

The Evolution of Mating Preferences and Sexually Selected Traits Group Report

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Abstract. This report covers three topics: a) the meaning of some important concepts in sexual selection theory, b) a critical evaluation of models for the evolution of female mating preferences, and c) suggested topics and methods of approach for empirical research. Female choice results from the expression of mating preferences, which are phenotypic traits of females that can cause sexual selection in males. Female mating preferences may evolve as a result of direct selection if females differ in viability or fecundity in relation to their mating preferences. They may also evolve as a result of selection of other traits with which the preferences are genetically correlated (indirect selection). Genetic models for the evolution of mating preferences differ in the degree to which the viability selection or female choice is the primary cause of indirect selection for a preference. We evaluate two particular sets of models: a) the "Fisherian models" of O'Donald, Lande, and Kirkpatrick in which female choice can lead to a self-reinforcing increase in the preference, and b) the Hamilton-Zuk and Andersson "viability indicator" models in which sustained viability selection can promote the evolution of mating preferences. Resolution of open questions about these mechanisms depends on three types of empirical research: a) assessing the pattern of phenotypic selection on attractive traits, b) measuring the genetic variation and correlation of male traits and female mating preferences, and c) measuring the genetic relationships between attractive male characters and components of fitness. We discuss the relevance of such studies to testing the different models. In two appendices, we suggest empirical tests and some topics in need of further theoretical investigation.

INTRODUCTION

Mechanisms for the evolution of extreme male displays and the female mating preferences for them are probably the most controversial subjects in sexual



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selection. A variety of biological processes have been proposed, and a number of these have now been formalized into explicit mathematical models. An intense debate has arisen over two classes of models — the viability indicator (sometimes called “good genes”) and “Fisherian” models — that have been framed as alternative explanations for the evolution of mating preferences for extreme displays. The primary aim of our group was to evaluate the logical scope, biological merits, and empirical implications of models of these two general types and to attempt to generate a set of testable hypotheses that could be used to evaluate the relative importance of the different processes in nature.

This report begins with a discussion of some terminological problems that have hindered the development of a common language for sexual selection workers. We follow this with a critical discussion of some important current models. We then review the kinds of questions subsumed under the idea of “critical tests” of different models and present some suggestions for such tests. Our report ends with a review of some methodological approaches to testing sexual selection theory.

Definitions of fitness

Behavioral ecologists and population geneticists traditionally use quite different languages in discussing evolutionary processes. Members of both disciplines are actively involved in research on sexual selection and terminological differences have often obscured common concerns. Especially troublesome in this regard has been the use of the term “fitness.”

Within population genetics, the goal of making precise predictions of evolutionary change has not been met through the use of any single definition of fitness. However, in many cases fitness can usefully be defined as the lifetime progeny count of an individual. For populations having discrete generations, this is equal to the product, $V \times F$, of viability (the probability of survival from conception to reproductive age) times fecundity (the number of zygotes contributed by surviving adults). Lifetime progeny counts also may provide an *approximate* definition of fitness in populations having overlapping generations (Charlesworth 1980). Population geneticists normally define individual fitness over the time period from zygote-to-zygote, for this separates processes of inheritance from those of selection and renders mathematical analysis more tractable. Unfortunately, empirical measurement of fitness defined in this way is difficult, perhaps impossible. Populations of zygotes are not amenable to censusing and even when censusing is done at a later age, components of lifetime fitness may be the most that can be measured effectively. Empiricists, then, must generally use alternative and indirect measures of fitness components from which to infer total fitness.

Defining fitness becomes especially difficult when there are direct parental

effects on offspring phenotypes other than through the genes that are passed. Parental care is the most obvious and perhaps the most biologically important example of this type of effect. Male nuptial feeding is another example of special relevance to discussions of mate choice. In such instances, the post-zygotic survival of progeny is directly affected by variation in parental reproductive traits, and the zygote-to-zygote definition of fitness is therefore inappropriate. We believe that direct parental effects are very important in the evolution of mating preferences. However, we excluded them from our discussion both because of the lack of a well-developed theoretical framework for dealing with this class of characters and because of our group's focus on the evolution of elaborate male traits that are apparently unrelated to parental care. Unless otherwise noted, the following discussion is therefore restricted to cases where parental care or other forms of direct investment are either absent or are independent of the male traits and mating preferences being considered. [It has been suggested that the problem of direct parental effects might be addressed using inclusive fitness formulations, by considering the component of offspring survival accounted for by the parental character as a fitness component due to nepotism (Grafen 1985).]

Another source of terminological confusion has been the use of the terms “direct” versus “indirect” selection in discussing the Fisherian and viability indicator models. Both classes of models assume that male parental care and resource contributions are absent; rather, mating preferences evolve as a result of differences in fitness between the progeny of females that possess genotypically different mating preferences. The process that creates these differences in progeny fitness is selection on the traits of the offspring themselves and not selection directly on the female mating preference. We therefore refer to differential effects of mating preferences on progeny viability or mating success as cases of “indirect selection” on female mating preferences. “Direct selection” on mating preferences occurs only when differences in preference lead to differential viabilities of the females themselves (e.g., through predation) or to differences in numbers of progeny born (differences in fecundity). We recommend this usage both for the sake of terminological consistency and because it retains our view of natural selection arising from the actual biological relationships between the traits of organisms and their survival and reproductive success.

Definitions of “choice” and “preference”

The words “preference” and “choice” have often been used as if they were synonymous in the population genetics and ethological literature. Yet in ordinary language “choice” and “preference” denote different types of phenomena. Choice denotes an action, whereas preference denotes a disposition or propensity that an individual possesses whether or not it is exercised. In practice,

female mating preferences can only be observed by observing female choice under conditions where the object of the preference is separated from other factors that may influence its expression. For example, Andersson (1982) was able to demonstrate a female preference for long tails in widowbirds by manipulating tail length while simultaneously controlling for other factors, such as territory quality, that might confound the expression of the preference of interest with other responses of females.

With respect to definitions of "female choice" per se, we favor Halliday's definition of female choice as differential mating by females as a result of their possession of mating preferences (Halliday, this volume). Note that this definition requires that female mating preferences simultaneously be both ordinary phenotypic traits and potential agents of sexual selection on males. We disagree with Maynard Smith's suggestion (1985) to reserve the term "female choice" only for those cases in which we consider the preference to have evolved as a result of the selective forces associated with it. Historical inferences about the evolutionary causes of mating preferences are difficult to make and frequently contentious; reserving the term for cases in which particular inferences have been made would probably render it useless. Halliday's definition, on the other hand, lends itself to reasonably straightforward operational definitions that allow us to detect female choice using currently observable processes.

Female mating preferences are most readily detected if individual females differ in their preferences, and these differences can be observed as differences in their choices between alternative male types. In such a case at least some variation in the relative mating probabilities of different male types will be attributable to individual differences between females, and mating preferences in Halliday's sense can thus be inferred. Variation among females in their mating preferences may or may not be genetic; showing that female mating preferences are heritable requires explicit genetic investigations (discussed below). If females are all alike in their responses to different male types, they may still possess preferences that are genotypically invariant.

Given that a mating preference is found, there are three general types of preferences that differ with respect to their evolutionary history and behavioral expression in females. First are what could be called *direct preferences*, where the male character we identify with the preference is indeed the trait to which females differentially respond and through which evolution of the mating preference has been mediated. This class of preferences corresponds to Maynard Smith's definition (1985). The second class of preferences might be called *indirect preferences*. These differ from direct preferences in that the male character we identify with the preference is not the trait to which females actually respond but is phenotypically correlated with it. Identifying whether a particular male trait is the object of a direct or an indirect mating preference requires either experimental manipulation, such as that used by Andersson

(1982) to infer preference for tail length in widowbirds, or a multivariate analysis of the male characters associated with attractiveness (see below and Wilkinson et al., this volume, for a discussion of one such method). The third class of mating preferences could be called *pleiotropic preferences*. These are mating preferences that arise as a result of pleiotropic expression of genes that determine some other female behavior, such as food choice. Like indirect preferences, pleiotropic preferences lead to apparent female choice for male characters that are actually incidental to the ecological function of the preference. Indirect preferences arise from correlations between traits in males, whereas pleiotropic preferences arise from correlated effects of genes in females. Pleiotropic preferences may not therefore be distinguishable from direct preferences by experimental or statistical manipulation; the distinction instead will depend on the identification of genetic correlations between different female behaviors, combined with studies of the relative importance of the different observable preferences in nature.

CRITIQUE AND DISCUSSION OF CURRENT THEORY

Two main schools of thought exist as to whether or not mating preferences for extreme male characters will generally be adaptive. A variety of different mechanisms of sexual selection have been proposed in support of alternative views, and the feasibility of several of these has been investigated theoretically using population genetic models. These models make diverse assumptions about mechanisms of inheritance (e.g., two or three loci versus polygenic inheritance) and use different methods of analysis (e.g., analytic versus computer-simulated results); such differences in modelling techniques complicate the task of comparing their empirical implications. Furthermore, models that differ substantially in their basic assumptions may nevertheless lead to very similar outcomes, making it difficult to identify empirical predictions that discriminate between them. A considerable part of our group's discussion was therefore aimed at identifying the major differences between models, the assumptions most vulnerable to criticism on biological grounds, and common features that might lead to qualitatively indistinguishable results.

Fisherian models

The joint evolution of female mating preferences and male secondary sexual characters in polygamous species has been analysed by O'Donald (1967, 1980), Lande (1981), Kirkpatrick (1982), and Seger (1985). These have confirmed that Fisher's (1930, 1958) basic description of the process is indeed feasible and can decrease male viability through the evolution of exaggerated male traits. During this process, natural and sexual selection may initially reinforce each

other, but at equilibrium they act in opposite directions on the male character. In this sense, the evolution of the sexually selected trait may be maladaptive in that female mating preferences lower the mean viability of males.

A primary point of agreement among the various Fisherian models is the existence of a neutral line of equilibria (Lande 1981; Kirkpatrick 1982). The possibility that the line itself can become unstable when the genetic correlation between the female mating preference and male trait is sufficiently large was first demonstrated for polygenic models (Lande 1981), and similar behavior has subsequently been found in other models. Two-locus models like those of O'Donald (1967), Kirkpatrick (1982), and Seger (1985) permit only fixation of alternative alleles and thus do not explicitly model continued and exaggerated evolution of secondary sexual traits. Nevertheless, the requirements for rapid fixation of the male trait in the two-locus models are similar to those for instability in the polygenic models in that fixation occurs when the correlated evolutionary response of the female mating preference is sufficiently large relative to the direct response of the male character to sexual selection.

The realism of the Fisherian models, or at least their applicability to many biological situations, has been questioned on several grounds. Most important is the assumption that female mating preferences are not subject to direct selection, by which we mean that females have different viabilities or produce different numbers of progeny as a consequence of differences in mating preference. In many species, there may be direct costs to females associated with mate choice. Examples include risks associated with searching for mates, increased fecundity as a result of male parental care, and infertility caused by species hybridization. However, the widespread existence of costs to mate choice *per se* must be distinguished from the subset of cases in which these costs create direct selection on a female mating preference of interest. For example, females who fail to recognize a species-specific character may have reduced fecundity as a result of hybridization. Given that females recognize the trait, however, there may be no differential fecundity as a result of discriminating among conspecific males that differ in the degree of its elaboration. The relative importance of different kinds of costs to mating preferences is virtually unknown and is a critical topic for future research. Note also that the existence of direct selection on female mating preferences applies as a criticism not only to the Fisherian models but also to the various viability indicator models discussed below.

If costs associated with mate choice lead to direct selection on mating preferences, general theoretical considerations show that this will eliminate the neutral line of equilibria. The preference can only equilibrate at a point that balances the forces of selection acting directly on females. Kirkpatrick has studied two explicit models that provide detailed predictions for special cases. The first examines the situation in which males provide females with material benefits, such as a resource (Kirkpatrick 1985). In this situation, females

evolve to maximize the quality or quantity of resource they receive. The second model examines the effects of search costs that arise, for example, from predation risks or energetic costs associated with differences in mating preferences (Kirkpatrick, this volume). Under some ecological conditions this model produces evolution of the male trait and female preference toward the viability optimum for the male character. Under other conditions, however, the trait and preference both equilibrate at values that deviate from the viability optimum. In general, both models indicate that direct selection on female mating preferences leads to evolutionary equilibria that are adaptive from the standpoint of females, in that mean female fitness is maximized, but that may be maladaptive with respect to mean male viability. These models still retain the theoretical possibility of an unstable runaway process in which preference and trait evolve in an unpredictable and overall maladaptive way.

A second criticism of the biological applicability of the Fisherian models is that the mating preference rules considered are too simple, and the introduction of more complex behavioral mechanisms of mate choice can strongly affect the models' results. The most dramatic effect is on the stability of the line of equilibria. In the simplest models of female choice studied by O'Donald (1980), Lande (1981), and Kirkpatrick (1982), females are assumed to have access to all males in the population and to evaluate potential mates according to fixed preferences that are unaffected by the frequency with which they encounter males of different types. In Lande's model, the line of equilibria becomes unstable only when the genetic covariance between the preference and trait becomes sufficiently large, as discussed previously. More detailed models of how females choose their mates, however, show that the behavioral mechanism of mate choice can itself affect the stability of the equilibria.

For example, Seger (1985) has extended Kirkpatrick's (1982) model to consider situations in which females choose the most preferred male from a sample of size N , such as might occur when females visit males at a lek. In these models the line of equilibria can become unstable as a direct consequence of this particular behavioral mechanism. O'Donald and Karlin have studied encounter models that assume that females have a variable threshold that determines the number of encounters required before they will mate with nonpreferred males (O'Donald 1980). These models give rise to frequency-dependent expression of mating preferences that can stabilize equilibria that would be unstable under simpler behavioral models. Furthermore, these effects arise even though there is no genetic variance for the female mating preference, and hence no genetic covariance between trait and preference that could contribute to the stability conditions. The above examples show that the mechanism of expression of mating preferences can strongly influence the range of possible evolutionary outcomes of sexual selection. In order to make detailed empirical predictions from theory, we therefore may require knowledge not only of the genetic system but also of the behavioral process by which mate choice occurs.

A third source of criticism of the Fisherian models is that the mating preferences they assume may be vulnerable to invasion and eventual replacement by alternative preferences (Fisher 1915; Borgia, this volume). The equilibria in the Fisherian models are intrinsically immune to invasion by *quantitatively* different mating preferences directed toward more viable values for the male character. However, there is a need for theoretical investigation of the possibility that mating preferences for maladaptive male traits can be replaced by *qualitatively* different preferences involving either different behavioral mechanisms or different male characters.

The argument that preferences for maladaptive traits will be replaced by preferences for adaptive traits is based on the widespread observation of apparently adaptive mate choice in resource-based systems. Existing models of choice in such systems suggest that female mating preferences are adaptive in that they maximize mean female fitness (but not necessarily male fitness). It is proposed that adaptive mating preferences arise in resource-based systems because of selection among alternative mating preferences, wherein preferences for male traits that enhance female fitness are more likely to evolve than preferences that do not have this effect. By analogy, it has been argued that in nonresource-based mating systems, mating preferences for male traits that enhance viability will outcompete mating preferences for male traits that have no effect or that decrease viability (Borgia, this volume). It is feasible that traits that increase male viability could bias the evolution of novel mating preferences in their favor yet still lead ultimately to the Fisherian trade-off between sexual and viability selection. The possibility that competition among alternative mating preferences could lead to the prevalence of preferences for adaptive male traits is an area in which explicit genetic models are needed.

Viability indicator models

Several mechanisms have been proposed that might lead to the evolution of predominantly adaptive mating preferences. By "adaptive mating preferences," we mean preferences that cause females to mate with males carrying genes that increase the viability of their progeny. The following is a list of several ways in which a mating preference could have this effect.

- (A) Females choose mates directly on the basis of viability (e.g., if courtship vigor were perfectly correlated with viability; see Maynard Smith and Charlesworth, both this volume).
- (B) Females choose mates using a character that indicates viability.
 - (B1) The indicator itself increases viability (e.g., Kodric-Brown and Brown 1984).
 - (B2) The indicator itself decreases viability (i.e., is a handicap) but is positively correlated with total viability through other traits (models reviewed by Maynard Smith 1985; Andersson 1986).

The following discussion is restricted to mechanisms of type (B2) above, because they are the most pertinent as explanations for the evolution of mating preferences for exaggerated male characters that must typically entail some cost to their possessors.

The first of the viability indicator models to be analyzed genetically was Zahavi's (1975, 1977) handicap mechanism. In its original form, this model was criticized by Maynard Smith (1976), who showed that under realistic conditions the survival of males with an unconditional handicap could not serve as an indicator of overall genetic quality. The male handicap and the female preference for it would then be lost from the population. Following this a variety of mechanisms involving "facultative," "conditional," or "revealing" handicaps have been suggested (Hamilton and Zuk 1982; West-Eberhard 1979; Dominey 1983; and others) in which a slightly deleterious indicator trait is fully expressed only in the most viable males. These models represent extensions of the basic Fisherian model to include genetic variance for viability in one or more characters in addition to the male trait. They are reviewed and analyzed by Maynard Smith (1985) who concluded that a male viability indicator and a female mating preference for it can spread if they reach a threshold frequency, but neither will spread if initially rare.

A version of the viability indicator hypothesis suggested by Hamilton and Zuk (1982) has received much attention. They proposed that the coevolution of species and their parasites can produce cyclical selection on genes in the host that confer resistance to particular species of parasites. When the parasite load of an individual affects the expression of a male secondary sexual trait, parasite selection will drive the evolution of a mating preference for the parasite indicator, thus giving resistant males a further advantage under sexual selection. It is postulated that population mean fitness increases by this process and that the mechanism represents a major cause for the evolution of exaggerated male traits in nature.

The first genetic models proposed by Hamilton have been studied by Kirkpatrick (1986) and Pomiankowski (unpublished manuscript). These models have found that the fluctuating selection produced by the parasites leads to different evolutionary equilibria than do the basic Fisherian models or those viability indicator models that assume constant viabilities. The neutral line of equilibria is lost, and the trait and preference either both spread or are both lost. In the simple haploid models studied thus far, the trait and preference will not spread when rare but require some other process to raise the preference allele to some critical threshold frequency needed to initiate effects from the parasite mechanism. Two important criticisms of the parasite hypothesis have been raised on the basis of these results. First, evolution need not be unidirectional. If external forces can initiate the process, they may also reverse it by causing the preference to drop below the threshold frequency. Which outcome will be more prevalent depends on the parameters of the model; it is a

question that can only be resolved by empirical measurement of those quantities. For example, the mechanism as originally formulated depends on special quantitative relationships between host and parasite life spans and the periodicity of fluctuating selection; the frequency of these conditions in nature is not known. A second criticism is that the current models do not lead to an increase in mean population fitness as proposed by Hamilton. Thus, although the parasite mechanism can influence the direction of sexual selection and can have strong effects on its outcome, current models have neither shown that it can initiate the process nor that it will lead ultimately to an adaptive outcome. There is a need for more theoretical and empirical work before the importance of the parasite hypothesis can be assessed.

Recently, Andersson (1986) analyzed a model of a conditional handicap in which a male indicator trait has no effects on viability or mating success except when associated with a high viability allele at another locus. To assess whether the mechanism suffices for the spread of trait and preference when there is no Fisherian mating advantage, the model assumed a monogamous mating system without variation in female fecundity. (In principle, indicator mechanisms can also operate in polygynous systems although their importance relative to the Fisherian mating advantage mechanism should decrease as the level of polygyny increases.) Andersson's model showed that under these conditions a male facultative handicap and female mating preference for it can evolve solely by association with genes for high viability. In this model there is neither sexual selection, in the sense of differences between males in the numbers or fecundities of mates, nor is there direct selection on female mating preferences, which evolve only as a correlated response to viability selection. Andersson's model accommodates Borgia's (1979) idea of a female preference for a trait that indicates dominance. It also covers, as a special case, variation in male viability caused by differences in resistance to parasites. This type of indicator model seems even more favorable for the evolution of trait and preference than does the Hamilton-Zuk host-parasite model. For these reasons, studies of indicator processes should not be restricted to parasite cycles as a cause of heritable viability differences but should consider also recurrent mutations and other environmental or genetic processes that might maintain additive genetic variance for fitness (e.g., Charlesworth, this volume).

An important criticism of the conditional indicator mechanism as a widespread explanation for mating preferences is that, operating alone in monogamous mating systems, it cannot account for the frequent occurrence of sexual dimorphism in monogamous species. This is because in the absence of any initial asymmetry in the expression of the characters in males and females there is no intrinsic force of selection for sexual dimorphism. This is easily seen where a conditional handicap character reveals genetic resistance to parasites by being fully expressed only in healthy individuals that are parasite-free. In such a case, with monogamous matings it would equally benefit either sex to choose

healthy mates, either by increasing their own fitness if parasites are transmitted during copulation (direct effect) or the fitness of their progeny (indirect effect). Thus, to the extent that the conditional handicap mechanism occurs in natural populations, it must operate in conjunction with other mechanisms that are capable of creating the sexual asymmetry required for the evolution of sexual dimorphism.

An alternative mechanism that *can* explain the existence of sexual dimorphism in monogamous species was proposed originally by Darwin (1871) and elaborated later by Fisher (1958). This postulates nonheritable differences in female fecundity wherein the most fecund females breed earlier in the season and have first choice of mates. This creates a force of sex-limited sexual selection on male traits that can lead to evolution of both the mating preference and sexual dimorphism via the classic Fisherian mechanism. Evidence for sexual selection of this sort has been found in arctic skuas by O'Donald (1983) and in kittiwakes by Coulson and Thomas (1983), and genetic models of its operation have been studied by O'Donald (1973, 1980). Although the Darwin-Fisher mechanism by itself can account for mating preferences and sexual dimorphism in monogamous populations, it could also operate in conjunction with a facultative handicap mechanism so as to bias evolution in favor of male traits that indicate viability.

The criticism that conditional handicaps cannot explain the evolution of sexual dimorphism also applies to polygynous mating systems. Here, however, a force of sexual selection will arise once mating preferences have begun to evolve, and it is probable that the Fisherian process, once initiated, will be a stronger force than the viability mechanism. Empirical tests of conditional handicap models should therefore be designed not only to indicate whether these mechanisms are operating but also to assess their importance relative to other processes that are expected to be operating simultaneously.

Commonalities of the models

Although the different models make strikingly different assumptions about underlying genetic mechanisms and the relationship between male traits and viability, they all share a common requirement for a mechanism that initiates a female mating preference from a prior state in which females show no bias in their mating. Either a mechanism is built into the models to create a force of viability selection that will lead to increase of an initially rare mating preference (as in Andersson's model) or alternative mechanisms, extrinsic to the models themselves, are required to bring mating preferences to a threshold frequency needed to initiate sexual selection. Several such extrinsic mechanisms have been suggested by Kirkpatrick (this volume). The ability of viability mechanisms to lead to the origin of mating preferences for quantitative characters has been examined in models by Heisler (1984, 1985). However, theoretical work

is needed to investigate other mechanisms for the origin of mating preferences and, especially, to examine the period of transition from a primarily viability selected to a sexually selected phase of evolution.

A second feature common to both the pure Fisherian models and the viability indicator models that also include Fisherian mating advantages is that as long as there is no direct force of selection on mating preferences and viabilities remain constant over time, there exists a neutral line of equilibria. In some models the equilibria are always unstable and therefore play no role in the evolutionary outcome of sexual selection. In either instance, however, there appears to exist a region of genotypic or phenotypic space in which initial conditions will lead to maladaptation on the part of the male character. Viability mechanisms reduce the set of initial conditions that will lead to maladaptation, but the Fisherian process appears always to be able to induce maladaptive evolution under at least some conditions.

ARE THERE DISCRIMINATING TESTS OF ALTERNATIVE MODELS?

Kinds of tests

Any discussion of the nature of critical tests of sexual selection theory must draw distinctions between the explanatory aims of different types of tests. Most fundamental is the difference between tests of historical hypotheses about the long-term processes that gave rise to the types of traits we observe across a range of taxa and tests of hypotheses about processes currently in operation within specific populations. Workers on sexual selection are interested in both kinds of questions, and failure to identify differences in perspective has sometimes hindered communication within the field.

Tests of hypotheses about current selective processes can be used to refute the existence of particular processes in individual instances and to strengthen evidence for the presence of alternatives. In aggregate many such tests can be used to make inferences about the relative frequency of different processes in other species and in the past. Models for how selection is currently affecting mating preferences and male characters can be tested using either critical assumptions that differ between the models or distinctive predictions. Andersson (this volume) has argued that tests of assumptions are especially desirable, so long as the assumptions are responsible for critical differences between alternative models. An example of one such critical assumption is the absence of direct costs or benefits that create direct selection on female mating preferences, an assumption required for the neutral line of equilibria. Likewise, discriminating tests of predictions about ongoing processes can be used in much the same way as tests of assumptions. An example of one such prediction is the existence of a positive correlation between the attractiveness of males and the average viability of their daughters, predicted by some of the viability indicator models (Boake 1986).

Tests of hypotheses about current processes, however, provide only indirect evidence about the relative importance of different processes in the past. To address questions about the historical origin and elaboration of different classes of characters, predictions are needed for the long-term results of different evolutionary mechanisms. Such tests do not require that the assumptions of different models currently be met in populations; they use long-term extrapolations from processes postulated within species to test predicted patterns of character distribution across species. An example of one such prediction is that male characters that reveal parasite loads should be more highly developed in species that are subject to high parasitism than in species where parasites are less common. The explanatory scope of historical tests is much larger than that of tests of current processes. However, it often may be difficult to obtain the kinds of predictions desired, in that models that have quite different assumptions may nevertheless be indistinguishable in their long-term results. Furthermore, the results of historical tests will typically be more subject to dispute than will tests of current processes, since the former tests depend on a larger number of biological assumptions, such as long-term constancy in the pattern of selection on traits.

The relative roles of genetic and phenotypic studies

An integrated approach to studying evolution requires both genetic and ecological investigations. The Fisherian and viability indicator models differ in specific statements about the genetic relationship between female mating preferences, male characters, and components of total fitness. These genetic relationships can be measured as genetic correlations, and such correlations may be of different magnitude and even different sign than the corresponding correlations based on phenotypic observations (Falconer 1981). Testing hypotheses that involve statements about such relationships necessarily requires explicit genetic analyses. Consequently, it has been questioned whether the different models can ever be distinguished without conducting arduous genetic investigations, an impossible task for many of the species whose traits are of most interest. Although genetic studies are indispensable for answering many important questions about the evolutionary consequences of mate choice, we believe that at least some discriminating tests can be done without explicit genetic information, using purely phenotypic observations.

Phenotypic studies

One approach to investigating sexual selection is to measure the selective pressures acting in a contemporary population. The idea is to exploit natural variation in traits that are presumed to be sexually selected and to analyze associations with measured components of fitness. This approach yields estimates of the strength of selection that are analogous to the selection

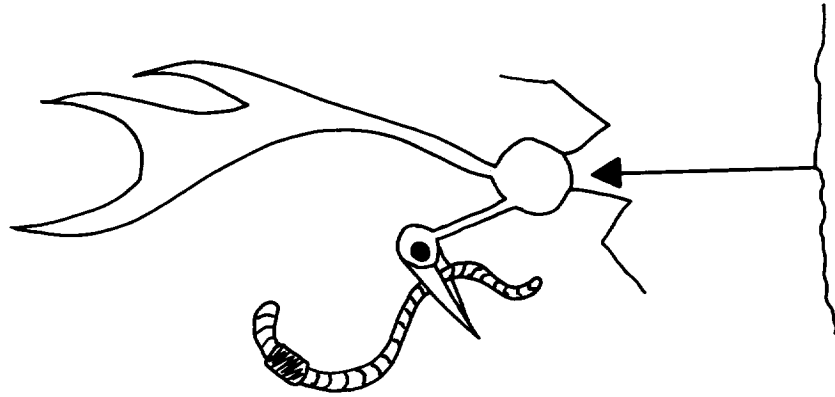


FIG. 1: Arnold's Bird-of-Paradise, illustrating three kinds of sexually selected traits. Tail size is sexually dimorphic and extravagant in males. The vigor of the male's courtship dance, measured as the average height of leaps, is a potential viability indicator. The average size of worms presented to a female at the end of the dance has potential effects on many male fitness components and on the fitness of his progeny.

coefficients used in equations for evolutionary change (Lande and Arnold 1983; Arnold and Wade 1984). A limitation of the method is that it cannot by itself address questions about ongoing evolutionary change, for which information about the pattern of genetic variation is required. The phenotypic approach treats selection as a process that can be studied separately from the analysis of inheritance. Even in the absence of genetic information, it permits a number of important questions to be explored. Some examples of these are illustrated in Figures 1 and 2. Wilkinson et al. (this volume) lists the assumptions implicit in the particular statistical approach discussed here.

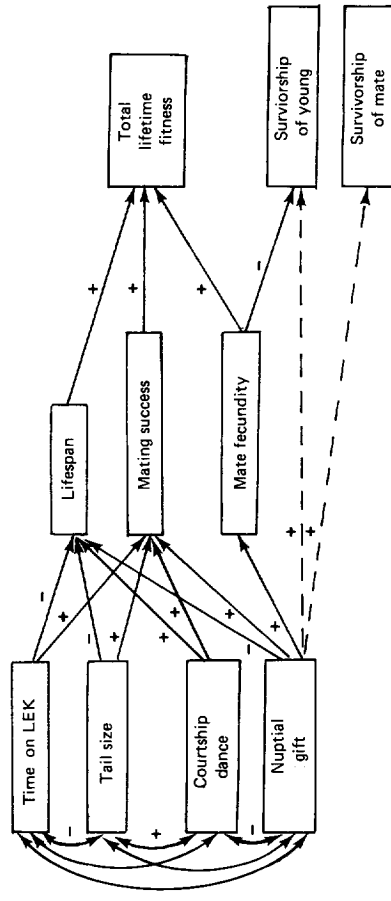


FIG. 2: An example of sexually selected traits that are phenotypically correlated with various components of fitness. Double-headed arrows represent phenotypic correlations between traits. Solid single-headed arrows represent partial regression coefficients of the fitness components on the individual characters. Dashed single-headed arrows represent maternal and paternal phenotypic effects on the survivorship of offspring. Lifespan is measured in units of time, mating success in numbers of mates per unit time, and male fecundity in units of average number of offspring per mate. The product of these three fitness components is total lifetime fitness in units of numbers of offspring (see text for discussion).

The hypothetical male shown in Figure 1 is a member of a lek-breeding species in which the male displays his extravagant tail to the female while displaying in front of her and offering her a nutritious nuptial gift. Assume that we have measured four phenotypic traits in males: time spent on the lek, tail size, vigor of the courtship dance, and the average size of nuptial gifts. Assume also that we have measures of three components of individual fitness — lifespan, mating success, and mate fecundity — that completely account for total lifetime fitness. Because we measure total lifetime fitness as a simple zygotic progeny count, we also score the survivorship of each male's progeny in order to assess maternal and paternal phenotypic effects on offspring quality (mediated, e.g., through the nuptial gift).

The hypothetical male traits are chosen to illustrate major categories of sexually selected traits that are presumed to exist under different selective regimes. Thus, tail size is the kind of trait commonly considered in Fisherian models (e.g., Lande 1981), and for it we have the expectation that opposing forces of sexual and viability selection balance in an equilibrium population. From the Darwin-Fisher hypothesis we might therefore predict that tail length would be positively correlated with mating success, negatively correlated with lifespan, and uncorrelated with total fitness.

However, to illustrate the kind of complications that arise due to character correlation suppose that tail size is negatively correlated with time on the lek

(perhaps because males with the largest tails exhaust quickly and retire sooner from the lek each day), but that time on the lek is a major phenotypic determinant of mating success. In this case the simple correlation coefficient between tail length and mating success might be negative or zero, giving the misleading picture of a mating preference for short tails or of no preference at all. A multiple regression analysis, however, would provide partial regression coefficients of lifespan and mating success on tail length, and these would control for the correlations between tail length and time on the lek and the other characters. Experimental manipulations of tail size could subsequently be used to assess directly the effect of tail length on mating success.

The vigor of the male's courtship dance illustrates how we might test expectations derived from a viability indicator model. We hypothesize that dance vigor is an indicator of male viability and, accordingly, we expect both lifespan and mating success to have positive partial regression coefficients associated with this trait. As before, experimental manipulations may be necessary to verify our interpretation of the statistical results.

Finally, the size of the male's nuptial gift illustrates the case of a male trait that is presumed to have complicated effects both on the fitness of his mates and on the fitness of his progeny. For example, suppose we wish to test the expectations that the male's nuptial gift has positive effects on his own mating success, on his mate's fecundity, on his mate's survivorship, and on the survivorship of his young. In addition, we expect a negative effect on the male's lifespan (because large gifts increase his risk of predation) as well as a negative correlation with dance vigor (because a large gift lowers his agility). As before, we could use partial regression analysis to sort out direct effects of the nuptial gift on these different components of fitness. In a situation this complex, however, experimental research would surely be needed to ascertain the actual biological processes occurring.

Genetic studies

Some types of genetic investigations will be essential to evaluate the applicability of different models. However desirable, it will not normally be feasible to perform analyses of both selection and inheritance on the same species, although in exceptional cases reasonable estimates of genetic parameters may be possible using field-collected data. Generally, however, genetic studies require species which can be reared in the laboratory in large numbers. Furthermore, if laboratory-based estimates are to be used to infer heritabilities in nature, the species must behave normally in an experimental environment.

Perhaps the most crucial information needed at present concerns the genetic basis and magnitude of heritable variation for female mating preferences. Artificial selection is a direct but as yet little-used approach to investigating this question. Unfortunately, selection on mating preferences is more difficult than

selection on simpler behavioral or morphological traits, owing to difficulties both in measuring the character itself and in separating its selection from selection on other traits that influence mating probabilities. Preferences under investigation may be directed at discrete male characters or at quantitative traits, and methods of selection will differ somewhat in the two cases. In general, the procedure is to assess female choice and retain those females that mated with "preferred" males as mothers of the next generation. As the preference increases in response to selection, the population will naturally come to consist more and more of the preferred phenotype. A complication arises, unless special measures are taken, in that this will alter both the intensity of selection on the preference and the level of frequency-dependence in its expression. In selecting on preferences for discrete traits, one can artificially start each generation with the same proportion of preferred and nonpreferred males. For example, Majerus et al. (1982) used a ratio of 3 melanics: 7 nonmelanics in each generation of selection for a mating preference in ladybirds. In selecting for a preference directed at a quantitative character, the intensity of selection can be held constant by selecting some fixed proportion of females that mated with the most extreme males. Because the distribution of the male trait changes over time, however, measuring the response to selection requires that females must periodically be tested using males from a control line having a standard distribution of phenotypes.

During the course of selection for a mating preference, male competition may cause evolutionary change in male characters other than the one under investigation, and this may confound the response to selection for the mating preference with unknown genetic changes. This problem can be avoided if it is possible to measure female preference using males from an unselected line and subsequently to breed the selected females at random with males from within their population. An alternative and less time-consuming procedure is to test males and females from the selected and unselected lines in various combinations, so as to assess the degree to which male characters have evolved (Majerus et al. 1982).

Several other types of genetic studies may be important in evaluating hypotheses about sexual selection. These include estimation of the number of genetic loci influencing male characters and/or female mating preferences and measurement of the genetic covariance (linkage disequilibrium) between male traits and female preferences. A particularly crucial class of measurements is the genetic correlations between sexually selected male characters and other male traits, most importantly components of male fitness.

To estimate genetic covariances for a set of characters, an efficient procedure is to use the regression between parental and offspring traits. The technique is to measure a set of behavioral and/or morphological traits in males, breed the males, and measure the same traits in their sons. The details of such designs are covered in several texts (e.g., Falconer 1981). An important

consideration is that each design has its own limitations and advantages. One such limitation is that genetic analyses often require large sample sizes if reasonable standard errors for the estimates are to be obtained (Bulmer 1980). An alternative procedure for estimating genetic covariances is artificial selection, but this method is hazardous because genetic correlations can be generated through unintentional assortative mating.

Although some of the viability indicator models are falsifiable using solely phenotypic observations, such as demonstrating that male parasite loads are not negatively correlated with attractiveness, other models require explicit genetic analyses of the correlations between male attractiveness and components of offspring fitness. The general procedure for obtaining such estimates is to evaluate male attractiveness and subsequently measure the viability of their progeny (Boake 1986). A correlation between fathers' attractiveness and daughters' viability will often avoid the problem of nongenetic parental effects on progeny, though this may not be the case if males contribute resources or care to their mates or offspring.

Genetic analyses should only be undertaken after careful consideration of their utility in answering the questions of interest for a particular species. Since the labor involved in genetic studies is considerable, experimental designs require careful development to ensure that the results will yield reasonably precise estimates. A variety of pilot procedures can provide information important in designing successful experiments. For example, measures of the repeatability (correlation between subsequent measures on the same individual) of behavioral traits should always precede heritability tests, since behavioral measures often have large components of random variation that place an upper limit on the magnitude of the heritability that can be detected.

CONCLUSION

This report summarizes a discussion that has not ended. A number of specific predictions were proposed that, if tested empirically, should be capable of falsifying particular models as explanations in specific instances. Some suggestions for such tests are listed in Appendix A. The list is not complete — there may well exist tests that are either more decisive or more readily conducted than those suggested. It is also possible that future research will show that some proposed tests are not in fact decisive. Nevertheless, the list includes enough important empirical questions to keep field and laboratory workers occupied for some time to come. Meanwhile, more theoretical work is needed. For example, some of the equilibrium phenotypic or genetic correlations between either mating preferences or male indicator traits and the various components of fitness are expected to differ among the Fisherian and various indicator models. These potentially distinguishing relationships have yet to be detailed

in full for any single model. Not only do we need new theory to address empirically reasonable proposals that as yet lack formal treatment, but perhaps more importantly, we need to examine more fully the empirical implications of the theory we already possess.

APPENDIX A: PROPOSED TESTS OF SOME MODELS OF SEXUAL SELECTION

Below we list some empirical predictions that could be used to test different proposed mechanisms of sexual selection. Some of these tests involve measuring relationships within particular species while others are comparative tests across a range of species.

Fisherian models

The pure Fisherian models of O'Donald (1967, 1980), Lande (1981), and Kirkpatrick (1982) make the following equilibrium predictions. Showing that any of these fails to hold demonstrates that the Fisherian mechanism cannot solely account for the pattern observed (i.e., is a partial falsification of the model).

- 1) Across a range of species, attractive male traits should be "arbitrary" in the sense that they should not be demonstrable predictors of male or offspring viability or total fitness.
- 2) Within populations assumed to be in evolutionary equilibrium, viability and sexual selection should act in opposing directions on attractive male traits.
- 3) Female mate choice should not positively influence the viability or total fitness of her progeny.

Viability indicator models

Several kinds of male characters have been suggested as possible indicators of the ability of males to sire viable progeny. Four of these are listed below with specific predictions that, should they fail to hold, would eliminate the mechanism as the sole explanation of the trait in question.

- 1) *Indicators of Male Age*. This model postulates that females prefer traits that accurately indicate male age because older males have demonstrated viability. The specific predictions are: (a) females preferentially mate with older males; (b) the male trait in question is an accurate indicator of age; and (c) females use the proposed indicator during mate choice.
- (2) *Indicators of Male Dominance*. This model postulates that males that win dominance contests produce progeny having high viability or total fitness. The

specific predictions are: (a) females prefer to mate with dominant males; (b) the proposed indicator is correlated with dominance; and (c) females use the proposed indicator during mate choice.

3) *Parasite Indicators*. This is the model of Hamilton and Zuk (1982), described in detail in the text. Four specific predictions are: (a) females within a given species prefer males in inverse relation to the number of their parasites; (b) individual display quality (e.g., plumage brightness) declines with increasing parasite loads; (c) display quality is favored by females during mate choice; and (d) in comparisons between related species, species that are heavily parasitized should possess more elaborate displays. (This last test requires careful control for confounding effects of mating systems and the degree of aggregation, which also should affect parasitism).

4) *Indicators of Male Vigor*. This model postulates that vigorous males carry genes for high viability or total fitness and indicate their vigor with elaborate traits. Three specific predictions are: (a) male vigor is positively correlated with mating success; (b) the proposed indicator is positively correlated with male vigor; and (c) females use the indicator during mate choice.

APPENDIX B: SUGGESTIONS FOR FUTURE THEORETICAL WORK

A. Exploration of Existing Models

1. Dynamical properties of models — trajectories of approach to equilibrium, rates of evolution in different areas of phenotypic space
2. Further examination of fluctuating selection (e.g., the parasite hypothesis)
3. Equilibrium correlations between traits and fitness components in various models

B. Addition of New Factors to Existing Models

1. Explicit models of female choice behavior — further examination
2. Effects of limited polygyny
3. Further examination of costs to female mating preferences

C. New Models

1. Mate choice and sexual selection in hermaphrodites
2. Effects of learned or culturally inherited mating preferences.
3. Interactions between male dominance/competition and female choice
4. Elaboration of specific 'good genes' models
 - a. Mate choice based on genome-wide viability differences generated by mutation-selection balance.
 - b. Mate choice based on male age as an indicator trait
 - c. Effects of heterozygote advantage for male characters

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Sexual Selection: Games between the Sexes

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Abstract. Mating involves several conflicts between the sexes. These conflicts are discussed from a game theoretic point of view. In order to mate, the sexes must first meet. If one sex exerts a high search effort, individuals of the other sex can profit by countering this pattern with low mobility; in view of the costs of moving, each sex would be better off if the other took on the high search effort. The problem of who moves thus shows the characteristic of a game between the sexes. We present a new model, the mobility game, in order to deal with the following question: why is the mobility pattern so typically linked with sex and why do females so often win this conflict? It may seem intuitively obvious that males should be the more mobile sex if females invest far more in the offspring and represent a limiting resource for males. This would mean that the sex who "loses" the parental investment game should "win" the mobility game. Surprisingly this intuitive logic turns out to be fragile; in our model both the "roaming male strategy" and the "roaming female strategy" are alternative ESSs for the same game. One sex may thus represent the loser of both the conflict over parental investment and the conflict over mate searching! We make a first attempt to show why the case of losing both these games seems less likely to occur in evolution than the case of winning one and losing the other. Another problem area is more directly related to sexual selection: even when the sexes meet they may not want to mate. A game-like situation arises in this context if it pays one sex to mate but not the other. Conflicts over mating decisions concerning incest, superfluous matings, mate quality, and hybridization are discussed. A previous model by Parker on disagreement between the sexes with regard to incestuous matings is modified. Conditions for the existence of this conflict are discussed. Interestingly, this discussion is related to that of the evolutionary maintenance of sexual reproduction. From the incest model we also conclude that incest avoidance does not seem to be the major principle which would explain sex-specific animal dispersal patterns. The final part of this paper deals with parental investment games. Once again, the problem of multiple ESSs for the same game occurs. This problem seems typical for many models of conflict between the sexes.