

CHAPTER 4

SEXUAL SELECTION, GOOD GENES, AND HUMAN MATING

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Abstract. Sexual selection is selection due to differential access to quantity and quality of mates. One form of it, intersexual selection, is due to differential access to mates driven by the mate preferences of individuals of the other sex. The major question about sexual selection pursued in theoretical investigation during the past two decades is, what accounts for mate preferences that drive intersexual selection? Several plausible models have been developed, one or more of which may apply to any particular species. This chapter has two major aims. First, evolutionary psychologists are interested in the linked tasks of inferring historical selection pressures that shaped psychological adaptations governing behavior, and describing the nature of those adaptations. Williams (1966) proposed that the criterion for inferring selection pressures, and thereby identifying adaptations that resulted, is special design. The logic of Williams' approach is briefly described. Second, one particular process of interest is good genes sexual selection. This form of sexual selection occurs when members of one sex (I focus here on females) prefer as sexual mates individuals who possess markers of good genes, whose gametes benefit the chooser's offspring. The criterion of special design applied to good genes sexual selection is: Are there any features of female mate choice that possess special design for choosing mates for their gametes, such that it is unlikely that such features would have evolved were they not designed by selection for this function? After discussing relevant background theory, I present several lines of evidence that are suggestive of such special design.

INTRODUCTION

Sexual selection refers to selection on genes due to differential access to quantity and quality of mates. Although it received very little attention in the first 100 years after Darwin introduced it, sexual selection has been a hotspot of theoretical and empirical research in the past two decades. Darwin (1871) distinguished two forms of sexual selection. Intrasexual selection refers to selection due to differential access to mates due to competition between individuals of the same sex (e.g., physical intimidation). Intersexual selection refers to selection due to differential access to mates driven by the mate preferences of individuals of the other sex.

Probably the major question pursued in theoretical investigation over the past two decades is, what accounts for mate preferences that drive intersexual selection? At least four answers have been offered (see, e.g., Andersson, 1994; Cronin, 1991). The first is that the preferences have been selected because of genetic benefits passed on to offspring of the chooser. This view, the “good genes” sexual selection theory, states that choosers prefer mates who possess markers of genetic fitness (Trivers, 1972). The benefits that select for preferences in this instance do not directly affect the chooser’s fitness but rather affect the fitness of her genes through effects on offspring quality and, hence, this form of sexual selection is referred to as indirect (e.g., Kirkpatrick & Ryan, 1991). A second is that the preferences have been selected because of material benefits passed on to either the offspring of the chooser or the chooser herself (Trivers, 1972). These benefits may come in many forms, and different theorists have emphasized different benefits (e.g., food, direct parental care, physical protection from predators or conspecifics, lack of disease that could be passed onto mates). These benefits directly affect the chooser’s reproductive success and, hence, this form of sexual selection is referred to as direct (Kirkpatrick & Ryan, 1991). A third is that sensory biases of the mate chooser, which are presumed to have evolved for other reasons, are exploited by members of the opposite sex. Cross-assortative mating between individuals who have particularly strong forms of the sensory bias and those who have the trait that exploits the bias can result in selection for greater forms of the trait. This view, though elaborated and refined in recent years, is the one Darwin (1871) favored. Fisher (1930) noted that selection could amplify traits favored by sensory bias, a process he called “run-away selection”. A fourth view introduced very recently is “chase-away selection” (Holland & Rice, 1998). This view is based on the

same initial premise of runaway selection that individuals of the chosen sex will evolve to exploit sensory biases of choosers. Because selecting mates on the bases of these exploitive traits does not benefit choosers, however, selection is presumed to operate on choosers to lower preference for the exploitive trait. This selection, like runaway selection, can result in exaggeration of the exploitive trait to "trigger" the preference due to sensory bias. The conflict between the sexes hence results in what is perhaps a counterintuitive outcome: a coevolution of greater degrees of the exploiting trait in the chosen sex and lesser preferences for the trait on the part of choosers. This last form of selection may explain why some highly exaggerated, sexually selected male traits (such as extravagant plumage in some species of birds) may not be associated with male mating success (e.g., widow birds: Andersson, 1982; jungle fowl: Ligon & Zwartjes, 1995).

These selection processes are not mutually exclusive. All may operate in nature and, indeed, all may operate on preferences for the different traits within the same species. Hence, if females prefer mates who possess traits X, Y, and Z, it is possible that trait X is a marker of good genes, trait Y promises material benefits and trait Z is disfavored by sensory biases. A primary question with regard to the sexual selection operating on any specific species is, then, what forms account for the selection of which traits?

In this paper, I will focus on attempts to document and test the effects of one form of sexual selection, specifically good genes sexual selection, on human mating. In so doing, I do not assume that this form of sexual selection has historically been the most important form operating on humans (for other views of the evolution of human mating, see Buss & Schmitt, 1993; Campbell, Simpson, & Orina, *in press*; Hrdy, 1981, 1997; Symons, 1979). Rather, I focus on this form of selection as one illustration of how selectionist theories can be applied to a study of human mating and address questions of the form just posed. Good genes sexual selection is perhaps a good theory to examine from this standpoint because it has been controversial over the years. Recent theoretical as well as empirical developments, then, have been important to its application to humans. Because evolutionists must have some means of distinguishing the role that different selection processes have had on traits, before discussing good genes sexual selection specifically I briefly discuss criteria for evaluating adaptationist accounts, including sexual selection accounts.

A DIGRESSION INTO METATHEORY

Evolutionary biology is an historical science. Evolution consists of changes in gene frequencies in populations over time. Evolutionary explanations purport to explain why a genetic system (as well as the phenotypes of individuals in the system) evolved from some prior state S to a later (e.g., current) state S' . These explanations invoke laws or phenomena that are not dependent on the precise system under consideration or the time period under consideration. Thus, for instance, only four phenomena are recognized as forces of evolutionary change and, hence, all evolutionary explanations must invoke at least one of these phenomena: mutation bias, migration, random drift, and selection (e.g., Crow, 1986). In addition to these time- and system-independent phenomena, evolution depends on events specific to time and system. These events can often be thought of as constraining the nature of evolutionary change that can take place. Thus, for instance, some phenotypes may be less subject to variation due to mutational changes, which limits their evolution. Similarly, developmental constraints may limit what array of traits can simultaneously evolve (Gould & Lewontin, 1979). An evolutionary account of the evolution of a trait in a population often cannot specify *a priori* time- and system-dependent constraints or even specify them after the fact. Hence, evolutionary explanations are rarely complete in the sense that they specify all conditions relevant to the evolution of a trait. Yet evolutionary explanations invoking time-independent phenomena (in particular, explanations of adaptations due to natural selection) can be compelling. An evolutionary account is often rendered persuasive (despite incompleteness) because: 1) it is based on a model that predicts a specific outcome that is observed, even without taking into consideration extraneous constraints; and/or 2) a compelling case is made that facts are coherent when viewed through the lens of the evolutionary account, even when constraints have not been specified. In both instances, the epistemological appeal of the account is due to the fact that, given what we know in terms of general phenomena responsible for evolution, no other evolutionary account can do as good a job at fitting the facts. (See Holcomb, 1993, 1996, for excellent treatments of the epistemological issues underlying evolutionary explanation of human behavior.)

Adaptationism is an attempt to understand the evolutionary outcomes of natural selection. Within the adaptationist framework, there are two major forms of explanatory argument, each following these general lines: tests of optimization models and arguments from design.

Tests of optimization models

An optimality approach attempts to specify the strategy or set of strategies that would result from natural selection in the absence of genetic or developmental constraints (see Parker & Maynard Smith, 1991). An optimization model must first identify a set of all possible strategies in a given domain. For instance, a model of the optimal sex ratio of offspring should identify all possible sex ratios of offspring, a model of optimal allocation of effort to investment in an offspring should identify all possible amounts of investment, and a model of optimal preference for a trait should specify all possible preferences. Next, the benefits and costs of each strategy associated with each strategy must be specified. They must be expressed in terms of fitness gains or losses to include those associated with giving up the opportunity to allocate the effort to other endeavors). In some cases, the benefit and cost functions may be empirically estimated through experimentation. In other cases, they must be specified on an intuitive or theoretical basis. The optimal strategy is that which maximizes net benefits. Complexities can be taken into account, such that optimal strategies may be contingent on the relative frequencies of each strategy in the population (frequency-dependent optima) or the condition or phenotype of the individual (conditional or phenotype-limited optima) (See Parker & Maynard Smith, 1991, for a fuller discussion.)

A test of an optimization model entails asking whether the optimal strategy is found in nature. If so, the data are taken as evidence that natural selection has acted on the organism under investigation in ways specified within the model. If not, the model is not supported. A model may fail for a variety of reasons: The entire range of strategies may not have been specified, the cost-benefit functions may be incorrectly specified (perhaps due to a missing component of the selection process), or the model may be right in so far as specifying what natural selection would produce in absence of genetic or developmental constraints, but constraints prohibit the evolution of what is optimal. Model failure gives reason to explore these different possibilities (see Mayr, 1983).

Arguments from design

Dynamic sufficiency of a model is the extent to which the model can state fully the parameters and laws by which evolutionary change takes place (Lewontin, 1974). In a dynamically sufficient optimization model, all parameters relevant to the evolution of the trait under con-



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