### Menelaos Apostolou

# 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 postindustrial 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 postindustrial 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 inlaw, 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.

Nicosia, Cyprus

Menelaos Apostolou

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#### **About the Author**

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#### 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. 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