also the case that men compete more intensively between them for gaining access to the reproductive capacity of women, predominantly through acquiring status and material goods (Buss, 2003). This places women in a position to be able to exercise choice, which means that female choice constitutes a strong sexual selection force responsible for shaping male adaptations. This force is also present in other animals, such as birds, where we observe, for example, large tails with vibrant colors evolved predominantly to make males more appealing to females (Zahavi & Zahavi, 1997). The use of sexual selection models which have a strong

female choice component could potentially promote our understanding of sexually selected adaptations in humans.

Nevertheless, there is a critical issue here: Sexually selected adaptations have been shaped by selection forces not in contemporary post-industrial societies like the USA and the UK but in ancestral pre-industrial societies which differ considerably from the current post-industrial ones. One main difference, relevant to sexual selection, is the regulation of mating. As opposed to post-industrial societies, where people exercise mate choice relatively freely, in pre-industrial societies, mate choice is regulated by parents who control their children's mating decisions, especially those of their daughters, and choose spouses for them (Apostolou, 2014).

Current models of sexual selection cannot account for these mating patterns. For instance, the model of female choice predicts that women will be in a position where they can choose desirable mates. However, across pre-industrial societies, what we actually observe is that a daughter's freedom to exercise mate choice freely is severely impaired by her parents, who control her mating decisions and are exercising in effect mate choice for her. The model of female choice does not account for this pattern, and consequently, it is inadequate for explaining how sexual selection works in humans. Accordingly, I have proposed the model of parental choice (Apostolou, 2016), which attempts to provide an account of these patterns and thus to promote our understanding of sexual selection in humans. The heart of the model constitutes the parent-offspring conflict over mating, which predominantly accounts for why parents control their children's mate choices and why they do not allow them to choose mates for themselves.

Parents and children are genetically related but not genetically identical. This means that their interests overlap but also diverge. One area where this divergence is manifested is mate choice (Trivers, 1974): Certain traits are more beneficial in a spouse than in an in-law, while others are more beneficial in an in-law than in a spouse (Apostolou, 2008a, 2008b). This asymmetry practically means that if children are left to exercise mate choice on their own, they will choose mates who are not optimal for their parents. As a consequence, there are fitness benefits for parents if they place mate choice under their own control and are able to choose in-laws who increase their own fitness (Apostolou, 2007, 2010).

Furthermore, because parents and children are genetically related, they have common interests. This is another source of motivation for parents to control their children's mating decisions: By being young and inexperienced, children are likely to make erroneous mate choices. Daughters and sons may also have certain dispositions or traits, such as poor health or displeasing looks, which impair their success in the mating market. These factors have an adverse effect for their own and for their parents' fitness (i.e., lower their chances for reproductive success). Thus, parents have an incentive to interfere and assist their children in attracting and securing mates.

Overall, by influencing and controlling mate choice, parents become an important sexual selection force: Traits which make an individual more likely to be chosen as an in-law are sexually selected and spread in the population. Parental choice is unique in humans as, to my knowledge, there is no other sexually reproducing species on the planet in which parents choose mates for their children. In the book, this selection force and its contingencies will be explored in detail. In the following section, I am going to provide a brief plan of the book.

The Plan of the Book

In Chap. 1, it is argued that sexual selection is not a homogenous force, but it is composed of different constituent selection forces. It is argued further that in the human species, the main forces are parental choice, male-male competition, individual mate choice, and sexual coercion. In parental choice, traits that make an individual more likely to be selected as an in-law are selected and increase in frequency in the population. In male-male competition, traits which enable men to fight other men and monopolize reproductive access to women are selected. In individual mate choice, traits which enable individuals to be chosen as mates by members of the opposite sex are selected. Finally, in sexual coercion, traits which enable men to circumvent parental and female choice and force sex on women are selected.

This chapter explores the interrelation between these different sexual selection forces. It is argued that there is an inverse relationship between the strength of parental choice and individual mate choice: When one selection force strengthens, the other weakens. In the same vein, there is an inverse relationship between parental choice, individual mate choice, and male-male competition. If, for instance, male-male competition strengthens, parental choice and individual mate choice forces weaken. As a consequence, understanding the strength of one force enables us to understand the strength of the others. The chapter argues also that the presence of different sexual selection forces translates into different reproductive niches being present: Individuals can promote their reproductive success by appealing to parents, by monopolizing access to mates by force, by appealing to opposite sex individuals as mates, and by forcing sex on members of the opposite sex. The size of each niche, and thus the prevalence in the population of the traits that address it, depends on the strength of each selection force, which in turn is determined by environmental conditions.

The parental choice sexual selection force is predominantly the consequence of diverging genetic interests between parents and children, giving rise to parent-offspring conflict over mating. Accordingly, understanding parental choice requires a solid understanding of parent-offspring conflict over mating, which is the purpose of Chap. 2. It is argued that, due to differences in genetic relatedness between parents and children, specific traits in a mate give different fitness benefits to each party. As a consequence, when the latter exercise mate choice, they make compromises which are not in the best fitness interest of the former. Thus, if parents were to exercise choice for their children, they would make different compromises, ones which would be less fitness-decreasing for them. In consequence, children's free mate choice involves an opportunity fitness cost for parents, which gives rise to parent-offspring conflict over mating.

In addition, this chapter examines the trade-off hypothesis which has been put forward as an alternative explanation for parent-offspring conflict over mating. It is demonstrated that evolutionary trade-offs do not result in such conflict; however, they affect parent-son conflict over mating. It is further argued that the degree of parent-offspring conflict over mating is contingent upon the prevailing environmental conditions and the mate value of children. Furthermore, this chapter reviews the literature on which traits give different fitness benefits to parents and children.

In Chap. 3, a formal model of parental choice is introduced. In this model, parental choice arises from parental control over mating, which is motivated by the opportunity cost of free mate choice. This opportunity cost has two components: the diverging opportunity cost and the converging opportunity cost. The diverging opportunity cost emerges from the differences in genetic relatedness between parents and their children and children choosing mates with traits which give them more fitness benefits than they give to their parents. The converging opportunity cost arises from the overlap in genetic relatedness and from children being young and inexperienced to risk making erroneous mating decisions that their parents would not make if they were to exercise choice in their place.

In addition, this chapter explores the contingencies in the opportunity cost of free mate choice and, thus, the contingencies in parental control over mating and the strength of parental choice. It is argued that the opportunity cost of free mate choice is higher for daughters than for sons. This difference translates into parents being more interested in exercising control over their daughters than over their sons, and as a consequence, parental choice is stronger on men than on women. It is further argued that the opportunity cost of free mate choice is usually higher for male than female parents, which translates into fathers exercising more control over their children's mate choices and male parental choice being stronger than female parental choice.

Chapters 4, 5, and 6 examine whether the predictions of the parental choice model are consistent with the patterns of mating prevalent in different society types. More specifically, in Chap. 4, the model is applied to societies that base their subsistence on hunting and gathering. It predicts that parental choice is a strong sexual selection force, with male-male competition and individual mate choice being also strong sexual selection forces. It predicts further that parents exercise more control over their daughters than over their sons, while fathers are more influential than mothers over their children's mating decisions. Anthropological evidence from hunting and gathering societies is presented that strongly supports these predictions.

In Chap. 5, the model of parental choice is applied to societies that base their subsistence on agriculture and animal husbandry. As in the case of societies that base their subsistence on hunting and gathering, the model predicts that parental choice is a strong selection force, with more control exercised over daughters than over sons and male parents being more influential than female parents over their children's mating decisions. It is further predicted that individual mate choice is a weak sexual selection force. Evidence from the anthropological and historical records on agropastoral societies is presented that provides a strong support for these predictions.

In Chap. 6, the model is applied to understanding the mating patterns in post-industrial societies. The model predicts that individual mate choice is the primary sexual selection force, with all other sexual selection forces being weak. It also predicts that, in terms of parental choice, female parents exercise more influence than male parents over mate choice. Consistent with these predictions, in post-industrial societies, individuals choose their own mates. Parents still exercise influence, but they do so indirectly with the use of several manipulation tactics.

In addition, mothers demonstrate a stronger interest in intervening in their children's mate choices than fathers.

Chapter 7 applies the model to make comparisons between societies of different subsistence types. Subsequently, it employs these predictions in order to make inferences about how the strength of parental choice and other sexual selection forces has changed through the course of human evolution. In accordance with the predictions of the model, evidence from anthropological and historical studies indicates that parental choice is stronger and male parents are more influential in pre-industrial societies which base their subsistence on agriculture and on animal husbandry than in societies which base their subsistence on hunting and gathering. On the basis of these findings, it is argued that the agropastoral revolution, which took place approximately 10,000 years ago, has resulted in the strengthening of male parental choice and the weakening of individual choice. This pattern has been reversed, however, following the industrial revolution and the eventual transition to post-industrialism.

Chapter 8 aims to understand the variation in the strength of parental choice between societies of the same subsistence type, as well as the variation in parental control over mating within societies. It is argued that societies of the same subsistence type differ in the factors that predict the opportunity cost of free mate choice, and as a consequence, they differ also in the influence that parents exercise over mate choice. In the same vein, it is argued that the factors predicting the opportunity cost of free mate choice vary across families, which explains why some families exhibit more control over their children's mate choices than others. In addition, these factors also change with the age of the children, predicting that parental control over mating will vary during a child's lifespan.

In-law preferences determine the course that sexual selection follows when it is driven by parental choice. Accordingly, Chap. 9 explores the qualities parents look for in a prospective spouse for their children. Several studies on in-law preferences converge in the conclusion that parents place considerable value in specific personality traits, family background, similarity, economic prospects, sexual behavior, and capacity to have a family. These preferences are contingent upon the sex of the in-law, as traits are valued differently in a prospective daughter-in-law and in a prospective son-in-law. The in-law preferences of fathers and mothers largely converge, but there is some divergence over specific traits. Last but not least, in-law preferences are contingent upon the specific environmental context, and consequently, they vary across societies of different subsistence types.

Chapter 10 nominates adaptations which are likely to have evolved in order to enable individuals to address parental choice. It further nominates possible adaptations which have evolved to enable men and women to communicate their desirable qualities to prospective parents-in-law. It also nominates adaptations which enable parents to appeal to other parents as beneficial marital allies. Finally, the chapter addresses the question why not all people share the same sexually selected adaptations. In particular, it is argued that, as there are several reproductive niches, individuals are likely to have evolved traits to enable them to address one or more niches.

In Chap. 11, it is argued that the transition from pre-industrialism to post-industrialism has brought a radical change in the relative strength of the different sexual selection forces, resulting in a considerable mismatch between the environment adaptations involved in mating that have evolved to function optimally and the demands of the environment they actually have to function currently. As a consequence, several mechanisms may fail to meet the demands of the modern context, causing individuals difficulties in the mating domain. The chapter nominates such mechanisms, including mechanisms responsible for sexual functioning, certain personality traits, and attention to looks.

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Dr Menelaos Apostolou was born in Athens, Greece. He completed his undergraduate studies at the Lancaster University, UK, and his graduate studies at the University of Warwick, UK. He currently lives in the Republic of Cyprus, and he is an associate professor of psychology at the University of Nicosia, Cyprus. He has published several peer-reviewed articles, and he is the author of *Sexual Selection Under Parental Choice: The Evolution of Human Mating Behavior* and *Feeling Good: An Evolutionary Perspective on Life Choices*. His research interests include evolutionary theory, mate choice, human sexuality, individual differences, and well-being.

Chapter 1
Sexual Selection Forces

Sexual selection is not a homogenous force, but it is the result of a number of nonindependent component forces, one of which is parental choice. Accordingly, in this chapter, I am going to examine the different component forces of sexual selection and how they are related to each other. I will begin by addressing the question why sexual selection arises in the first place.

Sexual Selection

The first life-forms lacked complexity and reproduced asexually (Beukeboom & Perrin, 2014). The environment has, however, many ecological niches which, in order to be occupied successfully, require more complex organisms (i.e., multicellular ones). Such organisms need to spend some time in developing the biological machinery necessary for occupying the niche they have evolved to fill. For instance, although it takes a few minutes for a newly born single-cell organism to be able to reproduce, doing so requires several years for a human being. The reason is that humans spend considerable time in developing the sophisticated biological hardware, such as a large brain, which is required for occupying their specific ecological niche.

The long period that more complex organisms need to allocate in development makes them vulnerable to the attacks of less complex organisms such as parasites. More specifically, a complex organism can be born with a resistance to parasites. In its lifetime, however, parasites, by virtue of being able to reproduce fast, can evolve ways to bypass this resistance. For the more complex organism to be able to build resistance to the newly evolved strain of parasites, it would need to reproduce and create many copies of itself, some of which, through mutations, will have the capacity to resist the new strains of parasites. Nevertheless, due to their capacity to reproduce fast, parasites would have surpassed the defenses of the organism long before it is able to become mature enough to reproduce.

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In effect, parasites set a constraint in the occupation of ecological niches that require complex organisms. That is to say, these niches cannot be occupied unless an organism finds a way to bypass the constraint of parasites. Sexual reproduction is the solution evolution has found to achieve this end (Ridley, 1995). In particular, an organism, instead of reproducing asexually, i.e., producing almost identical copies of itself, can combine its genetic material with the genetic material of another organism of the same species in order to produce other organisms which are similar but different to their parents.

Parasites which have evolved to bypass the defenses of the asexually reproducing parent can easily bypass the defenses of its offspring, because the two are almost identical. They cannot do the same, however, in sexually reproducing organisms because, even if the parasites have evolved ways to bypass the defenses of parents, these ways may not work on their offspring, as the latter are genetically different from the former. Thus, parasites need to evolve new mechanisms, giving time to the offspring to develop and be able to reproduce.

In effect, sexual reproduction makes possible the occupation of niches which require more complex organisms: At any point in time, there can be complex organisms which are not taken down by parasites before they are able to reproduce. When a sexually reproducing organism procreates, it does not pass its entire genetic material to future generations, and a part of it may be lost. This is the price complex organisms have to pay in order to be able to occupy the niches they do.

Sexual reproduction solves the problem of occupying ecological niches which require more complex biological hardware, giving at the same time rise to a new selection force, namely, sexual selection.

Sexual Selection and Conflict

The reproductive resource of an asexual reproductive organism is itself, but it is 100% genetically related with itself, so it does not have conflicting interests. On the other hand, the evolution of sex has resulted in more than one party to be involved in reproduction, parties which are not genetically identical and, thus, do not have identical interests over mating. In particular, due to sexual reproduction, individuals who comprise a given population are not genetically identical. One consequence of this fact is that they differ in their value as mates. For instance, some individuals may carry harmful genetic mutations that can pass to their offspring and thus have a lower mate value than others who do not carry such mutations.

In addition, sexual reproduction involves costs, including resources for producing gametes, time and energy to locate an opposite sex partner, time and energy allocated to having sex, and resources allocated to raising offspring. Accordingly, each individual is constrained by the cost involved in the number of mates it can copulate with. These two factors result in conflict of interest. Mates differ in their mate value, and there is a limited number of mates an individual can gain access to; thus, it is to the best interest of individuals to gain reproductive access to high mate

value individuals, but it is not to the best interest of high mate value individuals to provide such access to low mate value individuals. To put it another way, an individual of a given mate value has resources for gaining access only to a limited number of mates, so when it mates with an individual of a lower mate value, it forgoes the opportunity to mate with an individual of high mate value, i.e., it suffers an opportunity cost. This opportunity cost is a benefit to the low mate value individual, who finds itself to be mated with an individual of higher mate value than its own.

Thus, it is not to the best interest of sexually producing individuals to provide indiscriminate sexual access, because doing so involves suffering an opportunity cost which, in turn, selects for choosiness. Individuals would evolve mechanisms to prevent indiscriminate access to their reproductive capacity. In other words, conflict of interest generates a strong selection pressure on sexually reproducing individuals to discriminate between mates in order to reduce the opportunity cost arising from not getting the best mates they can. This force can be conceptualized as sexual selection.

In particular, natural selection can be understood as the process by which alleles that code for traits that make individuals well adapted to their environment increase in frequency in the gene pool relative to alleles that code for traits that make individuals less well adapted (Nettle, 2009). Sexual selection can be understood as a natural selection on the capacity of individuals to gain access to the reproductive capacity of the opposite sex. Since prospective mates are not identical, one aspect of this capacity is to be able to discriminate between prospective mates with respect to their mate value. This is because an individual's capacity to gain reproductive access to the opposite sex is compromised if it chooses indiscriminately. For instance, it will allocate the same effort in getting a mate who is not fertile as to a mate who is.

In effect, mechanisms are selected that augment the capacity of an individual to gain access to the reproductive capacity of the opposite sex through enabling effective discrimination of prospective partners. Evolved choosiness means that there is a filter in the way toward gaining reproductive access to the opposite sex that not everybody can pass. Accordingly, individuals need to compete between them over who will pass this filter. Consequently, selection pressure is generated, favoring traits that enable individuals to win this competition and gain reproductive access to the opposite sex.

To put everything together, sexual selection can be understood as a force that gives rise to traits that enable individuals to filter mates and to pass through this filter. How sexual selection comes about can be summarized as follows:

$$\begin{aligned}&\text{Sexual reproduction} \rightarrow \text{Conflicting of interest} \rightarrow \text{Opportunity cost} \rightarrow \\ &\text{Sexual selection} \rightarrow \text{Discriminating mating} \rightarrow \text{Competition} \rightarrow \text{Sexual selection}\end{aligned}$$

Environmental factors are likely to influence the degree of conflict of interest between the different parties involved in mating, affecting the strength of sexual selection. To use one example, imagine that a fertile man and a fertile woman are marooned on an uninhabited island and do not expect to be rescued. With respect to mating, the two parties have no conflicting interests as there are no alternative mating options.

Therefore, there is no opportunity cost involved in mate choice, and there is no reason for any party to be discriminating toward the other. Consequently, the two would readily provide access to each other's reproductive capacity, so the strength of sexual selection would be zero.

Now, if say several other fertile men and women maroon also on this island, the conflict of interest would turn positive. Individuals of low mate value would want to mate with individuals of high mate value, but it is not to the latter's interest to mate with the former. Mate choice would involve an opportunity cost, which would make people choosy, and choosiness would give rise to competition for mates. In different words, the change in the environment due to the arrival of other individuals would have a substantial effect in strengthening sexual selection.

Sexual Selection and Genetic Relatives

An allele is sexually selected over another allele if it augments more an individual's capacity to gain access to the reproductive capacity of the opposite sex. This being the case, it has a higher probability to be represented in the future generation, as the individuals who carry it will have more offspring, who are also likely to carry it, relative to the individuals who carry the other allele. An allele, however, can be represented in future generations by augmenting the capacity to gain access to the reproductive capacity of the opposite sex of the genetic relatives of the individuals who carry it. That is to say, an allele that acts so as to enable the individuals who carry it to assist its genetic relatives, who are also likely to carry it, to gain access to the reproductive capacity of the opposite sex, will have an elevated probability to be represented in future generations.

On this basis, it can be argued that there would be sexual selection pressure for traits or mechanisms to evolve that would enable an individual to augment the capacity of its genetic relatives to gain access to the reproductive capacity of the opposite sex. Such mechanisms may involve assisting genetic relatives to find mates by diverting resources to them, by assisting them to become more appealing to the opposite sex, and by assisting them to keep a relationship. In this respect, the definition of sexual selection can be expanded as follows: Sexual selection can be understood as a natural selection on the capacity of individuals or their genetic relatives to gain access to the reproductive capacity of the opposite sex.

Sexual Selection Forces

There are different ways an individual can employ to pass the selection filter that stands in the way of gaining reproductive access to the opposite sex. In turn, these different ways require different traits in order to enable individuals to achieve their

goal successfully. Thus, there are different selection pressures for different traits to evolve. An individual can gain access to the capacity of the opposite sex in three main ways: (1) It can exclude other individuals of the same sex and monopolize access to the opposite sex, (2) it can be chosen as a mate by members of the opposite sex, and (3) it can force sex to members of the opposite sex. Accordingly, three types of sexual selection pressure emerge, namely, intrasexual competition, intersexual competition, and sexual coercion.

Starting with intrasexual competition, men can win the competition by excluding other men and monopolizing access to women. As a consequence, male-male competition arises which is a selection force that favors traits that enable men to exclude other men from the competition. In the same vein, women can win the competition by excluding other women and monopolize access to men. As a consequence, female-female competition arises, which is a selection force that favors traits that enable women to exclude other women from the competition. Note that, if men and women were providing access to their reproductive capacity indiscriminately, there would be no need for men to exclude other men and for women to exclude other women from the competition, as there would be no competition. Overall, intrasexual selection has two main components, namely, male-male and female-female competition.

Moving on to intersexual selection, in female choice, a man can win the competition by being selected as a mate by a woman over other men. In particular, women are choosy, so men compete with each other in demonstrating that they have qualities women desire. Female choice then arises, which is a positive selection force on traits that enable a man to be chosen as a mate by a woman. Moreover, a woman can win the competition by being selected as a mate by a man over other women. More specifically, men discriminate over which women they desire, so women compete with each other in demonstrating that they have the qualities men desire. Male choice then arises, which is a positive selection force exercised on traits that enable a woman to be chosen as a mate by a man.

In addition, conflicting as well as converging interests over mating (see Chap. 3) motivate parents to place their children's mating decisions under their control. Parents discriminate over which men and women they desire as sons- and daughters-in-law, respectively, so men compete with other men, and women compete with other women in demonstrating to their prospective parents-in-law that they have the qualities they desire. Parental choice then arises, which is a positive selection force on traits that enable men and women to be chosen as sons- and daughters-in-law by parents. Overall, intersexual selection has three component forces, namely, female choice, male choice, and parental choice.

Finally, an individual can win the competition by forcing sex to the opposite sex, bypassing in effect individual choice, parental choice, and other competitors. This possibility gives rise to sexual coercion, which is a positive selection force on traits which enable individuals to gain reproductive access to the opposite sex through forcing sex on them.

Interrelation Between Sexual Selection Forces

The sexual selection force is subdivided in three selection forces: intrasexual selection, intersexual selection, and sexual coercion (Andersson, 1994; Dixson, 2009; Smuts, 1992; Smuts & Smuts, 1993). In this section, I will focus on the interrelation between the former two. In intersexual selection, the selection pressure is among alleles that turn individuals more likely to be chosen by the opposite sex or the ones who control this access. In the intrasexual selection, the selection pressure is among alleles that make individuals more effective in monopolizing reproductive access to the opposite sex.

The two forces are reversely related, so that when the strength of intrasexual competition increases, the strength of the intersexual competition decreases. The reason is that the strength of intersexual selection is positively related to the capacity of the individual or those who control this access, to exercise choice, and the strength of intrasexual selection is negatively related to the capacity of the individual or those who control this access, to exercise choice. More specifically, if the capacity of individuals or those who control this access to exercise choice increases, the capacity of other individuals to monopolize sexual access decreases, while if the capacity of the individuals or those who control this access to exercise choice decreases, the capacity of other individuals to monopolize sexual access increases. To put it the other way round, when the capacity of individuals to monopolize sexual access increases, the capacity of individuals or those who control this access to choose mates on their own decreases.

To illustrate why this is the case, assume that there is a population consisting of several tribes that live peacefully with each other and that individuals choose their own mates. In this setting, intersexual competition is the dominant contributor to the sexual selection pressure exercised on the different alleles. That is to say, selection pressure is stronger on alleles that affect the likelihood to be selected by the opposite sex, than on alleles that increase the effectiveness of monopolizing access to the opposite sex. For example, an allele that makes an individual more appealing as a mate to the opposite sex will spread more rapidly to the population than an allele that makes an individual more effective in fighting others and getting their mates.

Assume now that, for some reason, these tribes start fighting with each other. As a consequence, the environmental context changes dramatically, and raids become frequent. Tribe members engage in such raids in order to get the resources of the other tribes, one being individuals with high reproductive capacity. In this setting, individuals lose a substantial part of their capacity to exercise mate choice. Accordingly, selection forces are stronger on alleles that contribute to the effectiveness of monopolizing access to the opposite sex than on the alleles that contribute to the effectiveness of being selected by the opposite sex. For example, an allele that makes an individual more effective in fighting others and gaining access to their mates (e.g., predisposes for stronger muscles) will spread rapidly in the population, something which will not happen in times of peace. Similarly, an allele that makes

an individual more appealing to members of the opposite sex will spread at a lower rate in the war context than in the peace context.

In sum, in a peaceful context, people have a high capacity to choose their own mates, so the intersexual selection is the primary contributor to the sexual selection force. However, if say war erupts, and individual rights protection systems collapse, individuals' capacity to exercise choice is reduced, and the contribution of the intersexual selection on the sexual selection is reduced in favor of the intrasexual selection.

Overall, intrasexual and intersexual selections are inversely proportional related forces, so that when the strength of the one increases, the strength of the other weakens:

$$\text{Sexual selection force} = \text{Intersexual selection} + \text{Intrasexual selection},$$

where

$$\text{Intersexual selection} = a \,/\, \text{Intrasexual selection}$$

Equally,

$$\text{Intrasexual selection} = a \,/\, \text{Intersexual selection}$$

Thus,

$$\begin{aligned}\text{Sexual selection force} &= a^{*} \,/\, \text{Intersexual selection} + a \,/\, \text{Intrasexual selection} \\ &= a^{*}\left(1 \,/\, \text{Intersexual selection} + 1 \,/\, \text{Intrasexual selection}\right)\end{aligned}$$

In this formulation, the (a) describes the inverse relationship between the two forces which is assumed to be linear. We can also assume that neither intrasexual selection nor intersexual selection pressures become zero.

Males Versus Females

One sex usually makes a larger initial parental investment, and it is called the female sex (Trivers, 1972). This difference can be seen in the large size of eggs and the relative tiny size of spermatozoa. In more complex organisms, this initial asymmetry in parental investment is further augmented by the investment required for internal gestation. Complex organisms require some period of growth within the body of a parent before they are able to survive on their own in the outside environment. In effect, evolutionary pressure is exercised on one sex, usually the female one, to specialize in accomplishing this goal. Accordingly, females not only make a higher initial parental investment but make also a higher parental investment during the time required for incubation.

This investment results in time off the pool of individuals available for mating, meaning that a female cannot conceive additional children until the ones inside her are born, so she remains effectively outside the mating pool. Consequently, after a mating episode that leads to conception, females reenter the mating pool later than males, who invest less in their offspring. This difference affects the operational sex ratio, which is the ratio of males and females who are available to mate (Emlen, 1976; Emlen & Oring, 1977), so that, at any given point in time, there are more males than females available to mate. As a consequence, males compete more intensively for access to females, experiencing as a result stronger sexual selection.

In the human species, men also provide parental care. More specifically, because pregnancy is demanding and because a child needs several years before it becomes sufficiently autonomous, selection pressures are exercised on men to provide parental care to their offspring (Trivers, 1972). To put it another way, men who provide care to their pregnant partners and to their young children would enjoy higher fitness than those who do not, as they are likely to have more children that would survive to sexual maturity and reproduce. Paternal investment affects also the operational sex ratio because, after a mating episode that leads to pregnancy, men stay out of the mating pool and divert their resources to their offspring. To put it another way, there will be women who are ready to mate but may experience shortage of mates as many men will be outside the mating pool, caring for their pregnant partners or their children.

Even so, women invest more in their offspring, which means that the operational sex ratio is usually biased against men; thus, at any given point in time, there will be more men in the mating pool than there will be women. For instance, a man can enter in the mating pool even if his mate is pregnant, but his pregnant mate cannot enter in the mating pool.

Intrasexual Selection: Male-Male and Female-Female Competition

Men experience stronger intersexual and intrasexual selection. With respect to the latter, selection pressures can result in adaptations which enable men to exclude other men from the competition. Such adaptations include strong muscles and a more aggressive disposition (Puts, 2010, 2016). For instance, an allele that predisposes for stronger muscles in male bodies is selected because it enables men endowed with it to be more effective in fighting other men over women.

Since male parental investment tends to equalize the operational sex ratio, women experience also intrasexual selection pressure. This pressure may result in adaptations which enable a woman to exclude other women from the competition and monopolize mating access to men. Such adaptations may take the form of psychological mechanisms. For instance, women may spread rumors about the sexual life of their competitors, turn them less attractive to men, and effectively exclude

them from the competition. To use one example, men value chastity in women, so a woman can spread rumors that a competing woman is "easy" and has had many sexual partners (Buss, 2003). This strategy may exclude the competing woman from the long-term mating market, as men will not see her as a desirable partner.

Still, because the operational sex ratio is usually biased against men, men will experience stronger intrasexual selection than women, resulting in male-male competition to be more intense than female-female competition. Furthermore, since the relative strength of male-male and female-female competition depends on the operational sex ratio, it has to be that, when the strength of the female-female competition increases, the strength of the male-male competition decreases and the reverse. That is to say, at a given point in time, it is not possible for the ratio to be biased against both sexes. For instance, assume that war erupts. This event increases significantly the number of men who are ready for mating, as these men may have been effectively outside the mating market before the war. For example, they may have been with their families or unable to attract mates. But now they are soldiers who fight others and can get their women. The war increases significantly the ratio, strengthening male-male competition. On the other hand, female-female competition is weakened because women do not compete for mates who are forced on them.

Assume now that, after a prolonged period of fighting, the war is over, but many young men have died. Consequently, the operational sex ratio is affected, as we have a relatively high number of women being ready for mating and a relatively low number of men being ready for mating, resulting into stronger intrasexual completion exercised on women. Overall,

$$\begin{aligned}\text{Intrasexual selection force} = {} & \text{Male-male competition} \\ & + \text{Female-female competition},\end{aligned}$$

where

$$\text{Male-male competition} = b / \text{Female-female competition}$$

Equally,

$$\text{Female-female competition} = b / \text{Male-male competition}$$

Thus,

$$\begin{aligned}\text{Intrasexual selection force} = {} & b^{*}\left(1 / \text{Male-male competition}\right. \\ & \left. + 1 / \text{Female-female competition}\right)\end{aligned}$$

In this formulation, the (b) describes the inverse relationship between male-male and female-female competition. We can also assume that male-male and female-female competition never become zero.

Intersexual Competition: Individual and Parental Choice

Individual Choice

Turning to intersexual selection, individuals can gain reproductive access by being selected as mates by members of the opposite sex. Alleles which make an individual more likely to be selected experience positive selection (i.e., they increase in frequency in the gene pool), while alleles which make an individual less likely to be selected experience negative selection (i.e., they decrease in frequency in the gene pool). The asymmetry in parental investment, with women allocating more parental investment to their offspring, and the subsequent consequences of this difference on the operational sex ratio result into men being usually under stronger intersexual selection pressure than women (Dixson, 2009).

In particular, at any given point in time, there are more males than females available for mating, which means that males need to compete more intensively between them for gaining reproductive access to females. This asymmetry results in the latter being in a position to exercise choice, with female choice becoming a significant intersexual selection force. Traits in a male that make him more likely to be chosen as a mate experience positive selection and increase in frequency in the population. As discussed above, in the human species, men also allocate parental investment to their children which tends to equalize the operational sex ratio, strengthening in effect male choice. That is to say, at any given point in time, the surplus of men is limited because some of them are home providing for their children. In effect, women need to compete with each other in order to be selected by high-quality men, so male choice is exercised on them. Traits in a woman who make her more likely to be selected by men experience positive selection and increase in frequency in the population. Women with such traits attract the attention of more men, so they have a larger pool from which they can choose the higher-quality mates.

The strength of female choice is reversely related to the strength of male choice, since it cannot be the case that at any point in time, there are more males and more females available for mating. That is to say, when female choice strengthens, male choice weakens and the reverse. In the war example above, in the prewar state, assuming that there have been a roughly equal number of men and women, there would be more men available for mating than women, because many women were outside the pool of available mates being either pregnant or caring for their children. For one woman available, there would be several men seeking reproductive access. In effect, women would be in a position to exercise choice, and female choice would be driving intersexual selection. If, however, following a prolonged period of war, many young men have perished, there would be as a consequence more women than men available for mating in the mating pool. This difference would place men in a position where they could exercise choice, and, thus, male choice would be driving intersexual selection. Overall,

$$\text{Individual mate choice force} = \text{Female choice} + \text{Male choice},$$

where

$$\text{Female choice} = c / \text{Male choice}$$

Equally,

$$\text{Male choice} = c / \text{Female choice}$$

$$\text{Individual mate choice force} = c^{*}\left(1/\text{Female choice} + 1/\text{Male choice}\right),$$

where the (c) describes the inverse relationship between female choice and male choice. We can also assume that that female choice and male choice never become zero.

Parental Choice

Parents and children are genetically related but not genetically identical. As a consequence, their genetic interests overlap but also diverge (Trivers, 1974). One area where this overlap and divergence of interests is manifested is mate choice. In particular, several traits in a prospective mate make different fitness contributions to parents and children and, consequently, are valued differently by each party (Apostolou, 2008, 2014). Thus, if children are left on their own, they will make choices which maximize their own and not the fitness of their parents. In consequence, selection pressures are exercised on parents to place their children's mating decision under their control and choose in-laws that maximize their own fitness (see next chapter for a more detailed account of this argument).

When parents succeed in doing so, they become a significant intersexual selection force (Apostolou, 2007, 2014). In particular, individuals need to compete in order to gain access to the reproductive capacity of the opposite sex, not by being selected by the opposite sex but by the parents of the opposite sex. In this case, intersexual selection would be driven by parental choice: Alleles that code for traits that increase the probability to be selected as a son- or a daughter-in-law experience positive selection, while alleles that code for traits that decrease this probability experience negative selection.

Accordingly, intersexual selection has two components, namely, individual mate choice and parental choice, the strength of one being inversely related to the strength of the other. The reason is that, as parental grip over children's mating decisions strengthens, the latter's capacity to exercise choice is reduced. In the same vein, as children become more independent in exercising choice, the capacity of their parents to control their mating decisions weakens. Thus,

$$\text{Intersexual selection force} = \text{Individual mate choice} + \text{Parental choice},$$

where

$$\text{Individual mate choice} = d / \text{Parental choice}$$

Equally,

$$\text{Parental choice} = \text{d} / \text{Individual mate choice}$$

$$\text{Intersexual selection force} = \text{d}^{*}\left(1 / \text{Individual mate choice} + 1 / \text{Parental choice}\right),$$

where the (d) describes the inverse relationship between the individual mate choice and parental choice. We can further assume that parental choice and individual mate choice never become zero.

Parental choice is not a homogenous force, as it can be exercised by both mothers and fathers, with each party varying in how much control it has over children's mate choices (see Chap. 3). Thus, parental choice can be decomposed into male parental choice and female parental choice. For a given level of parental control over mating, if male parental control strengthens, female parental control weakens. Similarly, if female parental control strengthens, male parental control weakens. To put it differently, it is not possible for children's mate choices to be controlled at the same time predominantly by their fathers and predominantly by their mothers. Accordingly, there is an inverse relationship between the two forces so that

$$\text{Parental choice} = \text{Male parental choice} + \text{Female parental choice},$$

where

$$\text{Male parental choice} = \text{e} / \text{Female parental choice}$$

Equally,

$$\text{Female parental choice} = \text{e} / \text{Male parental choice}$$

$$\text{Parental choice force} = \text{e}^{*}\left(1 / \text{Female parental choice} + 1 / \text{Male parental choice}\right),$$

where the (e) describes the inverse relationship between female parental choice and male parental choice. We can also assume that female parental choice and male parental choice never become zero.

Sexual Coercion

Individuals can also gain reproductive access to the opposite sex by using force. This possibility translates into selection pressure that gives rise to adaptations that enable individuals to do so. Such pressure can be considered to be different to intersexual and intrasexual sexual selection forces (Smuts & Smuts, 1993). A forced-sex mating strategy or rape is an example of a mechanism that has evolved through this force (Smuts, 1992).

In more detail, due to the asymmetry in parental investment, men experience stronger competition in finding mates (Trivers, 1972). Accordingly, they need to

allocate considerable amounts of resources in mating effort, so as to be selected by women as mates or by their parents as in-laws, or to fight other men and get their women. Still, a man can avoid paying this cost by forcing sex to a woman. Such a strategy would be optimal when the cost of adopting it is low, so that the reproductive benefit exceeds it, for instance, when a woman has no relatives to retaliate or the society where she lives does not punish rape severely. This strategy can also benefit men who lack the traits that would enable them to be selected by women (e.g., good looks) or their parents (e.g., good family background) or to monopolize access to women (e.g., physical strength). Accordingly, a strategy would have evolved through sexual coercion that motivates men to force sex to women when the cost of doing so is low and/or when they lack the qualities to gain reproductive access to them through other venues.

Due to the asymmetry in parental investment, the operational sex ratio usually favors women, in the sense that the men available for mating are in surplus. Thus, a woman who wants to have casual sex can easily do so as there are many available men who would provide it. Therefore, women do not have to force sex on men. This is not the case for men, however, as women who are available for mating are usually in short supply and, thus, choosy.

Women are also choosier than men, because a sexual contact can be more consequential for them. A brief sexual encounter may have few costs for a man, but it can commit a woman's parental investment for 9 months to the child of a man who is not beneficial to her fitness. It pays then for women to be always choosy over whom to have sex with (Buss, 2003). The choosiness of women may place men in a position where forcing sex may be the only way to gain reproductive access to the opposite sex. It also has to be said that strong intrasexual competition has resulted in men having adaptations such as larger body size and stronger muscles than women (Puts, 2010), which can facilitate a forced-sex mating strategy.

There are several parameters that can affect the strength of this force. To begin with, ceteris paribus, a large population size favors sexual coercion. In a small population, there is more social control, and a man who engages in such a strategy can be more readily identified and punished. Also, the presence of powerful social institutions, such as the law, that punish this strategy severely weakens sexual coercion. In general, a state of anomie favors sexual coercion, as men who follow a forced-sex strategy do not suffer considerable costs.

For the purposes of this work, I will enter sexual coercion as a separate component of sexual selection so that

$$\text{Sexual selection force} = \text{Intersexual selection} + \text{Intrasexual selection} + \text{Sexual coercion}$$

Nonetheless, further modeling can be done as sexual coercion is not independent from the other two selection forces. For instance, adaptations that have been shaped by this force, such as a forced-sex mating strategy or rape, undermine female and parental choice and weaken intersexual selection. They may also undermine male-male competition as they can lead to impregnating women that have been controlled by other men.

Sexual Coercion Versus Other Sexual Selection Forces

With the term sexual coercion, I refer to forcing sex to a partner outside the context of marriage and male-male competition. More specifically, in male-male competition, men monopolize access to women, usually by exercising force on other men. They can either get these women as wives or concubines or just have sex with them. In this scenario, women did not choose these men, so they may not consent to have sex with them. Accordingly, men need to bypass possible resistance and force sex to women. This is a form of sexual coercion, which has evolved, however, in the context of male-male competition. In the same vein, in an arranged marriage context, the husband is not likely to appeal to the preferences of his wife as he is not her choice. Accordingly, she may resist allowing him reproductive access to her. In this case, the husband needs to bypass this resistance and force sex to his wife. This strategy has evolved in the context of parental choice to enable men to gain reproductive access to the opposite sex.

Sexual Selection Force

Putting the arguments made above together, we can get a more detailed picture of the major components of sexual selection and how they relate to each other:

$$\begin{aligned}\text{Sexual selection force} = a^{*}\left(1/\text{Intersexual selection} + 1/\text{Intrasexual selection}\right)\\ + \text{Sexual coercion}\end{aligned}$$

Substituting

$$\begin{aligned}\text{Sexual selection force} = a^{*}\Big\{1/\Big[d^{*}\left(1/\text{Individual mate choice} + 1/\text{Parental choice}\right)\Big]\\ + 1/\Big[b^{*}\left(1/\text{Male - male competition}\right.\\ \left. + 1/\text{Female - female competition}\right)\Big]\Big\} + \text{Sexual coercion}\end{aligned}$$

or

$$\begin{aligned}\text{Sexual selection force} = a^{*}\Big\{\Big[d\left(1/\text{Individual mate choice} + 1/\text{Parental choice}\right)\Big]^{-1}\\ + \Big[b^{*}\left(1/\text{Male - male competition} + 1/\text{Female - female competition}\right)\Big]^{-1}\Big\}\\ + \text{Sexual coercion}\end{aligned}$$

In the expression above, individuals belonging to sexually reproducing species are under a given sexual selection pressure. This sexual selection pressure can be decomposed into intersexual selection pressure, intrasexual selection pressure, and sexual coercion. Intersexual selection pressure can be decomposed to selection pressure coming from individual mate choice and selection pressure coming from parental choice, the latter force being unique in our species (Apostolou, 2007, 2014). Intrasexual competition can be decomposed into male-male competition and female-female competition.

An individual is likely to experience more than one selection force. For instance, a man needs to appeal to a woman as a mate, to her parents as an in-law, to fight other men who may try to get his partner, and to exploit opportunities to force sex to women. Nevertheless, the balance of power between different sexual selection forces varies with the environmental context. That is to say, certain environments may turn one sexual selection force stronger than the other. For instance, in Western societies, the protection of individual rights favors individual mate choice over parental choice and over intrasexual competition. In pre-industrial societies, lack of protection of individual rights favors parental choice and intrasexual competition over individual mate choice.

Since the different selection forces are interrelated, by identifying the factors that affect one, we can predict what will happen to the others. For instance, if a certain environmental factor strengthens individual mate choice, the strength of parental choice and male-male competition will decrease. To use one example, the adoption of a legal system that protects individual rights strengthens individual choice and weakens parental choice, as parents cannot force mates to their children, and intrasexual competition as individuals is constrained from fighting others and getting their mates. Sexual coercion will also weaken, as the space of individuals to force sex without or with little consequences decreases considerably. The abolition of this system will bring the opposite results.

Sperm Competition

Competition between males over fertilizing an egg continues after a mating episode, if the sperm of two or more males overlap near the site of fertilization in females (Parker, 1970). Sperm competition can be understood as a distinct sexual selection force which gives rise to adaptations that promote the success of sperm in direct competition, promote sperm success by preventing competition between different ejaculates (e.g., by blocking access to the female reproductive tract), or promote sperm success by removing, destroying, or inactivating the sperm of rival males (Wigby & Chapman, 2004).

To use a more concrete example of how this form of competition works, there is evidence that relative sperm numbers are important for sperm competitive success, and comparative studies show that species which experience higher risks of sperm competition invest in relatively larger testes that produce higher sperm counts (Wedell,

Gage, & Parker, 2002). Sperm competition may influence behavioral traits as well. For instance, a male can reduce the chances that sperm other than his own fertilizes the egg of a female by guarding her closely. That is to say, adaptations related to mate guarding may have been partially shaped by sperm competition (Simmons, 2001).

Although sperm competition is likely to affect several adaptations, it is predominantly responsible for shaping optimal ejaculate structure (Wedell et al., 2002). Thus, because the focus of this force is rather narrow, I will not integrate it in the arguments developed in this book. I will attempt, however, to examine in this section how this sexual selection force relates to other forces.

The strength of sperm competition is proportional to the strength of intrasexual selection and in particular of male-male competition. When raids, wars, and violent conflict are common, women would frequently find themselves victims of rape, which means that there is an elevated probability that the sperm of two or more men is found in the female reproductive tract. For the same reason, the strength of sperm competition is proportional in strength to sexual coercion. If environmental conditions turn sexual coercion more common, the probability that the sperm of two or more men is found in the female reproductive tract increases.

The strength of sperm competition is inversely related to the strength of intersexual selection. When individual or parental choice dominates, individuals establish long-term monogamous relationships which usually take the form of marriage, where there is a limited probability that the sperm of two or more men is found in the female reproductive tract. It needs to be said, nevertheless, that even in these scenarios, sperm competition is expected to be present. To begin with, women may marry men of similar genetic quality to their own, but then have extramarital relationships with men of superior genetic quality in order to have children of better genetic quality (Buss, 2003; see also Thornhill, 1983). This strategy can be even more pronounced when parental choice dominates. Parents value good genetic quality less than their children, so the latter are likely to find themselves married to individuals of a genetic quality which is inferior to what they desire, and so they would seek good genetic quality partners outside the wedlock (Apostolou, 2014).

Environmental and cultural factors that affect how easily individuals can have parallel relationships would affect the strength of sperm competition. For instance, in a theocracy like the Byzantine Empire, where extramarital relationships were severely sanctioned (Cavallo, 1997), sperm competition would be weaker than in the Roman Empire where extramarital relationships were less severely penalized (Rawson, 1991).

Reproductive Niches

In a given environmental context, all sexual selection forces are expected to be present. Thus, there are four ways through which an individual can gain access to the reproductive capacity of the opposite sex, namely, to be chosen by parents, to be chosen by members of the opposite sex, to monopolize access to members of the

opposite sex, and to force sex to members of the opposite sex. In effect, there are four distinct reproductive niches, i.e., slots in the environment with reproductive resources. The specific attributes of the environment determine the relative strength of each selection force, i.e., how big a reproductive niche is. If, for instance, a specific environmental context favors parental choice over the other selection forces, then the niche for parental choice is larger than the rest of the reproductive niches.

Accordingly, the equations above can be understood as depicting how the size of one reproductive niche relates to the size of the other reproductive niches. For instance, I have argued that the strength of parental choice is inversely related to the strength of individual mate choice. Thus, if parental choice strengthens, individual mate choice weakens. That is to say, when the parental choice niche increases in size, the individual mate choice niche decreases in size. The size of reproductive niches can be interpreted as indicating the probability that an individual will come across the opportunity to exploit a given niche. For instance, in a context where parental choice dominates and individual mate choice is limited, individuals seeking a mate will come across parental choice (i.e., prospective parents-in-law deciding whether to provide them with such access or not) more frequently than individual choice (i.e., prospective partners deciding whether to allow them such access).

In effect, individuals who have alleles that predispose for traits that enable them to increase their chances to be selected as sons- or daughters-in-law are better off than individuals who do not carry these alleles. Therefore, alleles that predispose for these traits will be in higher frequency in the gene pool, because individuals, who carry them, spread them in future generations by successfully exploiting the parental choice niche.

Accordingly, different reproductive niches mean that there is variation in sexually selected traits. Some individuals will be endowed with traits that enable them to address one niche, while others will be endowed with traits that enable them to address a different niche. Thus, in order to understand the prevalence of specific traits today, inferences about the size of ancestral niches need to be made. In addition, the observed frequencies of traits today can tell us about the size of ancestral niches. This argument will be explored in detail in subsequent chapters.

In summary, in this chapter I have argued that sexual selection is not a homogenous force, but is the resultant of different sexual selection forces. The different selection forces are, to a degree, inversely related to each other, as for a given level of sexual selection pressure, the strengthening of one selection force would inevitably mean the weakening of one or more other forces. I have argued that all sexual selection forces are present in every environmental setting, with the specific environmental factors in this setting determining the strength of each selection force. The presence of different sexual selection forces with different strengths translates in the presence of different reproductive niches of different sizes.

The chapters that follow aim to explore how parental choice works and to identify the factors that predict its strength. This endeavor can lead to a better understanding of the balance of selection forces on an individual and consequently on the evolution of sexually selected traits. The primary reason why parents are motivated to control the mating decisions of their children is conflicting interests over mating, so the next chapter will be devoted to accounting for this divergence in interests.

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Chapter 2
Parent-Offspring Conflict over Mating

If parents and children had identical interests over mating, the former would have had a weak incentive to control the latter's mating decisions: Children's mate choices would maximize their fitness, as well as the fitness of their parents. Therefore, parent-offspring conflict over mating is critical for understanding the parental choice sexual selection force. The purpose of this chapter is to explain why parents and children have conflicting interests over mating and how this conflict leads the former to control the mate choices of the latter.

Why Parents and Children Do Not Have Identical Interests over Mate Choice

Parents and children do not have identical genetic interests because they are not genetically identical (Trivers, 1974). The coefficient of genetic relatedness between parents and children is 0.5, meaning that a parent and a child share half of their genes. Consequently, a parental action that increases the parent's fitness (i.e., the probability that his/her genes will be represented in future generations) will also increase the child's fitness, but not as much. Similarly, a child's action that increases the child's fitness will increase also the parent's fitness, but not as much. In the same vein, a parent's action that decreases the child's fitness will decrease the fitness of the parent, but not as much. Similarly, a child's action that decreases the parent's fitness will decrease also the child's fitness but not as much. In this respect, each party is motivated to engage in actions that maximize its own fitness, even though these actions do not maximize the fitness of the other party.

This difference in interests is manifested in the allocation of parental investment (Trivers, 1974): Ceteris paribus, it is optimal for parents to divide their parental investment equally between their children, as they are equally genetically related to all of them (0.5). From a child's point of view, equal allocation is not optimal, as it

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is more closely related to itself (1) than to its siblings (0.5). Simply put, a unit of parental investment allocated to it will increase its fitness twice as much than if it is allocated to one of its siblings. Therefore, it would be best for a child to extract more than its fair share of parental investment because, by doing so, it increases its net fitness: It will suffer inclusive fitness costs by decreasing the fitness of its siblings, but these costs will be lower than the benefits that it will derive. Therefore, any strategy that will enable the child to get more than its fair share of parental investment will be favored by selection forces.

This argument can also be examined from the side of the parent: It can be evolutionary optimal for the parent to punish a child for exhibiting selfish behavior toward its siblings. Doing so would be beneficial for the parent, because it would allow it to have more resources available to distribute in a fitness-increasing manner, while the cost of the punishment to the child will be half the cost the parent will suffer. Consequently, any strategy that punishes selfish behavior and restores equality in the distribution of parental investment is likely to be favored by selection forces.

Overall, we expect conflict to arise, with children fighting to extract more resources than their parents are willing to give them and parents punishing and discouraging any such behavior. However, the allocation of parental investment is not the only domain of parent-offspring conflict.

Parent-Offspring Conflict over Mating

Another domain, where the difference in genetic relatedness between parents and their children asymmetry leads to conflict, is mate choice (Apostolou, 2007; Schlomer, Del Guidice, & Ellis, 2011). The conflict is generated because specific traits in a mating candidate give unequal benefits to parents and to their children (Apostolou, 2008a, 2008b). One example of this difference constitutes the looks of a prospective mate that summarize information about genetic quality, health, age, and offspring's reproductive success.

Starting from the former, poor genetic quality (i.e., mutations that affect the proper expression of genes or alleles which cannot deal effectively with the challenges of the environment) compromises individuals' survival success. Individuals of poor genetic quality are more likely to die or become incapacitated, leaving their partners and their children with no support. Furthermore, poor genetic quality means poor reproductive success, because individuals pass their genetic material to their children, who are also likely to suffer survival costs. Poor genetic quality is likely to have an effect on an individual's looks. For instance, individuals with alleles which cannot deal effectively with parasites may suffer during their development, which can affect their body's symmetry (Gangestad, Thornhill, & Yeo, 1994; Thornhill & Gangestad, 1993).

Furthermore, poor health relates to genetic quality, but it may not necessarily be the outcome of it. For instance, an accident may cause damage to body organs that results in poor body functioning. Individuals with poor health may die, become

incapacitated, and, thus, be unable to provide for their family, or they may even transmit the disease that caused them the poor health to their partners. Poor health usually reflects on looks; for instance, individuals may have pale skin color and falling hair and experience considerable loss in body weight.

Age constitutes another important predictor of fitness. More specifically, as people age, their reproductive capacity declines, and in older age it is lost completely (Eskenazi et al., 2003; Nelson, Telfer, & Anderson, 2012). With age, not only the reproductive capacity diminishes but also the capacity to provide for one's children and partners, since older individuals have fewer years ahead of them to provide to their family than younger ones. Individuals' age reflects also on their looks: As people get older, their hair and teeth fall, their skin becomes less smooth, and so on.

Last but not least, a certain observable trait may appeal to members of the opposite sex even if it does not summarize any information about genetic quality, health, and age. This can happen for various reasons (e.g., runaway selection, see Fisher, 1958), but the important point is that this trait is fitness increasing in a prospective mate: It can pass to offspring, turning them also appealing to members of the opposite sex. Accordingly, individuals who mate with partners who have this trait increase their fitness by having children who are more successful in the mating market.

Overall, there is substantial information about the fitness contribution prospective partners can make, which is summarized in their looks. As a consequence, the strong evolutionary pressures exercised on individuals to distinguish between potential mates and in-laws have shaped the mind to interpret traits which indicate high fitness, such as smooth skin and high symmetry, as beautiful (i.e., preferable), and traits which indicate low fitness, such as falling hair and teeth, as ugly (i.e., not preferable), and to tend to prefer the former than the latter in both prospective mates and in-laws. Nevertheless, the fitness contributions of attractive traits differ on the basis of whether they are found in a mate or in an in-law.

To begin with, if individuals' mates die due to poor genetic quality or poor health, the fitness loss will be higher than if their sons- or daughters-in-law die. One reason is that mates contribute more resources to their partners than to their partners' parents. Another reason is that the loss of partners involves considerable reduction in the resources diverted to their children; in the case that these individuals are partners, one's children will suffer losses, but in cases they are in-laws, one's grandchildren will suffer losses. Nevertheless, because individuals are more closely related to their children than to their grandchildren, the latter case is more fitness reducing than the former.

Furthermore, unattractive traits may indicate a contagious disease that individuals are more likely to catch from their mates than from their in-laws, as they have closer and more frequent interactions with the former than with the latter. In addition, attractive traits indicate that individuals' children and grandchildren will enjoy higher fitness. Still, because individuals are more closely related to their children than to their grandchildren, the fitness contributions of these traits are different when they are found in a mate and in an in-law.

As a consequence, different evolutionary pressures are exercised on in-law and mate preferences, with the two diverging over looks, a trait which is valued more in a spouse than in an in-law (Apostolou, 2008a). Apart from good looks, empirical research has, so far, identified that exciting personality is preferred more in a spouse than in an in-law, while well-off and similar family background are preferred more in an in-law than in a spouse (Apostolou, 2008a, 2008b, 2011a,b, 2011c, 2015; Apostolou et al., 2014; Buunk, Park, & Dubbs, 2008; Perilloux, Fleischman, & Buss, 2011).

The Nature of Mate Choice and Conflict over Mating

Differences in genetic relatedness indicate that certain traits have differential fitness benefits in a spouse and in an in-law, but this does not necessarily lead to conflict over mating. The differential benefits are not a sufficient condition for conflict to exist; for conflict to exist, the choices one party makes need to inflict a cost to the other. If they do not, there would not be disagreement between the two. For instance, a good looking mate is beneficial to both parents and their children, albeit more beneficial to the latter than to the former. As both have to gain, there should not be any conflict. But conflict exists, predominantly because mate choice involves compromises, and the compromises that children are willing to make in order to get desirable traits are not optimal for their parents.

More specifically, children are constrained by their own mate value with respect to the mate value of the individuals they can attract (Li, Bailey, Kenrick, & Linsenmeier, 2002). That is to say, individuals looking for long-term mates cannot attract mates of much greater value than their own, because these mates would not be willing to enter in such a relationship, as it would not be optimal for them to accept mates of a lower mate value to their own (Apostolou, 2011c; Buss, 2003). Therefore, mate choice inevitably involves compromises: In order to be able to attract and keep a long-term partner, mate-seekers have to accept mates who score lower in desirable traits than they would prefer.

The asymmetrical fitness benefits that certain traits provide result into mate-seekers making compromises which are not to the best interest of their parents (Apostolou, 2011c). For example, mate-seekers would have to compromise on traits such as social status and family background, in order to get a mate of high genetic quality. Nevertheless, because this trait is not as beneficial in an in-law, the accrued benefits will not balance the losses from the compromises in other desirable qualities. Therefore, from the parents' point of view, these compromises are not optimal, and if they were to exercise mate choice for their children, they would prefer a different mix of trait, a mix that would involve less of good genetic quality and more of other traits.

In order to examine the compromises in desirable trait hypothesis more thoroughly, a simple model of mate choice can be considered, where there are only two desirable traits in a prospective mate, namely, good looks (G) and well-off family

background (F) (see also Apostolou, 2017). We can further assume that (a) is the degree of the fitness benefits that mate-seekers derive from the good looks and that (b) is the degree of fitness benefits that mate-seekers derive from the well-off family background. We can consider further that when individuals enter in the mating market, they have a budget of mate points that they can allocate to different desirable traits in a mate. The amount of mate points they have available depends on their mate value (V); individuals who have a high mate value have more points to allocate, and so, they can get mates of high mate value. Finally, the amount of mate points allocated to a trait depends on the fitness benefits it confers: The higher the fitness benefits individuals receive from this trait, the more points they will allocate to it.

When children exercise choice, they are constrained by their own mate value in the value of a mate they can get, so that the fitness benefit they can derive from a mate (B_{child}) cannot exceed (V). As it would be suboptimal for a child to get a mate below (V), it is expected that children will strive to get mates so that $B_{child} = V$. Thus,

$$B_{child} = aG + bF \leq V \tag{2.1}$$

In the same way, if parents were exercising choice for their children:

$$B_{parent} = cG + dF \leq V \tag{2.2}$$

where (c) is the fitness benefit that the parent derives from the good looks and (d) is the fitness benefit that the parent derives from well-off family background.

Now, let us assume that due to differences in genetic relatedness, good looks are more beneficial to children than to parents ($a > c$) and well-off family background is more beneficial to parents than to children ($b < d$). This being the case, the mate choices of children of a given mate value involve a fitness loss for parents that can be estimated as follows:

$$B = B_{child} - B_{parent}$$

Substituting:

$$\begin{aligned} B &= (aG + bF) - (cG + dF) \\ &= aG + bF - cG - dF \\ &= (a - c)G + (b - d)F \end{aligned} \tag{2.3}$$

This formulation enables us to estimate the fitness cost inflicted to parents by the mate choices of their children. In Appendix 1, the Eq. 2.3 is employed in estimating the cost to parents using empirical data. This cost arises from differences in genetic relatedness resulting in $a \neq c$, and $b \neq d$. If parents and children were genetically identical, fitness benefits would be equal for both ($a = c$ and $b = d$), which means that the Eq. 2.3 would be zero. In that case, the mate choices of children would not be costly for their parents, and no parent-offspring conflict over mating would exist.

Note that conflict would arise even if there was only one conflicting trait. For instance, if the (G) would give asymmetrical benefits to parents and their children so that $a \neq c$, and the (F) would give the same benefits so that $b = d$, there would still be conflict expressed in this case as: (a−c)G.

Another possibility where there would be no conflict is when mate-seekers allocate zero mate points to the traits that give different benefits to parents and children and spend their budget in other traits which give similar benefits to each party (not included in this model). Yet, this is unlikely to happen, as it would not be optimal. For instance, a mate with extremely poor genetic quality would soon perish or would have children that would be unlikely to reach sexual maturity. Accordingly, we expect that mate-seekers would make a minimum allocation of mate points to most of the traits in a prospective mate (see also Li et al., 2002).

Furthermore, the fitness differentials (i.e., a−c and b−d) indicate that each trait makes different contribution to the fitness of parents and children. Each party would prefer to allocate more mate points to the traits that give it more benefits. In this scenario, children would allocate more mate points to (G) and fewer mate points to (F), whereas if parents were to exercise choice for their children, they would allocate fewer mate points in (G) and more mate points in (F).

The compromises in trait hypothesis have received empirical support. In particular, in one study I gave individuals and their parents a fixed amount of mate points (depicting mate-seekers' mate value), and I asked them to allocate them across several traits, including good looks and good family background (Apostolou, 2011c). I found that children allocated more points to good looks than their parents, and they did this by saving in other traits such as good family background and favorable social status. Parents, on the other hand, allocated more points to traits such as good family background saving, however, in other traits such as good looks.

Conflict and Mate Value

A further implication of the argument developed above is that the degree of conflict between the two parties is a function of children's mate value (V). In more detail, when mate value is low, children have fewer mate points to allocate to each conflicting trait, so the cost of forgone traits for parents is small. When mate value increases, children have more mate points available to allocate to conflicting traits, imposing a bigger cost to their parents. Thus, as children's mate value increases, parent-offspring conflict over mating increases as well. But conflict increases up to a point.

In particular, the score of a specific trait, such as good looks, is not infinite; in different words, children or their parents cannot allocate an infinite amount of mate points to a given trait. Returning to Eq. 2.3, children would allocate more mate points to (G) than to (F). If their mate value increases, they have extra mate points at their disposal, and they will allocate more of these extra points to (G) than to (F) as the former gives them more fitness benefits than the latter. But let us say now that they have reached the maximum of mate points they can allocate to (G). If their mate value increases further, they cannot spend their extra points on (G), as it has

already reached the maximum. Thus, they have to spend these points on (F), and doing so reduces the conflict with their parents.

Accordingly, the fitness cost that children's mate choices inflict to their parents, and, thus, the degree of parent-offspring conflict over mating, is a function of children's mate value. Nevertheless, this function is not linear but inverted U-shaped: As mate value increases, the conflict increases as well but up to a point, reaching eventually a maximum; after that point it decreases. Thus, conflict follows a quadratic function:

$$Conflict = eV^2 + fV + \mathrm{g}, \quad where\ \mathrm{e} < 0 \tag{2.4}$$

We can find the mate value for which the parent-offspring conflict is maximized by differentiating function (2.4):

$$\mathrm{v} = -\mathrm{f} / 2\mathrm{e} \tag{2.5}$$

Empirical estimation of (f) and (e) will enable us to calculate the (v).

In order to examine whether this model fits empirical evidence, I analyzed the data available from the budget allocation study (Apostolou, 2011c). Consistent with the above prediction, when we move from low to medium mate values, the fitness cost increases, and when we move from medium to high values, it decreases (Appendix 2).

According to the above argument, when children are of very low mate value (e.g., very unattractive, very low social status, etc.), the conflict with their parents over mating would also be low. This is because the outcome would be similar if parents would be the ones to choose spouses for their children: They would not be able to achieve much better results for themselves, because they have few mate points at their disposal to allocate. Nevertheless, when children's mate value is not very low, conflict is higher. In that case, if parents were the ones choosing spouses for their children, they would have more points to allocate to traits that give fitness benefits to them but not necessarily the same fitness benefits to their children. Finally, when the mate value of children is very high, the conflict with their parents would also be low, because the risk of children not getting a mate that fits the desires of their parents is low. To put it differently, children who score "10" in everything will get mates who score "10" in everything as well; if parents were to exercise choice for their children, they would not be able to do any better.

In summary, differences in genetic relatedness result in specific traits giving different benefits to parents and to their children. The nature of mate choice, where individuals are constrained by their own mate value in the mate value of a mate they can choose, leads into making compromises. The compromises of children are costly for their parents, who prefer different kinds of compromises. This cost gives rise to the parent-offspring conflict over mating which motivates parents to control their children's mating decisions in order to minimize it. It should be noted that the compromises in trait hypothesis apply to any trait that gives differential benefits to parents and to their children and is not confined to genetic quality and good family background.

A Note About Theoretical Models

Before moving on, it is useful to say that one problem with theoretical models is that their conclusions are strongly linked to their underlying assumptions. Thus, if these assumptions are not solid, the derived conclusions are not solid as well. The model on parent-offspring conflict over mating developed above makes the following assumptions:

1. Specific traits give different fitness benefits to parents and their children.
2. Mate-seekers are constrained by their own mate value in the mate value of a mate they can get.
3. The allocation of mate points in a given trait is a positive function of the fitness benefits that this trait gives to individuals.
4. How much of a trait mate-seekers can get is finite.

Starting from the first assumption, the proposed model works only if traits in a prospective mate give different fitness benefits to parents and to their children. This assumption is well grounded to evolutionary theory: Due to differences in genetic relatedness, specific traits are expected to give different benefits depending on whether they are found in a spouse or in an in-law. Considerably more theoretical and empirical work is required to identify such traits and work out how they provide different fitness benefits. Yet, this is not a requirement for the proposed model; the model requires only that traits give differential benefits to parents and children. When theoretical and empirical work finds these traits and estimates their respective fitness contributions for each party, these estimates can be plugged in the model so as to calculate the fitness costs of children's mate choices.

The second assumption is also well grounded to evolutionary theory: Selection forces have shaped mechanisms involved in mate choice so as to enable individuals to get the most fitness-increasing mates (Buss, 2003). Accordingly, when entering in the mating market, individuals would look for mates who have a similar or higher mate value than their own, and they would refuse to engage in relationships, especially long-term ones, with mates of lower mate value. Assortative mating, i.e., individuals choosing mates who are similar to them, is a well-known phenomenon (Domingue, Fletcher, Conley, & Boardman, 2014; Tognetti, Berticat, Raymond, & Faurie, 2014). As a consequence, individuals are constrained in attracting higher to their own mate quality mates.

In the same vein, because mate effort is costly in terms of resources, and resources are finite, individuals are expected to have evolved to be choosy and to allocate this effort in what gives them more fitness benefits. To put it differently, individuals who would allocate the same effort toward getting a trait in a mate that gives them few fitness benefits and toward getting a trait that gives them more fitness benefits would be worse off than those who would allocate more of their mating effort toward getting traits that give them more benefits. Consequently, people would tend to allocate more mating effort in getting individuals who score high in traits that give them more fitness benefits and less effort in attracting mates who score high in traits that give them fewer fitness benefits. This is another way to say that the allocation of

mate points in a given trait is a positive function of the fitness benefits that this trait gives to individuals.

Finally, the third assumption is based on reason and empirical observation: Traits in a prospective mate can vary, but up to a point. That is to say, there is an upper and a lower limit in how much an individual can score to a trait. For instance, being tall is a fitness-increasing trait, but mates do not get infinite tall. Therefore, the amount of a trait mate-seekers can get is finite.

Finally, a sound model needs to make predictions that fit the empirical evidence. The proposed model makes two key predictions, namely, each party would make different allocations in traits, allocating more units to traits which give it more benefits. A further prediction is that the fitness cost that the mate choices of children have for parents is a reverse U-shaped function of their mate value. These predictions are consistent with the available evidence (see Appendixes 1, 2, and 3); yet, there is only one budget allocation study on parent-offspring conflict over mating, and future studies need to replicate these findings.

Can the Theory of Evolutionary Trade-Offs Account for Parent-Offspring Conflict over Mating?

The theory of parent-offspring conflict is crucial for the arguments that will be developed in this book; thus, it is useful that alternative explanations are explored, so that the reader can gain a more solid understanding of the phenomenon in question.

The theory of evolutionary trade-offs proposes that individuals who have high genetic quality are likely to become poor-quality parents, as they tend to invest more effort in mate seeking than in raising children (Gangestad & Simpson, 2000). For instance, a man who enjoys superior genetic quality may be better off, in terms of maximizing his reproductive success, by allocating his resources in attracting different mates than in raising children with one mate. The reason is that genetic quality is a valuable trait in the mating market, so a man's mating effort can result in multiple instances of mating and ensuing offspring. For the same reason, a man of poor genetic quality will have a lower success in the mate market; therefore, he would be better off allocating his resources in attracting one mate and invest subsequently in the children that he will have with this mate.

This theory has been employed in explaining how the difference in genetic relatedness leads to parent-offspring conflict over mating (Buunk et al., 2008; Dubbs, Buunk, & Taniguchi, 2013). In particular, children, in comparison to their parents, benefit more from mating with an individual of high genetic quality, because genetic benefits will be delivered to the resulting offspring. If the partner is of poor-quality parent, the children can rely on their parents for extra support in raising any resulting offspring. On the other hand, if the children opt for partners with traits indicating high parental investment and lower genetic quality, then the parents would not have to invest extra resources into their grandchildren, which might then be diverted to themselves or to other relatives (Buunk et al., 2008; Dubbs et al., 2013).

Van de Berg, Fawcett, Buunk, and Weissing (2013) put forward a more formal model of a different version of this argument. In their formulation, a woman can receive resources both from her parents and from her chosen mate. The total amount of resources she receives determines her fecundity. Assuming that men vary in terms of the amount of resources they provide to their mates, one reason being that some score high in genetic quality and thus they focus less on parental effort, if parents have more than one mated daughter, these daughters may differ in the amount of resources they receive from their respective mates. If a daughter is mated to a man of high genetic quality and of poor parental investment, whereas another daughter is mated to a man of poor genetic quality and of high parental investment, parents would divert more parental and grandparental investment to the former than to the latter daughter in order to compensate for this loss. The argument of the authors is that daughters exploit their parents' willingness to make such provision, offering resources to them and their children, in order to get a mate of superior genetic quality who may, however, be of poor-quality parent.

Unsupported Assumptions

The trade-offs explanation of parent-offspring conflict over mating assumes that the cost of the loss in parental investment from the high genetic quality mate falls more heavily on parents than on their daughters. Evolutionary reasoning suggests, nevertheless, that the opposite is true. In particular, if, for example, a good genetic quality man abandons his wife and children for a younger woman and provides no resources to them, both the wife and her parents will increase their parental and grandparental effort in order to compensate for this loss. Nevertheless, the wife, who is more closely related to her children than her parents are to their grandchildren, will increase her parental effort more than her parents will increase their grandparental effort and not the other way round.

To put it differently, if both the wife and her parents fail to increase their parental effort, the survival chances of their children and grandchildren will be compromised. Yet, the fitness cost of this compromise is higher for the wife, who is more closely related to her children, than it is for her parents who are less closely related to their grandchildren. This reasoning indicates that the wife will increase her parental effort more than her parents will increase their grandparental effort, because she has more to lose than her parents. Consequently, the costs coming from the losses in parental investment, due to the trade-offs between genetic quality and parental effort, would fall more heavily on the wife than on her parents and not the other way around.

In this scenario, the cost for the wife will be higher than the respective cost for her parents, but she will also receive more benefits from the genetic quality of her ex-husband that can balance this cost. Her parents will receive fewer genetic benefits, as they are less closely related to their grandchildren, benefits which can balance the cost of the increase in their grandparental investment. Therefore, the

trade-offs between genetic quality and parental effort are not likely to lead to parent-offspring conflict over mating, simply because the gains and losses are proportionally similar for children and for their parents.

The assumption that the cost from a mate's poor parental investment will fall more heavily on parents than on their children is the primary weakness of the trade-offs explanation of parent-offspring conflict over mating, but it is not the only one. A child needs heavy parental investment to reach sexual maturity, while this parental investment continues even after sexual maturity is reached. Grandparents are likely to be absent due to death or be incapacitated, because of their older age or an illness, and, thus, be unable to help in providing for their grandchildren, especially for their older grandchildren. These issues would be more pronounced in a pre-industrial context, where life expectancy is shorter and medical care is limited. Therefore, it is not an optimal strategy for individuals to rely on grandparents for the provision of the substantial and long-term investment that their children need and that they may not receive from the high genetic quality parent.

An additional problematic aspect of this hypothesis is that, even if we accept that the assumptions of the trade-offs hypothesis are valid, this argument accounts for parent-offspring conflict between parents and daughters and not between parents and sons. More specifically, the trade-offs between good genetic quality and parental effort apply predominantly to men (Gangestad & Simpson, 2000): A man of good genetic quality may engage in more mating effort and less parental effort, since mating effort is likely to result in additional offspring. On the other hand, a woman of good genetic quality may not adopt this strategy, because the extra mating effort will not result in additional offspring.

In the trade-offs argument, women will not differ considerably in their parental investment versus mating effort. Thus, a man who attracts a woman of high genetic quality does not actually compromise on her parental effort and places no potential burden to his parents. In this respect, there would be no parent-offspring conflict over mating between parents and sons. Nonetheless, research indicates that there is also disagreement between parents and sons with respect to the sons' mate choices (Apostolou, 2014, 2015; Perilloux et al., 2011), and this disagreement is not explained by the trade-offs hypothesis.

Last but not least, the trade-offs argument refers solely to a potential disagreement over good genetic quality. Yet, empirical research indicates that the disagreement over mate choice is not limited to this trait, but involves also other traits including family and religious background and exciting personality (see above). These additional domains of disagreement are not explained by the trade-offs hypothesis.

The Relationship Between Evolutionary Trade-Offs and Parent-Offspring Conflict over Mating

Although the evolutionary trade-offs between good genetic quality and parental effort do not account for parent-offspring conflict over mating, they are not irrelevant to it. In particular, these trade-offs reduce the fitness benefit that mate-seekers

get from good genetic quality, which in turn decreases the conflict with their parents. As discussed previously, mate choice involves compromises, which suggest that mate-seekers will have to compromise on specific traits, such as good social standing, in order to get a mate of good genetic quality. Since mate-seekers gain more from good genetic quality when trade-offs are not present, they would be willing to make larger compromises in order to take more of this trait, inflicting in effect a higher cost to their parents.

This argument can be demonstrated in the framework of the proposed model of parent-offspring conflict over mating. In the presence of trade-offs, the fitness differential of good looks (which constitute a proxy of good genetic quality) will decrease, because the fitness benefits that come from this trait have to be discounted for the potential losses in parental investment. Therefore:

$$\left(a-c\right)_{no-trade-offs} > \left(a-c\right)_{trade-offs} \tag{2.6}$$

Assume, for instance, that in the absence of trade-offs, a = 1 and c = 0.5, so the difference is 0.5. Now assume that trade-offs decrease the value of the (G) by half so that a = 0.5 and c = 0.25; in this case the difference is 0.25. Consequently, from Eq. 2.3, it follows that in the presence of trade-offs, the conflict between parents and children over good genetic quality would be lower than where such trade-offs are not present.

Daughters and Sons

This is not the end of the story, however, because the presence of trade-offs predominantly affects the conflict over good genetic quality between parents and sons and not between parents and daughters. More specifically, daughters and their parents, when they exercise mate and in-law choice, respectively, need to discount the possible losses in parental investment. On the other hand, when sons or their parents exercise mate and in-law choice, respectively, they do not need to make such discounting. In different words, the fitness contribution of good genetic quality (i.e., the (a) and (c)) will be higher for sons and parents than for daughters and parents, which means that their difference would be higher for the former than for the latter pair:

$$\left(a-c\right)_{trade-offs\_sons-parents} > \left(a-c\right)_{trade-offs\_daughters-parents} \tag{2.7}$$

From Eq. 2.3, we can see that that trade-offs decrease the contribution that the (G) makes to the fitness cost to parents from the mate choices of daughters, reducing in effect the conflict between the two over this trait. Furthermore, how many mate points each party allocates to each trait is a function of how beneficial this trait to the party exercising choice. The presence of trade-offs renders the (G) more beneficial in mate for sons than for daughters (i.e., $a_{sons} > a_{daughters}$), which indicates that the former will allocate more mate points to it than the latter. Thus, sons save more than

daughters on other desirable traits, increasing in effect the fitness cost to their parents. Indeed, in the aforementioned budget allocation study (Apostolou, 2011c), sons allocated more mate points to the good looks of a prospective wife than daughters to the good looks of a prospective husband, inflicting a higher fitness cost to their parents (see Appendix 3).

Overall, evolutionary trade-offs decrease conflict over good genetic quality between parents and their daughters, but it has no such effect in the conflict between parents and sons. This argument should not be interpreted to indicate that, in the presence of trade-offs, there is more disagreement between sons and parents in general, but that there is more disagreement between sons and parents over good genetic quality in particular.

Environmental Contingencies

The compromises women are willing to make depend on the nature and quality of their local environment (Gangestad & Simpson, 2000). More specifically, if the local environment is difficult and demands considerable biparental care, women are expected to place more weight on the investment potential of prospective mates and less weight on indicators of good genetic quality. In this scenario, the environmental conditions effectively reduce the benefit of good genetic quality, so women desire less of this trait and, thus, have to make fewer compromises in other desirable traits.

On the other hand, if local conditions favor good genetic quality, for instance, when pathogens are prevalent, women would place more weight to the good genetic quality of their prospective mates (Gangestad & Simpson, 2000). In different words, prevailing environmental conditions would increase the value of good genetic quality, making women to desire it more, motivating more compromises in other desirable traits, and inflicting a higher cost to their parents. This argument suggests that the effective degree of parent-daughter conflict over good genetic quality is contingent on environmental conditions: Being more pronounced in environmental settings, where good genetic quality is more important, and less pronounced in environmental settings, where it is less important.

In sum, in this chapter I have argued that because parents and children are not genetically identical, their interests diverge resulting in parent-offspring conflict over mating. This conflict is the primary factor which gives rise to sexual selection under parental choice which I am going to examine next.

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Chapter 3
The Model of Parental Choice

In Chap. 1, I discussed the different sexual selection forces and I investigated how they interrelate. In Chap. 2, I examined the parent-offspring conflict over mating and how the children's free mate choice leads to fitness costs for parents. In this chapter I will focus on parental choice, putting forward a model which can account for the variation in strength of parental choice across different environmental settings.

The Model of Parental Choice

In the model that will be discussed below, parental choice constitutes a significant sexual selection force which arises from the parental control over mating, motivated by the opportunity cost of free mate choice. This cost is a consequence of the diverging and converging interests over mating that arise from the degree of genetic relatedness between parents and children. Accordingly, it has two main components, namely, the diverging opportunity cost and the converging opportunity cost (Apostolou, 2016). I will start by discussing the former first.

Diverging Opportunity Cost

The previous chapter demonstrated that free mate choice involves an opportunity cost coming from diverging genetic interests ($o_{diverging}$)—see Appendix 4 for a full list of the factors in the model—which is what parents forgo when they allow their children to exercise mate choice freely on their own. Parents lose desirable traits such as good family background, and these losses are not compensated by the gains in other traits, such as good looks, which are not as valuable to them.

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The opportunity cost of free mate choice results into evolutionary pressure exercised on parents to place their children's mate choices under their control. In particular, parents who are predisposed to control mating have a selective advantage over those who are not, as the former are likely to have in-laws who maximize their inclusive fitness, while the latter are likely to have in-laws who maximize their children's inclusive fitness (Apostolou, 2014a). When parents succeed in controlling mate choice, they become a significant sexual selection force: Traits that make an individual more likely to be chosen as an in-law are selected and increase in frequency in the population (Apostolou, 2007, 2010).

The strength of sexual selection under parental choice depends on the strength of parental control over mating (m), which is a positive function of the opportunity cost of free mate choice: $m = o_{diverging}$ (Apostolou, 2016). The higher the opportunity cost, the more beneficial will be for parents to control mate choice, the more effort they will divert in controlling mate choice, the more control they will exercise over mate choice, and the stronger sexual selection under parental choice will be.

The opportunity cost depends positively on the benefit parents receive in terms of desirable traits when they control mate choice, which is over and above the benefit that they would receive if their children were to exercise choice on their own (b) (see Chap. 2 for how this benefit is derived). Moreover, since control over mating involves parents allocating resources, such as time chaperoning their children and effort to punish them in order to align them with their will (see below), the (b) needs to be seen as a net benefit, i.e., it is the benefit minus the cost that parental effort to control mating involves.

The benefit that parents can extract depends on how different the compromises their children make are in comparison to their own if they (the children) are to exercise choice freely. If, for instance, children make identical compromises to their parents, then the (b) would be zero. As demonstrated in the previous chapter, the divergence of compromises between parents and children follows a reversed U-shaped function of the children's mate value (v) (see Chap. 2), which indicates that the (b) follows also a reversed U-shaped function of children's mate value: $b = f(v)$. When children have a low mate value, the (b) is low; that is, parents cannot extract much benefit from controlling their children's mate choices. However, when children do not have low mate value, parents can extract more benefits by controlling their mate choices, so the (b) is higher. Nevertheless, when children have a very high mate value, their compromises converge with the compromises of their parents, so the benefit that parents can extract by controlling their mate choices (b) declines.

The (b) needs to be adjusted by its potential (f) to be converted into fitness benefits [f = potential for increasing fitness directly (i.e., by having children) + potential for increasing fitness indirectly (i.e., by benefiting genetic relatives)] (Apostolou, 2014a). Nevertheless, in order to receive this benefit, parents have to make compromises which are costly to their children (c). But this cost is also their cost, because they are genetically related to their children. Accordingly, in order to estimate the actual cost that parents suffer, the (c) needs to be adjusted by the degree of genetic relatedness (r). In order to get a more precise measure of genetic relatedness, let's

call it adjusted r or ($\bar{r}$), the (r) needs to be multiplied by the probability (p) that one is actually an individual's genetic relative (i.e., $\bar{r} = r \times p$). Therefore, the net benefit of a mating deal to parents and, thus, the opportunity cost of not controlling mate choice is: $o_{diverging} = b \times f - c \times \bar{r}$.

The benefit that parents receive from controlling their children's mate choices comes predominantly from gains in family background, which usually translates into benefits from political support and resources. Parents gain further in terms of resources as, potentially, they compromise less in the resource acquisition capacity of their prospective in-laws, than their children would do so for their prospective spouses (see Apostolou, 2011). Therefore, the level of the benefit (b) is a positive function of the level of available resources (a). For instance, parents make compromises in traits such as beauty in order to forge a beneficial alliance with another family. If the other family controls more resources, the benefit of this alliance will be higher than if it controls fewer resources. The cost (c) is not a function of available resources (a), because when parents exercise choice, they inflict a cost to their children predominantly in terms of beauty and exciting personality (Chap. 2).

The Cost That Parents Can Inflict on Their Children to Align Them with Their Will

The size of the diverging opportunity cost of free mate choice depends on the parents' capacity to inflict a cost to their children in order to align them with their will (d). If parents can inflict no cost to their children, the latter would have no reason to allow the former to choose a spouse who is not optimal for them. In different words, when the (d) becomes zero, the converging opportunity cost of free mate choice becomes zero as well, since parents cannot impose a mate on their children. Accordingly, $o = o_{diverging} \times d$.

The (d) is almost always positive because parents have several advantages in their hands which are predominantly derived from the fact that they are older than their children. To begin with, during their lifetime, parents have accumulated material resources, such as money and land, which are diverted to their children in the form of parental investment (w). These resources also include nonmaterial ones, such as physical protection. The more resources parents have control over, the more their children have to lose from defying them.

By being younger than their parents, children are less experienced in subsistence activities and are less likely to have control over the means of producing wealth, such as land and cattle. They are also less experienced in defending and protecting themselves from external threats. Moreover, children depend on their parents' resources in order to procreate. For instance, in many pre-industrial societies, a man has to pay the bridewealth for the marriage to proceed, with these resources coming predominantly from his family (Goody & Tambiah, 1973). Overall, daughters and sons are dependent on their parents' resources, and the degree of this dependence

(e) positively predicts the cost that parents can inflict on their children. The more dependent children are on their parents, the more cost parents can inflict on them by discontinuing parental investment. Note that the (w) and the (e) are treated as separate factors, because even if children are totally independent from their parents' resources, they still have a lot to gain from these resources, which means that they are at risk of losing if their parents decide not to divert these resources to them.

Furthermore, by being older, parents are up to a certain age physically stronger than their children. Accordingly, they can use this strength differential, and they may also seek the assistance of physically strong relatives, in order to impose their will by means of physical force (h). For instance, they can physically punish a daughter for undesirable sexual behavior, or for refusing an arranged marriage. Therefore, the cost that parents can inflict on their children is positively related to their ability to use physical force in order to impose their will.

Apart from physical cost, parents can also inflict psychological cost to their children (j). For instance, parents can threaten their children with potential consequences, or they can exercise emotional pressure on them by crying, looking sad, withholding affection, etc. (Apostolou, 2013a; Apostolou & Papageorgi, 2014; Sussman, 1953). This capacity to emotionally manipulate their children does not necessarily stem from their older age per se; the age difference between themselves and their children contributes to more life experience, which enables parents to refine and enrich the manipulation tactics they can use on their children.

Finally, parents can inflict a cost to their children through the use of social institutions (i). Ascending the social hierarchy usually takes time; thus, most social institutions (e.g., organized religion) are controlled by the older generation (Apostolou, 2013b). In effect, parents may find themselves in higher positions or have relatives and friends in high places in these institutions. Accordingly, they may have the capacity to use these social structures to impose a cost on their children for deviating from what is considered desirable behavior. For instance, a religious institution may punish a premarital sexual relationship, or the law may prevent a marriage to take place if it does not have the approval of parents. Overall, $d = w + e + h + j + i$.

When parents inflict a cost on their children in order to align them with their will, they also inflict a cost on themselves as the two are genetically related; so, the net cost they can inflict on their children is over and above the cost they inflict on themselves. Accordingly, the (d) needs to be adjusted by the $\bar{r}$ multiplied by the cost inflicted on parents through inflicting a cost on their children (q) so that $d = (w + e + h + j + i) - (q \times \bar{r})$.

Finally, when parents inflict a cost on their children, the latter have a capacity to absorb or resist it. For instance, children who score low in agreeableness and conscientiousness may be more resistant to psychological manipulation than higher scorers; children of considerable social status may be more resistant to the mandates of social institutions; physically stronger children can better resist when their parents apply force on them; older children are less dependent on their parents for protection and resources; and the wealth of parents matters less to children who are wealthy themselves. Thus, the (d) should be considered as a net cost, which is the

cost over and above the one their children can absorb when inflicted by parents on their children to align them with their will.

$$\text{In } sum\text{: } o_{\text{diverging}} = \left[\left(b \times f\right) - \left(c \times \bar{r}\right)\right] \times d.$$

Converging Opportunity Cost

The genetic relatedness between parents and their children (i.e., r = .5) indicates that the two parties, except from diverging, have also converging interests over mating; that is to say, parents and children both agree in the latter getting a mate who is beneficial for them. In several instances, parents, by influencing mate choice, can enable their children to get better mates than they could get for themselves. To put it differently, if parents do not interfere, they stand to lose, because their children may not get the best possible mates. Therefore, there is an additional opportunity cost accrued to parents by the free mate choice of their children, which in this case comes from parents and children having converging interests over mating ($o_{\text{converging}}$) (Apostolou, 2016).

This cost is predicted by the risk children face to make mistakes when they exercise free mate choice that their parents are less likely to make if they were to exercise choice for them (k). For instance, if children are left on their own to exercise mate choice, they may fall prey to individuals who wish to exploit or harm them. Parents, on the other hand, are less likely to fall prey to such individuals because they are older and more experienced, and their judgment is not clouded by high levels of libido and romantic love.

The (k) is positively predicted by children's traits which may turn them prone to making unwise mate choices and becoming vulnerable to unfit suitors. One such trait is experience (ex), which correlates positively with age, with older and more experienced children to be less likely to make erroneous choices. These two factors are inversely related so that, when experience increases, the chances of making erroneous mate choices decrease: k = 1/ex.

Personality traits (pe) are also important factors in making optimal mate choices; for instance, a highly conscientious child is less likely than a low conscientious child to be carried away by a sexual adventure. Other personality dimensions are likely to have such an influence, but more research is required to identify their effects. Thus, for now, I will keep only the conscientiousness: When individuals score high in this dimension, the (k) falls. Thus, k = 1/ex + pe, where pe = 1/conscientiousness. Note that the (pe) enters as a separate factor, so that in future revisions of the model, additional personality traits can be added. Intelligence is yet another predictor, as children of higher intelligence can better protect themselves and make wiser mate choices (int). Accordingly, intelligence is inversely related to (k). Overall, k = 1/ex + pe + 1/int.

Furthermore, the (k) is positively predicted by the children's mate value (v). This is because children of high mate value are likely to become more frequently the target of intense mating effort than children of low mate value, which may often involve deception and assault. For example, low mate value men who follow a forced-sex mating strategy usually target young and fertile women (Thornhill & Palmer, 2000). Overall, $k = ex^{-1} + pe + int^{-1} + v$.

It has to be said at this point that experience and mate value are not independent, as both are predicted by age. I am not going to factor age out, one reason being that the contribution of age to the (v) depends on the sex of the child. In particular, although experience is always positively predicted by age, the contribution of age to the mate value is more complicated. For a sexual mature female child, the contribution is usually negative, but for a sexually mature male child, it is at first positive and subsequently it becomes negative. Future work can model the (v) and factor out the effect of age separately for each sex. Also, it has to be said that not all predictors of the (k) have an equal weight. Empirical research is required in order to estimate these weights, but I believe that personality constitutes the most important one.

In sum, children with specific traits such as being less experienced, scoring low in conscientiousness, having low intelligence, and being of high mate value are more likely to make unwise mate choices which indicates a higher opportunity cost for their parents if they leave them to exercise mate choice on their own. This is not the end of the story though, because the (k) needs to be adjusted by the impact a wrong mate choice will have on children and, thus, on their parents (n). The (n) is a function of several variables, including the presence of grave sexually transmitted diseases. For instance, the (n) is higher when HIV prevalence is high and lower when HIV prevalence is low. Similarly, the (n) is lower where the use of contraceptives is widespread than where it is not, i.e., it is less likely that an erroneous mate choice would result in an unwanted pregnancy in the former than in the latter case. Accordingly, $o_{converging} = k \times n$.

The converging opportunity cost is also predicted by the child's risk to be unable to attract a mate (l). This is costly for parents, who have allocated considerable parental effort to bring this child to sexual maturity, and they risk forfeiting it, in case it is unable to provide them with grandchildren. This risk is positively predicted by the children's personality traits, which negatively influence success in attracting a mate (s). For instance, if left to exercise choice on their own, children who score high in introversion are more at risk of not being able to attract mates. Thus, the higher a child scores in such traits, the higher the (s). This risk is also a negative function of a child's mate value (v): As the mate value of a child decreases, the risk of not being able to attract a long-term partner increases. Overall, $l = s + v^{-1}$.

The intervention of parents can decrease the (l). For instance, parents may find mates for their children when the latter's personality traits prevent them from doing so. In addition, parents may interfere, diverting more resources to their children in order to increase their mate value. For example, parents may augment the dowry of a daughter to compensate for a physical deformity that impairs her mating success. Finally, the converging opportunity cost needs to be multiplied by the adjusted r ($\overline{r}$) in order to get an actual estimate of the cost that parents will suffer if their children

make erroneous mate choices or are unable to get a mate and procreate. Accordingly, $o_{converging} = \left[\left(k \times n\right) + l\right] \times \bar{r}$.

The converging opportunity cost gives parents an additional incentive to control their children's mate choices, a control which is also beneficial for the latter. Thus, children may consider some parental intervention and control over their mate choices as acceptable or even desirable, and they are also likely to ask the advice of their parents in matters of mate choice, opening in effect a window for parents to influence their mating decisions. The opportunity cost from converging interests strengthens parental choice as a sexual selection force since, even in those cases when parents attempt to control the mate choices of their children primarily for the children's benefit and not their own, when they succeed, they are more likely to get in-laws who best appeal to their own preferences. For instance, if a son is constrained by a physical defect in finding a mate, his parents may arrange a marriage for him paying a high bridewealth and making compromises on the traits of a prospective daughter-in-law. But, the compromises they are going to make will be in accordance to their own preferences and not to their son's preferences. What is important in sexual selection is who exercises choice, not why (Apostolou, 2016).

It has to be said that empirical work is required to investigate and model in detail the risks that give rise to the converging opportunity cost (i.e., the k and the l). For instance, the mate value of children affects both risks but differently. As mate value increases, the (k) increases, since children are more likely to become the target of unwanted mating effort, but, at the same time, the (l) decreases as children become less likely to stay single. The two effects, to some degree, counterbalance so the mate value may not have a considerable quantitative effect in the converging opportunity cost. It is likely to have a qualitative effect though, as when the (k) is high and the (l) is low, parental interference will take the form of guarding, acting aggressively toward, or threatening unsuitable mates. On the other hand, when the (k) is low and the (l) is high, parental interference will take the form of finding mates and/or increasing the mate value of their children.

Note that the level of converging opportunity cost is not determined by the cost parents can inflict on their children to align them with their will (d), because children will be willing to surrender to their parents some control over mate choice, as this will also be beneficial for them. The degree of control children will be willing to surrender would be equal to the converging opportunity cost; in order to get more control over their children's mate choice and, thus, to gain from minimizing the diverging opportunity cost, parents need to inflict a cost to their children (d). Therefore, even if parents can inflict no cost to their children in order to align them with their will, they will still be influential over mating, because their children will be willing to surrender some of their freedom to exercise mate choice to them.

Converging Opportunity Cost and Conflict

In Chap. 1, I argued that a necessary condition for sexual selection to arise is conflict of interest. Without such conflict there would be no discrimination between mates, no competition, and, thus, no sexual selection. The converging opportunity cost

indicates that sexual selection under parental choice may arise from converging interests over mating, which suggest that there may be a contradiction with the conflicting interests argument. However, there is no such contradiction.

In particular, the converging opportunity costs arise from the conflicting interests over mating between children and prospective mates. It is optimal for low mate value mates to access the reproductive capacity of the higher mate value children, but it is not optimal for the latter to grant such access. But it is also not optimal for their parents, who are genetically related to their children, and they also have to lose. Therefore, diverging interests of children with prospective mates, and converging interests of children with their parents, result in parents having conflicting interests over mating with prospective mates for their children. In turn, such convergence and divergence of interests select for mechanisms that enable parents to control their children and be selective over who to give access. This parental control and choosiness lead to prospective mates to compete with each other for reproductive access and sexual selection under parental choice to arise.

Overall, in the diverging opportunity cost case, parents are in conflict with their prospective in-laws as well as with their children, but, in the converging opportunity cost case, parents are in conflict only with their prospective in-laws. Thus, both opportunity costs involve conflict of interest between the parties involved.

In sum, free mate choice involves an opportunity cost which motivates parents to control the mate choices of their children:

$$\mathrm{m} = \mathrm{o}$$

where

$$\mathrm{m} = \left(\mathrm{o}_{\mathrm{diverging}} + \mathrm{o}_{\mathrm{converging}}\right)$$

Substituting for the ($\mathrm{o}_{\mathrm{diverging}}$) and the ($\mathrm{o}_{\mathrm{converging}}$):

$$\mathrm{m} = \left[\left(\mathrm{b} \times \mathrm{f} - \mathrm{c} \times \bar{\mathrm{r}}\right) \times \mathrm{d}\right] + \left\{\left[\left(\mathrm{k} \times \mathrm{n}\right) + \mathrm{l}\right] \times \bar{\mathrm{r}}\right\}$$

Substituting for the (d):

$$\mathrm{m} = \left\{\left(\mathrm{b} \times \mathrm{f} - \mathrm{c} \times \bar{\mathrm{r}}\right) \times \left[\left(\mathrm{w} + \mathrm{e} + \mathrm{h} + \mathrm{j} + \mathrm{i}\right) - \left(\mathrm{q} \times \bar{\mathrm{r}}\right)\right]\right\} + \left[\left(\mathrm{k} \times \mathrm{n}\right) + \mathrm{l}\right] \times \bar{\mathrm{r}}$$

Substituting for the (k) and the (l):

$$\begin{aligned}\mathrm{m} = &\left\{\left(\mathrm{b} \times \mathrm{f} - \mathrm{c} \times \bar{\mathrm{r}}\right) \times \left[\left(\mathrm{w} + \mathrm{e} + \mathrm{h} + \mathrm{j} + \mathrm{i}\right) - \left(\mathrm{q} \times \bar{\mathrm{r}}\right)\right]\right\} \\ &+ \left[\left(ex^{-1} + pe + \mathrm{int}^{-1} + \mathrm{v}\right) \times \mathrm{n} + \left(\mathrm{s} + \mathrm{v}^{-1}\right)\right] \times \bar{\mathrm{r}}.\end{aligned}$$

Sexual Selection Under Individual Mate Choice

Older age offers parents the capacity to inflict a cost on their children in order to align them with their will (d). This cost exercises evolutionary pressure on children to become resistant to it. In turn, evolutionary pressure is exercised on parents to bypass their children's resistance, which in turn exercises further pressure on children to evolve resistance to their parents' attempts to inflict a cost on them and so on. As a consequence, parents will never manage to dominate their children's mate choices completely, but their children can never evolve to be totally resistant to their parents' attempts to influence their mating decisions. In effect, at any given point in time, parents will be able to exercise some influence over their children's mate choices, and children will have some space to exercise mate choice.

In addition, the presence of the converging opportunity cost mandates that parents will have an influence over their children's mate choices, even if they can inflict no cost on them for deviating from their will. Accordingly, in the scenario where the (d) is very low, parental influence over mating will still be present, predominantly in the form of parents attempting to influence their children's mating decisions in order to reduce the converging opportunity cost of mate choice. Overall, parental choice and individual choice are sexual selection forces that are copresent, with the balance of power between them depending on the environmental factors that affect the opportunity cost of free mate choice (see also Chap. 1).

Contingencies in Parental Choice

Daughters Versus Sons

Women divert more parental investment to their children, and so they become the scarce reproductive resource to which men seek access (Trivers, 1972). As a consequence, male children and their parents are more likely to seek access to wives and daughters-in-law than the other way round (Apostolou, 2014b); thus, parents can extract more benefits by controlling their daughters' than their sons' mate choices ($b_{daughters} > b_{sons}$). Moreover, women usually control less wealth than men (Whyte, 1978), which means that daughters are more dependent upon their parents' resources than sons.

In addition, as people age and accumulate more experience, they become more proficient in gaining their subsistence and in accumulating wealth; thus, older children are less dependent on their family's resources than younger ones. Because women mature and marry earlier than men, women of marriage age are more dependent on their parents than sons of marriage age. In addition, women are usually physically weaker than men, which translates into daughters being more dependent than sons on their family's protection ($e_{daughters} > e_{sons}$). Furthermore, because daughters are physically weaker than sons, parents can more easily employ physical force

to inflict a cost on the former than on the latter ($h_{daughters} > h_{sons}$). Overall, the diverging opportunity cost of free mate choice is higher for daughters than for sons ($o_{diverging\_daughters} > o_{diverging\_sons}$).

A sexual adventure can commit a daughter's parental investment (i.e., pregnancy) to a man who is not necessarily best for her. An unwanted pregnancy is not something that can be easily resolved, particularly in a pre-industrial context. Also, not only a son does not need to bear the cost of pregnancy, but he can also deny paternity, since in the pre-industrial context, this is not something that can be easily proven. Moreover, due to parental uncertainty, men value chastity in a woman, one of the reasons being that this preference reduces the risk of cuckoldry (Buss, 2003). For a similar reason, parents prefer a daughter-in-law who is chaste; this preference reduces the risk of diverting resources in grandchildren who are not their own (Apostolou, 2014b). In addition, due to menopause, following sexual maturity, the reproductive value of daughters decreases more rapidly with age than the reproductive value of sons. Thus, erroneous mate choices can have more detrimental consequences for the fitness of daughters than for the fitness of sons ($n_{daughters} > n_{sons}$).

Furthermore, because women constitute the scarce reproductive resource, they are the target of more intense mating effort, and, thus, they face a higher risk of deception and assault by nonoptimal men, who attempt to gain access to their reproductive capacity. Overall, the risk of erroneous mate choices is higher for daughters than for sons ($k_{daughters} > k_{sons}$).

On the other hand, by being the scarce reproductive resource, women are less at risk than men of not being able to attract a mate ($l_{daughters} < l_{sons}$). As the (i) and the (k) are higher, but the (l) is lower for daughters than for sons, and assuming an equal contribution of each factor, the converging opportunity cost of free mate choice is higher for daughters than for sons ($o_{diverging\_daughters} > o_{diverging\_sons}$). In turn, as both diverging and converging opportunity costs are higher for daughters than for sons, parental control over mating would be stronger over daughters than over sons ($m_{daughters} > m_{sons}$).

It has to be said that this conclusion reflects the general trend and does not apply to all situations. It may be the case, for instance, that parents have two children, a young son who is still dependent on them and an older daughter who has passed the age of menopause and is financially independent. In this scenario, the opportunity cost of free mate choice is higher for the son than for the daughter, which predicts a stronger parental control on the former than on the latter.

Mothers Versus Fathers

The asymmetry in parental investment enables men, not only to compete between them in being selected by women or by their parents (intersexual selection) but also to fight directly between them (intrasexual selection). The consequence of intrasexual selection forces for men is to be physically stronger than women and to tend to monopolize resources, to dominate the political scene, and to have exclusive

access to weaponry (Puts, 2010). Thus, fathers and other male relatives control more resources than mothers and other female relatives, and these resources can be withheld if their children disobey them ($w_{fathers} > w_{mothers}$).

One clarification that needs to be made at this point is that, although mothers usually divert more parental investment than fathers to their children, this difference does not mean that they have a stronger say in their children's mating decisions. One reason is that they divert more of what they have (i.e., time, affection, caring, effort, etc.), but not more in absolute terms. Since fathers usually control more resources (i.e., wealth, land, weapons, etc.), they can potentially divert more of these resources to their children. Therefore, children risk losing more if they disobey their fathers than if they disobey their mothers, even though mothers divert more of what they have toward them (Apostolou, 2016).

Another reason is that mothers divert more parental investment to their children when the latter are young (e.g., breastfeeding, keeping them warm and safe, etc.). Nevertheless, older children are less dependent on maternal investment (e.g., they do not breastfeed) and more on general family resources, which are typically controlled by the father. For instance, in pastoral societies, sexually mature offspring base their subsistence on the herding of animals, which belong to the father (e.g., the pastoral Fulbe, see Hopen, 1958).

Furthermore, the defense and safety of the family unit predominantly rest with its male members, who are typically physically stronger, control weaponry, and have political connections. Therefore, children are more dependent on their fathers than on their mothers for protection ($e_{fathers} > e_{mothers}$). Also, because fathers are physically stronger than mothers, they can inflict a higher cost by using physical force on their children ($h_{fathers} > h_{mothers}$). In the same vein, because men have better access to political institutions (Apostolou, 2013b), fathers can easier than mothers employ or appeal to these institutions to inflict a cost on their children ($i_{fathers} > i_{mothers}$).

On the other hand, by being physically weaker than men, women have to rely on psychological manipulation in order to promote their interests (Apostolou, 2013a). As a consequence, mothers are typically more effective psychological manipulators than fathers (Apostolou & Papageorgi, 2014), and, thus, they can inflict a higher psychological and emotional manipulation cost on their children ($j_{fathers} < j_{mothers}$).

In addition, due to internal gestation, mothers are 100% certain that their children are their own; however, this is not the case for fathers, who are far less certain about paternity. As a consequence, the adjusted r is lower for fathers than for mothers ($\bar{r}_{fathers} < \bar{r}_{mothers}$), which means that the cost parents have to suffer from inflicting a cost on their children ($q \times \bar{r}$) is lower for the former than for the latter. Overall, fathers can inflict a higher cost than mothers on their children to align them with their will ($d_{fathers} > d_{mothers}$).

A further implication of paternal uncertainty is that the costs from making compromises in order to get benefits from in-law traits ($c \times \bar{r}$) are lower for fathers than for mothers. In consequence, fathers can potentially gain more from a mating deal than mothers, as they are less constrained by the cost that this may have on their children.

Moreover, due to menopause, women conclude their reproductive careers at an earlier age than men do. This difference means that the residual reproductive value (i.e., the contribution to the population through future reproduction) is less for older women—to the point of being zero if they have passed the age of menopause—than it is for men of the same age (Apostolou, 2014b). As a consequence, a mating deal involving their children can be more beneficial for fathers, as it can provide them with resources, which can be used for future reproduction.

In addition, men have a higher reproductive variance than women, as they are not constrained by their biology in the number of children they can father. Men's reproductive success is positively related to the resources they control (Buss, 2003), with men being able to deploy resources in such a way that enables them to practice polygyny and/or to attract multiple casual mates (Goode, 1982). On the other hand, because women are constrained by their biology, polyandrous marriage and having multiple casual mates will not increase their reproductive success. Accordingly, a mating deal for their children which provides parents with resources can potentially be more beneficial for a father than for a mother, as the former could use these resources to directly increase his reproductive success: For instances, the resources from a mating deal have the potential to increase the direct reproductive success of the father to a considerably greater extent than the direct reproductive success of the mother ($f_{fathers} > f_{mothers}$) (Apostolou, 2016).

In sum, because fathers can inflict a higher cost on their children, and because they can convert more of the benefits they extract by controlling mate choice into reproductive success, they have more to lose if they allow their children to exercise mate choice freely ($o_{diverging\_fathers} > o_{diverging\_mothers}$). This difference refers to the average case, and it does not preclude the possibility that the diverging opportunity cost is higher for a mother than for a father. For instance, in a family where the father is very old but the mother is relatively young, the latter can inflict more cost to children, and she is more likely to convert benefits from a mating deal into a direct reproductive success (e. g., in order to get a desirable husband after her husband dies).

On the other hand, due to paternal uncertainty, if children make erroneous choices which reduce their fitness, mothers have potentially more to lose because they are certain that the children are actually their own; consequently, $o_{converging\_fathers} < o_{converging\_mothers}$. When the diverging opportunity cost is higher than the converging opportunity cost, influence over mating will be dominated by fathers ($m_{fathers} > m_{mothers}$), but when the diverging opportunity cost is lower than the converging one, influence over mating will be dominated by mothers ($m_{fathers} < m_{mothers}$). Which opportunity cost is going to be higher, and, thus, which one of the parents exercises greater control over mating, depends on the specific conditions prevailing in a given society and in any given family.

Overall, sexual reproduction gives rise to conflict of interest between parents, children, and children-in-law; conflict of interest exercises selection pressure on parents to control their children's mating decisions and choose daughters- and sons-in-law who best promote their own interests. In addition, sexual reproduction results in parents to have converging interests with their children but diverging interests

with their prospective children-in-law. These interests exercise selection pressure on parents to exercise influence over mate choice and screen prospective mates for those who are not best for their children. Parental control over mating, and parental choosiness, gives rise to competition between individuals to be chosen as daughters- and sons-in-law, which gives rise to sexual selection under parental choice. In the next three chapters, I will attempt to explore how the model developed here can account for the variation in the strength of parental choice across different society types.

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Chapter 4
Sexual Selection Under Parental Choice in Hunting and Gathering Societies

The determinants of the opportunity cost of free mate choice, and thus the strength of parental choice as a sexual selection force, are affected by environmental factors which vary across societies. Accordingly, in this and the following three chapters, I will attempt to examine how parental choice and other sexual selection forces vary across different society types.

Human societies can be classified in two main categories on the basis of the level of technological development on which they base their subsistence, namely, pre-industrial and post-industrial societies. Pre-industrial societies can be further classified into the ones which base their subsistence on hunting and gathering and the ones which base their subsistence on agriculture and animal husbandry. Further subdivision of pre-industrial societies is possible, but, in order to keep the argument simpler, I will focus mainly on these two divisions. In this chapter I am going to explore sexual selection under parental choice in hunting and gathering societies and in the next chapter sexual selection under parental choice in agropastoral societies.

A Typical Foraging Way of Life

Hunters and gatherers do not establish permanent settlements, but they set temporary camps in which they stay for a limited amount of time (Lee & Devore, 1968). Subsistence is based predominantly on gathering plants, vegetables, fruits, honey and seeds, and hunting animals. There is a clear division of labor, where gathering is almost exclusively the job of women and hunting is almost exclusively the job of men. During hunting trips, it is not uncommon for men to gather some seeds or honey for individual consumption. Women may also engage in small animal hunting, such as hunting turtles. Gathering is based on a very simple technology, with women using only a wooden stick, which they employ to extract roots. Hunting is based on a more complex technology, with hunters employing bows, arrows, and spears (Kelly, 2013; Lee & Devore, 1968).

Overall, the technological development of foraging societies is not advanced, and, as a consequence, they do not produce enough food to allow the maintenance

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of large community sizes. Thus, hunters and gatherers live in small bands, which usually do not exceed 150 people (Kelly, 2013). In the same vein, not much wealth is produced, and people have few material goods in comparison to people living in societies of different subsistence types. Moreover, simple technology translates into low specialization, which, in turn, results into people being relatively self-sufficient. Furthermore, small size, limited wealth, and low specialization make well-developed institutions, such as the church and the law, not needed for the smooth function of hunting and gathering societies; thus, these institutions are usually lacking in these societies (Apostolou, 2013a).

Sexual Selection in Foraging Societies

I will now turn to examine how the model of parental choice accounts for the patterns of mating found in a pre-industrial foraging context. Starting from the diverging opportunity cost [$o_{diverging} = (b \times f - c \times \bar{r}) \times d$], in this setting there are no social protection mechanisms, and individuals are heavily dependent on each other for survival. Alliances between families are of paramount importance, which means that there is a considerable benefit for parents to use their children's marriage in order to establish beneficial alliances with other families. However, due to their low technological level, hunting and gathering societies produce limited surpluses of goods, constraining in effect the material benefits, which parents can accrue from a marriage alliance.

In foraging societies, children are usually married young (Apostolou, 2007; Kelly, 2013), meaning that their parents are also relatively young, and they have not terminated their reproductive careers. Thus, as part of the benefits parents can extract from a beneficial marriage arrangement, they can convert into direct reproductive fitness, i.e., to have additional children, turning in effect the (f) to be considerable.

I now turn to the parents' capacity to inflict a cost on their children for deviating from their will [$d = w + e + h + j + I - (q \times \bar{r})$]. Starting from the resources parents control and they can divert to their children (w), in this setting material goods are rather limited; however, the provision of physical protection constitutes an important resource that parents provide to their children. Children's dependence on their parents for their subsistence is limited, the reason being that subsistence is based on individual effort. That is, whether people decide to hunt or gather constitutes an individual choice, and it is not controlled by parents. Even so, due to the lack of social protection systems, children have to rely on their family for protection, turning the (e) important. Moreover, parents have a high capacity to inflict a cost on their children through physical force (h) because in this setting there are no social protection systems, and individual rights are not well protected.

It is also expected that parents have a high capacity to inflict psychological cost on their children (j). This capacity emerges from the fact that parents and children are genetically related, so the latter have an interest in the welfare of the former,

who use this interest to promote their own goals through manipulation (Apostolou, 2015). As the genetic relatedness between parents and children does not change, this capacity is likely to remain high across different society types. Thus, among hunters and gatherers, parents are expected to have a good capacity to impose costs on their children through using psychological manipulation. Finally, foraging societies do not have well-formed institutions, such as the church and courts of law. As a consequence, parents have a low capacity to inflict costs on their children for deviating from their will through the use of social institutions (i).

Overall, in a pre-industrial context where subsistence is based on hunting and gathering, parents can benefit from controlling their children's mating decisions, and they have a capacity to inflict a cost on them in order to align them with their will. In effect, there is a considerable diverging opportunity cost of free mate choice ($o_{diverging}$).

Turning to the converging opportunity cost $\{o_{converging} = [(k \times n) + l] \times \bar{r}\}$, it is expected that in this setting there is a high risk that children make mistakes when they exercise free mate choice, which their parents are less likely to make if they were to exercise choice for them (k). The (k) is inversely related to experience (ex) and intelligence (int) and positively related to personality traits (pe) and mate value (v). These traits exhibit substantial variation, so in this context, as in all other contexts, many children have levels of these traits which make them vulnerable to erroneous mate choices. In addition, among foragers, as technology is relatively simple, there is no need for individuals to spend considerable time in training before they enter in the production process. Accordingly, they enter in the long-term mating market soon after they reach sexual maturity, which means that they are inexperienced and prone to make mistakes, resulting in a high (k).

Furthermore, in a foraging context, there are limited means to prevent conception (e.g., there are no condoms) and to terminate unwanted pregnancies; there is also limited capacity to treat sexually transmitted diseases. As individual rights are not well protected in these societies, an erroneous mate choice may have a considerable negative impact on children and, consequently, on their parents (n). For instance, a daughter may form a relationship with a man who is physically abusive, or end up pregnant by a man who abandons her. A son may engage in sexual conduct with a promiscuous woman and contract a sexual transmitted disease which cannot be treated. Accordingly, the high (n) contributes considerably in increasing the converging opportunity cost.

Turning to the other component of the converging opportunity cost, namely, the risk that a child faces to be unable to attract a mate (l), it is positively predicted by the personality traits of a child that have a negative impact on a mate (s), and it is inversely related to a child's mate value. Since personality traits exhibit considerable variability in this context, as in all other contexts, we expect that many children have levels of these traits which make them vulnerable to staying single. Therefore, the (l) is expected to be positive. Overall, in this setting, there is a significant converging opportunity cost of free mate choice.

As parental control over mating (m) is a function of diverging and converging opportunity costs $[m = (o_{diverging} + o_{converging})]$, which are both positive in a hunting

and gathering setting, it is predicted that in societies of this type parents would exercise substantial control over their children's mating decisions.

Consistent with this prediction, in one study I collected data from a sample of 190 contemporary foraging societies and I analyzed their mating patterns (Apostolou, 2007). I found that the most frequent mode of long-term mating, in approximately 70% of cases, was arranged marriage, where parents choose spouses for their children. This was also confirmed in a subsequent study of a smaller sample of societies which base their subsistence on hunting and gathering (Apostolou, 2010). In particular, I found that, in approximately half of the foraging societies in the sample, marriages were arranged.

Contingencies

Daughters Versus Sons

Women divert more parental investment to their children, and they become the scarce reproductive resource to which men seek access (Trivers, 1972). As a consequence, men and their parents tend to seek access to wives and daughters-in-law rather than the other way round (Apostolou, 2014); so parents can extract more benefits by controlling their daughters' than their sons' mate choices ($b_{daughters} > b_{sons}$).

In a foraging context, individuals are relatively autonomous from their parents with respect to their subsistence, as hunting and gathering is based on individual effort rather on the exploitation of family resources. That is to say, sons and daughters at sexual maturity have roughly equally low dependence on their parents for their subsistence. Nevertheless, daughters are more dependent on their family for protection than sons. More specifically, by being physically stronger and by having access to weapons, sons are less vulnerable to attacks from wild beasts, individuals from other tribes, and individuals from their own tribe. Also, daughters are much more vulnerable than men to sexual assault as well as to physical abuse from their partners. Consequently, daughters are more dependent on their parents for protection than sons ($e_{daughters} > e_{sons}$). In addition, because daughters are physically weaker than sons, and because there is no constrain in using physical force on children, parents can more easily employ physical force to inflict a cost on their daughters than on their sons in order to align them with their will ($h_{daughters} > h_{sons}$).

Overall, parents can gain more by controlling the mating decisions of their daughters than their sons, and they can inflict a higher cost on their daughters than on their sons to align them with their wishes ($d_{daughters} > d_{sons}$). As a consequence, the diverging opportunity cost of free mate choice is higher for daughters than for sons ($o_{diverging\_daughters} > o_{diverging\_sons}$).

In the hunting and gathering setting, there are no effective ways to prevent or terminate an unwanted pregnancy, which means that an erroneous mating decision can be particularly costly for a woman. This is not the case for a man, because he

does not have to bear the costs of pregnancy, and he can deny paternity as there is no way to prove it. It needs to be said, nevertheless, that infanticide, which is practiced in these societies (Whyte, 1978), can partially correct erroneous mating decisions. Also, because chastity is valued more in a woman than in a man (Buss, 2003), engaging in relationships which do not have long-term prospects may harm the reputation of women more than the reputation of men. Furthermore, since following sexual maturity, reproductive value decreases more rapidly with age for women than for men, allocating time in relationships which do not have long-term prospects can be more costly for daughters than for sons. In sum, erroneous mate choices in hunting and gathering societies can have more detrimental consequences for the fitness of daughters than for the fitness of sons ($n_{daughters} > n_{sons}$).

Furthermore, because women constitute the scarce reproductive resource, they are the target of more intense mating effort, and, thus, they face a higher risk of deception and assault by men who attempt to force access to their reproductive capacity, consequently ($k_{daughters} > k_{sons}$). On the other hand, by being the scarce reproductive resource, women are less at risk of not being able to attract a mate than men ($l_{daughters} < l_{sons}$). As the (n) and the (k) are higher, but the (l) is lower for daughters than for sons, and assuming an equal contribution of each factor, the converging opportunity cost of free mate choice is higher for daughters than for sons ($o_{converging\_daughters} > o_{converging\_sons}$). Overall, because in a foraging context both diverging and converging opportunity costs are predicted to be higher for daughters than for sons, parental control over mating is expected to be stronger over daughters than over sons ($m_{daughters} > m_{sons}$).

Consistent with this prediction, in one study I employed a database of coded mating patterns on pre-industrial societies, including a subset of societies which base their subsistence on hunting and gathering (Apostolou, 2010). I found that there was a considerable difference over the control that parents exercised on their daughters and sons. More specifically, in approximately 53% of the societies, marriage was arranged for women, and in approximately 8% of the societies was based on free mate choice. For men, however, the percentages were 31% and 40%, respectively, indicating that they had a much larger space than women to exercise mate choice.

Mothers Versus Fathers

We can now move on to examine differences in parental control over mating between fathers and mothers. Starting from the wealth that parents control and can divert to their children in the form of parental investment (w), men control more material wealth than women, but because in the foraging setting not many material resources are produced, this sex difference is expected to have a limited effect on the (d).

Moreover, hunting and gathering societies are not free from aggression, with raids from external groups, but also internal conflict being common (Chagnon, 1992; Kelly, 2013). Women are frequently the target of these aggressive acts; for instance, the Yanomamo organizes raids against neighboring groups in order to

capture their women (Chagnon, 1992, 2013). In addition, men within the group attempt to force sex on women in order to bypass female and parental choice (Apostolou, 2013b). Fathers and other male relatives, by virtue of being physically stronger and more aggressive and by controlling access to weaponry, are predominantly the ones who provide physical protection to their family. In effect, children are more dependent on their fathers than on their mothers for physical protection ($e_{fathers} > e_{mothers}$).

In the same vein, because fathers are physically stronger than mothers, they can inflict a higher cost on their children through physical force ($h_{fathers} > h_{mothers}$). This is facilitated by the fact that, in the hunting and gathering setting, individual rights are not well protected. Also, as stated earlier, in foraging societies, social institutions such as the church and the law are not present or they are not well developed, meaning that any difference in access to and influence in these institutions between fathers and mothers would have little impact on the (d). On the other hand, as mothers are usually more effective manipulators than fathers, they can inflict a higher psychological manipulation cost on their children than fathers ($j_{fathers} < j_{mothers}$).

Finally, because in this context there is no technology to allow the testing of paternity, fathers are less certain than mothers that their children are indeed their own, which translates in the cost parents have to suffer from inflicting a cost on their children ($q \times \bar{r}$) being lower for fathers than for mothers. Overall, fathers can inflict a higher cost on their children to align them with their will than mothers ($d_{fathers} > d_{mothers}$).

As discussed in Chap. 3, a further implication of the paternal uncertainty is that the cost from making compromises in order to get more desirable traits ($q \times \bar{r}$) is lower for fathers than for mothers. Thus, fathers can potentially gain more from a mating deal than mothers, as they are less constrained by the cost that this may have on their children. Also, because women conclude their reproductive careers at an earlier age than men, and because men have a higher reproductive variance than women, the resources from a mating deal have the potential to increase the direct reproductive success of fathers to a considerably greater degree than the direct reproductive success of mothers ($f_{fathers} > f_{mothers}$). Yet, because in this context not many resources are produced, the benefits that fathers can extract and convert into reproduction may not take the form of material wealth, but favor which can be returned at a future time. For instance, among the Tiwi in Australia, it is common for fathers to arrange the marriages of their daughters before they are even born, with the purpose of gaining reproductive benefits for themselves (Hart, Pilling, & Goodale, 1988).

Putting everything together, within the hunting and gathering setting, fathers can inflict more cost on their children, and because they can extract more benefits from controlling mate choice, they have more to lose if they allow their children to exercise mate choice freely ($o_{diverging\_fathers} > o_{diverging\_mothers}$).

On the other hand, due to paternal uncertainty, if children make erroneous choices (k) and stay without a mate (l), which reduces their fitness, mothers have potentially more to lose because they are certain that their children are actually their own, so that ($o_{converging\_fathers} < o_{converging\_mothers}$). Still, this difference is not extensive

because it is based only on the difference in parental certainty. On the other hand, the difference between the diverging opportunity costs between fathers and mothers is expected to be more substantial, as fathers differ from mothers in several dimensions (see above) so that ($o_{diverging\_fathers} - o_{diverging\_mothers} > o_{converging\_mothers} - o_{converging\_fathers}$). Therefore, in this context fathers experience an overall higher opportunity cost from the free mate choices of their children, which predicts that they would be more influential in controlling mate choice than mothers ($m_{fathers} > m_{mothers}$). Still, mothers are expected to have a strong say as they also face a high opportunity cost.

Consistent with this prediction, in one study I coded for the mating patterns of a sample of 190 foraging societies (Apostolou, 2007). In about 44% of the societies in the sample, fathers and other male relatives arranged the marriages of their children, with little input from mothers and other female relatives. Nevertheless, in about 16% of the societies, fathers dominated arrangements, but mothers had an important say; in about 34% of the societies, both fathers and mothers had a roughly equal contribution, and in about 8% of the societies, both parties contributed, but mothers dominated the arrangements. In a different study, which involved a smaller sample of hunting and gathering societies, I analyzed preexisting codes and found that in about 18% of the cases, fathers and other male relatives monopolized marriage arrangements; in about 23.5% both parties contributed, but fathers had more say in arrangements; in about 47% both parties had roughly an equal say; and in about 12% both parties participated, but mothers had more say (Apostolou, 2010).

Other Sexual Selection Forces

Individual Mate Choice

The anthropological evidence on the mating patterns of pre-industrial societies is consistent with the predictions of the model of parental choice developed in Chap. 3: Parents exercise a strong control over their children's mating decisions; male parents dominate marriage arrangements, and parental control over mating is stronger over female than over male children. Even so, the power of parents over their children is not and cannot be absolute, which allows space for individual choice to be exercised. Hunting and gathering is based on individual effort, which means that parents have little control over it that, in turn, results into children enjoying more autonomy over subsistence, which translates into more autonomy over mate choice. For instance, parents have limited control over the subsistence needs of a sexually mature daughter, who can go on her own to gather food. Thus, they cannot threaten her with withholding food in order to impose their will. As expected, the anthropological record on hunting and gathering societies indicates that in this context individual mate choice is strong.

In more detail, although in a typical foraging society marriages are arranged, individuals can exercise mate choice in a variety of ways: They can engage in premarital relationships or they can elope with mates of their own choice; they can

influence their parents so as to direct marriage arrangements toward individuals they like; following an arranged marriage, they can engage in extramarital relationships with individuals of their own choice; they can divorce the spouses their parents have selected for them; and they can arrange later marriages (Apostolou, 2014).

In my study of 190 hunting and gathering societies (Apostolou, 2007), 13.5% of the cases based their marriage on courtship subject to parental approval. In this type of marriage, individuals have a considerable space to exercise choice as they choose who to marry, but their choices are subjected to their parents' approval. Furthermore, in 13.9% of the cases, individuals found their own spouses, with little input from their parents. Divorce was found in 65.8% of the societies in the sample, and it was reported as common in 59.3% and as rare in 40.7% of them. Note that in societies where divorce was not reported, this does not mean that it was not practiced, but rather that the anthropological record was incomplete. Instances of extramarital affairs were also frequent in this sample, although their prevalence rate was not estimated. Finally, elopement was reported in 23.7% of the societies in the sample.

In my study which was based on the Standard Cross-Cultural Sample (Apostolou, 2010), I found that in 8.3% of the foraging societies women could choose their own spouses with little influence from their parents; in 36.1% of the cases, they could choose their own spouses, but their choices were subject to their parents' approval; and, finally, in 2.8% of the cases, both arranged marriage and free courtship marriage were practiced. For men, in 40% of the cases, marriage was based on free courtship, in 22.8% on courtship subject to parental approval, and in 5.7% of the cases, both arranged marriage and courtship marriage were practiced. Furthermore, when marriages were arranged, parents consulted their daughters in 71.5% of the cases, and in 28.6% of the cases, the daughter's consent was necessary for the marriage to proceed. In 85.7% of the cases, parents consulted their sons, and in 57.1% of the cases, the son's consent was necessary for the marriage to proceed. Finally, divorce was reported in almost all societies in the sample, and in 78.9% of the cases, both men and women could initiate it.

It needs to be said at this point that children are likely to use different tactics of manipulation in order to influence their parents (Apostolou, 2015). In the case of arranged marriage, children can influence their parents to choose someone they like or at least not to choose someone they dislike. In courtship subject to parental approval, children can manipulate their parents in accepting a partner they have selected. Manipulation can take many forms; children, for instance, can threaten with suicide to avoid an undesirable partner to be imposed on them, or to make their parents accept a desirable partner (Apostolou, 2015). To the degree that manipulation is successful, it provides children with space to exercise choice through manipulating their parents into getting the mates the children want. There are several instances where anthropologists report such manipulation. For example, among the !Kung foragers in Africa: "Girls have been known to attempt suicide rather than allow a marriage to be consummated. (We know of no successful suicide attempts, and in all cases the marriage was called off)" (Lee, 1984, p. 79). Manipulation of this kind has not been studied systematically in pre-industrial societies, so at present we lack evidence about its prevalence and effectiveness.

Finally, due to the asymmetry in parental investment, when mate choice is exercised, it is expected that female choice would be stronger than male choice. That is, men would be courting women who would be in a position to exercise choice. Unfortunately, there are no systematic studies to examine whether this is actually the case.

Male-Male Competition

In the hunting and gathering context, there is opportunity for men to monopolize reproductive access to women either within their group or outside their group. Starting from the latter, some groups may become stronger than other neighboring groups. This can be due to various reasons, several of which are stochastic, for instance, a disease hitting a neighboring group, or certain groups occupying areas where there are more resources, which allow them to grow in size more than other groups. Unbalanced strength between groups provides the stronger groups with the opportunity to attack the weaker groups and monopolize their resources, one such resource being women of reproductive age. This usually takes the form of coalitions of men who organize raiding parties in order to attack neighboring groups (Puts, 2010).

Although large-scale warfare does not exist in foraging societies, raids and attacks on neighboring tribes are common (Kelly, 2013). A good example, albeit not a representative one, is the Yanomamo, a group of foragers living in South America. In this group, raids are frequently organized, and raiding parties of men are formed to attack neighboring groups with one of the primary objectives being to get their women (Chagnon, 1992, 2013).

Within the group, there is variation in the power men have: Some are physically strong, others are physically weak, and some are influential others less so. Men who find themselves in a favorable position can use their advantage to exclude other men from the reproductive process and monopolize women. In a foraging context, for instance, chiefs and other influential men marry several high mate value women, while less influential men get one wife of inferior mate value or even no wife at all (Apostolou, 2014). In my study of 190 hunting and gathering societies, polygyny is found in 73.7% of them (Apostolou, 2007).

Sexual Coercion

Women are physically weaker than men, while their parents and husbands are not always present to protect them. Moreover, in a foraging context, there are not well-developed institutions, such as the police or courts of law, to protect individuals. Thus, there is space for men to attack women and force sex on them. Sexual attacks and rape are reported in this context, albeit their actual rate is difficult to be estimated (Broude & Greene, 1976; Minturn, Grosse, & Haider, 1969; Roze-Koker,

1987; Sanday, 1981). It has to be said also that, because hunting and gathering societies are small-scale, a man who follows such a strategy faces a high chance to be detected and socially penalized, constraining in effect the fitness benefits from such a strategy.

Analysis of Selection Pressures in a Typical Hunting and Gathering Society

In the sections above, I examined the presence of different sexual selection pressures in hunting and gathering societies. This analysis can enable us to identify the strength of the different selection pressures exercised on men and women living in this setting.

Men

Most probably, the strongest selection pressure exercised on men in a hunting and gathering context is male parental choice: Men are under strong selection pressure to appeal to parents, and particularly to male parents, as spouses for their daughters. In this context, mothers have also an important role to play in marriage decisions, and in many societies, their selection power is similar to men's (Apostolou, 2014). Therefore, sexual selection under female parental choice would be an important sexual selection force exercised on men.

When they exercise choice, parents do not only choose daughters- and sons-in-law, but also other families to align with. That is to say, in parental choice, younger individuals are selected as spouses and their parents as allies. Consequently, fathers are also under strong selection pressure to appeal to parents in other families and in particular to male parents, as beneficial allies. To put it differently, fathers who do not appeal to parents as allies will suffer considerable reproductive consequences, as they will not be able to establish fitness-increasing marital alliances, and they may have to accept daughters- and sons-in-law of inferior family background.

A strong, but most likely weaker, sexual selection force exercised on men is female choice. Parents have a strong influence on deciding with whom their children will get married, but following marriage, their strength declines; so, this force is exercised predominantly within the context of marriage. Still, because female choice is present in later marriages, in relationships before marriage and in extramarital relationships, it is expected that female choice would be exercised also outside the context of marriage.

In this setting, fights between men for gaining access to resources, including women, are frequent. Accordingly, strong intrasexual selection forces are exercised on men, favoring traits that enable them to become effective in fighting other men and monopolize access to women. Finally, sexual coercion force is also exercised on

men, favoring adaptations that would make them more effective in forcing sex to women. This selection force is expected to be relatively weak however, as the chances of using this strategy without paying considerable social costs are low.

Overall, I have argued that in a hunting and gathering context, the stronger sexual selection force exercised on men is parental choice and predominantly male parental choice followed closely by female choice, and male-male competition, with sexual coercion being a significant but weak sexual selection force.

Women

Parental choice is a strong selection force exercised on women. It is usually the parents of a man who take the initiative arranging a marriage for their son (Apostolou, 2007), and part of their choice depends on the qualities of the prospective bride (Apostolou, 2014). In effect, the traits that make a woman more appealing to prospective parents-in-law as a wife for their son are selected. This is because women who have these traits are more likely to attract the attention of a larger number of prospective parents-in-law, giving their parents the opportunity to choose the most fitness-increasing offer, which presumably is fitness-increasing (probably not to the same extent) for the daughters themselves.

Moreover, older women parental choice, and especially male parental choice, is exercised in being selected as allies. That is, mothers are also under selection pressure to appeal to parents in other families and in particular to male parents, as beneficial allies. Women who are not appealing as allies suffer fitness penalties as they have to accept as spouses for their children individuals of inferior family background.

Male choice constitutes a significant sexual selection force exercised on women living in foraging societies. To begin with, as men have considerable autonomy over mate choice, and they also have an influence on their parents, women who have traits that make them more desirables as wives enjoy fitness benefits: Several men would come seeking them in marriage, which would give their parents a greater choice in selecting the most fitness-increasing ones. Also, in later marriages which are not arranged by parents, such traits will enable women to have a greater selection of prospective spouses to choose the most fitness-increasing one.

Male choice is exercised also within marriage, where men decide whether they would divorce their mates or whether they would stay married, but establish relationships with other women outside marriage. Thus, traits which enable a woman not to be divorced or make her husband to prefer her over other women will be selected. Male choice is also exercised on women in premarital relationships and in extramarital relationships. That is, traits which turn a woman more likely to be selected by men as premarital or extramarital partners confer fitness benefits to women because they enable them to attract more men and choose among them those who are more beneficial for them.

Female-female competition is also exercised on women. Women compete with other women in order to keep their husbands, or exclude other women from the

mating game. Traits that enable women to exclude other women from the competition are selected. For instance, traits that enable women to efficiently spread rumors that a competitor is promiscuous, has a disease, etc., or threaten competing women, effectively excluding the from the competition, would be selected. Nevertheless, given that in this context women are controlled by their parents, and there is also strong male-male competition, this force is expected to be weak.

Overall, I have argued that male choice and parental choice are the two primary sexual selection forces exercised on women living in a foraging context. Although parents have a strong say in this context, sons have also considerable space to exercise choice, which means that male choice would be strong over women. Female-female competition is the weakest force, with sexual coercion not to be present.

In sum, in this chapter I examined how the model of parental choice is consistent with the mating patterns found in pre-industrial societies which base their subsistence on hunting and gathering. I have also examined the strength of the other than parental choice sexual selection forces. In the next chapter, I am going to examine whether the model is consistent with the mating patterns found in pre-industrial societies which base their subsistence on agriculture and animal husbandry.

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Chapter 5
Sexual Selection Under Parental Choice in Agropastoral Societies

In the previous chapter, I examined sexual selection under parental choice in pre-industrial societies which base their subsistence on hunting and gathering. In this chapter, I am going to examine sexual selection under parental choice in pre-industrial societies which base their subsistence on agriculture and animal husbandry. These societies range from the ones which base their subsistence predominantly on agriculture to those which base their subsistence predominantly on animal husbandry. Despite such variation, for simplicity, these societies will be treated as a single category, but some space will be devoted in discussing the differences between societies which base their subsistence predominantly on agriculture and societies which base their subsistence predominantly on animal husbandry.

A Typical Agropastoral Way of Life

Despite their considerable differences, agropastoral societies have several patterns in common. To begin with, they have sophisticated technology for producing food, for instance, to plow the land, plant grain, process grain into flour, and use flour to make bread. Complex technology requires specialization, for example, people who specialize in plowing the land, people who specialize in manufacturing the machinery required for doing so, people who specialize in processing grain into flour, and people who specialize in processing flour into bread. Such specialization means that individuals cannot themselves produce what they need for their subsistence, and they have to rely on other people's output. For instance, the farmer supplies grain to the miller who supplies flour to the baker who provides the former two with bread.

Specialization leads to the problem of exchange, because the farmer who wants bread cannot provide grain to the baker in exchange for it, since unprocessed grain is not useful to him. This problem is solved with the use of money, so that the farmer can sell its product to the miller and use the money to buy bread from the baker. Consequently, these societies are characterized by the use of money, which is further employed to store wealth.

The sophisticated technology allows high food production, which in turn allows a higher population density. As a consequence, agropastoral societies are generally

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numerous, ranging from a few hundreds to several thousands or even millions. Their population is sedentary, as it pays to find fertile land and build permanent settlements to exploit it. A sedentary way of life is also mandated by the fact that the facilities required for food production, such as a mill, are not readily portable.

The sophisticated technology demands specialization and allows large group numbers to be maintained and wealth to be produced and guarded. In turn, these factors give rise to sophisticated social institutions which are necessary for coordinating the different aspects of the production process, for regulating the living of a large number of people in close distance, and for regulating the distribution and safekeeping of the produced wealth. Thus, agropastoral societies are characterized by having sophisticated social institutions such as the church, the law, and the army (Apostolou, 2013). For instance, a sophisticated judicial system is necessary for protecting people's wealth from internal threats, while a well-trained army is necessary for protecting wealth from external threats. To use another example, a religious institution, such as the church, can spread and enforce a sophisticated religious dogma that can enable the harmonious coexistence of a large number of people in close proximity.

Sexual Selection in Agropastoral Societies

I can now turn to examine how the model of parental choice accounts for the patterns of mating found in pre-industrial agropastoral societies, starting from the diverging opportunity cost [$o_{diverging} = (b \times f - c \times \overline{r}) \times d$]. In this setting, considerable wealth is produced, which takes the form of food surpluses, material goods, land, and animals. In addition, social protection systems are not well developed, and individuals have to rely on each other for subsistence and protection. Therefore, there are potentially many benefits that parents can receive from an arranged marriage (b) in this context. For instance, parents who can arrange a marriage with a family who controls considerable wealth, such as land and animals, are likely to receive substantial benefits in the form of bridewealth or gifts. Furthermore, in this setting, there are well-developed social institutions which regulate the functioning of a society. An alliance with an influential family, that is, a family whose members hold important positions in these institutions, can also benefit parents as it will increase their own influence and access to different social institutions.

In addition, in agropastoral societies children are married young, when their parents are also relatively young (Apostolou, 2010). As a consequence, the benefits that parents can extract from a marriage arrangement are they can convert them into direct reproductive fitness, i.e., to have additional children, or get additional wives increasing the overall (f).

In agropastoral societies, parents enjoy a high capacity to inflict a cost to their children for deviating from their will [$d = (w + e + h + j + i) - (q \times \overline{r})$]. Starting from the resources that parents control and can divert to their children (w), in many instances they are substantial. In particular, because these societies produce

considerable material wealth, and because the means of production are individually owned and can pass from parents to children (Apostolou, 2011), the (w) can be considerable. For instance, parents can divert part of the money they have accumulated to their children that their children can use to increase their fitness. Furthermore, since social protection systems are not well developed or are totally lacking, physical protection is another important resource that parents can divert to their children.

In this setting, children are heavily dependent on the resources their parents control (e). More specifically, subsistence activities are based on the cultivation of land and the herding of animals, which are usually under parental control. Therefore, children are heavily dependent on their parents for their subsistence. In addition, because social protection and individual rights systems are not well developed, individuals are dependent on their family for physical protection. The lack of these systems results also in a high capacity of parents to inflict a cost to their children through physical force (h). Furthermore, it is expected that parents have a high capacity to inflict psychological cost to their children in order to align them with their will (j).

Agropastoral societies are relatively large, there is high specialization in the production process while surplus wealth is produced, all of which require the development of sophisticated social institutions that regulate these societies. Social institutions such as the law, the army, and the church play a critical role for the functioning of a society, and consequently, they have a considerable power in regulating people's behavior. These institutions are controlled by older society members, which translates into parents having preferential access to these institutions, and they can employ them in exercising control over their children's mating decisions (Apostolou, 2013). Accordingly, parents in an agropastoral context enjoy a high capacity to inflict costs on their children for deviating from their will through manipulation of social institutions (i).

In sum, in a pre-industrial context where subsistence is based on agropastoralism, parents can derive substantial benefits from placing their children's mating decisions under their control, and they have a large capacity to inflict cost on them in order to make this control possible. In effect, in these societies there is a substantial diverging opportunity cost of free mate choice ($o_{diverging}$).

Moving on to the converging opportunity cost [$o_{converging} = [(k \times n) + l] \times \bar{r}$], in this context there is a high risk that children make mistakes when they exercise mate choice, which their parents are less likely to make if they were to exercise choice for them (k). As defined in Chap. 3, the (k) is inversely related to experience (ex) and intelligence (int) and positively related to personality traits (pe) and mate value. Children vary in these traits, with many having levels that make them vulnerable to erroneous mate choices. Furthermore, because technology is relatively simple, an extensive period of training is not required before individuals are ready to enter in the production process. As a consequence, individuals enter in the long-term mating market soon after they reach sexual maturity (Apostolou, 2010), which means that they are inexperienced and prone to make mistakes, resulting in higher (k).

In the pre-industrial agropastoral context, there are few if any means to prevent conception and terminate unwanted pregnancies, there are no effective ways to treat

sexually transmitted diseases, and individual rights are not well protected. As a consequence, an erroneous mate choice may have a considerable negative impact on children and, thus, on their parents (n). The (n) is further augmented by the strong rule of social institutions, which can impose heavy cost to individuals for deviating from acceptable behavior. For instance, in a theocracy like the Byzantine Empire, a daughter who loses her virginity before marriage is likely to suffer heavy costs, coming predominantly from the religious institutions (Cavallo, 1997). Similarly, the rule of law is strong in many of these societies, so, for instance, a son who engages in a sexual relationship with a married woman and enters in a fight with her husband and kills him may suffer severe consequences such as life imprisonment or even death.

Turning now to the risk that a child faces in being unable to attract a mate (l), it is positively predicted by the personality traits of a child that negatively influence success in attracting a mate (s), and it is also inversely related to a child's mate value. As discussed previously, in this context, as in all other contexts, we expect that several children have levels of these traits which make them vulnerable to staying single. In effect, the (l) is expected to be positive. Overall, in the agropastoral context there is a considerable converging opportunity cost of free mate choice.

As parental control over mating (m) is a function of the diverging and the converging opportunity costs $m = (o_{diverging} + o_{converging})$, which are both positive in an agropastoral setting, it is predicted that in societies of this type, parents would exercise considerable control over their children's mating decisions.

Consistent with this prediction, in one study I employed evidence from the Standard Cross-Cultural Sample, which included a large number of societies which based their subsistence on agriculture and animal husbandry. I found that arranged marriage was the prevalent mode of long-term mating (Apostolou, 2010). More specifically, in societies which based their subsistence predominantly on agriculture, for women, arranged marriage was the most frequent mode of long-term mating in 40.3% of the cases, followed by courtship subject to parental approval in 28.1%, arranged marriage and free courtship marriage both practiced in 24.5%, and courtship marriage in 7% of the cases. For men, these rates were 30.4%, 23.2%, 23.2%, and 23.2%, respectively. In societies which base their subsistence predominantly on animal husbandry, for women arranged marriage was practiced in 72.7%, courtship subject to parental approval in 18.2%, and both arranged marriage and courtship in 9.1% of the societies, while there were no cases where marriage was based predominantly on courtship. For men, the respective ratings were 41.7%, 25%, and 16.7%, while in 16.7% of the cases marriage was based on free courtship. In societies which based their subsistence on a combination of agriculture and animal husbandry, for women, in approximately 53% of the cases, marriages were arranged, in 21% were based either in arranged marriage or free choice, in 16% were based on courtship subject to parental approval, and in approximately 10% were based on free mate choice, with the respective rates for men being, 39%, 17%, 11%, and 33%.

In another study, I coded the mating patterns of 16 historical agropastoral societies (2012). I found that in 15 of them, marriages were arranged, and in one society in the sample, the sources were not clear about which was the dominant form of long-term mating.

Contingencies

Daughters Versus Sons

Women, by diverting more parental investment to their children than men, they become the scarce reproductive resource to which men seek access (Trivers, 1972). In effect, it is usually the case that men and their parents seek access to wives and daughters-in-law than the other way round (Apostolou, 2014); so, parents can extract more benefits from controlling their daughters' than their sons' mate choices ($b_{daughters} > b_{sons}$). Yet, in this context, sons enjoy a high mate value, which means that parents can also extract considerable benefits by controlling their sons' mating decisions. Accordingly, the ($b_{daughters} - b_{sons}$) difference is not expected to be considerable.

In agropastoral societies, parents are likely to possess considerable wealth that they can divert to their children. Nevertheless, the transfer of the wealth is asymmetrical in favoring sons. In particular, wealth passes from the parents to the son in terms of inheritance (Apostolou, 2011). Inheritance, in this context, can be considerable as it can take the form of land, animals, and money. Accordingly, sons have more to lose in terms of resources if they disobey their parents, which in turn gives parents more power over their sons' than over their daughters' mating decisions so that ($w_{daughters} < w_{sons}$).

In this context, both daughters and sons are dependent on their parents' resources (i.e., land and animals for their subsistence). Yet, because in these societies men enjoy higher social status, and women are much less autonomous and secluded, sons are less dependent for their subsistence on their family than daughters. For instance, they can more easily look for subsistence-generating activities outside their family; work, for example, in somebody else's field; shop; join the army; etc., things that daughters cannot do. In the agropastoral setting however, children depend also on their parents' resources for success in the reproductive effort. More specifically, in agropastoral societies, men usually have to pay a considerable amount of resources to their prospective parents-in-law for the marriage to proceed, a wealth which frequently comes from their own parents (Goody & Tambiah, 1973). Accordingly, sons are more dependent than daughters on their parents' resources for securing a spouse. An exception to this pattern is societies where dowry is practiced, that is, societies where the daughter has to bring to the marriage a considerable amount of resources, resources which come from their parents (Goody & Tambiah, 1973). Nevertheless, the dowry is much less common than bridewealth (Murdock, 1981), so it cannot be considered to be typical of these societies (see Chap. 8 for further discussion on dowry).

On the other hand, because in this context social protection systems are not well developed, and because women are physically weaker than men, they do not have access to weapons, and they are more frequently the target of sexual assault, and daughters are more dependent on their parents for physical protection than sons. Overall, daughters are more dependent than sons for their subsistence and protection on their parents, but sons are more dependent than daughters on the resources

of their parents for securing spouses. Thus, $e_{daughters} > e_{sons}$, but the difference is not expected to be considerable.

In addition, because daughters are physically weaker than sons, and because parents have few constraints in using physical force on their children, they can more easily employ physical force to inflict a cost on the their daughters than on their sons in order to align them with their will ($h_{daughters} > h_{sons}$). In sum, the cost that parents can impose on their children to align them with their will is higher for daughters than for sons ($d_{daughters} > d_{sons}$), but the difference is not expected to be extensive. Overall, the diverging opportunity cost of free mate choice is higher for daughters than for sons ($o_{diverging\_daughters} > o_{diverging\_sons}$), but the divergence is not expected to be substantial.

In the agropastoral context, there are no effective ways to prevent or to terminate an unwanted pregnancy, and there is no effective way to prove paternity. It needs to be said however, that infanticide, which is frequently found in these societies (Whyte, 1978), can reduce the cost of unwanted pregnancies. In addition, in most societies of this type, chastity is very highly valued in women, and it is not infrequent for an unchaste woman to be considered "damaged good" and not a marriage material (Campbell, 1964). Last but not least, following sexual maturity, the reproductive value of women decreases faster with age than the reproductive value of men; thus, allocating time in relationships which do not have long-term prospects can be more costly for daughters than for sons. In sum, erroneous mate choices can have more detrimental consequences for the fitness of daughters than for the fitness of sons ($n_{daughters} > n_{sons}$).

Moving on, because women constitute the scarce reproductive resource, they are the target of more intense mating effort, and thus, they face a higher risk of deception and assault by men who attempt to force access to their reproductive capacity so that ($k_{daughters} > k_{sons}$). Nevertheless, women, by being the scarce reproductive resource, they are less at risk of being unable to attract a mate than men ($l_{daughters} < l_{sons}$). As the (n) and the (k) are higher, but the (l) is lower for daughters than for sons, assuming an equal contribution of each factor, the converging opportunity cost of free mate choice is higher for daughters than for sons ($o_{diverging\_daughters} > o_{diverging\_sons}$). In sum, because in the agropastoral context both diverging and converging opportunity costs are higher for daughters than for sons, parental control over mating is expect to be stronger over daughters than over sons ($m_{daughters} > m_{sons}$). Nevertheless, because the diverging opportunity cost for sons is substantial, it is predicted that parents would exercise a considerable control over their sons.

As discussed in the previous section, in my study which was based on the Standard Cross-Cultural Sample (i.e., Apostolou, 2010), I found that parental control over mating was stronger over daughters than over sons, with parents however exercising considerable influence over the mate choices of the latter. For instance, in societies where subsistence was based predominantly on agriculture, for women, in approximately 40% of the cases, marriages were arranged, while for men the respective rate was 30%. Similarly, in societies where subsistence was based predominantly on animal husbandry, for women, in approximately 73% of the cases, marriages were arranged, while the respective rate for men was 42%. In societies

where subsistence was based on a combination of agriculture and animal husbandry, for women, in approximately 53% of the cases, marriages were arranged, while the respective percentage for men was 39%.

In my study of 16 historical societies which based their subsistence on agropastoralism (Apostolou, 2012), I found that in 90% of the cases for which data were available, parents controlled the mating decisions of their daughters more than those of their sons, and only in 10% of the cases both sexes were equally controlled. No case was reported where parents exercised more control over their sons than over their daughters.

In sum, consistent with the predictions of the model, in societies which base their subsistence on agriculture and animal husbandry, parents exercise more control over their daughters than over their sons' mating decisions, with the control that they exercise over their sons to be also substantial.

Mothers Versus Fathers

I will now move on to examine differences in parental control over mating between fathers and mothers. Starting from the wealth that parents control and can divert to their children in the form of parental investment (w), agropastoral societies produce considerable wealth which is predominantly controlled by male members (Whyte, 1978). Accordingly, fathers have a much higher capacity than mothers to inflict a cost on their children by discontinuing parental investment ($w_{fathers} > w_{mothers}$). For instance, fathers can exclude a son from inheriting cattle, but mothers cannot do so, as cattle usually belong to fathers.

In this context, subsistence is based on the cultivation of land and the herding of animals which are owned by parents, mainly fathers. This means that children are heavily dependent on the resources that their fathers control for their subsistence, which in turn gives to the latter a considerable capacity to inflict a cost on the former if they disobey their will. Many of these societies practice bridewealth, and some practice dowry, which also makes individuals dependent on their fathers' resources for their reproductive effort. In addition, wars and conflicts, motivated predominantly by the surpluses these societies produce, are not infrequent (Nolan, 2003). Fathers and other male relatives, by virtue of being physically stronger and more aggressive and by having exclusive access to weaponry than mothers and other female relatives, are predominantly the ones who provide physical protection to the family unit. In sum, children are more dependent on their fathers than on their mothers for the resources they need and for protection ($e_{fathers} > e_{mothers}$).

Similarly, because fathers are physically stronger and more aggressive and have access to weaponry, they can inflict a higher cost than mothers on their children by using physical force ($h_{fathers} > h_{mothers}$). This capacity is also augmented by the fact that in these societies, individual rights are not well protected. Mothers, however, are usually more effective manipulators than fathers, so they can inflict a higher psychological manipulation cost on their children ($j_{fathers} < j_{mothers}$).

Agropastoral societies are generally large scale, and they require sophisticated social institutions in order to make their functioning possible, but these institutions are predominantly controlled by older men (Apostolou, 2013). Fathers and older male relatives are likely to find themselves in positions of power within these institutions, and/or they are likely to know and be able to influence other men who hold such positions. They can use then this power to promote their control over mate choice. For instance, a father can influence a judge to punish a man for having an illegitimate relationship with his daughter, or a priest to excommunicate his son for not obeying his father's will. Thus, fathers have a higher capacity to inflict cost on their children through manipulating social institutions ($i_{fathers} > i_{mothers}$).

Finally, because in this context paternity cannot be proved, men are less certain than mothers that their children are their own, which translates into the cost that parents have to suffer from inflicting a cost to their children ($q \times \bar{r}$) being lower for fathers than for mothers. Overall, in an agropastoral context, fathers can inflict a higher cost on their children to align them with their will than mothers ($d_{fathers} > d_{mothers}$).

Paternal uncertainty translates also into the costs from making compromises in order to get benefits from controlling mate choice ($c \times \bar{r}$) to be lower for fathers than for mothers. Consequently, fathers can potentially gain more from a mating deal than mothers, as they are less constrained in the cost that this deal may have for their children. In addition, because women conclude their reproductive careers at an earlier age than men, and because men have a higher reproductive variance than women, the resources from a mating deal has the potential to increase the direct reproductive success of fathers to a considerably greater degree than the direct reproductive success of mothers ($f_{fathers} > f_{mothers}$). In this context, the benefits that fathers can extract (b) can involve considerable material wealth. For instance, a man who has a high mate value daughter can arrange a marriage and receive a high bridewealth from his son-in-law that can be used to pay his own bridewealth in getting additional wives.

Overall, in pre-industrial societies which base their subsistence on agriculture and animal husbandry, fathers can inflict considerably higher cost to their children than mothers in order to align them with their will. In addition, because they can extract more benefits from controlling mate choice, which they can convert into reproductive success, they have more to lose if they allow their children to exercise mate choice freely ($o_{diverging\_fathers} > o_{diverging\_mothers}$). Nevertheless, if children make erroneous choices (k) and stay without a mate (l), which reduce their fitness, mothers have potentially more to lose because they are more certain that their children are actually their own; so that ($o_{converging\_fathers} < o_{converging\_mothers}$).

Still, this difference is not considerable because it is based only on the difference in parental certainty, which is in general small. Furthermore, in this context, mate choice is strongly regulated (see above), while there are strong social institutions to punish undesirable sexual contact (Apostolou, 2013). These factors translate into paternal uncertainty not being that considerable, reducing the difference between the converging cost of mothers and fathers. On the other hand, the difference between the diverging opportunity cost between fathers and mothers is expected to be substantial so that ($o_{diverging\_fathers} - o_{diverging\_mothers} > o_{converging\_mothers} - o_{converging\_fathers}$). Therefore, fathers in this context experience an overall higher opportunity cost from

the free mate choices of their children, which predicts that they would be more influential in controlling mate choice than mothers ($m_{fathers} > m_{mothers}$). Mothers are also predicted to have a say, as they also face a considerable opportunity cost.

In my study which was based on the Standard Cross-Cultural Sample (Apostolou, 2010), in societies which based their subsistence predominantly on agriculture, in 25% of the cases, males monopolized marriage arrangements; in approximately 39% of the cases, both parents participated but men had more say; in 22% fathers and mothers had an equal say; and in 14% both parents participated but mothers had more say. In societies which based their subsistence on animal husbandry, in 71% of the cases, both parents participated in marriage arrangements, but fathers had more say, and in 29% of the cases, both participated with roughly equal say. Note that there were not so many societies in the sample which based their subsistence predominantly on animal husbandry, which may potentially explain the lack of variation found. Finally, in societies which subsistence was based on both agriculture and animal husbandry, in 80% of the cases, both parents participated but men had more say, in 10% men dominated marriage arrangements, and in 10% both parents had an equal say. Note also that in none of the society types investigated, there was any case where mothers dominated marriage arrangements.

In my study of 16 historical agropastoral societies, there was information for 14 societies (Apostolou, 2012). In ten societies, marriages were predominantly controlled by fathers, while in four societies both parents participated but fathers had more say. Furthermore, there was no case reported where women had more say, or they dominated marriage arrangements. Overall, consistent with the predictions of the model, in the pre-industrial context where subsistence was based on agriculture and animal husbandry, marriage arrangements are dominated by fathers, but mothers have also an important say.

Agricultural Versus Animal Husbandry Societies

Evidence from the anthropological record suggests that in animal husbandry societies, mate choice is controlled more and men are more dominant than in agricultural societies (Apostolou, 2010). It has to be said that this conclusion is based predominantly on one study, i.e., Apostolou (2010), in which there were not so many societies which based their subsistence on animal husbandry. Thus, more research is necessary in order to examine the degree that these society types differ in their mating patterns. Assuming that this difference is real, we can ask what can account for it.

In terms of the model of parental choice, it needs to be the case that the opportunity cost of free mate choice is higher in animal husbandry than in agricultural societies. In the latter societies, parents are more in need of their children to farm the land, which in turn, decreases their capacity to inflict a cost on them to align them with their will (d). On the other hand, the herding of animals is not so physically demanding and older individuals can perform it. Thus, the higher dependence of parents on the labor of their children in agricultural than in animal husbandry societies may be one of the reasons behind the observed difference in parental control.

In both society types, it is the father who controls subsistence-generating resources, so it is fathers in agropastoral society who are more in need of their children's labor in order to maintain their wealth. In effect, fathers in animal husbandry societies are less dependent on their children's labor, and so, they may have more power over their children than fathers in animal husbandry societies.

Other Sexual Selection Forces

Individual Mate Choice

In an agropastoral pre-industrial context, parents dominate marriage arrangements substantially reducing the space their children have to choose mates for themselves. Mate choice can still be exercised however, in manipulating parents, in extramarital relationships, and in later marriages. Mate choice is predominantly exercised through divorce, which is found in all agropastoral societies, and rests predominantly in the hands of children (Apostolou, 2014). Nevertheless, these avenues for exercising mate choice may not be that broad, because the wealth that agropastoral societies produce makes the stakes high, while the lack of social protection systems turns deviation from desirable mating behavior to be strongly punished by parents. In addition, social institutions, which are important in regulating agropastoral societies, are likely to function in a way that discourages such behavior. For instance, in the Christian dogma, marriage is supposed to last forever, and it is not up to the parties involved to dissolve it at will. In different words, breaking a marriage in a theocracy like the Byzantine Empire is likely to have severe divine consequences, which translate into severe earthly consequences, as individuals who break the marriage are likely to pay high costs, such as social exclusion.

Evidence from the Standard Cross-Cultural Sample indicates that, for women, in agricultural societies, approximately in 7% of the cases, marriage was based on free choice, but this percentage was zero in societies which based predominantly their subsistence on animal husbandry. while it increased to 10.5% for societies which base their subsistence on a combination of agriculture and animal husbandry (Apostolou, 2010). The respective percentages for men were 23.2, 16.7, and 33.3%. Furthermore, in many of these societies both parental arrangement and courtship are practiced, while many societies practice courtship subject to parental approval marriage (see above). Also, it is common for parents to ask the consent of their children before they proceeded with a marriage arrangement. Divorce was reported in most of these societies, and in the majority of the cases, both men and women have access.

In my study of 16 historical societies, there were no cases where marriage was based predominantly on free courtship (Apostolou, 2012). Nevertheless, the consent of the children, especially of sons, was sometimes asked. Extramarital relationships were reported in 11 societies, and divorce was reported in 11 societies, but men had an easier access. Note that when a given pattern (e.g., divorce) was not reported, this does not mean that it was not present, but most likely the historical records were incomplete.

When mate choice is exercised, the asymmetry in parental investment suggests that it would be predominantly men who would seek access to women, placing the latter in a position where they can exercise choice. Still, the importance of men in this context is likely to erode this difference. To my knowledge, there is no systematic analysis of individual mate choice patterns that would allow us to examine whether this is the case.

Male-Male Competition

Agropastoral societies produce surplus resources, which motivate aggression between groups that can take the form of raids but also larger scale conflict such as war (Nolan, 2003). The target of these aggressive acts is other groups' resources including women (Dow, 1983; Sugiyama, 2014). This is nicely depicted to the myth of the Trojan War, where the Greeks attack the Trojans to get back the Helen of Troy. These aggressive acts indicate strong male-male competition.

Furthermore, within the group, there is variation, with some men being physically strong, others being physically weak, and some being influential others less so. Men who find themselves in a favorable position can use their advantage to exclude other men from the reproductive process and monopolize women. This is demonstrated in harems where nobles, sultans, and emperors had monopolized access to a large number of high mate quality women, who were as a consequence, not available to other men.

Sexual Coercion

In agropastoral societies, the well-developed social institutions, such as the law and the church, turn such a strategy costly. On the other hand, the large size of these societies and the limited technology (e.g., no DNA testing) can make rapists less likely to be detected. Thus, these factors make sexual coercion strategies less costly. Overall, there is a niche for such strategies, which predicts that sexual coercion would be present. Consistent with this prediction, in my study of 16 historical societies, rape was reported in about half of them (Apostolou, 2012). Other anthropological studies report rape to be present in pre-industrial agropastoral societies (Broude & Greene, 1976; Roze-Koker, 1987; Sanday, 1981).

Analysis of Selection Pressures for a Typical Agropastoral Society

On the basis of the evidence discussed above, I will move on to discuss the sexual selection pressures exercised on men and women living in agropastoral societies.

Men

In the agropastoral context, perhaps the strongest sexual selection pressure exercised on sexually mature men is parental choice as they have to appeal to parents and particularly to male parents as spouses for their daughters. Moreover, strong sexual selection forces would be exercised on older men to appeal as in-laws to parents and particularly to male parents, who look to make alliances with desirable families. In this setting, where families are likely to control considerable wealth, and where one's property need to be protected, marital alliances are of high importance, so this pressure is expected to be considerable.

A strong, but most likely less strong, sexual selection force exercised on men is female choice. Parents have a strong influence in deciding with whom their children will get married, but once the marriage is arranged, their strength declines, so this force is exercised predominantly within the context of marriage. Moreover, as women have an influence on their parents, selection pressures are exercised on men to be chosen as mates. That is, a woman who desires a man having qualities she prefers can influence her parents to arrange a marriage with him. In this case, these traits are selected through female choice.

Strong intrasexual selection forces are also exercised on men, as fights between and within the group for access to resources, one being women, are frequent. Sexual coercion forces would also be exercised on men, as there is space to force sex to women.

Women

Parental choice is a strong selection force exercised on women in this context. It is usually the parents of a man who take the initiative in arranging a marriage for their son, and as the fitness of their choice depends on the bride they choose for him, they also consider the qualities of their prospective daughter-in-law. As a consequence, traits that make a woman more appealing to prospective parents-in-law are selected, because women who have them are more likely to attract the attention of several prospective parents-in-law, giving their parents the opportunity to choose the most fitness-increasing offer, which presumably is also fitness-increasing, even not to the same extent, for their daughters.

In addition, in older women, parental choice, and especially male parental choice, is exercised to be selected as allies: Traits that make a woman more likely to be chosen as an ally are selected because they enable mothers to get into more beneficial marital alliances. Mothers who are not appealing as allies suffer fitness penalties as they have to accept as spouses for their children individuals of inferior family background.

Male choice is also strong over women. It is exercised predominantly within marriage, where women have to retain their mates so as to avoid divorce or their spouses establishing extramarital relationships and diverting their parental

investment to other women. This selection force is exercised also in women entering in premarital relationships, in later marriages, and in extramarital relationships. Furthermore, as men have considerable autonomy over mate choice, and they also have an influence on their parents, considerable pressure is exercised on women to be selected by men. That is to say, traits which turn a woman more likely to be selected by men are sexually selected because they enable women to attract more men and choose between them the ones with the highest mate value. When parents exercise choice, they consider the preferences of their sons, so male choice is also exercised through parental choice.

Female-female competition is also present. Women compete with other women to keep their husbands, or exclude other women from the mating market. As in this setting, women are strongly controlled, and there is segregation of sexes; this selection force is probably weak.

Overall, the model of parental choice fits well the patterns of mating found in agropastoral societies: Male parental choice is the dominant sexual selection force, but other sexual selection forces are also present. In the next chapter, I will examine whether the model fits the patterns of mating in post-industrial societies.

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Chapter 6
Sexual Selection Under Parental Choice in Post-industrial Societies

In the previous two chapters, I explored how the predictions of the model of parental choice fit the patterns of mating in pre-industrial societies. In this chapter, I am going to examine how the predictions of the model fit the mating patterns in post-industrial societies.

A Typical Way of Life in a Post-industrial Society

Post-industrial societies are characterized by a high level of technological development which has several implications: To begin with, advanced technology allows for large population sizes. Accordingly, post-industrial societies are characterized by living in cities of thousands and frequently millions of inhabitants. The technological development allows also the production of considerable wealth: These societies generate substantial resources, which are considerably over and above of what is required for subsistence. The produced resources are not evenly distributed, and although most individuals have some surplus wealth that they do not need for their subsistence (e.g., money in their saving accounts), some have much more than others.

High technological development results in very high specialization and a long period of training. The combination of large population sizes, high specialization, and the production of considerable wealth requires well-developed social institutions which will make the living together in one place of many people possible, will coordinate the different production units, will provide the necessary training, and will guarantee the safekeeping and protection of the extra wealth from internal and external threats. Accordingly, societies of this type are characterized by well-developed social institutions such as the judicial system, the police, the higher education system, and the army.

One consequence of the presence of these institutions is that post-industrial societies are relatively peaceful. For instance, attacks and raids are rare, as institutions such as the police prevent them from occurring and institutions such as the judicial system impose heavy costs to those who engage in such actions (Pinker, 2011). Even so, internal strife and aggressive behavior are not totally eliminated. Fighting

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between different societies is also rare, but there are instances of conflict, motivated predominantly by getting resources such as oil, which are required for the production of wealth. The high technology results in the creation of more lethal mass destruction weapons, which allow large-scale wars between these societies with millions of victims (e.g., World Wars). Perhaps these destructive potential acts as a counter motive to the frequent occurrence of wars, by making the stakes very high (see also Pinker, 2011).

The high technology leads to surplus wealth, which in turn allows for the creation of several social protection systems. Thus, in most post-industrial societies, there are unemployment benefits; education and medical services are free or at least are free to those who cannot pay for them. In the same vein, the police, the fire brigade, and the army are paid by individuals through taxes, but provide their services to everyone irrespectively of whether they pay taxes or not or how much tax they pay. As a consequence, people living in post-industrial societies are not strongly dependent on others for survival; for instance, in times of need, they can rely on social protection systems instead on the help of their friends and relatives. Similarly, if they face internal threats, they can rely on the police instead of someone else to protect them, and in case of external threats, they can rely on their country's military force.

Sexual Selection in Post-industrial Societies

I can now proceed to examine how the model of parental choice accounts for the patterns of mating found in post-industrial societies. Starting from the diverging opportunity cost [$o_{diverging} = (b \times f - c \times \bar{r}) \times d$], post-industrial societies produce considerable wealth which is usually controlled by the older generation. Accordingly, in this setting there are potentially many benefits that parents can receive from manipulating their children's mating decisions (b). These benefits are moderated by the presence of well-developed social systems which turn individuals less dependent on each other. For instance, a parent who gets fired does not need to rely on his/her in-laws for support as he/she can receive an unemployment benefit. Thus, family alliances are less important for parents as they do not make a difference between life and death, which is the case in pre-industrial societies.

Furthermore, in post-industrial context, children are getting married relatively late (Coonz, 2006), which means that their parents are also old and they have terminated their reproductive careers. Consequently, parents have a limited potential to convert any of the benefits they have extracted into fitness through direct reproduction (f).

Even so, there are substantial benefits to be extracted by manipulating mate choice, which requires however that parents have a capacity to inflict a cost to their children for deviating from their will [$d = w + e + h + j + I - (q \times \bar{r})$]; this capacity is nevertheless limited. In particular, starting from the resources that parents control and can divert to their children (w), they are frequently substantial: Post-industrial

societies produce considerable surplus wealth, which is usually controlled by the older generation. Thus, through their lifetime, parents are likely to have accumulated substantial wealth in the form of money and property. As a consequence, children have potentially much to lose if they dissatisfy their parents, which increases the capacity of the latter to inflict a cost on them.

Nevertheless, at marital age children are weakly or not dependent at all on their parents' resources (e). More specifically, in post-industrial societies, individuals are usually married when they have completed their studies and have a stable job. Thus, they are financially independent from their parents, and they do not need the latter's resources for their survival and reproduction effort. In addition, the presence of effective social protection systems, found in most post-industrial societies, augments individuals' financial independence from their family. For instance, the police ensure that individuals do not need their families to protect them from thieves and other aggressors. Similarly, the welfare state ensures that individuals receive financial assistance in case misfortune finds them, and they do not need to rely on the assistance of their parents.

In addition, bridewealth and dowry are not practiced in post-industrial societies, which means that children do not need the financial assistance of their parents in order to get married. It has to be said however that individuals frequently receive substantial financial assistance from their parents in order to cover the expenses of marriage ceremony, but also in order to establish a new household. Yet, such assistance is not necessary for a marriage to proceed—individuals can get married without receiving any resources from their family.

Overall, in this context the (e) is low. Note however that the (e) varies with children's age. That is, teenagers are more dependent on their parents' resources than middle-age children. Thus, parents' capacity to influence children's mating decisions is usually higher in younger age where children are more dependent on their parents' resources. Note, however, that in young age, where parents may have more influence, individuals usually do not procreate, so parental control is likely not that consequential.

In the post-industrial context, institutions such as the law and the police ensure that individual rights are well protected. The protection of individual rights compromises the capacity of parents to inflict a cost on their children through physical force (h). This capacity is compromised even further by the fact that children are getting married several years following sexual maturity, so their parents are old and their capacity to use physical force is limited. Nevertheless, it is expected that parents have a good capacity to inflict psychological costs to their children in order to align them with their will (j) and they are likely to resort to exploiting this capacity to balance their limited capacity of doing so through physical means.

Post-industrial societies are large and complex, requiring sophisticated social institutions such as the law, in order to be able to function. Although the older generation is overrepresented in these institutions, their purpose is primarily to protect individual rights so they cannot be readily applied to impose parents' will on their children. Consequently, these institutions cannot be employed to inflict a cost on children for deviating from parents' will (i).

In sum, the diverging opportunity cost of free mate choice ($o_{diverging}$) is relatively low in a post-industrial context, predominantly because parents have a limited capacity to convert any benefits they extract into direct reproductive success and they have a limited capacity to inflict costs on their children if they deviate from their will.

Moving on to the converging opportunity cost [$o_{converging} = [(k \times n) + l] \times \bar{r}$], in this setting, there is a relatively high risk that children make mistakes when they exercise mate choice, which their parents are less likely to make if they were to exercise choice for them (k). As defined in Chap. 3, the (k) is inversely related to experience (ex) and intelligence (int) and positively related to personality traits (pe) and mate value. Children vary in these traits, with many having levels that turn them vulnerable to erroneous mate choices. Nevertheless, an extensive period of training is required for individuals to be able to secure a job and then move on to have a family. Thus, individuals enter in the long-term mating market when they are relatively old and experienced and, so, less prone to make mistakes, reducing somewhat the (k). On the other hand, the mismatch between ancestral and modern condition may augment the (k) considerably.

In more detail, individuals evolved in a context where mate choice was regulated. Parents chose spouses for their children, and they have evolved mechanisms such as in-law preferences in order to screen in-laws who can be harmful for their own and their children's fitness. As a consequence, the selection pressure on children to evolve such mechanisms is weak, which translates into daughters and sons not to be endowed with the mechanisms that enable them to effective do such screening on their own. Consequently, when parents move out of the picture, which is the case in the post-industrial context, the probability that children make erroneous choices augments considerably.

In a post-industrial context, technology advancements offer several means to prevent conception (e.g., the pill) and terminate unwanted pregnancies (e.g., abortion); there are effective ways to treat the majority of sexually transmitted diseases, while individual rights are well protected. Therefore, an erroneous mate choice may be corrected and so have a low negative impact on children and on their parents (n). Even so, such negative impact is far from zero: There are many sexually transmitted diseases which cannot be effectively treated, not everybody has access to abortion, which is not risk-free and can cause permanent damage (Atrash & Hogue, 1990), while, even if individual rights are well protected, people still abuse their partners and get away with it.

Moving on to the risk that a child faces to be unable to attract a mate (l), it is predicted by the personality traits of a child that negatively influence success in attracting a mate, and it is also inversely related to a child's mate value. In this context, as in all other contexts, we expect that many children will have levels of these traits which will make them vulnerable to staying single. In effect, the (l) is expected to be positive.

The (l) is expected to increase considerably also due to the mismatch between ancestral and modern conditions. More specifically, several mate choice mechanisms, which evolved in an ancestral context where mate choice was regulated, may

not be able to deal effectively with the demands of a free-choice context, resulting in the effective exclusion from the mating market (Apostolou, 2015). For instance, some people may exhibit very poor flirting skills, something which had limited effect in an ancestral context where their parents would find spouses for them, but it has a large negative mating success effect in a modern context where they have to find mates by themselves. I will explore this argument further in Chap. 11.

Overall, in the post-industrial setting, there is a considerable converging opportunity cost of free mate choice. As both diverging and converging opportunity costs are positive, we expect that parents would exercise a considerable influence on their children's mating behavior (m). Since parents in this context cannot impose their will directly on their children, parental control over mating would be exercised indirectly.

To begin with, Sussman (1953, p. 80) reported that parents employ means such as "cajolery, persuasion, appeals to loyalty, and threats" in order to influence their children's mating behavior. Another study found that modern Chinese parents in the USA attempt to create environments, such as staging a barbecue, in which their children can meet other individuals of Chinese descent and, therefore, of desirable background (Ikels, 1985). In a more comprehensive study of manipulation, I identified twelve tactics that parents employ on their children and four tactics that they employ on their children's mates (Apostolou, 2013a see also Apostolou & Papageorgi, 2014).

In more detail, when parents find their daughters and sons engaging in undesirable relationships, they attempt to undermine these relationships either by manipulating their children and/or by manipulating their children's mates in terminating the relationship. For example, in the former case, they advise their children against the relationship; they attempt to bribe them to dissolve the relationship, or they try to match them with different mates. In the latter case, they threaten their children's mates; they are rude to them or they try to find out things to use against them (Apostolou, 2013a). Parental manipulation can cause strain upon their children's relationship, effectively undermining it. Consistent with this prediction, one study found that manipulation of this kind can indeed be effective in weakening an undesirable relationship (Apostolou, Kasapi, & Arakliti, 2015).

Contingencies

Daughters Versus Sons

Since women constitute the scarce reproductive resource to which men seek access (Trivers, 1972), parents can potentially extract more benefits by controlling their daughters' than their sons' mate choices ($b_{daughters} > b_{sons}$). Moreover, in post-industrial societies, parents usually distribute their wealth evenly across their children, irrespective of their sex. Accordingly, daughters and sons face a similar risk of losing access to their parents' wealth if they disobey their wishes ($w_{daughters} = w_{sons}$).

In the same vein, because social protection systems do not discriminate between sexes, and in general, there is an overall equality between the sexes, both daughters and sons would be equally dependent on their parents' resources. It has to be said however that there is still an earnings' gap, with men earning more than women, while women frequently leave their jobs or work part-time in order to provide care for their young children (Blau & Kahn, 2007). These factors turn possibly dependent on their parents resources.

Such dependence can turn women more vulnerable to their parents' influence. Nevertheless, a woman may consider in advance that if she chooses someone her parents do not approve, she will have a hard time extracting resources from them later on when she will need them for raising her children (see also Apostolou & Zacharia, 2015). And her parents are likely to remind her of this need. In my study of manipulation tactics, parents tell their daughters to forget any support for them if they choose to marry a man they do not approve (Apostolou, 2013a). In sum, daughters are expected to be more dependent on their parents' resources than sons ($e_{daughters} > e_{sons}$); yet, this difference is unlikely to be substantial.

Overall, the diverging opportunity cost of free mate choice is higher for daughters than for sons ($o_{diverging\_daughters} > o_{diverging\_sons}$), but the difference is not expected to be considerable.

Moving on to the converging opportunity cost, women are physically weaker than men, which turns them more vulnerable to abuse from their partners. In addition, although in post-industrial societies there are effective ways to prevent or terminate unwanted pregnancies, such pregnancies remain a possibility. Furthermore, an abortion is not risk-free, and complications may compromise the capacity of a woman to conceive in the future (Atrash & Hogue, 1990). It needs also to be taken into consideration that religious believes may prevent several women from adopting contraceptive measures such the use of condom or the day after pill. In the same vein, in many countries, legislation may prevent women from terminating an unwelcomed pregnancy. In addition, men in post-industrial societies report a preference for chastity (Buss, 2003), indicating that erroneous mate choices can compromise women's mating success. Overall, erroneous mate choices can have more negative consequences for the fitness of daughters than for the fitness of sons ($n_{daughters} > n_{sons}$).

Moreover, because women constitute the scarce reproductive resource, they are the target of more intense mating effort, and thus, they face a higher risk of deception and assault by men who attempt to force access to their reproductive capacity so that ($k_{daughters} > k_{sons}$). Also, as discussed in the previous section, the mismatch between ancestral and modern conditions is likely to have augmented the (k) for both men and women. Nevertheless, because women were controlled more than men, it is likely this mismatch has a larger impact on them.

In particular, because daughters were controlled more than sons, there had been under weaker selection pressure to evolve mechanisms that would enable them to screen prospective spouses, which in turn translates into daughters being more prone to make erroneous choices when they are free to exercise mate choice. In addition, parents are expected to have evolved specific mechanisms that would

enable them to protect their daughters from any rape attempts, which in turn weakens the pressure for the daughters to have evolved such mechanisms (Apostolou, 2013b). That is to say, in ancestral human societies, daughters could have relied on the protection of their parents to avoid rape. In modern societies, where the parents are out of the picture, women may not be endowed with effective protection mechanisms, and thus, they may be more vulnerable to rape.

Because in ancestral human societies women had space to exercise choice, and because erroneous mate choices would have been more costly for them than for their parents, women are expected to have evolved mechanism that would prevent them from making such choices. Yet, my argument is that the mismatch between ancestral and modern conditions is likely to have affected daughters more than sons, because the former had been controlled more than the latter: Free mate choice prevailing in the post-industrial context constitutes a bigger mismatch for daughters than for sons.

Furthermore, women, by being the scarce reproductive resource, are less at risk of being unable to attract a mate than men ($l_{daughters} < l_{sons}$). Yet, the mismatch arising from a free mate context being larger for daughters than for sons is likely to reduce this difference. In particular, several women may lack the mechanisms that would enable them to attract long-term mates. It needs to be said however that the argument that the mismatch between ancestral and modern conditions is likely to affect daughters more than sons needs empirical investigation. On the basis of the results of such future research, additional adjustments to the model can be made.

Overall, as the (n) and the (k) are higher, but the (l) is lower for daughters than for sons, assuming equal contribution of each factor, the converging opportunity cost of free mate choice is higher for daughters than for sons ($o_{converging\_daughters} > o_{converging\_sons}$).

As it was discussed in the previous section, in a post-industrial context, the diverging opportunity cost is expected to be low, predominantly because parents cannot convert any extracted benefits to reproductive success, and because they have a limited capacity to inflict costs on their children in order to align them with their will. The main contributor to the opportunity cost of free mate choice should be then the converging opportunity cost. Since the converging opportunity cost is higher for daughters than for sons, parental control over mating is expected to be stronger over daughters than over sons ($m_{daughters} > m_{sons}$).

Accordingly, parents are predicted to be more interested in controlling the mate choice of their daughters than of their sons. As discussed in the last two chapters, the difference has been even more pronounced in a pre-industrial context where the converging opportunity cost is considerable and higher for daughters than for sons. The pre-industrial context is closer to the ancestral human condition (Apostolou, 2014), where it would be optimal for parents to exercise more control over their daughters than over their sons. Thus, parents are likely to have evolved such a disposition, which will be also present in a post-industrial context. As a consequence, mothers and fathers would exhibit a stronger concern about the mate choices of their daughters than it is justified by opportunity cost of free mate choice in the post-industrial context.

There are several studies which suggest that, in a post-industrial setting, parents are more concerned about the mating decision of their daughters than of their sons. In a comprehensive study, Perilloux, Fleischman, and Buss (2008) found that parents in the USA were more likely to control their daughters' sexual behavior and reported more emotional upset over daughters' sexual activity, and they controlled their daughters' mate choice more than their sons'. In a Greek-Cypriot sample, I examined the willingness of parents to apply 12 tactics of mate choice manipulation, separately on their daughters and sons (Apostolou & Papageorgi, 2014). I found that parents were more willing to apply manipulation for the purpose of influencing mate choice on their daughters than on their sons. In a related study, I asked Greek-Cypriot individuals to indicate how frequently they have perceived their parents to have attempted to use on them the 12 tactics of manipulation in order to influence their mating decisions. Female participants reported a significantly higher manipulation attempt by their parents than female participants (Apostolou & Papageorgi, 2014).

In a different study which employed Greek-Cypriot parents, participants indicated that that they were more interested in influencing the mate choices of their daughters than of their sons (Apostolou, 2011). Female participants indicated also a higher eagerness from their parents to influence their mate choices than male participants.

Mothers Versus Fathers

In a post-industrial setting, equality between sexes and protection of individual rights suggests that fathers do not have a higher capacity to inflict a cost on their children in order to align them with their will. In particular, fathers as well as mothers control wealth; however, there is still inequality with men controlling more wealth than women ($w_{fathers} > w_{mothers}$); yet, for the average case, this difference may not be considerable. Also, because children at marriage age are relatively independent from their parents, and they rely more for their protection on social institutions than on their family, the (e) is a relative insignificant factor. Similarly, because individual rights are well protected and children are married relatively old, fathers cannot use the advantage that they have over mothers to inflict a cost on their children through physical force (h). Also, although fathers are overrepresented in social institution, these cannot be employed to inflict a cost on children (i). Mothers, by being more effective manipulators than fathers, have a higher capacity to inflict a psychological manipulation cost on their children ($j_{fathers} < j_{mothers}$).

Paternal uncertainty translates also in the costs from making compromises in order to get benefits from traits ($c \times \overline{r}$) to be less for fathers than for mothers. Consequently, fathers can potentially gain more from a mating deal than mothers, as they are less constrained by the cost that it may have on their children. In the light of the fact that parents have a limited capacity to inflict costs to their children, this

difference is not of particular importance. We may also consider that technological advancements, such as DNA testing, reduce paternal uncertainty. Even so, the behavioral mechanisms of fathers evolved in a context where such technology was not available, so they may have evolved to behave as if they are uncertain about paternity. For instance, a father may discount more than a mother the cost that an action will have on his children, even if, following a DNA test, he is equally certain with the mother that his children are his own. Furthermore, when children marry, parents are old and effectively out of the mating marker; so, benefits from a marital alliance do not affect the direct reproductive success of fathers more than mothers ($f_{fathers} = f_{mothers}$). Another reason for this equality is that polygyny is not practiced in post-industrial societies.

In sum, in the post-industrial setting, the converging opportunity cost is low and roughly equal between fathers and mothers, as fathers can, for instance, inflict a higher cost on their children through manipulating their wealth and mothers through psychological manipulation.

Turning now to converging opportunity cost, if children make erroneous choices (k) or fail to attract a mate (l), mothers have potentially more to lose because they are more certain that their children are actually their own so that ($o_{converging\_fathers} < o_{converging\_mothers}$). Note that, as discussed above, even if modern technology eliminates paternal uncertainty, so that both parents would be equally certain that their children are their own, mothers would behave as they have less uncertainty than fathers. The reason is that technology that eliminates such uncertainty has emerged only recently, while the human mind has been shaped in a context where paternal and maternal uncertainty differed. Accordingly, because in this context we expect the converging opportunity cost to be higher than the diverging opportunity cost, and the former to be bigger for mothers than for fathers while the latter to be roughly equal between the two, the overall opportunity cost for mothers would be higher than the overall opportunity cost for fathers, which predicts that in a pre-industrial context, mothers would be more likely to attempt to control their children's mating decisions than fathers ($m_{fathers} > m_{mothers}$).

One study provided direct evidence in support of this hypothesis. In particular, I asked a sample of Greek-Cypriot parents to indicate their willingness to influence their children's mate choices (Apostolou, 2011). Mothers indicated a significantly higher willingness than fathers. In addition, participants were also asked to indicate whether their parents had or have been attempting to influence their mate choices. Participants reported that their mothers had or have been attempting to influence their mate choices more than their fathers. Moreover, in one study, I asked Greek-Cypriot parents to indicate their willingness to use 12 manipulation tactics in order to influence their children's mating decisions (Apostolou, 2013a). I found that for several tactics, mothers indicated a higher willingness than fathers. In a similar study, I asked Greek-Cypriot parents to rate their willingness to use these 12 tactics in order to influence the mate choices of their daughters and sons (Apostolou & Papageorgi, 2014). I found that mothers were more willing than fathers to use manipulation on daughters as well as on sons.

Other Sexual Selection Forces

Individual Choice

In the post-industrial setting, individuals are relative free to exercise mate choice, which means that individual choice constitutes the primary sexual selection force. The asymmetry in parental investment results in men competing more intensively to gain access to women, which places women in a position where they can exercise choice over whom they will grant such access. Thus, female choice is probably the stronger selection force in this context. Nevertheless, men in post-industrial societies control substantial wealth and divert a great part of what they control to their children. Given the considerable investment that fathers direct to their children, men constitute also an important reproductive resource over which women compete to gain access, which, in turn, gives to the former a considerable space to exercise choice. In effect, male choice constitutes a strong sexual selection force in the post-industrial setting.

Male-Male Competition

Post-industrial societies are relatively peaceful, although large-scale wars are not uncommon. The main motives of these wars are economic and not reproductive. Nevertheless, war rape is common (Stiglmayer, 1994), suggesting some reproductive gains for the winning party. Within a given society, it is not common for men to use force in order to monopolize access to women. One reason is that individual rights are well protected, so it is hard for men to exclude other men from gaining access to women by force and to force sex to women. Overall, male-male competition is expected to be a weak selection force in the post-industrial context.

Sexual Coercion

The sophisticated detection mechanisms allowed by technological development like DNA testing and fingerprint recognition turn a man who follows a forced-sex mating strategy more easily to be detected. The rule of law results further into men who are caught to pay heavy penalties, including spending several years in prison. Nevertheless, detection mechanisms are not perfect, so a rapist may not get detected, while the judicial system is also not perfect, so a rapist may escape conviction even if he is detected. In addition, many acts of sexual coercion are not reported because the victims want to avoid social stigma (Lalumiére, Harris, Quinsey, & Rice, 2005). Furthermore, the large size of post-industrial societies facilitates a man who follows such strategy to go undetected. Even if he is detected, he may suffer limited social

penalties as he can move to a different neighborhood or city where people do not know him. Accordingly, there is some space for sexual coercion to be exercised. For instance, to my knowledge there is not a single post-industrial society which is free from rape and acts of sexual coercion. Still, prevalence rates indicate that rape is rare; note however that these rates are not free from the bias of underreporting.

Analysis of Selection Pressures in a Post-industrial Society

Men

Female choice is the primary selection force exercised on men. Men need to appeal to women as short-term and long-term mates or else they risk being excluded from reproduction. This risk selects for adaptations that make men appealing as mates to women. Because parents have some influence in this context, there is some pressure on men to appeal to parents as in-laws, especially to mothers who are more willing to get involved in their daughters' mating decisions. Sexual coercion is present but not strong, and it can favor adaptations that make this strategy more effective. Finally, male-male competition is not a strong selection force exercised on men.

Women

Male choice is the primary sexual selection force exercised on women. Women have to appeal to men as short-term but especially as long-term mates. In particular, men have low mating standards when it comes to short-term mating (Buss, 2003), which translates into sexual selection forces being weak on female traits that would enable women to attract short-term mates. Still, men become much more selective when it comes to long-term mating (Buss, 2003), which mean that male choice is much stronger on female traits that enable a women to attract and retain a long-term mate. Women who lack these traits risk being excluded from the long-term mating market.

As parents have also some influence on mate choice, it is expected that there is some selection pressure on women to appeal to the parents of their mates as daughters-in-law. This is particularly the case for the mothers of their mates, who are more heavily involved in the mating decisions of their children. Finally, women can exclude other women from the mating market by spreading rumors about possible competitors. Women who are effective in doing so have an advantage over others, which means that female-female competition is a significant albeit weak sexual selection force exercise on women.

To conclude, post-industrial societies are characterized by strong individual mate choice, with parental choice being also present but a much weaker selection force. Sexual coercion and male-male and female-female competition are also present but weaker selection forces.

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Chapter 7
Sexual Selection Under Parental Choice Across Societies and Across Time

In the previous chapters, I examined how the model of parental choice predicts the strength of parental control over mating in different society types. In addition, the model makes specific predictions about how societies of different subsistence types differ between them with respect to the strength of parental choice. Accordingly, my first goal in this chapter is to examine whether these predictions hold. Furthermore, human evolution has been characterized by major transitions, which are associated with changes in the mode of subsistence; thus, my second goal is to examine how these predictions can be applied in understanding the way the strength of parental choice changed as a consequence of the major transitions. Finally, my third goal is to make inferences about the effects that the major evolutionary transitions had on adaptations involved in mating.

Sexual Selection Under Parental Choice Between Subsistence Types

Pre-industrial Societies Versus Post-industrial Societies

I will start my analysis by comparing post-industrial with pre-industrial societies, beginning with the diverging opportunity cost of free mate choice [$o_{diverging} = (b \times f - c \times \overline{r}) \times d$]. Post-industrial societies are more technologically advanced than pre-industrial ones, and they produce more resources ($a_{pre\text{-}industrial} < a_{post\text{-}industrial}$). Accordingly, parents, by controlling their children's mate choices, can gain more in the former than in the latter ($b_{pre\text{-}industrial} < b_{post\text{-}industrial}$).

In addition, children in post-industrial societies are married at an older age than children in pre-industrial ones, which means that their parents are also older and they have a lower reproductive capacity. Therefore, any potential gains from control over mating have a limited potential to be converted into additional offspring in

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post-industrial than in pre-industrial societies. This capacity is further reduced by the fact that polygyny is not allowed in the vast majority of post-industrial societies. This is not, however, the case in pre-industrial societies, where polygyny is usually allowed (Murdock, 1981; Zeitzen, 2008), and children are married young (Apostolou, 2014) and have relatively young parents who can convert benefits from a marriage deal into additional children. Therefore, ($f_{\text{pre-industrial}} > f_{\text{post-industrial}}$).

In terms of the capacity of parents to inflict a cost on their children for deviating from their will [$d = w + e + h + j + I - (q \times \bar{r})$], in post-industrial societies, parents control more wealth than in pre-industrial ones, which means that children have more to lose if they disobey their parents in the former than in the latter ($w_{\text{pre-industrial}} < w_{\text{post-industrial}}$).

On the other hand, technological orientation demands a long period of training before one is able to participate effectively in the labor market; thus, in post-industrial societies, children are married at a later age, when they are financially independent from their parents. In addition, the presence of social protection systems, such as the police, results into children being less dependent on their families for physical protection. In pre-industrial societies, however, children are married relatively young, since a long period of education or training is not required, and they are, as a consequence, more dependent on the resources of their parents (Apostolou, 2014). Also, because in these societies the social protection systems are not well-developed or they do not exist, children have to rely on their parents for physical protection. Accordingly, children are much more dependent on their parents' resources in pre-industrial than in post-industrial societies ($e_{\text{pre-industrial}} > e_{\text{post-industrial}}$).

In post-industrial societies, individual rights are well protected, and parents are prevented by the rule of law to use physical force on their children. But even if they were allowed to do so, such course of action would not be easy, since children are married at an older age when they are usually physically stronger than their parents. On the other hand, in pre-industrial societies, children are married younger, which means that their parents are also younger and thus better able to use physical force on them. In sum, the capacity of parents to apply physical force on their children is larger in pre-industrial than in post-industrial societies ($h_{\text{pre-industrial}} > h_{\text{post-industrial}}$).

In addition, in post-industrial societies, social institutions aim predominantly at protecting individual rights, and consequently, older generations cannot readily employ them to inflict costs on the younger generation. On the other hand, in pre-industrial societies, parents can more readily employ institutions, such as the church or the secular law, in order to impose their will. In effect, ($i_{\text{pre-industrial}} > i_{\text{post-industrial}}$). Overall, assuming an equal contribution of each factor, parents in pre-industrial societies have a higher capacity to inflict costs on their children in order to align them with their will than parents in post-industrial societies ($d_{\text{pre-industrial}} > d_{\text{post-industrial}}$). In sum, the diverging opportunity cost is lower in post-industrial than in pre-industrial societies ($o_{\text{diverging\_pre-industrial}} > o_{\text{diverging\_post-industrial}}$).

Turning now to the converging opportunity cost [$o_{\text{converging}} = [(k \times n) + l] \times \bar{r}$], in post-industrial societies, children are married at a later age, so they are more experienced, which means that they can make better choices; accordingly, ($k_{\text{pre-industrial}} >$

$k_{post\text{-}industrial}$). On the other hand, the mismatch between ancestral and modern conditions is likely to augment the chances that children make erroneous mate choices in post-industrial context (see previous chapter and Chap. 11), reducing in effect the magnitude of this inequality. In the same vein, the mismatch between ancestral and modern conditions is likely to turn children in post-industrial societies more prone to fail to attract long-term mates than children in pre-industrial societies so that ($l_{pre\text{-}industrial} < l_{post\text{-}industrial}$).

Furthermore, the widespread use of contraceptives and the after day pill, along with the effective treatment of most sexually transmitted diseases, turn erroneous mate choices in post-industrial societies less consequential ($n_{pre\text{-}industrial} > n_{post\text{-}industrial}$). In sum, the converging opportunity cost is expected to be lower in post-industrial contexts ($o_{converging\_pre\text{-}industrial} > o_{converging\_post\text{-}industrial}$), but with the difference being small.

Still, because it is expected to be a much bigger difference in terms of the diverging opportunity cost, which has the most weight in the overall opportunity cost of free mate choice, it is predicted that the opportunity cost of free mate choice is much higher in pre-industrial than in post-industrial societies ($o_{pre\text{-}industrial} > o_{post\text{-}industrial}$), which in turn predicts that parental control over mating is higher in pre-industrial societies than in post-industrial ones ($m_{pre\text{-}industrial} > m_{post\text{-}industrial}$).

Moving on to differences between parents, in pre-industrial societies, wealth is predominantly controlled by the male members of a society, while in post-industrial societies, it is more equally distributed across the sexes (Apostolou, 2014). Furthermore, men in pre-industrial societies are less constrained in employing their physical strength for controlling their children; thus, ($d_{fathers\_pre\text{-}industrial} > d_{fathers\_post\text{-}industrial}$) > ($d_{mothers\_pre\text{-}industrial} > d_{mothers\_post\text{-}industrial}$). Also, fathers can benefit more by a marriage arrangement (b) in a pre-industrial context as the extracted wealth goes under their control (e.g., the bridewealth; see Goody & Tambiah, 1973). In addition, pre-industrial societies are more aggressive than post-industrial ones (Pinker, 2011), and given that war and protection is predominantly the domain of men (Puts, 2010), children are more dependent on their male parents' protection in pre-industrial than in post-industrial societies ($e_{fathers\_pre\text{-}industrial} > e_{fathers\_post\text{-}industrial}$).

As discussed above, in pre-industrial societies, as opposed to post-industrial ones, polygyny is permitted and parents are relatively young when their children marry. Nevertheless, this pattern favors predominantly men who have a higher residual reproductive value and a higher reproductive variance than women. Accordingly, ($f_{fathers\_pre\text{-}industrial} > f_{fathers\_post\text{-}industrial}$) > ($f_{mothers\_pre\text{-}industrial} > f_{mothers\_post\text{-}industrial}$). Overall, the diverging opportunity cost for male parents is higher in pre-industrial than in post-industrial societies, which predicts that male parental influence is higher in the former than in the latter.

The diverging opportunity cost of free mate choice is likely to decrease dramatically in post-industrial societies, as parents can inflict little cost on their children to align them with their will, with the converging opportunity cost becoming the primary component of the overall opportunity cost. Nevertheless, due to paternal uncertainty, the converging opportunity cost is higher for mothers than for fathers ($o_{converging\_fathers\_post\text{-}industrial} < o_{converging\_mothers\_post\text{-}industrial}$); parental influence in post-industrial societies is expected to come predominantly from mothers.

In sum, it is predicted that parental control over mating is stronger in pre-industrial societies than in post-industrial ones and male parents to be more dominant in controlling mate choice in the former than in the latter.

Consistent with this prediction, in all post-industrial societies, marriage is typically based on free choice, but parents exercise an influence on their children's mate choices, primarily through manipulation. In particular, in one study I found that parents employed at least 12 different tactics to manipulate their children into accepting a desirable relationship or terminating an undesirable one (Apostolou, 2013a). They also employed at least four tactics on their children's partners in order to make them stay in the relationship if they considered them desirable, or to go away if they considered them undesirable (Apostolou, 2013a). In a further study, I found that mothers were more willing than fathers to use these tactics on their children (Apostolou & Papageorgi, 2014). In addition, mothers indicated a higher willingness to use manipulation than fathers. In another study, I found that mothers indicated a greater interest in influencing the mate choices of their children (Apostolou, 2011c).

I have also examined the effectiveness of manipulation tactics, by asking a sample of individuals to rate how likely each of these tactics would be on influencing their mate choices if they were used by their parents (Apostolou, Kasapi, & Arakliti, 2015). I found that, although they were effective, they were not that effective. Still, these findings are likely to be underestimates of the actual effectiveness of these tactics. One reason is that the findings are based on self-report data, and individuals may not be willing to admit that their parents can influence their mating behavior. Another reason is that they may not be able to accurately estimate the effectiveness of the manipulation tactics on their behavior. Effective manipulation is manipulation which is not perceived as such (Apostolou et al., 2015), so there is a good chance that parents manipulate their children without the latter being aware that they are manipulated, which, in turn, may lead to underreporting of manipulation effectiveness.

Available evidence is clear that parental influence is weaker in post-industrial societies than it is in pre-industrial societies, where parents are able to control mate choice directly. More specifically, in my study of 190 contemporary foraging societies, I found that the most common mode of long-term mating, in approximately 70% of the cases, was arranged marriage, where parents chose spouses for their children (Apostolou, 2007). In fewer than 5% of cases was the primary mode of marriage courtship, where children choose their own spouses with little input from their parents. In another study, where I employed data on mating patterns from the Standard Cross-Cultural Sample, which consists of 186 hunting and gathering as well as agropastoral societies, I found similar results; that is, arranged marriage was the most frequent form of long-term mating (Apostolou, 2010b). In both studies, marriage arrangements were dominated by fathers, with mothers having a weaker say in marital arrangements.

Hunting and Gathering Versus Agropastoral Societies

Agropastoral societies are more technologically advanced than hunting and gathering ones, and consequently, they produce more material wealth ($a_{agropastoral} > a_{foraging}$). Accordingly, individuals in the former are likely to have more wealth at their disposal than individuals in the latter. For instance, individuals in agropastoral societies are likely to own land, animals, food surpluses, and money. On the other hand, individuals in hunting and gathering societies are likely to own some artifacts, weapons, and household objects. This means that parents can gain more resources from controlling mate choice in agropastoral than in foraging societies ($b_{agropastoral} > b_{foraging}$).

In the same vein, parents are likely to control more wealth in agropastoral than in foraging societies, which means that children have more to lose if they disobey their parents in the former than in the latter societies ($w_{agropastoral} > w_{foraging}$). Furthermore, in hunting and gathering societies, individuals can rely on their own hunting and gathering effort in order to sustain themselves. In agropastoral societies, on the other hand, they need to rely predominantly on the cultivation of land or the herding of animals, which are owned by their parents. In effect, individuals are more dependent on their parents' resources in the former than in the latter societies ($e_{agropastoral} > e_{foraging}$).

Agropastoral are larger than foraging societies, as they produce more resources that allow the maintenance of bigger populations, and they are more complex, as there is a higher degree of specialization. These differences give rise to powerful social institutions, such as the law and the church, that can make the functioning of these societies possible. For example, a sophisticated legal system and a refined theological dogma are only found in agropastoral societies (Apostolou, 2013b). As discussed in previous chapters, these social institutions are controlled by the older generation, who has shaped them in such a way so as to regulate mate choice. Thus, parents can impose a higher cost on their children in agropastoral societies through manipulating social institutions ($i_{agropastoral} > i_{foraging}$). In sum, parents can inflict a higher cost on their children in agropastoral than in foraging societies ($d_{agropastoral} > d_{foraging}$), which means that the diverging opportunity cost of free mate choice is higher in the former than in the latter societies ($o_{diverging\_agropastoral} > o_{diverging\_foraging}$), predicting, in turn, a stronger control over mating in the former than in the latter ($m_{agropastoral} > m_{foraging}$).

Due to intersexual competition, men usually monopolize resources (Buss, 2003); so, when more resources are available, men have control over more of them. Accordingly, in agropastoral societies which produce more wealth, children have more to lose if they disobey their fathers than their mothers, in the former than in the latter [($w_{fathers\_agropastoral} > w_{fathers\_foraging}$) > ($w_{mothers\_agropastoral} > w_{mothers\_foraging}$)]. In addition, more resources increase the incentive of others to monopolize them, which means that there is a higher need to defend the family unit and its members. In effect, children are more dependent on their male parents' protection in agropastoral than in foraging societies ($e_{fathers\_agropastoral} > e_{fathers\_foraging}$).

The higher amount of produced resources results further in greater emphasis to be placed on military preparation, which is the realm of men (Apostolou, 2010b; Puts, 2010). As a consequence, more sophisticated and lethal weapons are produced to make defense of resources more effective and/or to get more effectively the resources of other groups. To these weapons, men usually have an exclusive access, which amplifies their ability to impose their will on their children by force ($h_{fathers\_agropastoral} > h_{fathers\_foraging}$). Finally, social institutions are controlled predominantly by older men, and since these institutions are more likely to be present in agropastoral than in foraging societies (Apstolou, 2013b), the male parents' capacity to use them for inflicting cost on their children is higher in the former than in the latter case ($i_{fathers\_agropastoral} > i_{fathers\_foraging}$).

Overall, fathers have a greater capacity to inflict a cost to their children in agropastoral than in foraging societies ($d_{fathers\_agropastoral} > d_{fathers\_foraging}$), which means that the diverging opportunity cost of free mate choice is higher for them in the former than in the latter societies ($o_{diverging\_fathers\_agropastoral} > o_{diverging\_fathers\_foraging}$). On this basis, it is predicted that male parental control over mating is stronger in agropastoral than in foraging societies.

Furthermore, in comparison to foraging societies, in agropastoral societies inheritance rights are more likely to favor male children (Apostolou, 2011a). Thus, sons have more to lose if they disobey their parents in the former than in the latter societies (d). Furthermore, male children are more dependent on their parent's resources in order to procreate (e). More specifically, bridewealth is much more prevalent in agropastoral societies than in hunting and gathering ones (Apostolou, 2010a). The bridewealth involves substantial resources, which are usually paid by the parents of the groom. If the parents disagree with their son's mate choice, they may refuse to pay the bridewealth, preventing him to proceed with the marriage. In effect, parents, and particularly male parents, can inflict a higher cost on their male children in agropastoral than in hunting and gathering societies, which increases the diverging opportunity cost of free mate choice for sons.

However, because men control more resources in agropastoral societies, and they play a more vital role in the defense of resources, they have the capacity to contribute more parental investment to their children. Accordingly, parents can potentially extract more benefits by controlling their sons' mate choices in agropastoral than in hunting and gathering societies ($b_{sons\_agropastoral} > b_{sons\_foraging}$). Consequently, the opportunity cost of male offspring's free mate choice is higher in agropastoral than in foraging societies ($o_{sons\_agropastoral} > o_{sons\_foraging}$), which predicts that parental control over mating is strongest over male offspring in agropastoral than in foraging societies.

The predictions of the model are consistent with the anthropological record. In particular, based on evidence from a cross-cultural sample, in one study I compared the patterns of mating between societies which base their subsistence on hunting and gathering and the ones which base their subsistence on agriculture and animal husbandry (Apostolou, 2010b). This sample contained both agropastoral and foraging societies, enabling comparisons between the two. The analysis indicated that parental choice was more dominant in agropastoral than in foraging societies, as

arranged marriage was more frequently found in the former than in the latter. Furthermore, in agricultural and pastoral societies, male parents and relatives had more decision-making power over marriage arrangements than female ones. Actually, there was not even a single case reported where female relatives dominated marriage arrangements. In addition, increased parental control came predominantly from controlling the mate choices of sons, as marriage was more frequently arranged for sons in agropastoral than in foraging societies.

Parasite Load

Another possible difference between the agropastoral and hunting and gathering societies is the parasite load. Agropastoral societies, in comparison to foraging societies, are larger and sedentary and have domesticated animals. These factors are likely to increase their parasite load. This being the case, good genetic quality would be valued more in agropastoral than in foraging societies. As a consequence, the parent-daughter conflict over good genetic quality would be higher in the former than in the latter (see Chap. 2). This difference can potentially increase the opportunity cost of free mate choice for daughters in agropastoral societies, giving an additional incentive to parents to control them. This hypothesis needs to be examined further by future research.

The Evolutionary Trajectory

The genus *Homo* appeared on earth approximately two million years ago, and for most of this period, our ancestors lived in small bands of hunters and gatherers (Lee & Devore, 1968); therefore, the greatest part of human evolution took place in this context (Tooby & Cosmides, 1990). About 10,000 years ago, the agropastoral revolution took place, and most of our ancestors shifted to a non-nomadic life and a mode of subsistence based on agriculture and the herding of animals (Price, 2000). Human societies were to be transformed once more with the industrial revolution, which began in the eighteenth-century Britain (Baten, 2016).

The model of parental choice can be employed in generating predictions about the strength of sexual selection in each period of human evolution: Starting with the former and the longest one, where our ancestors lived as hunters and gathers, we expect that parental choice would had been a strong sexual selection force, with individual mate choice, and male-male competition had been also strong selection forces. Sexual coercion would also have been present, as a weaker selection force. We lack direct information on ancestral hunter and gatherer mating patterns to enable us to test these predictions, as these societies did not leave behind any written records pertaining to the first and the longer period of human evolution. Even so, we have a good source of information, namely, contemporary hunters and gatherers whose mating patterns have been studied by anthropologists. The mating patterns

typically found in these societies are likely to be characteristic of the hunter-gatherer way of life and, consequently, are likely to be similar to those in ancestral hunter-gatherer societies (Apostolou, 2014; Ember, 1978).

Anthropological evidence indicates that the typical patterns in foraging societies are consistent with the above predictions about the strengths of different sexual selection forces (Chap. 4). Phylogenetic analysis, which attempts to reconstruct the conditions prevailing in ancestral societies, has provided additional evidence that the patterns of mating found across contemporary hunters and gatherers (e.g., arranged marriage) were also prevalent in ancestral ones (Walker, Hill, Flinn, & Ellsworth, 2011). Accordingly, there are good reasons to believe that during the foraging period of human evolution, parental choice had been a significant sexual selection force.

About 10,000 years ago, a different period of human evolution begun as our ancestors started shifting from a mode of subsistence based on hunting and gathering to a mode of subsistence based on agriculture and the herding of animals (Price, 2000). The model of parental choice predicts that this shift would have resulted in the considerable strengthening of parental choice, and especially of male parental choice, and in the weakening of individual choice.

Male-male competition is likely to have been strengthened as well. More specifically, the transition from hunting and gathering to agropastoralism has resulted in more wealth to be produced. More wealth gives rise to a stronger incentive in individuals within the society and to individuals and groups outside the society to monopolize it. Also, this transition has resulted into societies becoming sedentary. As a consequence, in a given region, different groups would compete for the same resources, which is not the case in a foraging context where a group could just move on to a different place, instead of staying in one to compete with other groups. These factors would predict that the transition to agropastoralism has resulted in more frequent conflicts, wars, and raids.

As we lack historical evidence about ancestral foraging societies, we cannot make comparisons between ancestral foraging and ancestral agropastoral societies. We can make comparisons, however, between contemporary hunting and gathering societies and agropastoral societies that can be revealing about the effects of the ancestral transition. Consistent with the predictions of the model, in comparison to foraging societies, in agropastoral societies, parental choice, mainly male parental choice, is stronger, and male children experience considerable loses to their freedom to exercise mate choice (Apostolou, 2010b). This prediction is also consistent with evidence from historical agropastoral societies, where male parental choice dominates and where both male and female offspring have a very limited space to exercise mate choice freely (Apostolou, 2012). Furthermore, comparisons between agropastoral and foraging societies indicate that warfare and conflict are more prevalent in the former than in the latter (Ember & Ember, 1997) which suggests a strengthening in male-male competition following the agropastoral revolution.

The model predicts that the transition to industrialism that started about 300 years ago would have resulted in considerable decline in the strengthening in parental choice, a considerable strengthening in individual mate choice, and a considerable weakening in male-male competition. It also predicts that mothers would exercise a

stronger influence on their children's mating decisions than fathers (see above). Consistent with these predictions, in modern post-industrial societies, mate choice is freely exercised, individual rights are well protected, and large-scale wars are relatively rare (Pinker, 2011). Parental choice is exercised predominantly through manipulation, with mothers being more involved than fathers in their children's mate choices (Apostolou, 2014).

With respect to sexual coercion, the exact factors that predict it, as well as its interrelations with other selection forces, are not yet known, so at this stage, it is difficult to generate hypothesis about how it has changed across major transitions. As discussed in previous chapters, in each major stage of human evolution, there are factors which strengthen it and factors that weaken it. For instance, in foraging societies there is strong social control but not well developed social institutions to protect individuals. In agropastoral societies, larger size weakens detection and social control, but well-developed institutions such as the church can turn a forced-mating strategy costly. In post-industrial societies, the very large population sizes reduce substantially the social control exercised and the chances to be detected, but the well-developed social institutions punish such behavior severely and also increase detection chances by using advanced technology. Accordingly, one reasonable hypothesis is that, across all the major stages of human evolution, there would be a small but significant niche for sexual coercion. This niche is likely to have changed in size following major transitions, but probably not substantially. Future work on sexual coercion can enable the generation of more refined hypotheses.

Overall, on the basis of the theoretical framework developed in this book and the available evidence, we can reach the following conclusions: During the earliest and longer period of human evolution, where our ancestors lived as hunters and gatherers, parental choice had been a strong sexual selection force. The transition to a mode of subsistence based on agropastoralism has increased considerably the strength of this force, while the transition to industrialism in the eighteenth century has resulted in a sharp decline of this force. Individual mate choice had been a strong sexual selection force, but probably weaker than parental choice during the foraging stage; it experienced a decline during the agropastoral revolution and a sharp increase during the industrial and post-industrial period. Male-male competition had been a significant sexual selection force in both the foraging and the agropastoral stages, albeit weaker than parental and individual choice, and experienced a sharp decline in post-industrial context. Sexual coercion had been present as a weak but significant sexual selection force, in all stages of human evolution.

The Effects of the Major Transitions on Adaptations Involved in Mate Choice

The anthropological and historical records allow us to make valid inferences about the relative strengths of individual sexual selection forces in different periods of human evolution and how these have been affected by the major transitions. In turn,

these insights can be used in order to speculate about the effects that these transitions have had on adaptations related to mating.

Parental Choice

To begin with, the transition from a social organization, where subsistence was based on hunting and gathering to a social organization which was based on agriculture and animal husbandry, would strengthen positive selection on traits that make an individual more appealing as an in-law. This would be particularly so for traits which promote an individual's appeal to other males. The reason is that this transition would have resulted in stronger male parental control over mating, and a reduction in the space individuals had to exercise choice. Accordingly, it is expected that adaptations such as young men being interested in displaying their abilities to other men would become more widespread and would change in significance, in the sense that men would attribute more importance in being appreciated by other men. In the same vein, because fathers and other male relatives would get more decision power over marriage arrangements, stronger selection pressures would be exercised on men to be able to screen other men on the basis of their abilities. Thus, it is expected that mechanisms which contribute to this capacity would be positively affected by the transition to agropastoralism. For instance, we expect that men's interest for the capacities of other men would strengthen.

The transition to post-industrialism has resulted in a deregulation of mate choice, which, in turn, has translated into selection pressures on adaptations that turn individuals appealing as in-laws to have weakened considerably. Accordingly, over generations we expect that such adaptations will become less pronounced.

Individual Mate Choice

The transition to agropastoralism would have weakened considerably the space that individuals had to exercise mate choice, resulting into substantial weakening of positive selection pressures on traits that make an individual appealing as a mate to the opposite sex: Some adaptations would become less pronounced, others would exhibit considerable variation due to weak selection pressures, while other adaptations, which have been predominantly evolved to appeal to prospective mates, would be modified to work on making individuals appealing to parents as prospective in-laws.

This pattern would be reversed following the transition to post-industrialism: Traits that turn an individual appealing to opposite sex partners would experience strong positive selection pressure. This pressure would result in these traits to become more pronounced, the variation they exhibit to decrease, while adaptations

that enabled individuals to appeal to parents may be modified to enable them to appeal to prospective mates.

Male-Male Competition

The transition to agropastoralism has enlarged the male-male competition reproductive niche. As a consequence, there would be stronger positive selection pressure on traits that enable a man to exploit it, such as a stronger muscles and aggression. This trend would be reversed with the industrial revolution, where male-male reproductive niche has been reduced considerably. As a consequence, such adaptations (e.g., aggression) are likely to experience negative selection and become less pronounced.

Sexual Coercion

At this stage it is difficult to say if this selection force has exhibited considerable change in strength as a consequence of major transitions. One possibility is that it has remained relative the same—that is to say, across time, there has been a small niche for men who follow a forced-sex mating strategy to be successful. If this is the case, the major evolutionary transitions are likely to have had little effect on the adaptations involved in sexual coercion.

Honest Signaling and the Major Evolutionary Transitions

Many of the traits which are desired by mate- and in-law-seekers, including the ability to provide resources, good health, and physical capacities, are to a considerable degree, not readily observable; that is to say, one cannot tell between two individuals, just by looking at them, who has say a better resource provision capacity. In addition, because the reproductive stakes are high, individuals have a strong incentive to lie about their capacities. As consequence, there is a need for reliable communication to take place between individuals with respect to their unobserved abilities. In turn, this need gives rise to honest signaling which enables individuals to make their unobserved capacities observable to other interested parties in a reliable cheat-proof manner (Zahavi & Zahavi, 1997). Accordingly, specific adaptations are expected to have evolved that motivate individuals to produce honest signals of their capacities and to be sensitive to the honest signals of others. In this way, individuals can distinguish themselves from others of inferior capacities, but also to distinguish between individuals those who have superior capacities.

The signaling produced will be contingent on the signaling needs of the context individuals occupy: In a context where population is small, there are plenty of opportunities for the abilities of an individual to become observable, while people know each other well, there is limited need for honest signaling. This translates into such adaptations not arising at all, or be adjusted by selection forces to divert limited resources in producing honest signaling. Nevertheless, in a context where the population is relatively large, there are not so many opportunities for individuals' abilities to be revealed, and people do not know each other well, so there would be strong selection pressures for such adaptations to arise, or if they are present to become more pronounced.

In the same vein, such adaptations are adjusted to the prevailing niches. For instance, if the parental choice niche becomes larger, there would be a higher need for honest signaling to be diverted from mate-seekers to parents. Thus, individuals would tend to demonstrate their abilities to parents, and selection forces would favor adaptations which enable individuals to do so effectively. These arguments suggest that the major evolutionary transitions, by affecting the strengths of the different sexual selection forces, have had an effect on the amount and kind of honest signaling produced.

More specifically, based on the knowledge of contemporary hunting and gathering societies, it can be inferred that ancestral hunting and gathering societies were small-sized and individuals knew each other relative well. In addition, survival was demanding and there were ample opportunities, such as hunting expeditions, for the abilities of individuals to be revealed. Consequently, there was limited need for honest signaling. The transition to agropastoralism, however, increased considerably the need for exchanging reliable information. In particular, this transition has resulted in larger population sizes, which translated into people not knowing each other well. In addition, the increase in technological development has increased specialization, which means that individuals did specialized jobs which required specific capacities. In turn, their full range of capacities could not be revealed by their job performance.

In sum, the transition to agropastoralism has resulted in a considerable increase in the need for honest signaling. It has also resulted in an increase in the strengthening of parental choice, especially of male parental choice, and in the weakening of individual mate choice. Therefore, the parental choice niche, and especially its male parental choice sub-niche, has expanded considerably. As women were controlled more, parental choice was usually exercised over men, who were then in higher need to produce honest signaling. Overall, the transition to agropastoralism has resulted in a considerable increase in the need for honest signaling, especially between men.

In effect, the agropastoral revolution would have resulted in social structures, which enable the exchange of honest signaling information, to become more refined, important, and numerous. It would also have also motivated the development of new social structures that served this function to emerge. One example of such structures is athletic competitions. It has been argued that sports have evolved to enable the exchange of unobserved physical abilities of individuals (Miller, 2000; Zahavi &

Zahavi, 1997). This being the case, it is expected that the agropastoral revolution should have been accompanied by the emergence of refined, elaborated, large-scale athletic competitions which would predominantly involve the exchange of reliable information between younger, those who looked for mates, and older men, those who looked for sons-in-law.

This prediction appears to be consistent with historical evidence, with the best example of such athletic competitions is the Olympic goals in ancient Greece. The Olympic Games had a great significance for ancient Greeks: Any conflict or war between city-states would stop, and athletes from all over Greece would gather to Olympia in Peloponnesus to compete in the games. Winners in the games enjoyed a substantial status increase in their homeland and all over Greece. The Olympic Games was also a business between men: The athletes were young men and the audience was composed of men of all ages, while women were strictly prohibited from competing and watching the games (Finley & Pleket, 2005).

The emergence of well-refined athletic competitions in ancestral agropastoral societies is also related to the strengthening of male-male competition. Young men would have an interest to signal their physical capacities to other men through sports, so as to be proffered as fighting allies and be avoided as enemies. Men would also benefit from observing such competitions by gaining information that would enable them to make better decision on who to approach as a fighting ally and who to avoid as an enemy (Lombardo, 2012).

Another institution which is predicted to have become more common and important in order to meet the signaling needs is the bridewealth. The agropastoral revolution would enable parents to exercise a stronger control over their daughters, but they would find themselves in a situation where they would have to choose sons-in-law with good resource provision capacity, between men for whom they had little information. One solution to this problem is to ask prospective in-laws to pay a considerable amount of wealth to them so as to allow the marriage to proceed. Since only men with high resource acquisition capacity would be able to gather the wealth necessary, the payment of the bridewealth would signal that a man has good resource provision capacity (Apostolou, 2010a). The practice of bridewealth is much more common in agropastoral than in hunting and gathering societies (Apostolou, 2010a), which suggests that it would become more frequently practiced following the agropastoral revolution.

The industrial revolution and the transition to post-industrialism have resulted in a considerable decrease in the strength of parental choice and male-male competition and a substantial increase in individual mate choice. This change has shifted the need to transfer reliable information to parents to transfer reliable information to prospective mates. The signaling needs would be also higher as the transition to post-industrialism is accompanied by a considerable population increase, which means the most people are unknown to each other. Given that men compete more intensively between them for access to the opposite sex, they would be the ones who would tend to generate honest signals of unobserved abilities. Most post-industrial societies are capitalistic, with one key characteristic of capitalism being to provide individuals with what they want.

Accordingly, the transition to post-industrialism was accompanied by the mass production of signaling goods, including expensive cars, watches, etc. For instance, a watch costing 10,000 euros does not tell the time better than a watch costing 100 euros, but it tells others that its owner can afford to spend 9900 more euros in something that does not provide additional utility value (see also Miller, 2010).

The Emergence of the Beauty Industry

Mating is extremely important for one's fitness, and much of social and economic life revolves around it. Thus, the major evolutionary transitions, by affecting mating patterns, would have also affected other socioeconomic aspects. In particular, parents place lower weight on beauty in an in-law than their children in a mate (Chap. 2), which indicates that the industrial revolution and the transition to post-industrialism, which made free mate choice the norm, have turned beauty to be a much more valuable commodity in the mating market that it has been before (Apostolou, 2011b). To put it another way, the transition to post-industrialism augmented substantially the individual mate choice niche, shrinking at the same time the parental choice niche. As opposed to addressing the parental choice niche, addressing the individual mate choice niche requires paying attention to one's looks as this is a trait which is valued considerably in a prospective mate.

Furthermore, mate-seekers, apart from attracting long-term mates, they are also interested in attracting short-term ones (Buss, 2003). On the other hand, parents are only interested in finding long-term mates for their daughters and sons, so when they control mate choice, they suppress the short-term mating strategies of their children (Apostolou, 2009). Consequently, in ancestral pre-industrial societies, where mate choice is regulated, the short-term individual mate choice niche is rather small, i.e., there are few individuals who look and find short-term mates. The transition to post-industrialism, and the resulting decrease in parental influence over mating, relaxed the parental constraint in following a short-term mating strategy; in turn, more people would look for casual mates, increasing the size of short-term reproductive niche. When individuals engage in casual mating, they weight beauty considerably more than when they look for a long-term mate (Buss, 2003). Accordingly, addressing the short-term reproductive niche requires paying considerable attention to one's looks.

Last but not least, the transition to post-industrialism brought a considerable improvement in the welfare of individuals. In post-industrial societies, food is plenty and inexpensive, while most individuals have access to health and welfare services. Social protection institutions such as the police provide protection to most individuals living in these societies. As a consequence, people in a post-industrial context care less about the traits that predict resource provision and protection than people in a pre-industrial context. Accordingly, they would be willing to compromise less on traits such as good looks in order to get more of traits that predict provision of resources and physical protection. In different words, such a change had an

effect on the individual mate choice reproductive niche, turning good looks to be a more important commodity.

Overall, the transition to post-industrialism increased considerably the value of good looks in the mating market. In turn, this change would place individuals under pressure to improve their looks, and so they would demand beauty products and services. Post-industrialism increased the surplus wealth individuals have, and they can allocate to improving their looks. The strong demand for improving looks along with the capacity to finance it indicates that there is profit to be made in helping individuals to improve their appearance, and the profit incentive gave rise to a huge beauty industry, producing beauty products (e.g., cosmetics) and services (e.g., beauty salons, plastic surgery). Thus, the rise of the beauty industry can be partially traced to the weakening of parental choice.

In sum, in this chapter I have examined how the model of parental choice predicts that this selection force would vary across societies of different subsistence types. I demonstrated that the predictions are consistent with the anthropological evidence. I employed this evidence in order to make predictions about how parental choice and the other sexual selection forces would have been affected by the major evolutionary transitions and what would be the effect of these transitions on the adaptations involved in mate choice. In the next chapter, I am going to examine how the strength of parental choice varies between societies of the same subsistence type and within individual societies.

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Chapter 8
Variation in the Strength of Parental Choice Within and Between Societies of the Same Subsistence Type

The previous chapters examined how the model of parental choice accounts for the variation in parental control over mating and consequently of the strength of parental choice as a sexual selection force among societies of different subsistence types. Nevertheless, the model predicts also that the strength of parental control varies among and within societies of the same subsistence type. In addition, it predicts that the strength of parental control varies across the lifespan of an individual. The purpose of this chapter is to examine these predictions.

Variation Among Societies of the Same Subsistence Type

Societies of the same subsistence type are likely to differ in the factors that predict the opportunity cost of free mate choice, $o = [(b \times f - c \times \bar{r}) \times d] + \{[(k \times n) + l] \times \bar{r}\}$, where $d = (w + e + h + j + i) - (q \times \bar{r})$, and consequently the degree of parental control over mating. To begin with, not all societies of the same subsistence type are equally wealthy. For instance, in Classical Greece, the Athenians were much more wealthy that the Spartans, although subsistence in both city-states was based on agriculture and animal husbandry (Powell, 2001). As a consequence, there was more to gain (b) from controlling mate choice in Athens than in Sparta. Furthermore, since parents also controlled more resources (w) in the former than in the latter, children had more to lose if they disobeyed their parents in Athens than in Sparta.

In addition, there is variation in children's dependence on their parents' resources (e) among societies of the same subsistence type. If we take the !Kung (Howell, 2000) and the Yanomamo (Chagnon, 2013) as an example, although both base their subsistence on hunting and gathering, the former are much less aggressive than the latter. In turn, high aggression level is expected to increase children's dependence on their parents for protection (e).

Furthermore, societies of the same subsistence type may differ in their social institutions which may have an important effect on the opportunity cost of free mate

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choice. For example, the rule of law is much stronger in the USA than it is in India. Consequently, parents are more constrained in using force on their children in the former than in the latter (h). In the same vein, in Scandinavian countries, there is a highly developed social protection system, but this is not the case in south European countries (Kvist, Fritzell, Hvinden, & Kangas, 2012). In effect, children are more dependent on their parents' resources (e) in the latter than in the former.

The difference in social institutions among societies of the same subsistence type is going to affect the impact of an erroneous mate choice on a child (n). For instance, the Byzantium was a theocracy, with the Orthodox Church exercising strong control over mating behavior (Laiou, 1993). In Rome however, sexuality was much less strictly regulated by social institutions (Rawson, 1991). Consequently, an act such as engaging in a sexual relationship that does not lead to marriage would have a higher negative impact on the individual in the former than in the latter society. For instance, in Byzantium the loss of virginity prior to getting married would compromise the capacity of a daughter to enter in any marriage, but this would not be the case in Rome. Accordingly, the converging opportunity cost ($o_{converging}$) had been higher in the Byzantium than in Rome, which means that parents would be more concerned about controlling mating in the former than in the latter.

Furthermore, although many agropastoral societies practice the bridewealth, several practice dowry instead (Goody & Tambiah, 1973). In the institution of bridewealth, a man has to pay a considerable amount of resources to his prospective parents-in-law for the marriage to proceed. In order to concentrate these resources, he needs to rely considerably on his father who controls the family's resources. On the other hand, in dowry cultures, the parents of the bride, particularly the father that controls the family's wealth, need to give a considerable amount of resources to their prospective son-in-law for the marriage to proceed (Goody & Tambiah, 1973). Accordingly, in agropastoral societies which practice bridewealth, a son is more dependent on his father for securing a wife than in agropastoral societies that practice dowry ($e_{son\_bridewealth} > e_{son\_dowry}$), which means that ceteris paribus, fathers can exercise more control over their sons in the former than in the latter societies. In the same vein, ceteris paribus, fathers would have more control over their daughters in dowry societies than in bridewealth societies, because in the former daughters cannot proceed with marriage unless their fathers pay for their dowry.

Overall, societies of the same subsistence type are likely to differ in the factors predicting the opportunity cost of free mate choice which, in turn, results in the strength of parental control over mating to vary among them. An analysis of why these differences exist is beyond the scope of this chapter. One possible reason is, however, that differences among societies do not depend only on the subsistence type. For instance, some of these differences are exogenous and stochastic. To use one example, when the British placed Australia under their control, they started imposing their social institutions on the local foraging tribes. As a consequence, parents' capacity to use physical force on their children was compromised by the imposition of the British rule of law (e.g., the Tiwi see Hart, Pilling, & Goodale, 1988). Accordingly, part of the variation in parental control among foraging societies

can be accounted by random exogenous factors such as the influence of one's neighbors.

Apart from stochastic factors, different factors, such as the political and the financial system, may be able to explain the differences in sexual selection forces among societies of the same subsistence type. For instance, the differences in the political and the financial system between Sparta and Athens can probably explain why the latter was much wealthier than the former, which, in turn, may explain why children may lose more in terms of wealth if they disobey their parents in Athens than in Sparta. This is not the end of the story, however, since it needs to be explained why the two societies differ in the political and financial systems in the first place. The reasons are partially stochastic and partially environmental. For instance, with respect to the latter, the Spartans occupied a mountainous area in Peloponnesus with no access to the sea, while the Athenians had such access through the port of Piraeus, which was a major hub of ancestral trade roots. This environmental difference is also a reason that may have caused different dynamics, making different social and political systems more likely to be adopted in each society, which, in turn, may have affected the strength of parental choice between the two societies.

The differences in factors other than subsistence among societies of the same subsistence type may account for differences in the strength of parental choice as well as the way parental influence over mating is exercised. That is to say, the strength of parental choice may be the same between two societies of the same subsistence type, but may be exercised in a different way. Going back to the example of Sparta and Athens, the former is more militaristic but less wealthy than the latter. In each society, parents may have exercised a similarly strong control over mating; in Sparta, however, they may have done so predominantly via force and, in Athens, through manipulating wealth.

Such qualitative differences are also relevant for sexual selection. In both Sparta and Athens, parents exercised considerable influence over their children's mate choice. In general, when parents exercise in-law choice, they are likely to value traits differently in a prospective in-law, depending on the specificities of their cultural setting. For instance, parents in Athens would value wealth and resource acquisition capacity in a prospective son-in-law more than parents in Sparta, while parents in Sparta would value fighting capacity in a prospective son-in-law more than parents in Athens. These differences may have had an effect on the underlying adaptations which address the parental choice reproductive niche. To put it differently, the parental choice reproductive niches in Athens and in Sparta may have been of similar size, but may have been qualitatively different. Accordingly, adaptations may require different optimizations for efficiently exploiting each one. Thus, the two populations may differ in their adaptations which have evolved through parental choice.

In sum, the factors that predict the strength of parental choice are likely to differ not only among societies of different subsistence types but also among societies of the same subsistence type. As a consequence, a variation exists in the strength of parental choice among societies of the same subsistence type.

Variation Within Societies

Variation in the strength of parental control over mating exists not only among societies of different subsistence types and among societies of the same subsistence type but also within societies. One of the reasons is that the factors that affect the opportunity cost of free mate choice vary not only among societies but also among families within a society. That is to say, the opportunity cost of free mate choice is higher for some families and lower for others, which means that some families will exercise more control over the mate choices of their children than others.

Variation Among Families

Families differ in the amount of resources they control, which affects the opportunity cost of free mate choice in several ways. Well-off families can make marriage deals with other well-off families, and so they can extract more resources and, thus, gain more benefits (b) from a marriage deal than less well-off families. Also, wealthy families can inflict more cost on their children by controlling more resources (w), such as money, influence, and protection, that their children risk losing if they disobey their parents. In addition, well-off families are likely to have more access and control over social institutions, and thus, they can inflict a higher cost to their children through these institutions (i).

Furthermore, well-off families have more resources they can divert to their children, who, in turn, can divert to their own children. Therefore, ceteris paribus, the children of wealthy families are likely to inherit more wealth and receive more support than the children of less well-off families that translates into the former having a higher mate value (v) than the latter. In turn, well-off parents can derive a higher benefit from controlling mate choice and thus experience a higher opportunity cost if they do not ($o_{diverging}$), than not so well-off parents. A similar argument can be made for high-status versus low-status families.

Overall, the opportunity cost of free mate choice is higher for the more well-off families, which predicts that parental control over mating, and thus, sexual selection under parental choice would be stronger in the upper strata than in the lower strata. Anecdotal evidence is consistent with this prediction (Goode, 1982). Also, in one study I found that the more wealth parents reported to possess, the stronger interest they exhibited in controlling their children's mate choices (Apostolou, 2011b). Furthermore, since part of the variation among families in the opportunity cost of free mate choice is accounted by the difference in the wealth they control, there should be less variation in parental control over mating between families in societies, where wealth more equally distributed, than in societies, where it is more unequally distributed.

Note further that the disparity in wealth among families will also affect the converging opportunity cost ($o_{converging}$). In particular, due to their higher mate value,

children of well-off families will attract more unsuitable suitors. That is to say, many suitors are likely to target parents' wealth instead of having a genuine interest in forming an intimate relationship with their children. Thus, the (k) component of the converging opportunity cost is expected to be higher for children of well-off families than for children of not so well-off families. On the other hand, because of their higher mate value, children coming from well-off families will find it less likely to stay single than children of less well-off families, meaning that the (l) component of the converging opportunity cost will be lower for well-off parents and higher for not so well-off parents. On this basis, it can be predicted that well-off parents will worry more about their children making erroneous choices and will divert more effort in guarding their children. On the other hand, less well-off parents will worry less about their children making erroneous choices and more about their children failing to get a mate. Thus, they may try to get a more active role in either enhancing their children's mate value or finding mates for them themselves.

Families differ also in their ability to inflict physical force on their children in order to align them with their will (h). One reason is that families differ in the number and age of male members belonging to the older generations. For instance, in one family the father may be absent or very old, and no other close male relative might be around, while in another family, the father may be present and relatively young and uncles and grandfathers may also be around. As a consequence, the former family has a higher capacity to inflict physical cost on children than the latter family.

Furthermore, families with older parents exercise less control on their children than families with younger parents, since the former are less likely to convert gains from controlling mating into additional children (f). Nevertheless, older parents are likely to have more resources under their control and a stronger say in social institutions that can compensate for the reduction in the opportunity cost from lower (h) and (f). It can be predicted, nevertheless, that if we consider two families of equal wealth and social influence, more control will be exercised over children in the family where parents are younger.

It has to be said also that in a given society, families will vary, not only in the degree of control they exercise over their members' mate choices but also on how they exercise this control. For instance, wealthy families will tend to employ their wealth in order to control their children. They may attempt, for example, to blackmail their children out of an undesirable relationship, saying that they will disinherit them if they do not comply with their wishes (w). There is an elevated probability that children will comply with their parents' wishes because they have much to lose if they do not. On the other hand, poor families that have limited material resources but have, for instance, physically fit older men cannot achieve much in terms of controlling mate choice by manipulating wealth, as younger family members do not have much to lose if they disobey their parents. They may have to resort then to using physical force on their children (h).

In sum, families differ in the factors that predict the opportunity cost of free mate choice, and consequently they differ in the degree of control they exercise over their children's mating decisions. Families differ also in the way they impose their

control, because they differ in the means they have in their disposal that enable them to do so.

Variation Within Families

The model of parental choice predicts that there is variation in the control exercised within the family, with the primary difference being that more control is exercised over female than male children, the reason being that the opportunity cost of free mate choice is higher for female than male children (Chap. 3). Yet, the opportunity cost varies also among children of the same sex. In particular, same sex children are likely to differ in their physical strength, which will affect the degree of control their parents can impose on them. For instance, one son may be physically stronger than the other, which means that parents will be more successful in controlling the mate choices of the latter than of the former through the use of physical force (h). Also, children of the same sex may differ in how dependent they are on their parents' resources (e). For example, in a foraging context, a daughter who is a skillful gatherer is likely to be more difficult to control than a daughter who is younger and less experienced gatherer and thus more dependent on her family.

Other traits, such as personality and intelligence, can also affect the dependence of children on their parents' resources. For instance, a hardworking daughter may be less dependent on her family's resources than a lazy one. In addition, personality traits can affect how resistant children are to their parents' psychological manipulation (j). For example, children who are low in agreeableness may be more resistant to psychological manipulation than children who are high in agreeableness. Furthermore, such traits will affect how children can protect themselves from making unwise mate choices. For example, an extroverted daughter may place herself more frequently in danger, increasing in effect the chances of making a non-optimal mate choice (k) and consequently the converging opportunity cost of free mate choice ($o_{converging}$).

The arguments above suggest further that parents may adjust the means they use in order to influence mate choice on the basis of the particularities of their children. Accordingly, they can use their wealth for manipulating a child who cares more about wealth; yet, for another child who is not so interested in wealth but is emotionally more sensitive, they may employ psychological manipulation instead (Apostolou, 2013).

Children vary also in their mate value, which predicts the opportunity cost of free mate choice. For example, if parents have two daughters and one of them is attractive but the other is not, they will divert more effort in controlling the former than the latter. This is because they can extract more benefits for themselves (b) by controlling the reproductive resource with the highest mate value (v). Similarly, the high mate value daughter will be the target of more intense mating effort and will be more likely to become a victim of sexual assault (k), increasing in effect the converging opportunity cost of free mate choice ($o_{converging}$). In this case, however,

parents will be motivated to guard her closely, but they will not be particularly concerned that she may stay single.

Note that in a scenario where the daughter is not just of high mate value but of very high mate value, the benefits her parents can extract by controlling her mate choices will not be much, the reason being that she can attract a man of high mate value herself (see Chap. 2). Nonetheless, parents are still expected to maintain a strong interest in controlling her mate choices, which arises from the high (k): The very high mate value daughter will face a high risk of sexual assault and deception, which will motivate parents to exercise a strong control over her in order to protect her.

The model also predicts differentiation in parental control over mating in the case a child is adopted and not genetically related to parents (i.e., $\bar{r} = 0$) (Apostolou, 2014a). In this scenario, parents are less constrained in inflicting a cost on their adopted children in order to align them with their will and in making costly compromises in mate choice so as to benefit themselves. In effect, the diverging opportunity cost ($o_{diverging}$) is going to be considerable, as parents can get benefits with minimum costs. On the other hand, the converging opportunity cost ($o_{converging}$) tends toward zero, as the genetic interests of parents are not compromised by their adopted children making a wrong mate choice and/or staying single. Thus, in such a scenario, parents may exercise considerable control over the adopted child, predominantly with the purpose of extracting benefits for themselves, and not for protecting the child or ensuring that it will find a mate (Apostolou, 2014a).

This argument predicts further that, in a context where parents can derive substantial benefits from regulating mating, they will be likely to exercise considerable control on their adopted children's mate choices, inflicting substantial cost to them (e.g., marrying a stepdaughter to a much older man) in order to derive benefits for themselves (e.g., get a considerable bridewealth), while they will be likely to make less costly compromises in mate choices for their genetic children. On the other hand, in a context where parents can derive few benefits from regulating mate choice, they may demonstrate a very low interest in their stepchildren's mate choices and a much higher interest in the mate choices of their genetic children.

Parents differ in the factors which predict the strength and the way they exercise control over mate choice. The way mothers and fathers differ has been examined in Chap. 3, where it was argued, for instance, that fathers are physically stronger than mothers, so they are more likely to employ physical force (h) in order to make their children comply with their wishes. Mothers, on the other hand, are better in manipulation, and accordingly, they are more likely to attempt to impose their will by using psychological manipulation (j). In pre-industrial societies, fathers usually have more to lose from the free mate choices of their children, so they exercise more control over them than mothers, a pattern which is reversed in post-industrial societies.

Moreover, parents of the same sex differ in the qualities that predict the opportunity cost of free mate choice, which indicates that they differ also in the strength and the type of influence they exercise over their children. For instance, a father may not be physically fit, but may control considerable wealth, so he will prefer to use his

wealth (w) to influence his children's mating decisions. Another father may be physically fit, but may control limited resources, so he would use physical force (h) instead of wealth to influence his children's mate choices. In the same vein, a mother may have inherited considerable wealth and may be very good in applying psychological manipulation, while another mother may not share these qualities. The opportunity cost of free mate choice is higher for the former than for the latter mother, since she can control her children's mating decisions more effectively, so she would exercise more control than her.

In sum, children and parents differ in the factors that affect the opportunity cost of free mate choice, which explains the variation in control over mating within a family. These factors also change over the lifespan of an individual, which predict variation in parental control over mating over this lifespan. I am going to examine this variation next.

Variation Across an Individual's Lifespan

Children

The strength of parental control over mating is expected to vary across an individual's lifespan. More specifically, when individuals enter puberty, their parents are more likely to control their mating behavior. The reason is that young individuals are more dependent on their parents for subsistence and protection (e), and their parents who are relatively young and thus physically fit can apply physical force on their children in order to impose their will (h). Accordingly, the cost that parents can inflict on their children to align them with their will (d) is considerable at this age, resulting in a high diverging opportunity cost ($o_{diverging}$).

Furthermore, following puberty, as women age, their mate value declines because they approach menopause, which decreases the diverging opportunity cost of free mate choice (unless their mate values are very high in the first place—in this scenario, when they get older and their mate value declines, the diverging opportunity cost increases, and subsequently, when their mate value keeps declining, the opportunity cost declines as well; see Chap. 2). On the other hand, following puberty, as men age, their mate value increases, as they accumulate wealth and social status, but eventually it starts declining as they come near the end of their lifespan. Consequently, following puberty, the diverging opportunity cost for sons is relatively low but, in an increasing trajectory, and starts to decline after a certain age. Thus, ceteris paribus, the interest of parents in controlling their daughter's mating decisions will be strong following puberty, but it will start declining as she ages. For a son, their interest will be relatively low following puberty, but it increases as he gets older, up to a certain age, and then it declines.

Moving on to the converging opportunity cost, the risk children face to make mistakes when they exercise mate choice, which their parents are less likely to make

if they exercise choice for them (k), is reversely related to experience ($k = ex^{-1} + pe + int^{-1} + v$): As people age, they tend to acquire more life experience, which reduces the (k). In addition, as sexually mature women get older, their mate value declines, so they tend to be less at risk of becoming the target of intense mating effort decreasing in effect the (k).

Nevertheless, as children age and their mate value decreases, the risk of not finding a mate ($l = s + v^{-1}$) increases. Sons face also such a risk as they age, but this risk increases less sharply than in the case for daughters. Yet, the contribution of the (k) to the converging opportunity cost of free mate choice declines sharply after an unmated daughter reaches menopause. The reason is that, even if the daughter finds a mate, doing so will make little contribution to her own and her parents' fitness, as children cannot be born out of this relationship. The (k) will remain, however, a significant contributor because, if a daughter finds a mate who can contribute to the survival effort of the family unit, her inclusive fitness, and therefore the fitness of her parents, will increase.

Overall, for both daughters and sons, the converging opportunity cost will be high following puberty, and it will remain high in later life as long as they remain single or have partners with poor prospects. In later life, however, the opportunity cost of free mate choice will be higher for unmated daughters than for unmated sons. Following menopause, this difference will reverse, with the opportunity cost for daughters declining sharply, while for sons declining less sharply, exceeding in effect that of daughters.

The variation of converging opportunity cost with children's age affects parental motivation to influence mate choice. More specifically, starting with daughters, when they are young, their parents would worry that they are not experienced enough, that they are prone to make erroneous mate choices, and that they may become the target for sexual assault and deception. Such concern will decline as daughters are getting older, but parents will then start to worry about their daughters not being able to attract a mate (assuming that they have not attracted one already). If they pass the age of menopause and they are still single, parents will lose interest in their daughters finding mates, because even if they do, these relationships will not lead to grandchildren. Similarly, parents will be concerned about their young sons making erroneous mate choices. As their sons age, this concern will be reduced, but after they reach a certain age and are single, parents will become concerned that their sons are not able to find a mate. As men to do not experience menopause, parents will still hope that their unmated sons will enter in a relationship and give them grandchildren, even if the latter have reached an advanced age.

We can conclude that the diverging cost of free mate choice will tend to decline with children's age, while the converging opportunity cost will experience qualitative change as children age. How diverging and converging opportunity costs are affected by age differs, however, for daughters and sons.

This variation has implications on the selection pressures exercised on the adaptations affected by parental choice. In this respect, mechanisms which have evolved to regulate in-law and mate choice are likely to have evolved to operate accordingly

to age. For instance, parental interest in children's mate choices would be stronger for children when the latter are young, but will start declining as children are getting older. Also, parents undervalue beauty in an in-law, which may lead children to overvalue beauty in a mate in order to pressure their parents to find more good-looking in-laws (Apostolou, 2014b). That is to say, if parents know that their children have a strong taste for beauty, they will be less willing to compromise on this trait in a prospective in-law, because doing so would increase the probability of the marriage to fail. But they would be less willing to do so if they knew that their children's taste for beauty was not that strong. In this respect, it would make sense for individuals to have a stronger taste for beauty when young and when their parents are more likely to control their mating decisions, and a weaker preference in older age, where they are more likely to make choices on their own.

Thus, the preference for beauty is expected to have been optimized by selection forces to reside with age. This effect has been found in different studies (Apostolou, 2008a, 2008b, 2011a), but it has to be said that what was discussed above may not be the only reason behind it. For instance, as people are getting older and accumulate more life experience, they may come to realize that beauty is something that will go away soon, or that it is not as important as other traits, so they place less emphasis on it.

We can approach this argument the other way as well. For example, family background is more valuable to parents, and so it pays for them to prefer it more than their children. This is likely to lead to conflict with their children, but this conflict is balanced by the benefits of a good alliance. However, when sexually mature children are getting older, and the opportunity cost of free mate choice resides, it would be more optimal for parents to converge their preferences with the preferences of their children. Otherwise, parents would overreact to the decisions of their children without being able to do much to change it, resulting in unjustified conflict. At this stage, such predictions are speculative, and future research efforts need to examine them.

Parents

As parents get older, their capacity to convert the benefits they can extract from influencing their children's mate choices (b) into direct reproduction (f) declines. In addition, their physical strength declines, and so does their capacity to inflict a cost to their children in order to align them with their will through using physical force (h). These factors reduce the converging opportunity cost of free mate choice as parents get older which decreases their incentive to control mate choice. On the other hand, as parents age, they accumulate more wealth and they can threaten to stop diverting this wealth to their children in order to align them with their will (w). They also gain higher rankings in social institutions which augments their capacity to inflict a cost to their children through them (i). These factors act to increase the diverging opportunity cost of free mate choice as parents get older.

This analysis does not allow us to make a clear prediction about whether the converging opportunity cost increases or decreases with parents' age, since the weights for each factor of the converging opportunity cost are not known. In addition, the level of impact of age on each factor is also not known. Yet, I would think that age, at least in the pre-industrial context, has a bigger impact on the (f) and the (h) than on the (w) and the (i). If this is the case, then the converging opportunity cost would decline as parents are getting older.

Finally, note that the opportunity cost of free-mate choice applies predominantly to unmated children. If for instance, parents have only one daughter for whom they have managed to arrange a successful marriage, the opportunity cost of free mate choice for her declines sharply, and so does her parents' interest in influencing her mating behavior. As parents are getting older, it becomes more likely that their children are married, which is another factor that is likely to decrease parental interest in controlling mating.

It also needs to be said that the opportunity cost of free mate choice does not become zero when a child marries. One reason is that a child can exercise mate choice within marriage, either by divorcing a spouse or by engaging in extramarital relationships. Such choice can undermine a marriage that parents have arranged. Furthermore, spouses may turn out to be abusive, infertile or unfaithful, and thus harmful to the fitness of the child and its parents. Last but not least, the marriage may not be the outcome of parental choice but of individual mate choice, and consequently, it may pay for parents to undermine it. These factors suggest the presence of a significant opportunity cost in children making mating decisions on their own following marriage. In turn, this cost predicts that parents would maintain a strong interest in their married children's mating behavior.

Mate-Seekers

The strength of all sexual selection forces exercised on individuals, including parental choice, weaken with age because people become more likely to have solved the problem of finding a mate as they get older. This is less the case for men though, especially in a pre-industrial context. Since men remain fertile even in late adulthood, it pays for them to continue their mating effort in older age. Thus, the strength of sexual selection exercised on mate-seekers declines with age, but the decline is less steep for men than for women.

Accordingly, adaptions, which have been sexually selected to address the different reproductive niches, are expected to be more pronounced in younger sexually matured individuals and less pronounced in older and in sexually immature ones. Sexual desire constitutes an example of an adaptation that has been selected to enable an individual to address all reproductive niches. Sexual desire motivates individuals to engage in behaviors that would enable them to address the different reproductive niches. It is inactive before sexual maturity; it turns on with sexual

maturity, reaches a peak, and starts declining with age, with this decline being much sharper for women than for men.

Moreover, men usually look for young women who have a high mate value, which means that both young and old men look for young women. But young women are controlled more by their parents than older ones, so both young and old men looking for mates have to pass through parental choice. That is to say, parental choice is strong on both older and younger men. On the other hand, parental choice is stronger on younger and weaker on older women. Older women are freer from their parents to exercise mate choice, while younger women are more dependent on their parents, and thus, their fate partially depends on how they appeal to other parents who look for spouses for their sons. On this basis, it can be predicted that traits involved in exploiting the parental choice niche would remain pronounced in older age, especially for men.

When parents exercise choice, they focus on the prospective spouses for their children as well as on their parents. In a way, the strength of parental choice is divided between individuals and their parents; for instance, even if individuals do not do very well in certain traits, these shortcomings can be compensated by their parents doing well in other traits. For example, a daughter's poor looks can be compensated by her parents' high social status. When individuals are older, however, their parents may not be present due to death, which indicates that the burden of mate choice falls predominantly on them. For instance, if individuals are not doing well in some traits, their parents cannot compensate for these shortcomings as they are not there.

The selection pressure coming from male-male competition is expected to decline fast with age. One reason is that it relates to physical abilities that decline as people get older. For instance, it may not pay for older men to fight younger men, as they are likely to lose. In addition, male-male competition is risky, and it pays more for younger men who do not have families to fight than men who have. The latter have already solved the problem of reproduction, so they have less to gain than the former who have not solved this problem. In effect, certain adaptations that enable men to effectively address the male-male competition reproductive niche may become less pronounced with age; for example, aggression will decline with age with older men being less aggressive than younger ones.

In an ancestral context, individual mate choice may be strong in adulthood, as individuals are getting married and decide whether they will remain married to each other or be looking for partners outside marriage, at the same time parental choice and male-male competition decline. The strength of individual mate choice declines less sharply for men as they keep seeking young women who are controlled by their parents.

To put everything together, in a pre-industrial context and most likely during human evolutionary time, we expect that sexual selection would be very weak on individuals before sexual maturity, it would strengthen considerably when individuals reach sexual maturity, and it would peak in the years following sexual maturity and would start declining afterward. The decline would be sharper for women than for men. With respect to the constituent forces of sexual selection, parental choice

would be stronger in the years following sexual maturity, it would decline after it, and the decline would be sharper for women than for men. Individual mate choice would be weaker than parental choice in younger age, but it would become stronger in later years. Male-male competition would be strong when entering puberty and some years after it, but it would then decline sharply. Following sexual maturity, sexual coercion would arise as selection force, but it would remain relatively weak throughout men's reproductive years.

Overall, in the pre-industrial context, a man who enters puberty needs to appeal predominantly to parents in order to get a wife and subsequently to appeal to his wife in order to keep her. When addressing parents, he also needs to appeal to their daughter, who has an influence on them with respect to her marriage. As he gets older and wants to have additional wives, he also needs to appeal to parents, who now focus more on him, as his parents are likely to be dead. He needs further to appeal to his newly acquired wives in order to keep them. As he is likely to have many children, his interest in mating declines, and the focus is shifted toward raising his children. When his children reach sexual maturity, he needs to appeal as a prospective in-law to other parents so that they would be willing to forge a marriage alliance with him and his family. On the other hand, a woman who enters puberty needs to appeal to parents as a daughter-in-law and as a wife to men who are not controlled by parents. She then needs to appeal to her husband in order to keep him and to extramarital lovers in order to get good genes and other benefits. When her children reach sexual maturity, she needs to appeal to other parents as good in-law to ally with.

To conclude, in this chapter I have argued that the factors that predict the strength of parental control over mating vary among societies of the same subsistence type, among families within a society, among individuals, and within individuals at different life stages. As a consequence, the strength of parental choice varies among societies of the same subsistence type, among families within a society, among individuals within families, and within individuals as they age. In the next chapter, I am going to explore in-law preferences which drive sexual selection in the parental choice reproductive niche.

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Chapter 9
In-Law Preferences: What Parents Want in a Prospective Daughter- and Son-In-Law

Sexual selection under parental choice arises when parents are in a position to exercise or influence their children's mate choices: parental influence over mating gives rise to the parental choice reproductive niche, and for individuals to address it, they need to appeal to parents who decide about granting reproductive access to their children. As a consequence, traits which make an individual more appealing to parents as an in-law experience positive selection. Nevertheless, in order to understand which traits are likely to have been favored by parental choice, we need to know first what parents want in a prospective daughter- and son-in-law. Accordingly, in this chapter, I will attempt to summarize and synthesize the findings of studies on in-law preferences.

The Structure of In-Law Preferences

When parents are able to control or influence their children's mate choices, they are effectively in a position where they can exercise in-law choice. In turn, they face the evolutionary problem of screening prospective daughters- and sons-in-law for fitness-increasing traits, which exercises selection pressure for well-refined in-law preferences to arise. To put it differently, alleles which give rise to preferences that enable parents to choose as in-laws the most fitness-increasing individuals are selected over alleles which do not do so or are less effective in doing so: parents endowed with the former alleles are more likely to have as in-law individuals who have traits that make a positive contribution to their fitness than parents who have the latter alleles.

In this respect, in-law preferences are sexually selected mechanisms that enable parents to increase their fitness by either augmenting their own or their genetic relatives' capacity to gain access to the opposite sex. For instance, by preferring a son-in-law who is wealthy and can provide a large bridewealth, a father can gain resources that he could use to get an additional wife for himself. By preferring a daughter-in-

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law who is chaste, a mother increases the chances that her son does not raise another man's children. By preferring sons- and daughters-in-law who come from high-status families, fathers and mothers can enhance their own and their genetic relatives' social standing, which in turn can enable them to attract higher mate value mates.

In order to be able to identify the structure of in-law preferences, that is, the domains over which in-law choice is exercised, all the traits that parents consider desirable in a prospective in-law need to be identified first and subsequently to be classified into broader preference categories. Accordingly, my first step was to administer an open-ended questionnaire to a sample of Greek-Cypriot families (Apostolou, 2011a). The parents in the sample were asked to indicate the traits that they considered desirable in a spouse for their children, while the children in the sample were asked to indicate the traits that they considered desirable in a spouse for themselves. The analysis of participants' answers revealed 86 distinct traits which were considered desirable in an in-law and in a spouse.

In order to make this list more inclusive, I added 2 additional traits that have been identified by ethnographic research, namely, "wealthy family background" and "from a family of similar social status," reaching a total of 88 traits. In order to identify the structure of the in-law preferences, I employed an extensive sample of 1717 Greek-Cypriot parents who were asked to rate how desirable they would consider each of the 88 traits in a prospective spouse for their children (Apostolou, 2015b). By applying principal component analysis, these traits were classified in ten broader preference categories, namely, "kind, understanding, and cooperative," "good looks," "spontaneous and selfless," "good cook-housekeeper," "well-off family background," "similar religious and ethnic background," "reliable and tolerant," "family oriented," "good economic prospects," and "exciting personality."

In the "kind, understanding, and cooperative" factor, apart from "kindness" and "understanding," the traits "patient," "cooperative," "reasonable," "down to earth," and "good manners" loaded as well, suggesting that parents wanted as an in-law someone who is kind and understanding and with whom they can cooperate with. In the "good looks" factor, the traits that loaded were "thin," "nice body," "good looking," "athletic," beautiful eyes," "tall," and "charming." In the "spontaneous and selfless" factor, the traits that loaded were "selfless," "spontaneous," "sensitive," "longsighted," "imaginative," "extrovert," "modest," "strong personality," and "open-minded." In the "good cook-housekeeper" factor, the traits that loaded were "good cook," "good housekeeper," and "tidy."

Moving on, in the "well-off family background" factor, the traits that loaded were "from a wealthy family"; "from wealthy," "good social status"; and "from a family of similar social status." The last trait indicated that parents had also a preference for finding an in-law coming from a family of a social status similar to their own. In the "similar religious and ethnic background" factor, the traits that loaded were the "same nationality," "religion," "religious" "similar political beliefs," and "good family background." In the "reliable and tolerant" factor, the traits that loaded were "tolerant," "serious," "calm," "reliable," "determined," "respectful," "ambitious," "generous," "good communication," and "polite." This factor clearly indicates that parents look for in-laws with whom they can work and deal with effectively.

In the "family oriented" factor, several traits loaded, including "loves my daughter/son," "loves children," "good father/mother," "loves his/her family," "wants children," "moral," "trustful," "honest," "faithful," "good character," "healthy," "sincere," "emotionally stable," "stable," and "family oriented." Here, parents were interested in finding an in-law who is family material, that is, he has the willingness and the capacity to have a family with their children. In the "good economic prospects" factor, the traits that loaded were "financially independent," "good provider," "good economic prospects," "educated," "industrious," "dynamic," and "intelligent." Finally, in the "exciting personality" factor, the traits that loaded were "cheerful," "good sense of humor," "sociable," "romantic," "entertaining," "exciting," "pleasant personality," and "easygoing."

I was also interested in examining whether the structure of in-law preferences is different for sons- and daughters-in-law. Toward this end, I asked a sample of 621 Greek-Cypriot parents to indicate how desirable they considered each of the 88 traits separately in a prospective son-in-law and in a prospective daughter-in-law (Apostolou, 2014a). Principal component analysis was applied separately on the answers that individuals gave for a daughter- and for a son-in-law. The produced factor structure was similar for a son-in-law and a daughter-in-law and similar to the factor structure produced in the study where there was no distinction between in-laws (i.e., Apostolou, 2015b).

One noteworthy difference was the emergence of an additional factor, namely, "chastity" in which only one trait loaded, namely, "few sexual experiences before marriage." This finding suggested that one of the reasons why chastity did not come as a separate factor in the Apostolou's (2015b) study was that it did not extract factors separately for a daughter- and a son-in-law. That is to say, since this factor is mainly relevant to a daughter-in-law, it did not appear when parents rated traits in an in-law in general. Accordingly, I consider chastity to be an important and distinct domain of in-law preference.

Overall, research indicates that in a post-industrial context, parents are interested in the personality of their prospective in-laws (kind and understanding, exciting personality, reliable and tolerant, pleasant personality), their family background (well-off family background, similar religious and ethnic background), their economic prospects (good economic prospects), their looks (good looks), whether they have the capacity to have a family (family oriented), their housekeeping abilities (good cook-housekeeper), and their sexual conduct (chastity).

In-Law Preferences in a Pre-industrial Context

The research on in-law preferences discussed above has been conducted in a post-industrial context which is considerably different from the pre-industrial context where most of human evolution took place. Assuming that in-law preferences have been shaped predominantly in ancestral pre-industrial societies, the factor structure found in post-industrial ones would be similar to the factor structure in a pre-industrial societies. Even so, it is important to examine in-law preferences in a pre-industrial context.

Toward this end, I conducted a study that was based on 148 societies, where parents had a considerable involvement in mate choice, taken from the Standard Cross-Cultural Sample (Apostolou, 2010). On the basis of the anthropological material available for these studies, I coded for the traits that anthropologists reported that parents value in a prospective spouse for their children. Identification of in-law preferences was possible for the 67 societies in the sample.

The analysis identified 13 desirable traits, namely, "good character," "good family background," "good worker," "industrious," "favorable social status," "good economic prospects," "wealthy," "similar family social status," "good heredity," "wealthy family background," "healthy," "good looking," and "chastity." The evidence produced by this study is informative on what parents value in a prospective spouse for their children in a pre-industrial context. It needs to be said that one major strength of this study was that it measured actual preferences recorded by anthropologists rather than answers to hypothetical questions.

Combining the results of this study with the results of the studies in post-industrial context, we can get a more complete picture of what parents want in a prospective daughter- and son-in-law. In particular, parents are interested in the personality of their prospective in-laws (good character), their family background (good family background, similar family social status, wealthy family background, favorable social status, wealthy), their economic prospects (good economic prospects, good worker, industrious, favorable social status, wealthy), their looks (good looking), whether they have the capacity to have a family (good heredity, healthy), and their sexual conduct (chastity). Note that I have placed the "favorable social status" and the "wealthy" in both economic prospects and family background, as they are relevant to both domains.

One difference was that in the pre-industrial context, the interest in housekeeping abilities did not emerge. A possible reason may be that this preference integrates to the "good worker" dimension. That is to say, because in pre-industrial societies housekeeping is almost exclusively the task of women (Whyte, 1978), when parents talk about a daughter-in-law who is a good worker, one of the dimensions they are referring to is being a good housekeeper. Another difference is that in pre-industrial societies, as opposed to post-industrial societies, there are no references to similarity in religious background and in nationality. This is because the majority of pre-industrial societies are homogenous in terms of these dimensions. Parents have a general preference for similarity (see below), and the way it is manifested depends on local conditions. In post-industrial societies, where there is variation in religion and ethnic origin, parents express a preference for similarity in these dimensions; in societies where there is no such variation, they do not.

Similarity

The studies on in-law preferences discussed above indicate that parents were also interested in similarity: across post-industrial and pre-industrial societies, we find traits such as "similar religious and ethnic background" and "similar family social

status." In addition, parents expressed a strong interest for good family background, with statistical analysis indicating that part of what parent considered being good family background was similarity in the family backgrounds. In particular, in my two studies of in-law preferences, I applied principal component analysis which indicated that the trait "good family background" loads in the "similar religious and ethnic background" factor (Apostolou, 2014a, 2015b).

In a different study, I took the 11 dimensions found in Apostolou (2014a), and I asked Greek-Cypriot parents to rate how they scored in these dimensions and how they would like their prospective daughters- and sons-in-law to score in these dimensions (Apostolou & Papageorgi, 2014). Subsequently, I correlated the scores that participants gave for each dimension for themselves with the scores that they gave for their prospective in-laws. Almost all correlations came positive and significant. The strength of the correlations ranged from strong to weak, with the majority being moderate to strong. The strongest correlations were over "religious and ethnic background," with personality dimensions such as "pleasant personality" to receive also high scores.

In order to investigate further which aspects of similarity in family background parents value more, I conducted several interviews with Greek-Cypriot parents, and I asked them to identify and discuss the various dimensions of the family background that they were interested in the families of their prospective daughter- and son-in-laws to be similar to their own family (Apostolou, 2014d). I identified nine dimensions of similarity, namely, same religion, same ethnicity, same values, same cultural background, same educational level, same social status, same interests, same financial condition, and same political views.

Subsequently, I asked parents to rate the importance of each of these dimensions, and by applying principal component analysis, I classified these nine dimensions in two main domains of interest. In the first domain, the "same religion," and the "same ethnicity" loaded, while the rest loaded in the second domain. Participants' scores indicated that parents ascribed more importance to the first domain (i.e., same religion and ethnicity) than to the second domain (Apostolou, 2014d). Overall, it appears that parents care predominantly about two aspects of similarity in the family background of a prospective in-law, namely, ethnic and religious background and socioeconomic and cultural background, which are composed of nine different dimensions of similarity.

In sum, parents across societies place considerable emphasis on similarity in the family background of a prospective in-law. One reason is that parents use marriage as a way to forge fitness-increasing alliances with other families, and similarity can enable more effective cooperation between the families and promote stability. Another reason is that a preference for similarity can enable parents to seek marital alliances which can be more easily forged. For instance, it would not be optimal for parents to allocate their marital alliance effort in finding sons- and daughters-in-law who come from families of say social standing much higher to their own, as such families would prefer to ally with families of similar or higher and not of lower to their own social standing.

The Hierarchy and the Contingencies of In-Law Preferences

In-law preferences vary in strength because traits in a prospective in-law have differential fitness benefits. More specifically, different traits make different contributions to the fitness of parents, so parents ascribe different weights on how much they value them—i.e., some traits are preferred more than others (Apostolou, 2007a). In addition, several traits provide different benefits depending on whether they are found in a daughter- and in a son-in-law. Accordingly, parents would ascribe different weights to these traits in a daughter- and in a son-in-law (Apostolou, 2014c). Finally, certain traits are likely to make different contributions to the fitness of mothers than to the fitness of fathers, so mothers and fathers ascribe different weights to them (Apostolou, 2014b, 2015a). In the following sections, I am going to discuss the empirical evidence on these contingencies.

In-Law Preferences in Hunting and Gathering Societies

In my study of mating patterns in foraging societies, I estimated how frequently each in-law preference was reported (Apostolou, 2007b). This frequency could be considered as an indicator of the importance ascribed to these traits, since it can be argued that traits which are considered more important are more likely to be reported. I found that the most frequently reported trait was to be a good hunter, followed by being hardworking, being a good provider, and coming from a good family. For a daughter-in-law, the most frequent trait was to be hardworking and to come from a good family. This study focused however predominantly on examining the type of marriage, and it did not provide a comprehensive account of in-law preferences.

In my study of 67 pre-industrial societies, which was specifically designed to investigate in-law preferences, the most frequently reported trait in the hunting and gathering societies was "industrious" followed by "good worker," "good character," "good economic prospects," "good family background," "favorable social status," "chastity," "wealth," "wealthy family background," "good looks," and "healthy" (Apostolou, 2010).

These findings suggest that, in a foraging context, parents are predominantly interested in the resource-generating capacities of a prospective in-law, their character, and their family background. Hunting and gathering societies generate few resources, and there is limited accumulation of wealth. Accordingly, it is not surprising that the focus is on the capacity of prospective in-laws to generate resources and not on the resources they actually control, as these are unlikely to be substantial.

In-Law Preferences in Agropastoral Societies

In my study of 67 pre-industrial societies, for the agropastoral societies, the most frequent in-law preference was "good character" followed by "good family background," "industrious," "good worker," "favorable social status," "wealthy," "wealthy

family background," "good economic prospects," "good heredity," "similar family social status," "chastity," "good looking," and "healthy" (Apostolou, 2010).

In my study of 16 agropastoral historical societies, I also examined in-law preferences (Apostolou, 2012). It has to be said however that the historical record is largely incomplete in terms of this dimension. Still, the available evidence indicated the most frequent preference was for good family background. Also, in several cases, parents were reported to prefer an in-law from a wealthy family background and from a family background similar to their own. Parents also valued wealth, good working ability, favorable social status, and good character.

Hunting and Gathering Versus Agropastoral Societies

The sample of 67 societies allows comparisons between different society types. It is found that "wealthy," "good family background," "similar family social status," "good character," and "good heredity" were found significantly more frequently in agropastoral than in foraging societies. Being a good hunter was reported only in foraging societies (Apostolou, 2007b).

Two key differences between agropastoral and foraging societies are that the former produce more material wealth and are predominantly regulated by well-developed social institutions such as the church. Accordingly, individuals and families in agropastoral societies are likely to vary in how much wealth they control and in how much access they have to these institutions; this variation would be much less pronounced in foraging societies where individuals control little material wealth and where these social institutions are not present or are less powerful in regulating people's lives. Therefore, parents in the former would have a stronger preference for wealth and good family background than parents in the latter societies.

Moreover, one reason that "good heredity" was not reported in hunting and gathering societies is likely to be that foragers do not have a clear concept of heredity, i.e., that certain traits are inherited from parents to children. Finally, it is no surprise that being a good hunter was reported only in foraging societies, as this trait has little relevance in agropastoral societies.

In-Law Preference in Post-industrial Societies

Moving on to in-law preferences in post-industrial societies, in a UK sample, I employed two different instruments to measure in-law preferences (Apostolou, 2007a). For the first instrument, at the top of the hierarchy of parental preferences were the "emotional stability," "dependable character," "good health," "pleasing disposition," and "desire for home children" traits. In the middle of the hierarchy were the "ambition industriousness," "education, intelligence," "sociability," "good

financial prospect," "refinement," "good cook-housekeeper," "similar education background," and "wealth" traits. Finally, at the bottom of the hierarchy, the "favorable social status," "similar religious background," "good looks," "similar political background," and "chastity" traits were found.

For the second instrument, at the top of the hierarchy, the "kind and understanding," "healthy," "compatible with you as a parent-in-law," and "easygoing" traits were found. In the middle of the hierarchy were the "have a job," "good family background," "wants children," "intelligent," "good housekeeper," "exciting personality," "good earning capacity," and "physically attractive" traits. At the bottom of the hierarchy were the "good heredity," "creative and artistic," "college/university graduate," and "religious" traits.

In another study, which employed a USA sample (Perilloux, Fleischman, & Buss, 2011), it was found that at the top of preferences were the "kind," "intelligent," and "healthy" traits. At the middle of the hierarchy were the "easygoing," "college graduate," "earning capacity," "religious," "wants children," "exciting personality," and "attractive" traits. Finally, at the bottom of the preferences hierarchy, the "heredity," "creative," and "housekeeper" traits were found.

In my study of in-law preferences, where I employed a Greek-Cypriot sample (Apostolou, 2014a), I found that at the top of parental hierarchy were the "family oriented," "kind and understanding," and "emotionally stable-mature" traits. In the middle of the hierarchy were the "pleasant personality and cooperative," "good economic prospects," "exciting personality," "similar religious and ethnic background," and "good looks" traits. At the bottom of the hierarchy were the "good cook-housekeeper," "chastity," and "well-off family background" traits.

In a subsequent study of in-law preference, also using a Greek-Cypriot sample (Apostolou, 2015b), I found that at the top of parental preferences were the "family oriented;" the "kind, understanding, and cooperative"; and the "reliable and tolerant" traits. In the middle of parental preference hierarchy were the "good economic prospects," "similar religious and ethnic background," "exciting personality," and "spontaneous and selfless" traits, while at the bottom of the hierarchy were the "good cook-housekeeper," "good looks," and "well-off family background" traits.

Overall, we can conclude that in a post-industrial context, place a strong emphasis on personality traits, particularly kindness and understanding. In addition, family oriented, good earning capacity, similarity, and healthy are also considered important.

Post-industrial Versus Pre-industrial Societies

In order to be able to make direct comparisons between post-industrial and pre-industrial societies, we need to ask parents to rate their preferences using the same instrument in both settings. No research attempt has materialized this task; still, on the basis of the research findings on in-law preferences in the two settings, we can reach some general conclusions about differences between the two.

One notable difference is that traits which are associated with family background were ascribed much higher importance in pre-industrial than in post-industrial societies. For instance, in my study of in-law preferences in pre-industrial societies, I found the "good family background" trait to be at the top of parental preferences (Apostolou, 2010), but in my study of in-law preferences in a post-industrial context, I found this trait to be in the middle of the hierarchy (Apostolou, 2007a).

This difference most probably reflects the decreasing importance of family alliances in post-industrial societies. In pre-industrial societies, there are no welfare and social protection systems, and individuals rely heavily on others for help in their struggle for survival and reproduction. Consequently, it is of paramount importance for parents' fitness to forge an alliance with another family through marriage. Accordingly, parents ascribe a high importance to the family background of a prospective in-law. On the other hand, in a post-industrial context, where welfare and social protection systems are present, individuals rely less on others for their survival and reproduction. Accordingly, an alliance through marriage with another family is less fitness consequential for parents, and this is one of the reasons why parents were found to be less sensitive to the family background of a prospective in-law in the post-industrial setting.

A more pronounced difference was that, in post-industrial studies, parents placed the desire to have children and to be family oriented traits at the top of their hierarchy (e.g., Apostolou, 2015b), but these or similar traits did not appear as desirable in the study of in-law preferences in pre-industrial societies (Apostolou, 2010). One possible reason is that having children and having a family are something which are considered as given in a pre-industrial context. Furthermore, the lack of effective contraception in this setting prevents individuals to choose when and whether to have children. Therefore, willingness to have children and a family is not something that effectively varies in a pre-industrial context, so parents would not consider it important. In post-industrial societies, however, having a family and children is not given, while there is effective contraception which gives the capacity to people to choose if and when to have children. An in-law who is not willing to have children can severely compromise the fitness of parents who risk not having any grandchildren. It is not a surprise then that parents in a post-industrial context place considerable value on this trait.

In the post-industrial setting, parents indicated a preference for in-laws with similar religious and ethnic background as their own, but such preferences were not observed in pre-industrial societies. The reason is that pre-industrial societies are generally homogenous in the dimensions of religion and ethnicity. Post-industrial societies are usually not so homogenous, predominantly due to the inflow of economic immigrants. Also, several post-industrial countries such as the USA were formed predominantly by immigrant populations, which varied in several dimensions. Therefore, the preference for similarity is also manifested in the post-industrial setting as preference for similarity in terms of religion and ethnicity.

Last but not least, it appears that kindness and understanding were valued more in post-industrial societies than in pre-industrial ones. This difference is likely to reflect differences in converging and diverging opportunity cost of free mate choice

between the two society types. In both societies, the converging opportunity cost is substantial, but in post-industrial ones, the diverging opportunity cost is much higher than in pre-industrial ones (see Chaps. 6 and 7). This difference is likely to have an impact on parental preferences: in post-industrial societies parents would place more emphasis on traits such as kindness, understanding, and good health, which can potentially harm the welfare of their children, than in pre-industrial societies. On the other hand, in pre-industrial societies parents would place more emphasis on traits which provide them with more benefits than they provide to their children, such as family background, than in post-industrial societies.

Sons-In-Law Versus Daughters-In-Law

The human species is sexually reproducing, with each sex having different specializations with respect to reproduction (Whyte, 1978). For instance, women specialize in providing the protected environment for the fetus to develop before it is able to survive in a non-protective environment. Consequently, after a successful mating episode, women have to remain longer than men outside the mating marker, which turns them the scarce reproductive resource over which men compete intensively in order to gain access (Emlen & Oring, 1977; Trivers, 1972). One way that men can achieve this objective is to fight other men and monopolize access to women (Puts, 2010). Accordingly, strong selection pressures are exercised on men to evolve adaptations that will enable them to do so. As consequence of these selection pressures, men are on average physically stronger and have a bigger body size, and they are more aggressive than women (Puts, 2010, 2016).

In turn, differences in traits make men and women fitter to fill different social niches and have different roles in the substance and survival effort of the societal unit. For example, in foraging societies, hunting and war effort, which require strength and aggression, are the domains of men, while gathering, which does not require scoring high in these traits, is the domain of women (Lee & Devore, 1968).

The division of labor by sex means that the fitness value of a trait for parents in a prospective in-law is contingent on the sex of the in-law. For instance, physical strength has a higher fitness value in a prospective son-in-law than in a prospective daughter-in-law. The reason is that a physically strong son-in-law will be an effective warrior and hunter and will provide protection and food to parents and their family, but a physically strong daughter-in-law will not be equally beneficial, as she will not engage in the protection and hunting effort.

Overall, sexual reproduction results in each sex to be endowed with different traits, which leads to a division of labor that turns the fitness benefits of specific traits in prospective in-laws to be contingent on their sex. In consequence, differential selection pressures are exercised on in-law preferences, making them to diverge over traits which have differential fitness potential in a daughter-in-law and in a son-in-law (Apostolou, 2007a, 2014c). Simply put, parents are expected to alter their preferences in specific traits depending on the sex of their prospective in-law.

Several studies find evidence consistent with this prediction. More specifically, in my study of 67 pre-industrial societies, the traits "good worker,'" "favorable social status," "good economic prospects," and "wealthy" were reported as important significantly more frequently in a son-in-law than in a daughter-in-law (Apostolou, 2010). The trait "chastity" was reported significantly more often in a daughter-in-law than in a son-in-law. In addition, "wealthy family background," "good looks," and "healthy" were more frequently reported as important in a daughter-in-law than in a son-in-law, but these differences in frequency did not pass the significance level. Differences between in-laws were not examined separately in a foraging and in an agropastoral context.

In my study of 190 hunting and gathering societies, I found that traits such as being a "good provider" and a "good hunter" were reported as important predominantly in a son-in-law but not in a daughter-in-law. Also, in my study of 16 historical agropastoral societies, I found that being "wealthy" was more frequently reported as important in a son-in-law than in a daughter-in-law (Apostolou, 2007b). The evidence on these preferences was inadequate however for more solid conclusions to be reached.

Turning to post-industrial societies, in a study of British parents, I found that "dependable character," "ambition," "industriousness," "education," "intelligence," "good financial prospects," and "wealth" were rated significantly more important in a son-in-law than in a daughter-in-law (Apostolou, 2007a). Nevertheless, the traits "refinement," "good cook-housekeeper," and "good looks" were considered as more important in a daughter-in-law than in a son-in-law. These results were replicated in two subsequent studies of British parents, where "chastity" was also found to be rated as more important in a daughter-in-law than in a son-in-law (Apostolou, 2008a, 2011b). In another study which used a different instrument, I found the "have a job," "good earning capacity," "intelligent," "good family reputation," and "good family background" to be considered more important in a son-in-law than in a daughter-in-law (Apostolou, 2008b). The traits "easygoing," "wants children," "good housekeeper," and "physically attractive" were rated as more important in a daughter-in-law than in a son-in-law.

In a different study, I asked Greek-Cypriot parents to indicate the traits that they would prefer in a son-in-law and in a daughter-in-law (Apostolou, 2011a). Mothers reported significantly more frequently as important "good looks," "cleanliness," and "good cook-housekeeper" in a daughter-in-law than in a son-in-law. On the other hand, they reported more frequently as important "industriousness," "pleasant personality," "good character," "faithfulness," "being a good provider," and "wealthy" in a son-in-law than in a daughter-in-law. Similarly, fathers reported "good cook-housekeeper," "love," and "good looks" more frequently as important in a daughter-in-law than in a son-in-law. On the other hand, they reported "industriousness," "good character," "emotional stability," and being a "good provider" more frequently as important in a son-in-law than in a daughter-in-law.

In a more comprehensive study of in-law preferences in a Greek-Cypriot sample, "good looks," "good housekeeping," and "chastity" were considered to be significantly more important in a daughter-in-law than in a son-in-law (Apostolou, 2014a).

On the other hand, parents ascribed more importance to "good economic prospects" for their prospective son-in-law than for their daughter-in-law. Finally, in a different study, I asked Greek-Cypriot fathers and mothers in the same family to rate the 88 traits used in the Apostolou (2014a) study (Apostolou, 2015b). I found that the "good looks" and the "good cook-housekeeper" were rated significantly more important in a daughter-in-law than in a son-in-law. The "family oriented" was also preferred more in a daughter-in-law than in a son-in-law, but the "trustful" component was valued significantly more in a son-in-law than in a daughter-in-law.

In addition, the "good economic prospects" trait was valued more in a son-in-law than in a daughter-in-law, while the "reliable and tolerant" was preferred more in a son-in-law than in a daughter-in-law, but the means practically overlapped mainly because its constituent traits were preferred similarly in a daughter-in-law and in a son-in-law, with the exceptions of the "determined" and the "generous" traits which were valued more in a son-in-law than in a daughter-in-law. For the traits which did not load in any domain, the "sweet," "few sexual experiences before marriage," "energetic," "conscientious," and "smiling" were preferred more in a daughter-in-law than in a son-in-law.

Overall, evidence indicates that in-law preferences are contingent on the sex of the in-law: parents place more emphasis on the resource acquisition capacities of a prospective son-in-law than of a prospective daughter-in-law, while they emphasize more on the looks and the chastity of a daughter-in-law than of a son-in-law. In a foraging pre-industrial context, parents place strong emphasis on the hunting abilities of a prospective son-in-law, while in an agropastoral pre-industrial and post-industrial context, they place more emphasis on the wealth of the son-in-law than of the daughter-in-law. The reason for this is that these societies produce surplus wealth which is usually controlled by men. Finally, in post-industrial societies, parents place more emphasis on the housekeeping capacities of prospective daughters-in-law than of prospective sons-in-law.

Mothers Versus Fathers

Certain traits in a prospective in-law are likely to give different fitness benefits to fathers and mothers. To begin with, due to menopause, women conclude their reproductive careers at an earlier age than men. As a consequence, the residual reproductive value (i.e., the contribution to the population through future reproduction) is less for older women—to the point of becoming zero if they have passed the age of menopause—than it is for men of the same age (Apostolou, 2014b).

In addition, men have a higher reproductive variance than women, as they are not constrained by their biology in the number of children they can father. Men's reproductive success is positively related to the resources they control (Buss, 2003), with men being able to deploy resources in such a way that enables them to practice polygyny and/or to attract multiple casual mates (Goode, 1982). On the other hand, because women are constrained by their biology, polyandrous marriage and having

multiple casual mates will not increase their reproductive success. In effect, a mating deal for their children, which would provide parents with resources, can potentially be more beneficial for a father than for a mother, as the former could use these resources to directly increase his reproductive success. To put is another way, the resources from a mating deal have the potential to increase the direct reproductive success of the father to a considerably greater degree than the direct reproductive success of the mother (Apostolou, 2014b).

Overall, it is expected that there would be traits in a prospective in-law that would benefit one parent differently than the other, and for these traits, preferences will diverge depending on the sex of the parent. For the areas where there is no differential fitness benefit, the preferences will not diverge. One nominated area where preference would diverge is resources, where fathers are predicted to place more emphasis than mothers, as historically resources would enable them to increase their fitness more than mothers. It can also be argued that traits such as kindness, which relate to the welfare of children, will be preferred more by mothers than by fathers. The reason is that, due to women not experiencing parental uncertainty and limited residual reproductive value, a prospective in-law harming their children will have a more negative impact to the fitness of mothers than to the fitness of fathers (see also Chap. 3). That is to say, because traits such as kindness, understanding, and emotional stability predict how well individuals treat their mates, they will be preferred more by mothers than by fathers.

The evidence is currently inconclusive. In particular, in one of the first studies of in-law preferences, involving a sample of 297 British parents, I found no significant differences in preferences between fathers and mothers (Apostolou, 2007a). Yet, the sample involved only 72 men, meaning that it may not had been powerful enough to detect any sex differences. In a more comprehensive research of in-law preferences, which involved participants assessing 88 traits which were classified in 11 dimensions, I found that mothers considered "pleasant and cooperative" and "exciting personality" more important in a son-in-law than fathers, while they considered "family oriented," "good economic prospects," "emotionally stable and mature," and "kind and understanding" more important in both a son- and daughter-in-law than fathers (Apostolou, 2014a).

One study in the USA compared the rankings that 117 fathers and 121 mothers gave for 13 traits in a prospective in-law (Perilloux et al., 2011). They found only one significant difference, where mothers ranked the "wants children" higher than fathers. In a different line of research, Dubbs and Buunk (2010) found that daughters perceived a low-quality partner to be more unacceptable to their mother when compared with their father and having a partner with traits indicating low social status as more unacceptable to their father when compared with their mother. This research did not investigate preference differences between fathers and mothers, but it hinted that such differences may actually exist.

These research efforts have compared the preferences of men and women who were not related to each other. Nevertheless, I am mainly interested in examining whether there is intrafamily conflict; that is to say, whether fathers and mothers in the same family agree or disagree. It may be, for instance, that two individuals have

different preferences, but when they have children together, their preferences converge, so there is no effective disagreement between the two. The opposite can also occur; and the current literature has not examined whether this is the case.

To allow for this limitation, I employed data from my Apostolou's (2015b) study, which involved ratings from fathers and mothers who had children together. I found that the "well-off family background" was valued more by fathers than by mothers, with the differences being predominantly over "from a wealthy family" and "wealthy" sub-traits. The "similar religious and ethnic background" was valued more by mothers than by fathers. Nevertheless, analysis of the constituent traits indicated that mothers valued the same nationality more than fathers, while fathers valued similar political beliefs more than mothers. There was also some evidence that kindness was valued more by mothers than by fathers. In particular, the "kind" trait was valued significantly more by mothers than by fathers, although there was no sex difference for the domain in which this trait belonged (i.e., "kind, understanding, and cooperative"). I also found a significant interaction, where mother valued "kind, understanding, and cooperative" more in a prospective son-in-law than in a prospective daughter-in-law. However, the interaction was close to the significance level, so this sex difference requires further investigation and replication (Apostolou, 2016).

The conclusions from the current literature are that mothers and fathers have largely converging but not completely overlapping in-law preferences. There is evidence that fathers place more emphasis to the wealth of their prospective in-laws, while mothers place more emphasis on the kindness, especially on the prospective son-in-law.

In-Law Versus Mating Preferences

In-law preferences need to enable parents to reduce the converging and diverging opportunity costs of free mate choice. For the in-law preferences that enable parents to reduce the diverging opportunity cost, we expect them to diverge from the respective mate preferences of their children. Good looks are an example of this: beauty constitutes a proxy of genetic quality, which is more beneficial to children than to parents (see Chap. 2). Accordingly, in-law and mate preferences diverge over this trait, with parents ascribing less importance to it, so that they would be able to get an in-law who scores lower in this and higher in other traits than their children would.

For the preferences which aim to reduce the converging opportunity cost, they are expected to be similar to the respective mate preferences of their children. For example, kindness is equally beneficial to each party, so preferences do not diverge. Thus, both parents and children value kindness similarly, but children, driven by libido, can make the erroneous choice to get an individual who is not kind, their parents who also have such strong preferences from kindness, but their judgment in not clouded by libido or romantic love will be driven by their references to intervene and kick out this individual.

Nevertheless, because the diverging opportunity cost is usually larger than the converging opportunity cost, parents may prioritize over reducing the former than the latter. This means that they may be willing to make compromises on traits which are equally beneficial to them and to their children in order to get traits which are more beneficial to them. There is no contradiction here: parents have preferences that protect their children from making erroneous choices and find good mates; however, they would be willing to make compromises that reduce the fitness of their children, if doing so increases more their own fitness. For instance, in a pre-industrial context, in order to forge a beneficial marital alliance, they may be willing to accept an in-law who is not especially kind.

Are In-Law Preferences Actually Mate Preferences?

It can be argued that, in ancestral human societies, there had not been substantial selection pressures for distinct in-law preferences to evolve; therefore, what it is measured here as in-law preferences are actually "masked" mate preferences. This can possibly explain the observed similarity in contingencies; for instance, beauty is valued more in wife than in a spouse, and it is valued more in a daughter-in-law than in a son-in-law. This argument is not valid for several reasons.

To begin with, evidence from the anthropological and historical records, along with phylogenetic studies, indicates that in ancestral human societies mate choice was regulated, with parents choosing spouses for their children and not the children for themselves (Chap. 7). Therefore, during human evolutionary time, parents faced recurrently the problem of choosing fitness-increasing daughters- and sons-in-law, which translates into substantial selection pressures for in-law preferences to evolve.

Moreover, if in-law preferences were simply "masked" mate preferences, then the two would be identical in strength, which is not the case. In particular, in one line of research, I tested the hypothesis that people have distinct in-law and mate preferences by asking individuals who had children to rate a set of traits in a prospective spouse for themselves and in a prospective spouse for their daughters and sons (Apostolou, 2008a; Apostolou et al., 2014). If in-law preferences were 'masked' mate preferences, there would not be any differences between the two ratings; yet, significant differences were found, with participants changing their preferences on the basis of whether they acted as in-laws or mate-seekers. Even more importantly, the observed differences were consistent with what evolutionary predictions on how in-law preferences would differ from mate preferences, namely, good looks were preferred more in a spouse than in an in-law, while good family background was preferred more in an in-law than in a spouse.

In the same line of reasoning, if in-law and mate preferences were identical, the sex differences in preferences between mothers and fathers would also mirror the difference in preference between male and female mate-seekers. More specifically, research on mate preferences has found that traits such as good economic prospects and being well-off are preferred more by women in a male partner, while traits such

as beauty and good housekeeping abilities are preferred more by men in a female partner (Buss, 2003). If in-law and mate preference were identical, then such differences would emerge when we compare the preferences of mothers with the preferences of fathers. Yet, these differences were not found, while with respect to wealth, the difference was to the opposite direction: fathers ascribed more importance to it than mothers.

Last but not least, if in-law and mate preference were identical, then the two would have the same structure, i.e., principal component analysis of in-law and mate preferences would produce identical or very similar factor structures. Research that employed such analysis on desirable traits in a mating candidate found that in-law preferences have a different structure than mate preferences (Apostolou, 2014a, 2015b). In sum, different lines of evidence converge to the conclusion that in-law preferences are distinct from mate preferences: in-law preferences are adaptations which have evolved to enable parents to choose fitness-increasing in-laws, while mate preferences are adaptations which have evolved to enable individuals to choose fitness-increasing mates.

In conclusion, parents have well-defined in-law preferences. Some traits are considered more important than others, with the value ascribed to each trait varying with the ecological context where parents find themselves in. In-law preferences are also contingent on the sex of the in-law and the sex of the parent. In the next chapter, I am going to explore the possible effects that in-law preferences have had in shaping specific adaptations.

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Chapter 10
Parental Choice and Its Impact on Adaptations Involved in Mating

In the previous chapters, I discussed evidence which indicates that parental choice constitutes a strong sexual selection force in pre-industrial context and that there are good reasons to believe that it had been also a strong sexual selection force in ancestral human societies. Consequently, parental choice should have been responsible for shaping several adaptations that would make an individual more likely to be selected as a son- or daughter-in-law. Accordingly, in this chapter, I will explore and nominate possible adaptations which have been favored by parental choice, i.e., have evolved in order to enable individuals to address the parental choice reproductive niche. Not everyone is expected to have such adaptations; thus, before doing so, I am going to discuss why people exhibit variation in their sexually selected adaptations.

Reproductive Niches and Variation in Sexually Selected Adaptations

In Chap. 1, I argued that the presence of different sexual selection forces translates into the presence of different reproductive niches. Distinct reproductive niches require individuals to have different adaptations in order to be able to address them. As a consequence, there is variation or polymorphism in the sexually selected adaptations. People vary in their sexually selected adaptations because they have evolved to address different reproductive niches. Such polymorphism can take two forms, namely, genetic polymorphism, in which the phenotype that an individual exhibits is genetically determined, or a conditional strategy in which the phenotype of an individual is set by environmental cues (Leimar, 2005). I will discuss the former first.

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Genetic Polymorphism and Balancing Selection

Let me start with a context where the parental choice is the largest reproductive niche. In this case, alleles that predispose for traits that enable an individual to address this niche would be in higher prevalence than alleles that enable an individual to address any of the other reproductive niches. To see why, let us assume that a population of individuals who do not have traits that enable them to specialize in addressing any niche is found in this context. Let us assume also that, through mutations, four alleles arise, namely, an allele that enables an individual to exploit the parental choice niche, an allele that enables an individual to exploit the individual choice niche, an allele that enables an individual to exploit the male-male competition niche, and an allele that enables an individual to exploit the sexual coercion niche. All four alleles will spread in the population, as they accrue more fitness benefits than alleles that do not enable the exploitation of any reproductive niche. Eventually, the latter will be replaced by the former alleles. Yet, the four beneficial alleles will not be in the same frequency in the gene pool.

The fitness of the alleles that predispose for traits that enable an individual to address a specific reproductive niche decreases as they become more common in the population (this is known as negative frequency-dependent selection; see Nettle, 2009). When there are few individuals with traits that enable them to address a reproductive niche of a given size effectively, the fitness of the alleles for those traits is high, as individuals who have them are better off than those who do not. The alleles will increase in frequency in the gene pool, meaning that individuals who have traits that enable them to address the niche in question will become more numerous.

However, as their number keeps rising, their fitness declines because the reproductive niche has space only for a limited number of individuals. For instance, if in a given context there are many women who have a considerable space to exercise mate choice, and few men with traits that enable them to address effectively the female choice reproductive niche, then these men would face little competition in gaining reproductive access to women and will have many children who also have these traits. Yet, as additional men are born with these traits, competition with other men who have similar traits increases, and so these men would enjoy lower fitness, i.e., they would have access to fewer women and have fewer children. At some point, the competition becomes so fierce that additional men who have these traits gain no fitness benefits, and as a consequence, the alleles that code for these traits stop increasing in the gene pool. In different words, the frequency of these alleles stabilizes at the point where there are enough men with these traits to address the female choice reproductive niche.

The equilibrium frequency is determined by the size of the niche in question. For instance, in the above example, if women are relatively free to exercise choice, the equilibrium frequency will be higher than if they are constrained in exercising choice. Consequently, at any point in time, we expect to find alleles for different niches in different frequencies that translate into people exhibiting variation in

traits: Some are endowed with traits that are effective in addressing the parental choice niche, others in addressing individual choice niche, and so on.

The argument above does not preclude the possibility that there are alleles that enable an individual to exploit more than one niche. This is more likely to be the case for more similar niches such as parental choice and individual mate choice. For instance, an allele that predisposes for status-seeking behavior in men can enable successful exploitation of both parental choice and individual choice niches, as high status is favored by women in a mate (Buss, 2003) and by parents in a son-in-law (Apostolou, 2010a, 2014a). Accordingly, alleles that enable an individual to address, say, two reproductive niches, would be in higher frequency than alleles that enable the individual to exploit only one niche. This argument indicates further that there are individuals with traits that make them able to occupy more than one niche.

Certain alleles can be effective in even addressing all the niches, such as physical strength in men. Alleles that predispose for a strong body (e.g., stronger muscles) enable a man to exploit the parental choice and individual choice niches, as parents and women prefer stronger to weaker sons-in-law and mates, respectively; the male-male competition niche, as men who carry these alleles would be more effective in fighting other men who do not; and the sexual coercion niche, as men who carry these alleles are more effective in forcing sex to women than men who do not. It is no surprise then that most men are bigger and stronger than most women (Puts, 2010).

Yet, alleles that address all niches would be in the minority, since different niches require different traits to be addressed effectively. For instance, women value kindness and understanding in a mate (Buss, 2003), so alleles that predispose for these traits enable a man to address successfully the individual mate choice niche. Such alleles would be an impediment in addressing the male-male competition and the sexual coercion niches, as men who are kind and understanding may not be willing or effective in killing other men and forcing sex to women. It is not a surprise then that these traits are less common in men than in women (Apostolou, 2016).

Overall, there are different alleles that code for traits which specialize in addressing one or more reproductive niches, with their fitness depending on their frequency in the population which in turn is determined by the size of the different reproductive niches, which is determined by the specific environmental conditions.

Conditional Development Strategy and Environmental Cues

In the scenario discussed above, individuals develop a trait for addressing a specific niche, depending on whether they carry or not the allele or alleles which predispose for this trait. Those who carry it will develop the trait, while those who do not will not develop the trait. There is still another possibility, namely, that individuals carry the allele, but whether it is expressed or not depends on the environmental conditions during an individual's development. For instance, an allele that predisposes for aggression that would enable a man to address the male-male reproductive niche may be expressed if the individual finds himself in a violent context at a young age,

which hints that the male-male niche is large, and by becoming aggressive, he will be readier to exploit it. On the other hand, if the individual finds himself in a peaceful and nonviolent setting, which hints that the male-male reproductive niche is small, then this allele may not be expressed as the man will not reap considerable reproductive benefits from becoming aggressive.

It has to be said also that the expression of alleles may be contingent on the presence of other traits, sometimes referred to as "reactive heritability" (Lukaszewski, 2011; Lukaszewski & Roney, 2015). In the example above, if alleles that predispose for aggression are expressed irrespectively of the traits that an individual has, they are likely to be expressed in men who are physically strong as well as in men who are physically weak. But in the latter case, the fitness of these alleles would be compromised, as individuals who are aggressive but physically weak will frequently end up in fights with physically stronger men, fights which are likely to lose. It would pay then for these alleles to remain silent and be expressed only when they are found in a physically strong male body. Thus, alleles for aggression, the expression of which is contingent on other traits, may be favored over alleles that are expressed irrespectively of the presence of other traits.

This argument adds some complication because the presence of these other traits may be contingent on environmental clues or on the presence of yet other traits. Therefore, a sexually selected trait, the expression of which is contingent on the presence of another trait, may be triggered by environmental factors, if the expression of the other trait is contingent on environmental factors. An environmental cue triggers the expression of the other trait, and the presence of this other trait triggers the expression of the sexually selected trait. Thus, many sexually selected traits may appear to be contingent on the environment, although in reality, they are contingent on the presence of other traits, the expression of which is contingent on the environment.

We can now ask in which case selection forces would favor alleles that are always expressed and in which case they would favor alleles the expression of which depends on environmental factors or the presence of other traits. The answer is that the former would be favored when the specific aspects of the environment that these alleles address are static, while the latter would be favored, when they are not static or when the other traits which are required to address a specific environmental niche are not always present. Starting with the static case, oxygen in the air and solid land are properties which do not vary (i.e., there are always there) in the specific ecological niche that humans occupy. Accordingly, people have evolved adaptations such as legs to walk around and lunges to extract oxygen from the air. Individuals without these adaptations cannot survive, so all individuals are endowed with genes which code for them, the expression of which is not contingent on environmental conditions or the presence of other traits. Alleles, that say code for lunges, the expression of which is contingent on environmental cues, will not be better off than alleles that are expressed irrespectively of environmental conditions, as humans cannot survive without lunges. Thus, selection forces will not favor these alleles, which are not expected to exist in the gene pool.

Moving on to the non-static case, we can use the male-male competition reproductive niche as an example. This niche may not be static; there may be, for instance, prolonged periods of conflict and war, followed by prolonged periods of piece. Thus, alleles that predispose for traits such as aggression, that enable a man to address effectively the male-male reproductive niche, and that are expressed irrespectively of the environmental conditions are worse off than the respective alleles whose expression depends on environmental conditions. The reason is that men who carry the former will be aggressive in times of conflict, gaining reproductive advantages, but will also be aggressive in times of peace, suffering reproductive and social exclusion costs. On the other hand, men who carry the latter will be aggressive in times of war, gaining reproductive advantages, and not aggressive in times of piece, not suffering reproductive costs.

Moreover, traits such as physical strength, which are required to exploit the male-male competition niche, vary across individuals, even if they are genetically related. For example, a man whose father is physically strong may not be physically strong because he got the genes for physical strength from his mother and not from his father. As these traits are expected to vary, it would pay for the expression of the alleles for aggression to be contingent on the presence of physical strength. In particular, even if the male-male competition niche is large, it would not pay for an allele that predisposes for high aggression to be expressed, unless it is found in a physically strong man. If it is expressed in a physically weak man, it would suffer reduced fitness as this man would get into fights he would lose. Thus, if men did not vary in physical strength, alleles whose expression is contingent on physical strength would not be better off than alleles whose expression is independent of the presence of physical strength and most probably would not exist in the population.

Another way to see it is that since the size of male-male competition reproductive niche and the physical strength trait which is required to exploit it vary, selection forces would favor alleles that code for an aggression mechanism which adjusts its developmental trajectory on the basis of environmental cues and the presence of physical strength. If environmental cues indicate a large male-male competition niche, and the alleles are found in a physically strong male body, then the man may turn to become aggressive; if any of these two conditions are not satisfied, the man may become less or nonaggressive.

The Ancestral Environment and the Nature of Sexually Selected Traits

Evolutionary theorizing, along with anthropological and historical evidence, suggests that in ancestral human societies, there were at least four reproductive niches of different sizes (see Chap. 1). Accordingly, following the balancing selection argument, we expect that in the contemporary gene pool, there are alleles in different frequencies that predispose for traits that enable individuals to address the

different reproductive niches. That is to say, some individuals carry alleles that enable them to address one niche, and other individuals carry different alleles that enable them to address another niche.

Whether the alleles individuals have to enable them to address a specific niche are contingent on environmental cues or the presence of other traits is more difficult to answer. Starting from the latter, due to the nature of sex and recombination, those who have the alleles for addressing one specific reproductive niche may vary considerably in the other traits which are required for addressing this niche. For instance, several men may carry an allele that predisposes for aggression, the expression of which is contingent on the presence of other traits such as physical strength, body size, stamina, etc. There may be several men who carry it, but in some of them, this allele will not be expressed, because they are not, for instance, physically strong. Accordingly, men will exhibit variation in how aggressive they are, even if they carry the same allele.

Moving on to the environmental contingencies, it is hard to say whether the size of different reproductive niches had been stable in each period of human evolution. Application of the model of parental choice along with empirical evidence indicates that these had been relatively stable—for instance, in agropastoral period, individual choice and sexual coercion would have been small and parental choice and male-male competition large. Even so, some variation is expected. There may have been, for instance, prolonged periods of peace (e.g., Pax Romana) that would increase the size of parental choice and individual mate choice niches and would decrease the male-male competition niches, a trend that would be reversed by prolonged periods of war and conflict (e.g., the fall of the Roman Empire). Thus, it is not unlikely there would be in the gene pool sexually selected alleles that respond to environmental cues.

To sum up, it is expected that in the contemporary gene pool, there are alleles for different traits which aim to address different reproductive niches. The expression of some of these alleles would be independent of environmental cues and of the presence of other traits, while the expression of some alleles would be contingent on environmental cues and the presence of other traits. I can now proceed to discuss some adaptations which are likely to have evolved to enable individuals to exploit the parental choice niche.

Attracting Mates and In-Laws

Men as Mate-Seekers

When parents are looking for sons-in-law, they are looking for individuals who come from a desirable family background, who have good character, who can contribute resources to their family unit, who have a capacity to have a family, and who are good looking (see previous chapter). These in-law preferences exercise selection

pressures on men to signal reliably their qualities to prospective parents-in-law. Men who have qualities that parents desire and are effective in demonstrating that they have them will be more likely to be selected as sons-in-law than men who have such qualities but are not as effective in demonstrating them.

Doing so would involve adaptations to enable a man to signal his family background and the social standing coming from his family background. For instance, he may have a taste for ornamenting himself or dressing in a way that is informative about his family background. He may also have a preference to put on display family artifacts and antiques that serve this purpose.

A man is also under selection pressure to demonstrate that he has a good character, e.g., that he is kind, cooperative, and reliable. Adaptations involved in serving this purpose are likely to include a motivation to engage in charity and in altruistic acts, such as helping the poor and those in need. With respect to demonstrating being tolerant and pleasant, men may have evolved mechanisms that enable them to exhibit good manners, smile, and be polite and accommodating when in a social context, especially when surrounded by older people.

A man needs to demonstrate further that he has good providing abilities and that he can be a valuable source of resources. Adaptations which can serve this purpose may include a motivation to demonstrate possession of wealth, possession of good social standing, and industriousness. As wealth and status are considered desirable qualities by parents, and unlikely other traits such as personality and looks, they can be acquired through one's lifetime. Accordingly, adaptations are likely to arise which generate a strong motivation for men to pursue high status and wealth. In addition, adaptations are likely to evolve which aim to prevent a man from losing accumulated status and wealth. For instance, a man may be very sensitive in losing face, especially among other men.

Parents are further interested in finding a son-in-law who is physically fit, so he can be a valuable asset in protecting their family and helping them in their subsistence activities. A predisposition to engage in physical competitions such as sports is likely to have evolved in order to serve this purpose (Apostolou, 2015d). Such competitions can enable men to demonstrate the physical competences, including physical strength and stamina.

Parents care also about finding a son-in-law who is healthy and has a capacity to give them healthy grandchildren. A mechanism that motivates men to take part in athletic competitions can also serve such a function, as those who do not enjoy a good health and do not have a good genetic quality are unlikely to be able to compete successfully in physically intensive sports (Zahavi & Zahavi, 1997). Since health and genetic quality predominantly reflect on looks, men are expected to have also evolved mechanisms that motivate them to maintain good looks. For example, a man would care about his appearance and would take action to improve it.

It has to be said that, since male parental choice is usually stronger than female parental choice, such adaptations should have evolved to appeal predominantly to other men, who in an ancestral context were likely to had been fathers, uncles,

and brothers looking for spouses for their daughters, nieces, and sisters, respectively.

Men as Parents

Parents place great emphasis on a prospective in-law's family background, which places individuals who are parents under selection pressure to demonstrate and preserve their family standing. This is particularly so for fathers, as they are usually the main players in marriage arrangements (Apostolou, 2010b). Older men are likely to have evolved adaptations which enable them to increase their own and thus their family's social standing and prestige, as doing so would enable them to ally with families of superior social standing. They are also expected to have adaptations which enable them to demonstrate their accumulated social standing and wealth, as these traits would turn them more attractive to other families looking for marital alliances. For instance, they may have a predisposition to exhibit their family's wealth and prestige by organizing fists to demonstrate wealth (e.g., the custom of potlatch; see Boas, 1966), living in large and expensive houses, etc. They may also be interested in particular rituals, dressing code, shaving, tattooing, and so on that demonstrate one's social class.

A man who suffers a compromise in his family standing would—among other things—suffer severe reproductive loses because other families would not like to ally with his family, so he would have either to compromise in arranging a marriage with a family of inferior social standing or even fail completely to find suitable spouses for his children. Accordingly, men are likely to have evolved adaptations that enable them to protect their family's status from being compromised. Such adaptations may involve sensitivity to anything that can compromise one's family name. For instance, inappropriate sexual behavior from a man's daughter can harm his family name and can trigger this mechanism leading him to punish her severely. For example, honor killings are often reported in the anthropological literature (see Campbell, 1964).

Taking such a course of action involves a substantial fitness cost, because a man who kills his daughter loses all parental investment he has allocated to her along with her potential to give him grandchildren. However, particularly in a pre-industrial context, men are likely to have several other children. For instance, in rural Greece of the last century, it was not uncommon for parents to have five or more children (Friedl, 1967). Accordingly, failure to act so as to preserve the social standing of his family could have involved a larger fitness cost, in the form of failing to secure desirable marriages for his other children. It also needs to be said that these mechanisms may act to deter children from engaging in behaviors that can harm their family's standing. If a daughter knows that an inappropriate relationship can cost her life, she will not engage in it. Thus, this mechanism will result in offspring behaving appropriately (i.e., as their parents wish), and in very rare instances, it would lead to the killing of a daughter or son.

Women as Mate-Seekers

Women need also to signal to prospective in-laws that they come from a good family background. Accordingly, the adaptations nominated above may also apply to women. In addition, women need to signal that they are going to be valuable in contributing to the subsistence and survival effort of the family unit. Women's strength and athletic abilities are less of a concern, since the division of labor in a pre-industrial context mandates that women do not hunt and play little role in the defense of the family. Women, however, contribute substantially to the subsistence of the family unit by gathering plants or by participating in the cultivation of land. They also have a critical role in keeping the household and raising children. Thus, traits such as industry and being effective in running a household are of interest to parents looking for daughters-in-law. Women may signal these qualities by engaging in acts demonstrating industry and good housekeeping capacity. For instance, they may be sensitive in their household being clean and orderly, especially in the presence of guests.

In addition, parents are interested in having a daughter-in-law who can be a functional new member to their family, which in turn demands good character properties such as kindness, cooperativeness, and reciprocity. Thus, women are under selection pressure to communicate these capacities. They may, for instance, engage in altruistic acts such as helping the poor and those in need.

Furthermore, the capacity of a prospective daughter-in-law to have a family and provide healthy grandchildren is important to parents (Apostolou, 2015c). This capacity is determined by a woman's age, health, and genetic quality, all of which are reflected in her looks. Accordingly, parents place an important emphasis on the good looks of a prospective daughter-in-law, which in turn exercises selection pressure on women to evolve mechanisms that motivate them to pay attention to their looks. In effect, women are expected to have adaptations which drive them to improve their appearance and be sensitive in avoiding anything that can compromise their looks. Women would also be motivated to improve their looks in ways that make them look younger and healthier.

Moreover, parents want to be certain that their grandchildren are their own and not other parents' grandchildren. Consequently, they place emphasis on a prospective daughter-in-law to be sexually constrained (Apostolou, 2015c), which in turn exercises selection pressure on women to demonstrate chastity and sexual constrain. Thus, women may be sensitive to anything that can compromise their chastity status. They may also be predisposed to engage in intimate relationships in secrecy.

Women as Parents

Older women are also under selection pressure to signal their family's social standing; accordingly, the relevant adaptation discussed above for men is likely to be found in women as well. Yet, because women in a pre-industrial context have a more

limited role in marriage arrangements, such adaptations may be less pronounced. In addition, women are emotionally closer to their children than men, predominantly due to lack of maternal uncertainty. Thus, older women, more than older men, may be predisposed to advise their children about how to behave in order to preserve their family' status. For instance, a mother may advise her children how to dress and how to behave in social occasions.

Adaptations to Retain Marital Alliances

Marriage is a long-term coalition, which means that individuals not only need to appeal to parents who look for spouses for their children, but they also need to remain appealing to them following marriage. Although parents' capacity to mandate mate choice decreases following marriage, they still have a say in divorce decisions. For instance, they can employ manipulation in order to undermine an undesirable marriage (Apostolou, 2013), while in several pre-industrial societies, it is not uncommon for parents to end the marriage deal unilaterally if they are not satisfied with their in-laws (Apostolou, 2014b).

That is to say, selection pressures are exercised on individuals to remain desirable to their parents-in-law. This leads to the prediction that specific adaptations would have evolved to serve this purpose, and adaptations which have evolved to serve different purposes have also been optimized to serve this purpose as well. Such adaptations are likely to include being sensitive to parents-in-law opinion, being responsive to their wishes, remain helpful and accommodating to their requests, buying them gifts, and so on.

In the same vein, when arranging a marriage, parents are after establishing a long-lasting alliance with another family. That is to say, there are selection pressures to enable parents to retain this alliance. They can do so by remaining appealing to their in-laws as allies. For instance, they may have evolved mechanisms that motivate them to supply the relatives of their daughter- or son-in-law with gifts, treat them well, and keep showing them their value, hiding from them any social status-compromising information, advising their children to treat them well, and so on.

Since individuals have a considerable space to exercise choice within marriage (Apostolou, 2014b), selection pressures are exercised on parents to be able to influence their daughters- and sons-in-law not to break up or to seek extramarital relationships which can undermine the marriage. For instance, parents may attempt to use manipulation such as threats or advice for this purpose. They may also be very sensitive to social information and gossip about their in-laws related to possible infidelity. This sensitivity could deter individuals from engaging in such relationships. In addition, if parents suspect any threats to marriage stability, they can take measures to prevent it from escalating to a divorce. They may threaten, for instance, those involved with severe consequences.

What Drives the Evolution of Sexually Selected Traits?

Comparisons between in-law and mate preferences indicate that there is substantial overlap, but there is also divergence, which is however predominantly quantitative and not qualitative in nature. That is to say, parents do not desire different things in a prospective spouse for their children than their children for themselves. For instance, both parents and children consider good looks desirable, but the latter consider them more desirable than the former (Apostolou, 2014b; Buss, 2003).

This overlap in preferences suggests that more than one sexual selection forces can drive the evolution of a trait. For instance, adaptations that motivate a man to display his resource-generating capacity are likely to have been driven by both parental choice and female choice, since both parents and female mate-seekers prefer good resource-generating capacity in a prospective in-law and in a mate, respectively. To use another example, strong muscles would be favored by intrasexual selection forces as they enable men to fight other men but would also be favored by parental choice, as parents would prefer strong men as sons-in-law, would be favored by female choice as women would prefer strong men as mates, and would be favored by sexual coercion as this trait would enable men to force sex on women. Another way to put it is that there is an overlap in the qualities an individual needs to have in order to be able to exploit the parental choice and the individual mate choice niches, which may favor traits such as a man having a desire to pursue high social standing, which enable him to address both the parental and the individual mate choice niches.

Such overlap may also have one further implication. Evolution works on what is available, so when the environmental factors change, it is likely to modify existing traits, instead of giving rise to new traits, to meet the demands of the modern conditions (Gould & Vrba, 1982). This is more likely to happen if the changes in the environment are not so drastic to require novel adaptations. The agropastoral revolution has resulted in the expansion of the parental choice reproductive niche and the shrinkage of the individual mate choice niche (Chap. 7). Thus, traits which have originally evolved to address the individual mate choice niche may have been modified to address the parental choice niche. For example, mechanisms which make men effective to communicate their social standing to women may have been modified to make men effective in communicating their social standing to older men who control access to women.

Overall, figuring out the evolutionary history, and thus the function of a sexually selected trait, is a challenging endeavor which requires an understanding of the variation in the strength of different sexual selection forces across human evolutionary time.

The Effect of Sexual Selection on Traits Which Are Not Sexually Selected

In the sections above, I made the argument that selection pressures would be exercised on individuals to evolve adaptations that enable them to signal qualities that they have and prospective parents-in-law find desirable, so as to be effective in

addressing the parental choice reproductive niche. Yet, selection pressures would also be exercised on traits that make individuals desirable as in-laws. For instance, parents value resource-generating capacity in a prospective son-in-law (Apostolou, 2010a, 2014a), which in turn exercises evolutionary pressure on men to evolve mechanisms that would enable them to signal such a capacity reliably. But it exercises also selection pressure on men to increase this capacity. In order to see why, assume that all men have mechanisms that enable them to signal effectively their resource acquisition capacity; in this scenario, men who have a high resource capacity would be better off in terms of reproductive success than those who have a low capacity, as they would be better able to address the parental choice reproductive niche. In turn, if these men are better off and have more offspring than others, the alleles that predispose for high resource-generating capacity in men would increase in frequency in the gene pool; simply put, men who have an increased capacity to generate resources would become more numerous in the population.

This example underlines the complexity of understanding the evolutionary trajectory of the different adaptations, the reason being that different selection forces are exercised on individual traits. In this case, selection pressures would have resulted in men being endowed with adaptations that give them the capacity to generate the resources they require in order for them and their family to survive—these adaptations have not been sexually selected. But, for various reasons, such as genetic mutations, accidents, and illness, men would vary in their capacity to provide resources. This variation would exercise selection pressure on parents to become sensitive to the resource acquisition capacity of their prospective sons-in-law. Parents who are predisposed to prefer as sons-in-law men with high resource acquisition capacity will be better off than parents who do not have such preferences, as they will have an elevated probability to have a son-in-law who will be a good provider of resources to their daughter and their grandchildren. As a consequence, alleles that predispose for such in-law preferences would spread in the gene pool, meaning that parents in the population would tend to prefer sons-in-law with a good resource-generating capacity.

These in-law preferences would in turn exercise selection pressure on men to increase their resource-generating capacity as well as to reliably signal this capacity. Consequently, alleles that predispose a man to produce resources over and above the ones needed to support himself and his family would be selected because they would confer to the man who has the reproductive advantages. As a consequence, the resource-generating capacity of men will increase in the population, with several men tending to generate more resources than they need for sustaining themselves and their family. Thus, part of the observed male resource-generating capacity has been sexually selected, i.e., it has been favored by selection forces in order to enable men to attract and retain desirable mates.

This scenario is likely to apply to several other traits which are preferred by parents. In particular, adaptations that enable individuals to increase their own and their family's social standing and several personality traits desired by parents are likely to have been "augmented" by sexual selection because they enable individuals to gain reproductive benefits by addressing parental choice or other reproductive niches.

Other Adaptations

In the sections above, I discussed the implications of parental choice in shaping adaptations which enable individuals to be selected as in-laws. Nevertheless, the presence of parental choice is likely to have given rise to several other adaptations which do not relate directly to turning an individual appealing as an in-law. I will explore some of these adaptations below.

Parents

Parents are not always able to control their children directly, especially if they are old and the latter are independent from them. In effect, selection pressure is exercised on the former to evolve ways to manipulate the latter over mate choice. That is, parents are likely to have evolved a battery of manipulation tactics that would enable them to influence their children's mating decisions. As discussed previously, research has identified several tactics that parents use for this purpose (Apostolou, 2013; Apostolou & Papageorgi, 2014).

Children are likely to find opportunities to escape parental control and exercise their own choice. This possibility would exercise selection pressure on parents that would give rise to adaptations which enable them to monitor their children's mating behavior and take action if it strays from what they consider optimal. Such adaptations may include being sensitive to cues that suggest romantic involvement, a strong interest in acquiring information about children's mating behavior, etc. These adaptations are also likely to monitor predominantly female children's mating behavior. Some evidence indicates that this is actually the case (Perilloux, Fleischman, & Buss, 2008).

Children

The strong parental control over children's mate choice exercises selection pressures on the latter to evolve mechanisms that would enable them to escape the former's control. Such adaptations may involve children manipulating their parents in the domain of mate choice. In one study, I found seven tactics used by children to manipulate their parents out of relationships they wished to impose on them and seven tactics children employed to persuade their parents to accept the mates they have chosen (Apostolou, 2015a). In addition, the presence of strong parental choice exercises selection pressure on mate-seekers to manipulate prospective parents-in-law in accepting them as mates. Accordingly, in one study, I found seven tactics that individuals employ for this purpose (Apostolou, 2015b).

There would also be selection pressure on children to become efficient in exercising their own mate choice without being detected by their parents or the

spouses that their parents have selected for them. Some of these adaptations may be more sinister. Individuals may try to isolate their partners from the influence of their parents and thus make their relationships more resistant to manipulation. For example, they can use manipulation to undermine the relationship of their partners with their parents, distance them from them, and reduce therefore parents' influence on the relationship.

To conclude, strong parental control over mating during most of the period of human evolution is likely to have influenced the evolution of several adaptations. As parental control over mating had been strong while individual mate choice had been weak, especially in the later stages of human evolution, we expect that several individuals today have traits that enable them to address the parental choice and not the individual mate choice niche. As a consequence, the transition to post-industrialism and the considerable increase in size of the individual mate choice niche, and the associated decrease in size of the parental choice niche, results in individuals facing difficulties in the mating domain. I am going to explore these difficulties in the next chapter.

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Chapter 11
Environmental Mismatches and Mating Effectiveness

In the previous chapters, I have argued that parental choice and the other sexual selection forces are not static, but they change in response to environmental conditions. Accordingly, when the environment changes, these forces are likely to change as well. In this chapter, I am going to focus on such environmental change caused by the industrial revolution and the transition to post-industrialism. I will argue that this transition has changed considerably the prevailing mating patterns, so that people today may not have adaptations which are optimized to deal effectively with the demands of the modern environment. I also aim to derive insights about phenomena such as same-sex attractions, the evolution of which cannot be readily explained in reference to the current environment, but can be explained in reference to the ancestral one.

The Mismatch Between Ancestral and Modern Conditions

Evolutionary theorizing, along with evidence from anthropological and historical records, indicates that in ancestral human societies, the parental choice reproductive niche was large. The male-male competition niche was also large, but the individual choice niche was relatively small. On the other hand, in contemporary post-industrial societies, the parental choice and the male-male competition niches are very small, while the individual mate choice niche is the prevailing one (Chap. 7).

The transition to post-industrialism and the associated changes in the size of the different reproductive niches, along with the fact that this transition has occurred very recently in evolutionary terms, lead to the mismatch problem: Selection forces have not had sufficient time to optimize the frequencies of the alleles that code for traits which are involved in mating for modern conditions. As a consequence, several individuals today may face difficulties in establishing and maintaining intimate relationships.

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In more detail, the evolutionary recent changes in the sizes of the different reproductive niches, brought by the transition to post-industrialism, have several implications. To begin with, traits that have evolved to address parental choice and male-male competition reproductive niches are in higher frequency, and traits that have evolved to address the individual mate choice niche are in lower frequency than what is optimal for post-industrial conditions. That is to say, several individuals today have traits that do not enable them to promote their reproductive success, because they have evolved to address different reproductive niches than the ones they can effectively address today. Furthermore, individuals may have traits that have evolved to enable them to address the parental choice and the male-male competition reproductive niches, which may not only be inadequate for addressing the individual mate choice niche but may actually impair individuals' capacity to do so. This issue particularly applies to traits that address the male-male competition niche (see below).

In addition, several individuals may lack the traits that enable them to address the individual mate choice reproductive niche effectively which is now the prevailing one. In most cases, different traits have not evolved to address different niches, but the same traits have been selected to work in a different range, depending on the niche they have evolved to address. For instance, aggression is higher in the male-male competition niche and lower in the individual mate choice niche. Therefore, one way to understand this argument is that many individuals have traits which have been selected to work in a range which is not optimal for modern conditions.

Overall, the industrial revolution, followed by the transition to post-industrialism, has brought a substantial mismatch between ancestral and modern conditions, with many individuals either lacking the traits necessary for meeting the demands of contemporary conditions or having traits that are actually impairing to their mating effort. In the following sections, I will nominate and discuss several of these traits. Before doing so, it is necessary to discuss the importance of the agropastoral revolution for the evolution of adaptations involved in mating.

The Importance of the Agropastoral Revolution

The agropastoral revolution took place approximately 10,000 ago. Human populations started becoming sedentary, cultivating the land and domesticating animals. The environment has changed drastically, triggering considerable evolutionary change. Even so, scholars in evolutionary psychology tend to ignore this period of human evolution as being very short to have significant consequences for the human mind (Tooby & Cosmides, 1990). Yet, evidence indicates that such time period is more than enough for substantial evolutionary change to occur (Cochran & Harpending, 2009).

In particular, humans reproduce slowly; therefore, 10,000 years translates to about 400 generations (Irons, 1998). Experiments with nonhuman animals have demonstrated that 400 generations are more than enough for substantial evolutionary

change to occur. For example, in one experiment, captive silver foxes were systematically bred for tameness by the mating of the tamest individuals of each generation. In 30 generations, foxes were produced that sought human contact and waved their tails when approached (Trut, 1999). In Galapagos finches, a drought resulted in large changes in beak size in only one generation (Weiner, 1995). Grant (1986) estimated that 23 such bouts of evolution could transform one species of finches into another. In humans, Mekel-Bobrov et al. (2005) have shown that a variant of a gene that regulates brain size appeared about 5800 years ago and has swept to high frequency under strong positive selection since then.

The significance of the agropastoral period can be better understood in the context of William Irons' (1998) concept of the adaptively relevant environment (ARE). The ARE of an evolved adaptation consists of those features of the environment that the adaptation must interact with in order to confer a reproductive advantage. An adaptation interacts only with a few selected elements, out of the organism's total environment, in order to confer its reproductive advantage, and different adaptations interact with different features of the environment. When long-lasting changes occur to the environment, those adaptations having changed AREs undergo evolution, while the rest remain the same (Irons, 1998).

The agropastoral revolution brought such a permanent change, namely, the strengthening of parental choice and male-male competition and the weakening of individual mate choice, and this change is likely to have affected the adaptations involved in mating. In different words, following the agropastoral revolution, the parental choice and the male-male competition niches have been expanded, and the individual mate choice niche has been shrunk.

The industrial revolution brought also a permanent change to the ARE of the mechanisms involved in mating, as it has resulted into a considerable weakening of parental control over mating and male-male competition, and an associated strengthening of individual mate choice. Nevertheless, this transition is very recent in evolutionary terms to have been able to eliminate the effects of selection pressures operating during the 10,000 years of pre-industrial agropastoralism. In fact, in many societies where free mate choice is now the norm, regulation of mating was the norm until only a few generations ago (e.g., England; see Stone, 1990). Thus, the transition to post-industrialism is unlikely to have resulted in significant changes in the allele frequencies of the mechanisms involved in mating, so as to optimize them for modern conditions.

Overall, the agropastoral revolution has resulted in changes in the strengths of different sexual selection forces and, consequently, in the size of different reproductive niches. There has been sufficient time for selection forces to affect the allele frequencies for traits involved in mating to be more optimal for these conditions. The post-industrial transition brought also considerable change, but there has not been sufficient time for selection forces to affect the allele frequencies for traits involved in mating to be more optimal for these conditions. Therefore, the allele frequencies of traits involved in mating reflect predominantly ancestral condition optimization, including the last 10,000 years, and they are not optimized for contemporary conditions.

The Role of Mutations in Optimal Functioning and the Agropastoral Revolution

The mismatch between ancestral and modern conditions is one reason why a trait does not work optimally. Genetic mutations are another. In particular, most traits are coded by several genes, with each gene making a small contribution to the trait. For instance, nearly 100 genes could affect skin color (Barsh, 2003). Thus, a fitness-decreasing mutation may experience weak negative selection, as it is likely that it does not have a considerable impact on a trait. The negative fitness effect is additive, which means that an individual who says has ten harmful mutations in a given trait would be worse off in terms of the functioning of this trait than an individual who has only three. To put it differently, a few harmful mutations in a given trait may not make a noticeable difference to its functioning. Yet, above a certain cutoff point of accumulated mutations, the difference would be considerable, causing difficulties to the individual. Accordingly, for any trait, we expect that individuals would vary in the number of harmful mutations they have which would result in a normal distribution of the functioning of a given trait in the population.

The dimensional view of mental disorders (Trull & Durrett, 2005) is consistent with this framework. Mental mechanisms are complex, and, as such, they are coded by many genes. Several individuals have mutations that turn these mechanisms not to work optimally, but still not to the extent of becoming impairing for the individual. Others have more mutations which impair the functioning of mental mechanisms to an extent that they classify as having a mental disorder. For instance, happiness regulation mechanism monitors people's life events and generates happiness when individuals do something that increases their fitness and unhappiness when they do something that decreases their fitness (Apostolou, 2016b). Accumulated mutations on the part of the genome that codes for this mechanism may result in some people becoming depressed or happy without a fitness-affecting reason. As a consequence, the happiness mechanism may not be effective in keeping them in a fitness-increasing path.

It needs to be said that not all genes make an equal contribution to the shaping of a trait, so there is a possibility that a single harmful mutation would have a substantial negative impact to its functioning. In general, however, we expect that the optimal functioning of a given trait would be reversely proportional to the number of mutations in the genes that code for it, with each mutation making a small negative contribution.

There are reasons to believe that the agropastoral and subsequently the industrial revolution has substantially increased the variance of the distribution of genetic mutations, especially for specific traits. As a consequence, the number of people who find themselves above the cutoff point has also increased. In particular, when a population of individuals is introduced in a previously unoccupied environmental niche, it starts increasing until it reaches the maximum capacity of the niche. From that point on, it stabilizes. Nevertheless, from the moment of the introduction until the point of reaching this maximum capacity, the selection pressures exercised on individuals are relative weak. The reason is that there are ample resources available,

and individuals do not have to compete intensively in order to get them. During the period when the selection pressure is relative weak, the number of harmful mutations is expected to rise. To put it another way, when resources are available, an individual with the mutation and an individual without it do not differ much in terms of their fitness; the reason is that they can both get access to resources without having to compete with each other. Yet, when the population starts approaching the maximum allowed by the specific environmental niche, the resources become scarcer. Consequently, the competition between individuals becomes stronger, and the negative selection pressures on fitness-impairing mutations strengthen.

It needs to be added that when selection pressures are relaxed, there may be a strengthening of a positive feedback cycle. More specifically, mutations impair the functioning of individuals' adaptations, reducing their capacity to make an optimal response to the environment. Consequently, these individuals have impaired fitness and, thus, low mate value. Due to the nature of mate choice, individuals are constrained by their own mate value in the mate value of a mate they can attract (see Chap. 2). Thus, individuals with a high mutation load are likely to have as mates individuals of a high mutation load as well, since the latter will have a similar mate value with the former. In effect, people with a high mutation load are likely to mate with people of an equally high mutation load.

The children from these unions have an elevated probability to have also a high mutation load, while some of them are likely to have a higher mutation load than each of their parents. That is, a child may inherit a considerable portion of the mutations of its mother and a considerable portion of the mutations of its father and so may have a higher mutation load than each parent. If selection pressures are relatively weak, this child is likely to survive and eventually mate with an individual of comparative mate value, leading to children with an elevated probability to have a similar or a higher mutation load than their parents. And as this process continues, the mutation load in the population increases. Such process would be constrained in a context where selection pressures are strong, as children with high mutation loads would not survive, but it would be less constrained in a context where selection pressures are weak.

Moreover, strong parental choice and male-male competition, along with weak individual mate choice, can allow a higher mutation load in traits which enable an individual to address individual mate choice. Starting with the former, when male-male competition is strong, men who have a high mutation load in traits which do not relate to male-male competition, but relate to traits which turn someone appealing as a mate (e.g., good looks), can pass these mutations to their children by forcing sex to the women they have monopolized. In a similar vein, parents do not set a high priority on good looks when choosing a spouse for their children (Chap. 9). Thus, individuals with a high mutation load that affects their looks can still be selected as daughters- or sons-in-law, especially if they have other desirable properties such as good family background. These individuals will then have children and will pass their mutations to future generations.

In sum, the technology that brought about the agropastoral revolution made possible the production of more food, which allowed larger population sizes to be maintained. Human populations which made the transition found themselves in a

new environmental niche which allowed for larger populations. In turn, these populations increased in size, experiencing weaker selection pressures (for instance, there was plenty of unexploited land to be farmed). Since agropastoral technology was not static but has been improving, and since the agropastoral revolution occurred recently in evolutionary terms, it is unlikely that these populations would have reached the population cap of the niche. This being the case, one consequence of the agropastoral revolution would be a high mutation load in the population.

In addition, by strengthening parental choice and male-male competition and weakening individual choice, the agropastoral revolution allowed a higher mutation rate on traits that turn an individual appealing as a mate. Since modern populations living in post-industrial societies have emerged from agropastoral societies, it is expected that there would be many individuals who have a high mutation load that affects their fitness. Moreover, it is expected that this mutation load would be especially high over traits that enable an individual to address the individual mate choice niche.

The process discussed above would repeat following the industrial revolution and the transition to post-industrialism. The new technology would relax the competition between individuals by making more resources available, allowing for higher mutation prevalence. The continuing technological process ensures that a population cap is never reached.

Overall, the industrial revolution and the transition to post-industrialism brought not only a mismatch between ancestral and modern conditions but also a higher prevalence of mutant alleles. In combination, these two factors can cause considerable difficulties to individuals in the mating domain. I can now turn to examine the different traits involved in mate choice that may not be able to meet the demands of the contemporary mating market.

Traits Involved in Mating That May Not Meet the Demands of Modern Environment

Mechanisms Regulating Sexual Functioning

Sex is required for reproduction, and, thus, good sexual functioning is of paramount importance to the fitness of an individual. Thus, it is at first a surprise that sexual dysfunctions are in high prevalence in post-industrial societies. More specifically, approximately 30% of adult men and 40% of adult women are considered to suffer from some sexual dysfunction (Lewis et al., 2004; Shifren, Monz, Russo, Segreti, & Johannes, 2008). This high prevalence of sexual dysfunctions becomes less surprising when examined in an evolutionary perspective.

We can consider, for instance, premature ejaculation, the most common dysfunction in men (Lewis et al., 2004; Wincze & Carey, 2001). Ejaculation time varies

considerably from a few seconds to more than 30 min following the initiation of intercourse (Waldinger, McIntosh, & Schweitzer, 2009). A substantial proportion of men ejaculate on average in less than 2 min following the initiation of intercourse, while there are many men who ejaculate in less than a minute after the initiation of intercourse (Waldinger et al., 2005). These prevalence rates raise the question why a predisposition for quick ejaculation, which limits the capacity of a man to provide sexual satisfaction to his partner, exists in such a high frequency in the population. The answer I put forward is that in an ancestral context, where parental choice had been strong and female choice weak, negative selection pressures on the predispositions to ejaculate soon after the initiation of intercourse had been weak. Since the sexual satisfaction of women had been a secondary concern, the fitness of a man with a predisposition to ejaculate soon after the initiation of sexual intercourse was not much different from the fitness of a man with a predisposition to ejaculate later on. Consequently, both predispositions are likely to have remained in the population, resulting in the variation we observe today (Apostolou, 2015a).

Furthermore, ejaculating soon after penetration is likely to be optimal for men who address the male-male competition reproductive niche. In this niche, the sexual satisfaction of women is irrelevant; yet, when men engage in a raid and force sex to the women of their opponents, delaying ejaculation means more time having sex, which may turn a man vulnerable to attacks. The relative high size of this niche in the ancestral past suggests that many men today carry the predisposition for quick ejaculation following penetration.

Turning to women, almost one in two women classify as suffering from hypoactive sexual desire (Shifren et al., 2008). Sexual desire is regulated by a specific mechanism which has evolved to motivate women to seek sex (Toates, 2014). In ancestral context, where women were exchanged between men as a reproductive commodity and husbands could force sex to their wives at will, the degree of sexual desire of a woman had little fitness consequences for her reproductive success. Thus, a woman who had low sexual desire would not differ considerably in fitness from a woman who had a higher sexual desire. That is to say, both women would have sex (willingly or less willingly) and would have children who would pass their predispositions to future generations. This is one of the reasons behind the high variation in the sexual desire contemporary women experience (Apostolou, 2016f).

To put everything together, the mechanisms involved in sexual functioning have been shaped by selection forces to work in a range which is optimal for ancestral pre-industrial societies and not for modern post-industrial ones. A proportion of this range is not optimal for modern pre-industrial conditions, as mechanisms working in this range cannot meet the demands of a free mate choice context. We have labeled this range of functioning as dysfunctional, although in the majority of the cases, such label does not reflect a mechanism not working properly, but a mechanism working as it should for the environment where it originally evolved and which is different from the environment in which it now needs to function.

Personality

Personality predicts many aspects of human interaction, including intimate relationships (Buss & Hawley, 2010). As personality traits have been shaped by selection forces operating in ancestral environments, it can be the case that several of these traits may impair the formation of intimate relationships in contemporary environments. For instance, traits such as introversion and shyness can be disadvantageous where individuals have to find mates on their own, but would have had few or even no negative fitness consequences in a context where marriage was the product of negotiation between families. Similarly, a need for intimacy, in a free mate choice context, constitutes an important prerequisite for establishing and maintaining a long-term, intimate relationship. For example, narcissists have a low need for intimacy, which make them less motivated and less willing to recognize and address the shortcomings of their character in order to make the formation of long-term intimate relationships possible (Campbell & Miller, 2011). A strong need for intimacy, however, was not a primary requirement for establishing and keeping a relationship, when the purpose of marriage was to establish a useful alliance between families.

In effect, evolutionary pressures on specific aspects of personality, such as shyness and need for intimacy, are weak in a context where mate choice is regulated. Such weak pressures translate into selection forces allowing more variation in these traits, as alleles that predispose for, say, a high level of shyness are not in a disadvantageous position (see Crespi & Vanderkist, 1996; Fisher, 1958). Part of this variation may, nevertheless, be dysfunctional in a free-mating context (Apostolou, 2016a). For instance, in an ancestral setting, introverted or shy individuals would find themselves married to spouses that their parents have selected for them, whereas in a post-industrial context, where they have to actively seek and find their own mates, they are likely to remain single for a prolonged period of time.

Furthermore, in the ancestral context, the male-male competition niche had been large. This reproductive niche requires specific personality traits in order to be addressed, including high aggression and low empathy. Peaceful men high in empathy would not be particularly effective in killing other men in order to get their women. These traits are therefore expected to have been favored by selection forces and to appear in the male population in high frequency. Nevertheless, the considerable reduction in the size of male-male competition reproductive niche in modern societies makes these traits no longer useful in men's reproductive effort. Actually, the opposite is likely to be true: These traits are impairing for gaining reproductive success. Men who score high in aggression and low in empathy are unlikely to be considered desirable mates and may face difficulties in participating effectively in the mating market (Apostolou, 2016a).

In sum, personality traits have been shaped by selection forces in a context where the parental choice and the male-male competition reproductive niches had been large. Accordingly, many individuals today may find themselves with personality dispositions that prevent them from addressing the individual mate choice niche, which is the dominant one.

Looks

One domain where parents and children disagree when it comes to the latter's mate choices is looks, with children ascribing more emphasis to this trait than their parents (Apostolou, 2014). This difference in preference suggests that in a context where parents control mate choice, good looks are much less important than in a context where individuals choose their own mates. In the same vein, good looks are not required for men addressing effectively the male-male competition niche.

Accordingly, individuals who address the parental choice and the male-male competition reproductive niches do not need to have especially good looks. As these niches had been large in ancestral human societies, mechanisms involved in regulating the attention individuals ascribe to their appearance have experienced weak selection pressures. This would also be the case for specific body traits that enhance good looks, such as large breasts in women.

Consequently, selection forces are likely to have allowed considerable variation in these traits, but much of this variation is not optimal for a context where individuals choose their own mates and place considerable emphasis on looks. Thus, several individuals today may be predisposed to pay little or no attention to their looks. For instance, they may care little about their clothing, hair, etc. In addition, several individuals may find themselves having physical traits such as a not well-shaped body, which impairs their looks. These traits may have had little importance in ancestral mating market, but may prevent individuals to participate effectively in the contemporary mating market.

Mate Preferences

Mate preferences are mechanisms that have evolved to guide mate choice (Buss, 2003). Yet, these mechanisms have evolved to do so in a context where mating decisions were largely determined by parents. In effect, these mechanisms may have been shaped so as to influence parental choice in a way that would lead to children getting more optimal mates. For instance, parents value beauty less in a mate for their children than their children in a mate for themselves (Apostolou, 2014). If children have a strong preference for beauty, this preference would constrain parents in making substantial compromises on this trait, as they would consider the fierce reaction of their children. Therefore, what is optimal for children is to value beauty more than it is justified by the benefits accrued from this trait, so as to get mates with beauty closer to the justified benefits.

Nevertheless, when parents are out of the picture, which is the case in a post-industrial context, such preferences may not be optimal to guide mate choice. That is to say, mate-seekers may tend to overemphasize beauty, and as a consequence, they would compromise more than it is optimal on other traits. To put it another way, mate-seekers may go after and spend much energy attracting mates who are

high scorers in beauty but poor scorers in other dimensions such as specific personality traits, working ability, social standing, etc., ending up with attractive mates who have nevertheless poor prospects for establishing a long-term relationship and raising a family.

In a similar vein, when male-male competition is strong, it may pay for women to prefer as husbands men who are physically strong and have personality traits such as dominance, aggression, and low empathy. Although these men may be abusive, reducing the fitness of women, they can protect them from being taken or raped by other men, which can balance this cost. Thus, in post-industrial societies, several women may be attracted to the "macho"-type men, only to find out that such men may not be appropriate for long-term partners, as they can be abusive and unpleasant to be with, while the protection they can provide is not needed since male-male competition is very weak and individual rights are well protected.

Pursuing Optimal Mates

Getting a fitness-increasing mate requires assessing one's own mate value and the mate value of prospective mates. Yet, selection pressures exercised on these mechanisms would have been weak during most of human evolutionary time, predominantly because much of the decision-making process had been undertaken by parents. In effect, considerable variation would have been allowed by selection forces that would not be optimal for the modern context (Apostolou, 2015a). As a consequence, several people today may overestimate or underestimate their own or their prospective partners' mate value. Doing so can result in diverting their mate effort toward individuals who are not attainable, e.g., toward mates who far exceed their own mate value. On the other hand, people may tend to accept mates who are far below their own mate value, suffering the fitness opportunity cost coming from the higher quality mates they could get but they do not. In sum, a considerable proportion of people today may not make optimal choices with respect to where they direct their mating effort, resulting in reduced reproductive success.

Screening Mates

As children's mate choices involve a considerable converging opportunity cost for parents (Chap. 3), when parents exercise in-law choice, they would employ mechanisms such as in-law preferences that would enable them to screen prospective mates for those who can potentially be harmful for the wellbeing of their children. During most of the period of human evolution, parents exercised considerable influence over their children's mate choices (Chap. 7), which means that they would have screened and selected out individuals who could potentially harm their children.

As a consequence, the selection pressure on children to do the screening themselves had been weak, as they would have relied on their parents to do the screening for them. Thus, children may not have evolved refined screening mechanisms that would enable them to select out individual who can harm their fitness (Apostolou, 2015a). In ancestral societies, this was not a problem as the choice of a mate, and thus the screening, was made by parents. It is a problem, however, in a modern context, where parents are out of the picture and children have to choose mates for themselves. Children may lack reliable screening mechanisms, which means that they may end up being with mates who can harm them or abandon them and, in general, with mates who are not fit to engage in a long-term intimate relationship.

Parents usually exercise more control over their younger than over their older children (Apostolou, 2014). Accordingly, the selection pressures for evolving reliable screening mechanisms are higher in younger than in older individuals. This argument suggests a developmental trajectory, where the screening mechanisms develop and work better in older than in younger individuals. On this basis, it can be predicted that younger individuals will be more prone to make erroneous choices than older ones.

Mating Effort

Getting a mate requires considerable effort, but the type of effort required in a post-industrial context is different from the one required in a pre-industrial one. In particular, in pre-industrial societies, individuals do not have to pursue prospective mates directly, as spouses come from their parents. Things are different, however, in post-industrial societies. Mates are not provided by parents, but individuals have to find mates on their own. Individuals' motivation mechanisms may not have been optimized to enable them to put the mating effort necessary to find a mate in a post-industrial context. Accordingly, several individuals living in post-industrial societies today may not make the mating effort required to attract a mate (Apostolou, 2015a). For instance, they may have other priorities, putting their effort and resources there instead in seeking a mate, and stay single as a consequence.

A similar argument can be made for keeping a relationship. Although divorce is present in almost all pre-industrial societies (Murdock, 1981), there are reasons to believe that it is not as common and as easily obtained than it is in post-industrial societies. In the latter context, people can rely on their salary and the welfare state to provide for their needs and not on their spouses and families, something which is not the case in the former. In effect, individuals in post-industrial societies are less constrained in the financial consequences of terminating a long-term relationship than individuals in pre-industrial societies; accordingly, they are more likely to initiate divorce if they are not satisfied from a relationship. In turn, more effort is required in order to keep an intimate relationship, as motivational mechanisms may not have been optimized for doing so, because this was not necessary in ancestral

pre-industrial societies. As a consequence, several individuals today may not put the necessary mating effort required to keep a long-term intimate relationship, facing in effect difficulties in keeping such relationships.

Status-Seeking Among Men

Status-seeking can be considered to be a special case of mating effort in men, which may not have been properly optimized for modern conditions. More specifically, in an ancestral context, men would usually receive women from other men through arranged marriage. Successful men, such as chiefs, would receive more than one wife and would marry polygynously, while less successful ones would receive one or even none (Zeitzen, 2008). To put it differently, in order to address effectively the parental choice niche, ancestral men needed to impress and appeal as sons-in-law to other men. One way to do so was to climb up the social status hierarchy. For instance, in pre-industrial societies, high-status men, such as chiefs, would receive women from other men who wished to form an alliance with them (Apostolou, 2014).

Thus, in a pre-industrial context, allocating considerable effort in order to climb the status hierarchy would constitute effective mating effort: The more time a man would allocate to go up, the higher up he would go and the more women would come in his way. Doing so may not work equally well in a post-industrial context however. In particular, high social status is considered a highly attractive trait by women in men (Buss, 2003). Nevertheless, for this trait to be useful in the mating market, men need to actively pursue women, something that was not necessary in the ancestral mating market. Therefore, many men may be predisposed to be too focused on their careers and in doing things to increase their standing among other men, leaving little time to allocate in pursuing women. In an ancestral setting, these predispositions might have led to polygyny, but in a modern setting, they may lead to stay single.

Jealousy and Aggression

Jealousy manifested in intimate relationships is a mechanism that has evolved to enable individuals to guard their mates and protect themselves from losing them to others or raising other people's children (Buss, 2000). For instance, jealousy may motivate behavior that turns infidelity costly for a partner. In particular, physical aggression against one's partner, coming usually from bouts of jealousy, has been hypothesized to be an adaptation that enables men to restrict their intimate partners' sexual behavior (Buss, 2000; Goetz, Shackelford, Romero, Kaighobadi, & Miner, 2008). Such aggression makes sexual infidelity costly to women, reducing their motivation to cheat, protecting in effect men from being cuckolded. In a pre-industrial context, where mate choice is regulated and the interests of the family come first and where additionally individual rights are not well protected, such

aggression may be a relatively successful strategy. Parents are also likely to tolerate it, as long as it is not particularly harmful for their daughter, because her husband is usually their choice. Moreover, if she would engage in extramarital relationships with men of her own choice, she would put at risk the marriage that they had arranged.

On the other hand, in a post-industrial context, where mating is not regulated, the individual rights are well protected and family alliances are less important, physical aggression may be a less successful strategy for ensuring paternity. This is because women have low tolerance for aggressive behavior from their partners (Bowlus & Seitz, 2006). Thus, although an adaptation which predisposes to physical violence against one's partner may decrease the risk of raising somebody else's children, it is also likely to increase considerably the chance of the relationship failing.

Desire to Settle Down and Have Children

Mechanisms such as a desire to settle down and have children have evolved to motivate individuals to have a family. In a pre-industrial context, such a strong motivation was not necessary, as individuals had much less of a freedom to opt out from the family-making process: Their marriages were arranged, and subsequently they would have unprotected sex that would usually have resulted in children. Accordingly, in order to address the parental choice niche, a strong motivation to settle down and to have children was not that necessary. In different words, selections forces would not be particularly strong on these mechanisms, allowing considerable variation in the range that they work. As a consequence, many individuals today may experience a weak desire to settle down and have children, or they may experience such a desire at a later age, when doing so is difficult or impossible. In a modern pre-industrial context, such desire is likely to compromise reproductive success, which in turn may have negative consequences for the individuals' wellbeing (Apostolou, 2016b).

Poor Flirting Skills

In a free mate choice setting, refined flirting skills are required to enable an individual to attract mates. Such skills are much less necessary in a context where parental choice and male-male competition dominate, i.e., good flirting skills are not required for appealing to parents or for monopolizing access to women by force. Accordingly, during human evolutionary time, selection pressures to refine flirting skills had been weak. As a consequence, a large number of people today lack good flirting skills and thus face difficulties in approaching other individuals with the purpose of mating.

Poor Lovemaking Skills

In addressing the male-male competition reproductive niche, refined lovemaking skills are not required. Actually, a tendency to have sex with a woman as soon as possible would be the optimal disposition. Such a disposition is not optimal nevertheless for addressing the individual mate choice niche. Thus, men with such dispositions may rash to have sex with their partners without foreplay, reducing in effect the sexual satisfaction the latter receive and increasing the chances that the relationship fails.

In a similar vein, since providing sexual satisfaction is not a concern in male-male competition niche and it is not the highest priority in the parental choice niche, selection pressures on the penis to be of a size that provides good sexual satisfaction had been weak. To put it another way, the range of sizes that would not cause fitness issues to men would be extensive, allowing for an extensive variation in size. Male penis' size exhibits considerable variation, with some of this variation not providing adequate sexual satisfaction to women, i.e., the penis is too small or too large. This is not much of an issue in a context where the dominant reproductive niches are the parental and male-male competition ones, but it is a problem in a context where the dominant niche is the individual mate choice (Apostolou, 2016c).

Similarly, as discussed above, high sexual desire has not been necessary for women to have sexual intercourse in the ancestral pre-industrial setting, which means that several women today may experience low sexual desire, which in turn can impair their capacity to provide sexual satisfaction to their partners. Also, because men could have sex with their female partners at will and would be relatively free to do as they wished, the selection pressure on women to develop refined lovemaking skills had been weak, resulting into several women today lacking them. Since in a post-industrial context a man cannot force his way to his partner, the latter's lovemaking skills become more important. Lack of such skill decreases the sexual satisfaction and increases the probability of the termination of a relationship.

Mutation Load

In the sections above, I nominated several mechanisms involved in mating which may not work optimally in a modern context due to the mismatch between ancestral and modern conditions. As discussed previously, these mechanisms may suffer from high mutation loads, which add to their poor performance. Maladaptive mutations may have accumulated in these mechanisms, because negative selection pressures on them had been weak. Accordingly, the combined effects of high mutation load and the mismatch between ancestral and modern conditions can augment further the difficulties that contemporary individuals face in intimate relationships.

Further Insights

The evolutionary framework developed in this book can also enable us to understand a range of additional phenomena related to mating. In the paragraphs that follow, I will examine briefly same-sex attractions, rape, and sports.

Same-Sex Attractions

Attraction to the opposite sex is a mechanism that enables individuals to address all reproductive niches: It motivates people to appeal to parents so as to gain reproductive access to their offspring, to fight other men and monopolize access to women, to pursue mates and persuade them to establish an intimate relationship with them, and to force sex to women. Given that this mechanism enables individual to address all niches, we would expect that almost all individuals experience heterosexual orientation. This prediction is partially confirmed: About 90% of individuals classify themselves as being attracted predominantly to opposite sex partners (heterosexual) (LeVay, 2010). However, a small percentage of individuals classify themselves as being attracted to both sexes (bisexual) and as being attracted mainly to the same sex (homosexual) (LeVay, 2010; Savin-Williams, Joyner, & Rieger, 2012). Furthermore, a considerable proportion of individuals experience varying degrees of same-sex attraction, although they have a heterosexual orientation (Calzo, Masyn, Austin, Jun, & Corliss, 2016; LeVay, 2010). These observations lead to the question why selection forces have not eliminated any dispositions for same-sex attraction from the population.

One possibility is that same-sex attractions have little consequences in addressing the parental choice niche, especially for women (Apostolou, 2016d). For instance, women are given by their parents in marriage to men, who can force sex to them at will (Apostolou, 2014). Thus, whether a woman experiences same-sex attractions or not is inconsequential for her reproductive success. In different words, selection pressures in ancestral human societies, where mate choice was regulated, had been weak on alleles that predispose for same-sex attractions, resulting in them to be in a relative high frequency in contemporary populations.

Another, not mutually exclusive, possibility is that same-sex attractions enable individuals, particularly women, to better address the individual mate choice niche (Apostolou, 2016e). In more detail, men face the problem of parental uncertainty; thus, if their partners experience same-sex attractions, they will divert part of their mating effort to same-sex outlets which reduces the chances of cuckoldry. Accordingly, men find the same-sex attractions of their partners desirable, which means that women who experience such attractions may better address the individual mate choice niche, i.e., by being more likely to keep a partner than women who do not experience such attractions.

I have also argued that homosexual orientation in men can be fitness-increasing if certain conditions are met, i.e., if they live in an agropastoral mate context and have several older brothers. In such a context, inheritance rules favor the firstborn sons (Apostolou, 2013a). Latter-born sons are usually left with little wealth to inherit, which compromises their chance to establish a good marriage. As a consequence, conflict is likely to arise between brothers for access to their family's resources. A homosexual younger brother will not have such conflict, which increases his inclusive fitness, while he can still be given to marriage by his parents and procreate, even if the marriage deal is not that good. In this respect, male same-sex orientation may have started increasing in prevalence following the agropastoral revolution (Apostolou, 2013a).

Note that the above arguments are not mutually exclusive. Strong parental choice reduces the fitness costs of same-sex attraction, while the reduction in paternal uncertainty and the reduction in conflict within the family increase its fitness benefits.

The puzzle of same-sex attraction has not yet been resolved, but the theoretical perspective developed in this book can provide several useful insights that can contribute to its solution.

Rape

The presence of sexual coercion reproductive niche indicates that specific mechanisms have evolved to enable individuals to exploit it. It has been argued that rape has evolved to enable men to circumvent female choice (Thornhill & Palmer, 2000). In the theoretical framework developed in the current book, this strategy has evolved to enable men to bypass parental choice as well as female choice. Given that parental choice was stronger than female choice in the ancestral past, it can be further argued that this strategy has evolved to enable men to predominantly circumvent parental choice (Apostolou, 2013b).

A further insight that can be derived from this perspective is that the presence of the forced-sex mating strategy exercises selection pressures on women and on their parents to evolve ways to protect their daughters and themselves, respectively. The pressure would be predominantly on parents who can evolve, for instance, strategies such as chaperoning their daughters. When parents are out of the picture, women's self-protection mechanism may not be adequate for protecting them from falling victims of rape.

Sports

Across different times and across different cultures, people exhibit considerable interest in taking part and in watching athletic competitions (Guttmann, 2004). Competing in sports and watching sports involve substantial resources, including

energy, money, and time. The fitness benefits of doing sports that balance these costs are not well understood, as it is not well understood why sports constitute mainly a male interest: Those competing and those watching are predominantly men (Guttmann, 1986, 2004). The proposed evolutionary framework can enable us to make sense of these patterns.

In particular, in ancestral times the parental choice and the male-male competition niches were dominant. In the former, men have to impress other men in order to choose them as sons-in-law, and in the latter, they have to signal to other men that they will be valuable allies to be preferred and dangerous opponents to be avoided. Athletic competitions can assist men in doing so. They can enable men to signal in a reliable fashion their athletic qualities to an interested audience, composed of men who look for spouses for their daughters and of men who look for potential allies to be preferred and enemies to be avoided (Apostolou, 2015b; Apostolou, Frantzides, & Pavlidou, 2014; Lombardo, 2012). In different words, a preference for doing sports has evolved because it enables men to address the parental choice and the male-male competition niches. A preference for watching men competing has evolved to enable men to address the male-male competition niche and to enable men to find fitness-increasing sons-in-law.

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Conclusion

The study of sexual selection is fascinating—sexual selection drives the evolution of complex adaptations which enable an individual to gain and to maintain access to the reproductive capacity of the opposite sex. Accordingly, theoretical biologists, evolutionary psychologists, and other evolutionary-minded scholars have placed considerable effort in studying this selection force and its consequences. Such efforts have produced a wealth of evidence that has increased considerably our understanding of how sexual selection works. Surprising however, almost all scholars have neither acknowledged nor studied the unique aspects that this force exhibits in the *Homo sapiens* species: In humans, sexual selection has an additional component force, namely, parental choice.

The failure to acknowledge parental choice as a sexual selection force is even more surprising in the light of the fact that, for several decades now, there has been detailed evidence from the anthropological record which indicates that mate choice in a pre-industrial context is regulated, with parents choosing spouses for their children. This evidence indicates further that parental choice is not just a simple component force but a primary force driving sexual selection.

Consequently, although we know much about the workings of sexual selection in non-human sexual reproducing species, our knowledge is incomplete about its workings in own species, mainly because there has been a considerable gap in understanding parental choice. In my work, I aimed to close this gap, and this book has attempted to synthesize and advance this effort. Accordingly, in Chap. 1, I examined the interrelation between different sexual selection forces and how parental choice is related to them. One major insight from this chapter is that selection forces are not independent, and when the strength of one changes, the strength of the others is likely to change as well. This area needs more theoretical and empirical work, especially in order to understand sexual coercion and how it relates to other selection forces.

Parent-offspring conflict over mating is the primary factor which gives rise to parental choice; thus, in Chap. 2, I attempted to demonstrate why parents and children have conflicting interests over mating and how this conflict motivates the

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former to control the mate choices of the latter. The important insight of this chapter is that the difference in genetic relatedness between parents and their children turns profitable for the former to place under control the latter's mate choices. Although the idea that parents and children have conflicting interests over mating is not new, researching it is. But despite being recent, I believe that we currently have a good understanding of this phenomenon, and I do not expect that future research will change considerably the conclusions reached in this chapter.

Chapter 3, where a formal model of parental choice is presented, constitutes the core of this book. The basis of this model is that the degree of genetic relatedness between parents and children results in the two having diverging as well as converging interests over mating, which, in turn, give rise to an opportunity cost that parents are to suffer if they leave their children to exercise mate choice on their own. This opportunity cost motivates parents to control the mate choices of their children, and such control gives rise to the parental choice sexual selection force. The main insight here is that, if parents do not control their children's mate choices, they are likely to suffer a considerable opportunity cost. I believe this model constitutes a good basis for understanding parental choice and its contingencies, but I expect that future work will be able to expand and revise it, producing a more refined and accurate formulation.

In Chaps. 4, 5, and 6, I examined how this model can account for the matting patterns found across different society types. In Chaps. 4 and 5, I demonstrated that parental choice constitutes a primary sexual selection force in pre-industrial societies, while in Chap. 6, I demonstrated that in post-industrial societies, it constitutes a secondary, but still a significant, sexual selection force. One important insight from these chapters is that the opportunity cost of free mate choice, and thus the strength of parental control over mating, changes across societies of different subsistence type. I believe that more cross-cultural studies in pre-industrial context would be useful in providing additional support for these arguments, but I do not expect their findings to diverge from the conclusions reached in these chapters. Still, much more cross-cultural research is needed in order to understand parental choice in a post-industrial context.

In Chap. 7, I made the argument that the evidence from the anthropological and historical records indicates that parental choice had been a dominant sexual selection force in ancestral human societies. The main insight of this chapter is that parental influence over mating has been present throughout human evolutionary time. I believe that this is an important insight, because it indicates that parental choice had an important role in shaping several of the adaptations involved in mating that we carry with us today. I think that this argument is solid, but additional historical and phylogenetic studies can strengthen it.

The anthropological and historical records indicate that there is substantial variation in the mating patterns found across societies of the same subsistence type. For instance, even though parental choice is strong in pre-industrial societies which base their subsistence on agropastoralism, there are societies of this type where this force is relatively weak. Accordingly, in Chap. 8, I attempted to examine whether the model of parental choice can provide insights that may account for this variation.

I also took a step further, and I attempted to examine whether the model can provide insights about the variation within a given society, in particular, why parental choice is stronger in certain social layers than in others. The primary insight is that opportunity cost of free mate choice, and thus the strength of parental control over mating, changes between and within societies of the same subsistence type. This chapter constitutes a good introduction and provides an incentive to start asking questions about variation in strength of sexual selection within and between societies of the same subsistence type. Considerable more theoretical and empirical work is required however for advancing this domain of inquiry.

If the effect of parental choice in driving the evolution of adaptations is to be understood, understanding first what parents want in an in-law is necessary. Accordingly, in Chap. 9, I have summarized the different research efforts on in-law preferences. The key insight of this chapter is that selection forces have endowed parents with well-refined preferences to guide their in-law choices. Although future studies can contribute in this domain, I believe that currently we have a good knowledge of in-law preferences. Moving on, in Chap. 10, I nominated several adaptations which are likely to have been shaped by parental choice. The main insight of this chapter is that parental choice has been important in shaping the human mind. This chapter is to a considerable degree speculative, and future work needs to advance our knowledge of the consequences of parental choice on human adaptations.

There are good reasons to believe that parental choice has contributed considerably in shaping several adaptations involved in mate choice. There are also good reasons to believe that parental choice had been stronger in ancestral pre-industrial societies than in contemporary post-industrial ones. This mismatch between ancestral and modern conditions is likely to result in several difficulties, as adaptations are likely to have evolved to work well in a context where mate choice is regulated, so they may not work equally well in a context where it is not regulated. This argument was explored in Chap. 11. The key insight is that a considerable part of observed maladaptive human behavior in the mating domain can potentially be explained by the mismatch between ancestral and modern conditions. This is a vast topic which can increase our understanding of certain aspects of normal and abnormal human behavior. It has also an important potential in enabling us to identify the adaptations which do not work optimally in a modern context and provide counseling or treatment that would enable individuals to become more successful in the domain of mating, increasing in effect their well-being.

Chapters 10 and 11 demonstrate the usefulness of evolutionary theory in understanding behavioral phenomena. This usefulness has been understood by scholars several decades ago, giving rise to the field of evolutionary psychology (Tooby & Cosmides, 1990). In evolutionary psychology, the evolutionary theory guides research on human behavior. But the evolutionary theory has been developed predominantly on research on non-human animals, so it does not take into consideration the peculiarities of the human species and the behavior of its members evolutionary psychologists try to explain. This issue has led to many claims such as that a large part of the human brain has evolved to enable individuals to flirt each

other (Miller, 2000). Yet, these claims are unfounded in the light of empirical and theoretical evidence on the ancestral human condition. Thus, there is potentially a great benefit in employing an evolutionary framework which takes into consideration the peculiarities of evolutionary process in our species.

Sexual selection under parental choice is a complex phenomenon, and not all of its facets have been explored in this work. One such facet is parents-parents competition: Parents strive to form the best alliances and find the best in-laws to integrate to their family. Thus, there is competition between parents of different families which means that there would be selection pressures that can give rise to mechanisms that enable parents to succeed in this competition. Mechanisms of this kind may include adaptations which enable parents to remove from the competition other parents, for instance, by spreading negative rumors about other families or by intimidating other families. Given that male parents are usually the primary decision-makers in marriage arrangements, these mechanisms are likely to be expressed predominantly in older men.

There are additional factors which play a role in understanding the strength of parental choice, which need to be identified and integrated to the parental choice model. For instance, the strength of parental choice is expected to be dependent on the extent of infidelity prevailing in a given environmental context. If parents choose spouses for their children and their children cheat on their spouses with individuals of their choice, doing so will undermine parental control over mating and the strength of parental choice as a sexual selection force. Last but not least, I have not addressed the issue why parental choice is not found in other species. I have done some speculation on this subject in a different publication (Apostolou, 2011); yet, in terms of the theoretical framework developed in this book, it can be argued that parental choice is not found in other species because the opportunity cost of free mate choice is zero or very low—thus, there is no sufficient selection pressure to motivate parents to control their offspring's mate choices. There may be many reasons for the absence of opportunity cost, including that sexually mature individuals are independent from their parents for their subsistence and they are equally or physically stronger than them. More theoretical work is required to explain why parental control over mating is unique in humans.

This book has been an attempt to increase our understanding of how sexual selection works in our species. It has to be said, however, that almost all of the arguments made in this book can be improved, refined, and extended, while some of the arguments need to be dropped if they are not validated by empirical research. Yet, this is expected as the argument of parental choice being an important sexual selection force has only being recently introduced, while most research attempts on sexual selection are focused on non-human sexual reproducing animals. The time is ripe now for research efforts to shift from extrapolating findings from other species to humans, to study sexual selection specifically in humans—human mating has several unique aspects, and consequently, the method of understanding sexual selection by extrapolation is not the most appropriate one.

To conclude, I hope that this book will contribute toward increasing our understanding of the working of sexual selection in our species. I also hope that it will

motivate evolutionary-minded scholars to place parental choice in their research efforts. Doing so will enable the derivation of more solid hypotheses about the evolution and the workings of human adaptations involved in mating.

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Appendix 1

In Apostolou (2011) study, children and their parents were given three different budgets of mate points to allocate to eight desirable traits, including good looks and good family background, in a prospective mate and daughter- and son-in-law, respectively. Assuming that good looks constitute a proxy of good genetic quality, and by making certain assumptions about the fitness contributions of genetic quality and good family background, I can employ formulation (2.3) from Chap. 2 in order to estimate the fitness cost that children's allocations inflict to parents. More specifically, let's assume that good genetic quality is twice as beneficial to children as it is to their parents, while good family background is half as beneficial to children as it is to their parents, so that a = 1, b = .5, c = 0.5, and d = 1. Substituting these values in formula (3), we get:

$$(a-c)G+(b-d)F=0.5G-0.5F$$

Now, I can take the actual allocations that children made in the Apostolou (2011) study. As an example, I am going to employ the allocations that children made for a prospective spouse in the medium budget—this budget can be considered to represent an average mate-seeker. In this scenario, children allocated an average of 4.71 mate points to good looks and 3.08 mate points to good family background. Substituting these values to the formula, we get:

$$0.5^{*}(4.71)-0.5^{*}(3.08)=0.815$$

The 0.815 represents the fitness cost to parents due to the allocations their children chose to make on these traits. Future work that will estimate the contributions that each trait makes to the fitness of each party (i.e., a, b, c, and d) will enable more precise calculations.

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Appendix 2

The Apostolou (2011) study gave parents and children three different budgets of mate points to allocate to different traits. The low budget had few mate points depicting a mate with low mate value, the moderate budget had more points depicting a mate of moderate mate value, and the high budget had even more points, depicting a mate of high mate value. Accordingly, this design can enable us to examine the hypothesis that the cost inflicted to parents is reverse U-shaped. More specifically, for each budget, I estimated the fitness cost inflicted to parents by the allocations of daughters and sons using formulation (2.3) from Chap. 2. I have made similar assumptions as in Appendix A about the fitness contributions of each trait, and I assumed further that good looks constitute a proxy of genetic quality.

Accordingly, children in a low budget allocated an average of 2.42 mate points to good looks and 1.45 mate points to good family background, so the formulation (2.3) from Chap. 2 becomes:

$$0.5^{*}\left(2.42\right)-0.5^{*}\left(1.45\right)=0.485$$

In the medium budget, they allocated 4.71 mate points to the good looks and 3.08 mate points to the good family background so that:

$$0.5^{*}\left(4.71\right)-0.5^{*}\left(3.08\right)=0.815$$

In the high budget, they allocated 6.28 mate points to good looks and 5.13 mate points to good family background so that:

$$0.5^{*}\left(6.28\right)-0.5^{*}\left(5.13\right)=0.575$$

We can see that the results of these calculations fit the prediction that the fitness cost inflicted to parents is a reverse U-shaped function of children's mate value. As we move from low to medium budget, the fitness cost increases, whereas as we move from medium budget to high budget, the fitness cost decreases.

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Appendix 3

In order to examine whether trade-offs result in more conflict between parents and sons than between parents and daughters over genetic quality, I employed data from the Apostolou (2011) study. Similar to Appendix 1, I assumed that good looks constitute a proxy of genetic quality, and I made also the same assumptions about the fitness contribution of each trait.

In the presence of trade-offs, daughters and their parents have to discount the loss in parental investment coming from the good genetic quality. In different words, the fitness contribution that the (G) makes is lower when trade-offs are present. Let's assume that trade-offs reduce the fitness contribution of (G) by 10% so that a = 0.9 and c = 0.45. Accordingly, the fitness cost to parents from the mate choices of their daughters is:

$$0.45(\mathrm{G}) - 0.5(\mathrm{F})$$

Furthermore, since $a_{sons} > a_{daughters}$, we would expect that sons would allocate more mate points to the good genetic quality than daughters. This is consistent with the evidence from Apostolou (2011) budget allocation study. In each budget level, sons allocated more mate points to good looks than daughters. I estimate the relative fitness costs to parents for the medium budget as follows:

Daughters allocated 3.88 to good looks and 3.1 to good family background so that:

$$0.45^{*}(3.88) - 0.5^{*}(3.1) = 0.196$$

On the other hand, sons allocated 5.53 mate points to good looks and 3.05 mate points to good family background so that:

$$0.5^{*}(5.53) - 0.5^{*}(3.05) = 1.24$$

As 1.24 > 0.196, we can see that the fitness cost that parents suffer is higher in the case of sons than in the case of daughters.

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Appendix 4

a	The level of available resources in a given contextb The benefit parents receive, in terms of desirable traits when they control mate choice which is over and above the benefit they would get if their children were to exercise choice on their own
c	The cost that children suffer when their parents control their mating decisions
d	Parents' capacity to inflict a cost to their children in order to align them with their will
e	The degree of children's dependence on their parents' resources
ex	The experience of children when they engage in mate-seeking
f	The potential of (b) to be converted into fitness benefits
h	The cost that parents can impose on their children by applying physical force
i	The cost that parents can impose on their children through social institutions
int	Children's intelligence
j	The psychological cost that parents can impose on their children
k	The risk that children face to make mistakes when they exercise mate choice that their parents are less likely to make if they were to exercise choice for them
l	The risk of not being able to attract a mate that a child faces
m	The strength of parental control over mating
n	The impact that an erroneous mate choice will have on children
$o_{converging}$	The opportunity cost of free mate choice coming from converging interests between parents and children
$o_{diverging}$	The opportunity cost of free mate choice coming from diverging interests between parents and children
p	The probability that one is actually an individual's genetic relative
pe	Children's personality traits which predict the quality of their mate choices

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q	The cost parents suffer when they inflict a cost to their children
r	The degree of genetic relatedness
$\bar{r}$	The degree of genetic relatedness (r) multiplied by the probability (p) that one is actually an individual's genetic relative
s	The personality traits of a child that negatively influence success in attracting a mate
v	An individual's mate value
w	Parental resources which are diverted to children in the form of parental investment
s	The personality traits of a child that negatively influence success in attracting a mate

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