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Editors

**Marco Apollonio**

*University of Pisa*

**Marco Festa-Bianchet**

*University of Sherbrooke*

**Danilo Mainardi**

*University of Venice*

Series Editor

**Antonino Zichichi**

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## SEXUAL SELECTION AND MATE CHOICE: TRADE-OFFS FOR MALES AND FEMALES

R. HAVEN WILEY

*Department of Biology, University of North Carolina  
Chapel Hill, NC 27599-3280, USA*

### ABSTRACT

This review addresses current issues in the study of mating systems and mate choice and shows how sexual selection results in trade-offs for both sexes. Arbitrary female preferences serve as a null hypothesis for comparison with the alternative hypotheses of direct and indirect net benefits for female preferences. Indirect benefits require heritable male traits and thus raise the issue of decreasing additive genetic variance which could eliminate selection for female choice based on indirect benefits. Whenever heritable traits and preferences affect mating, the consequent assortative mating will produce genetic correlation and the possibility for accelerating evolution. Accelerating evolution can also result from frequency-dependent selection on any signals and responses. An expanded view of mate choice includes indirect as well as direct choice. With this view, the coevolution of male and female traits is seen to have much greater scope than currently appreciated. Either form of mate choice can lead to the evolution of exaggerated traits and reliable signaling systems as a result of males optimizing fitness (survival X reproduction) and females optimizing decision-making in noisy conditions. Discordances between preferences and traits in a population can result either from phylogenetic constraints or from current selection on preferences and traits. This review thus emphasizes that the evolution of exaggerated traits and preferences depends on inevitable trade-offs for the individuals involved.

### 1. Introduction

Darwin (1871) proposed his theory of sexual selection in order to explain the evolution of male traits that appeared to reduce -- or at least not to promote -- an individual's chances of survival. He realized that females' preferences in choosing mates could explain the spread of these

traits in a population. Attention was thus directed to female preferences as a major force in evolution.

Not long afterwards Fisher (1915) emphasized that female preferences themselves must evolve. Mating preferences evolve, he proposed, both because a female's progeny inherit advantages unrelated to mating success (such as advantages in survival) and because a female's sons inherit advantages in mating. Advantages in mating, Fisher (1930) argued, can promote the evolution of female preferences even when advantages in survival are absent.

In the past decade biologists have developed a clearer understanding of these possibilities for the evolution of female preferences and now often present them as a series of hypotheses labeled by their characteristic features: "good genes for progeny", "direct benefits for females", or "Fisherian evolution". A review of the state of current investigations of sexual selection and mating systems might just as well start with an examination of these three hypotheses.

### 2. Costs and Benefits of Mate Choice

#### 2.1. *Costs and Benefits for Males and Females*

All models of sexual selection seek to explain the evolution of exaggerated traits that have advantages in obtaining mates (or fertilizations) but also disadvantages in survival. Individuals often face trade-offs in maximizing reproduction and survival, and males competing for mates are no exception. Of course, any male trait that had advantages in reproduction but no disadvantages in survival would raise no special problems for evolution.

Current models of sexual selection focus on the nature of costs and benefits for females with preferences. Direct costs and benefits are those that accrue to the female herself; indirect costs and benefits accrue to her progeny as a result of the genes they acquire from their fathers. We can classify these models by their assumptions about net direct benefits to females and indirect benefits of offspring (Fig. 1).

### Models for Evolution of Female Preferences

DB ... Direct Benefits Model  
 GG ... Good Genes Model  
 AP ... Arbitrary Preferences Model  
 X ... no evolution of female preference

Net Direct Benefit to Female	Indirect Benefit to Offspring		
	None*	Sexy sons	Vigorous daughters & sons**
>0	DB	DB	DB + GG
0	X	AP	GG
<0	X	X	GG

\* preferred male traits NOT heritable

\*\* if males make trade-offs between survival and mating success, then vigorous sons are also sexy sons

Figure 1. Models for the evolution of female preferences classified by net direct benefits to females and by indirect benefits to offspring

### 2.2. Direct Consequences of Preferences

Females might incur costs and benefits as a direct result of choosing mates. Costs might include decreased survival from the time, energy, or risks required. A female's costs might also include decreased fecundity if, for instance, choosing a mate meant a risk of missing the optimal time for reproduction.

A female's preferences might also yield direct benefits: either increased fecundity (if she chooses a mate that can fertilize more of her eggs or can provide more nutrients or protection for her eggs and young) or increased survival (if she chooses a mate that can reduce her exposure to predators or disease). The difference between these benefits and costs as a direct result of mate choice is the net direct benefit or cost of mate choice. Preferences that yield positive net direct benefits for females

should evolve to maximize these benefits. This possibility is the "direct benefits hypothesis" for the evolution of female preferences.

### 2.3. Indirect Consequences of Preferences

If there are net direct costs (negative net direct benefits), the evolution of preferences requires indirect benefits in the form of good genes for the female's progeny. There are two possibilities for indirect benefits from good genes. (1) A male successful in mating is likely to leave sons successful in mating (provided expression of the male trait is heritable). This idea is the "sexy son hypothesis" of mate choice. It is a component of Fisher's proposal for the evolution of female preferences. (2) A vigorous male is likely to leave vigorous progeny, daughters as well as sons with higher than average survival or reproduction (provided overall vigor is heritable).

Both of these kinds of good genes can promote the evolution of female preferences with net direct costs (Kirkpatrick 1988, Pomiankowski et al. 1991, Iwasa et al. 1991). The "good genes hypothesis" for the evolution of female preferences focuses on the second kind exclusively.

### 2.4. Arbitrary Preferences and the Sexy Son Hypothesis

Darwin (1871) first articulated the possibility of arbitrary female preferences. This suggestion was the most unsettling aspect of Darwin's theory of sexual selection. It is a proposal that entirely whimsical female preferences might result in the evolution of costly male traits. Lande's (1981) and Kirkpatrick's (1982) mathematical models provided the first demonstration that arbitrary female preferences might spread in a population.

These models include no net direct benefits and no indirect benefits of heritable vigor (the second kind of good genes above). They do include heritable male traits preferred by females and consequently good genes of the first kind above (those producing sexy sons). An "arbitrary preferences" model for the evolution of female preferences is thus equivalent to the "sexy son hypothesis". It proposes that the only benefits females obtain from mate choice are arbitrarily attractive sons.

Note that the hypothesis of arbitrary preferences has the epistemological role of a null hypothesis. There is no possibility of

obtaining positive evidence for arbitrary (hence unpredictable) preferences; this hypothesis is confirmed only by a failure to find positive evidence either for net direct benefits or for good genes for general vigor.

### 3. Heritability of Male Traits and the "Paradox of the Lek"

#### 3.1 Depletion of Genetic Variance for Preferred Traits

The "direct benefits hypothesis" for the evolution of female preferences does not require heritable variation in male traits. Variation among males in their ability to provide resources or protection for females and their offspring might result entirely from environmental variation. It would nevertheless pay for females to choose males with more to offer.

The "good genes hypothesis" and the "arbitrary preference hypothesis", on the other hand, by focusing exclusively on heritable variation among males, encounter the problem of the "paradox of the lek": directional selection, such as that produced by mate choice, will tend to reduce additive genetic variance in the trait selected. As genetic variation among males decreases, the advantages of mate choice by females likewise decrease. In these conditions, as generations pass, mate choice removes the conditions for its own evolution. One could say, mate choice puts itself out of business.

Simulations of sexual selection have clearly shown this influence of a depletion of additive genetic variance for the preferred traits (O'Donald 1980). This depletion of variance would also affect any traits, such as general vigor, that were correlated with preferred traits. Nevertheless, evidence for heritability of preferred male traits indicates that natural populations often retain additive genetic variance for these traits.

#### 3.2. Maintenance of Genetic Variation for Preferred Traits: the Red Queen's Predicament

The argument that mate choice must deplete genetic variance for male traits relies on the most general assumptions about evolution. Several more specific proposals can explain the maintenance of genetic variation for preferred traits and hence selection for preferences.

Of these specific proposals, the one by Hamilton and Zuk (1982, Hamilton 1982) is the most widely recognized. If parasites evolve to avoid their hosts' defences, then host-parasite evolution might resemble the Red Queen's situation of always having to run just to stay in one place. Under this hypothesis, the alleles associated with general vigor shift over periods of a few generations. As a consequence, females preferring male traits that indicate general vigor produce ever-shifting selection for different combinations of alleles. In essence, environmental conditions change so fast that directional selection on any one set of alleles never continues long enough to substantially deplete genetic variance.

To confirm the predictions and assumptions of this hypothesis, we need to show that preferred males produce more resistant progeny, that the effect is genetic not maternal (as a result of a female's allocation of nutrients depending on her choice of mate), and that the selected genes (those promoting vigor) shift over periods of several generations. Note especially the last condition: the genetic basis for resistance to parasites (general vigor) must change with time. No study of preferences for vigorous mates has yet demonstrated this temporal shift in the genetic basis for resistance to parasites.

This mechanism requires a delicate balance between the evolution of host and parasite. If parasites evolve too slowly in relation to their hosts, then female preferences will tend to deplete genetic variation for male traits associated with vigor. On the other hand, if parasites evolve too fast in relation to hosts (consider the limiting case in which genes for parasite resistance were completely uncorrelated from one generation to the next), then female preferences have less advantage in obtaining good genes for progeny.

#### 3.3. Maintenance of Genetic Variation for Preferred Traits: Mutation at Multiple Loci

Another proposal for maintaining genetic variance for preferred traits depends on mutations at multiple genetic loci. Mutations at any one locus are unlikely to maintain much genetic variance in equilibrium with directional selection from female mate choice (unless mate choice is extremely weak). If, however, vigor depends on alleles at a large number of loci, then moderate levels of mate choice might not substantially deplete

genetic variance for vigor. In other words, heritability of vigor could be maintained despite mating preferences for traits that indicate vigor (Charlesworth 1987).

Without knowing which genes contribute to general vigor, this hypothesis is the null hypothesis for maintenance of genetic variation during sexual selection. Evidence for a mutational mechanism consists of an absence of evidence for a Red Queen mechanism. Note also that evidence for heritable general vigor in preferred males does not discriminate between the two hypotheses. To support the Red Queen hypothesis, it is necessary to show that the genetic basis for vigor shifts from generation to generation.

#### *3.4. Maintenance of Genetic Variation for Preferred Traits: More Possibilities*

The paradox of the lek is a special case of the maintenance of genetic variation in populations subject to directional selection. The mechanisms just discussed fall into two categories of solutions to this problem: (1) temporal variation in selection and (2) mutation-selection balance. A third possibility with some similarities to these first two is (3) migration-selection balance. Migration might occur between local populations subject to selection for different alleles. The level of genetic variation in any one population would then depend on the balance between selection and immigration. In this case, there would be clear advantages to preferences for locally adapted mates. Even when populations differed only in alleles for sexy sons, migration could maintain genetic variation for these alleles despite continued directional selection from female preferences.

The paradox of the lek does not arise when female preferences do not create directional selection on particular alleles. For instance, attractiveness to females might result from heterosis in males. If so, the heritability of these traits would vanish, despite genetic differences between preferred and unpreferred males, and consequently any indirect genetic benefits of female preferences (either good genes for general vigor or for sexy sons) would also vanish. In this case, preferences for particular male traits could evolve only if they resulted in direct benefits for females.

Advantages of heterosis might instead favor preferences for disassortative mating in general, rather than preferences for particular traits.

In mammals, for instance, preferences for disassortative mating contribute to genetic complementarity of alleles at MHC loci. These preferences result in genetic benefits for progeny (and thus qualify as indirect benefits for these preferences), but they do not produce directional selection on particular alleles. They promote rather than reduce genetic variation for preferred traits (Potts et al. 1994, Penn and Potts 1998).

#### *3.5. Genetic Variation for Preferred Traits: Conclusion*

We still do not know what proportion of male traits preferred by females is heritable. Preferred traits that are not heritable could result from heterosis (or other forms of nonadditive genetic variance) or from environmental influences on males. Those that are heritable raise the issue of the paradox of the lek. To what extent continued heritability of these traits depends on a Red Queen mechanism, as opposed to mutation-selection or even migration-selection balance, is still moot.

### **4. Accelerating Evolution of Male Traits and Female Choice**

#### *4.1. Background for Fisher's Proposal*

In recent decades there has been a tendency to conflate arbitrary mate preferences with "Fisherian" evolution. "Fisherian" evolution refers to accelerating or runaway evolution of male traits or female preferences or both. Several issues need clarification to understand this process. It is useful to start again from the beginning.

When Darwin proposed his theory of sexual selection, he clearly saw that female preferences or male competition could result in the spread of some heritable traits over others. Particularly when discussing female preferences, he tended to emphasize their potentially arbitrary nature. The particular aspect of his theory that many of his contemporaries found incredible was his allusion to an "aesthetic sense" in nonhuman females (Darwin 1871).

Darwin's theory had two weaknesses: no clear physiological mechanism for female preferences; and, in common with the rest of his theory of natural selection, no clear genetic mechanism. The "Modern

Synthesis" solved both of these problems, in general if not in all particulars. First, the newly developed mathematical theory of population genetics viewed natural selection as differences in the spread of alleles in populations as a result of differences in the survival or reproduction of phenotypes associated with those alleles. Second, the newly developed field of ethology viewed a female's preference as any neural mechanism that resulted in a tendency to mate with males of one sort rather than another (Fisher 1930).

#### 4.2. Fisher's Proposal

Based on these two developments, Fisher proposed a mechanism for sexual selection. Although one of the great mathematicians of the century, he relied on a purely verbal account. His proposed mechanism consisted of (1) an initial advantage of a male trait for survival, (2) a consequent advantage of a female preference for this trait, (3) subsequent accelerating evolution of the trait and preference, (4) progressive increase in the disadvantage of the trait for male survival, and (5) eventual termination of the process once the disadvantage to survival exceeded any advantage in mating.

It is not clear what Fisher had in mind for the crucial features of the process, especially the transition from step (2) to (3) and the nature of step (3). His account suggests that he felt that the advantage of producing sexy sons would drive the evolution of female preferences beyond the point at which they ceased to have advantages for viability and that the advantage of a female preference would increase as it spread in the population.

#### 4.3. Mechanisms of Accelerating Evolution: Genetic Correlation

There are at least two possibilities for accelerating evolution of preferences and preferred traits (step 3 above): genetic correlation and frequency-dependent selection. The important role of genetic correlation between male traits and female preferences was first revealed by the mathematical models of Lande (1981) and Kirkpatrick (1982). A genetic correlation arises as a direct consequence of assortative mating: when females carrying alleles for a preference are more likely than others to mate with males carrying alleles for a trait, then the progeny are more likely than other individuals in the population to carry both sets of alleles,

both those associated with the male trait and those associated with the female preference. The former alleles are expressed primarily in sons and the latter only in daughters, but both sons and daughters carry both sets of alleles.

Population geneticists often use "linkage disequilibrium", rather than "genetic correlation", as a general term for an association of alleles at different loci (for instance, Hartl and Clark 1989). Genetic correlation can indeed result from close physical association of alleles on the same chromosome, but the genetic correlation that results from assortative mating would usually have nothing to do with chromosomal linkage. It is just an association across individuals between the alleles at two sets of loci.

Clearly a genetic correlation can cause self-promoting evolution of female preferences. As generations pass, it becomes more and more likely that a female choosing a male with a preferred trait (and thus one likely to carry the alleles for the male trait) is also choosing a male likely to carry the alleles for the female preference. When a female chooses a mate, she chooses an individual that is not only likely to carry the alleles for the male trait but *also likely to carry the alleles for the female preference*. The spread of alleles for the female preference is thus self-promoting. Evolution of both male trait and female preference accelerates (Lande 1987).

#### 4.4. Mechanisms of Accelerating Evolution: Frequency-dependent Selection

A second mechanism can also produce accelerating evolution. In many forms of communication, perhaps in all, the advantage to a receiver of having the capability for responding to a signal will often depend on how many individuals produce the signal. Consequently, the evolution of a novel signal encounters an initial hurdle: a novel signal rarely evokes a response when receivers with appropriate mechanisms for response are also rare. Conversely, the initial evolution of a new response usually encounters the reciprocal hurdle. Even if both signaler and receiver benefit from their interaction, neither is likely to receive much advantage at first. The signaler in particular incurs costs but would realize little benefit, because few receivers would respond appropriately. However, as the



alleles for the signal and the response spread, the net benefits for signalers and receivers would usually increase. The advantages are thus frequency-dependent, and evolution accelerates.

Eventually the advantage to both signaler and receiver might decrease as the signal spreads throughout a population. Imagine a signal used to identify a suitable social partner for foraging. As more and more individuals have the alleles making them suitable partners, the advantage of producing or responding to the signal would progressively decrease. In this case, evolution would first accelerate, when the alleles were scarce, then decelerate, when the alleles became common.

Note that accelerating evolution from frequency-dependent advantages requires no genetic correlation between signal and response. It thus does not depend on mating between the signaler and receiver. It could apply to the evolution of all communicatory signals, not just those between prospective mates. O'Donald's (1980) models of sexual selection included no provisions for genetic correlation and thus demonstrate the accelerating evolution of male trait and female response solely as a consequence of frequency-dependent advantages.

Fisher (1930) describes no specific mechanism for the accelerating evolution he proposes, but he seems to me to have had frequency-dependent selection in mind.

#### 4.5. Distinguishing between Mechanisms of Accelerating Evolution

So far no efforts have been made to discriminate genetic correlation and frequency-dependent selection as mechanisms for accelerating evolution of male traits and female preferences. It is not clear at this point how the dynamics of signal evolution by these two mechanisms might differ. Both would often encounter initial hurdles when alleles are scarce. In Lande's model, however, the initial threshold pertains to the magnitude of genetic correlation between trait and preference, not to the frequencies of the alleles themselves. Nevertheless, the correlation is likely to be low when the frequencies of alleles are low. Both would result in decelerating evolution if genetic variance for the signal decreases as the alleles go to fixation.

There is, nevertheless, at least one important difference between the two mechanisms: only a genetic correlation can produce runaway

evolution of an arbitrary male trait. Frequency dependent selection can only accelerate the evolution of a preference that has a net benefit.

#### 4.6. Genetic Correlation and Accelerating Evolution as Properties of Sexual Selection

Accelerating evolution as a result of genetic correlation can only apply to signals that affect mating. It is the mating between signaler and receiver that produces the genetic correlation. Furthermore, a genetic correlation always develops whenever heritable signals and responses affect opportunities for mating or fertilization. Regardless of the evolutionary origins of trait or preference (whether or not influenced by developmental/phylogenetic constraints) and regardless of the nature of any net benefits of preferences (direct benefits or good genes), mate choice produces genetic correlation and thus can promote accelerating evolution of signal and response.

Consequently, genetic correlation and accelerating evolution of trait and preference are not criteria for a distinctive form of "Fisherian" evolution. Despite Fisher's key insight that sexual selection could lead to accelerating coevolution of trait and preference, it is probably best to avoid the term "Fisherian evolution," at least without clear specification of which alternatives are intended.

### 5. Indirect and Direct Female Choice

#### 5.1. The Traditional View

In proposing his theory of sexual selection, Darwin argued that exaggerated male traits might evolve because of female preferences for them or because they promoted success in competition with other males. His two forms of sexual selection have pervaded discussions since then, often under the labels "intrasexual and intersexual selection".

These two terms conflate proximate and evolutionary mechanisms. I will use the term "selection" only for evolutionary mechanisms and the term "preference" or "choice" for proximate (behavioral/ physiological/ morphological) mechanisms (Wiley and Poston 1996). The terms "intrasexual" and "intersexual" also obscure the essential role of female behavior in all sexual selection.

prefer males that make certain kinds of sounds, have longer tails, make more intense or persistent displays, or carry more stones (Møller 1991, Soler et al. 1996, Westcott 1992).

In contrast, a female might choose mates indirectly, perhaps without ever perceiving them. In this case, a female establishes the conditions under which she will mate. The female has thus set conditions under which males compete for access to her; she simply mates with the winner.

#### 5.4. *An Example of Indirect Mate Choice: Penelope's Strategy*

A female danaid butterfly emits a sexual pheromone while still in her chrysalis and then mates before she ecloses with the male able to guard the chrysalis most effectively. She has chosen her mate as effectively as if she had examined a series of males in advance. Indeed, if the objective is to choose a competitive male, her optimal strategy might be to precipitate a contest rather than to assess the prospective suitors directly. Advertising availability and waiting long enough to assure a telling contest are useful components of this strategy.

We might call this form of indirect choice the "Penelope strategy", for Odysseus' patient wife who paid no heed to her suitors but accepted the winner. The eventual winner, in addition to defeating all comers, had also engaged in a number of extrapair copulations! Circumnavigating the island of Sicily (the site of the conference on which the present volume is based) might illustrate the sort of tests created indirectly by a mate adopting Penelope's strategy.

#### 5.5. *Other Varieties of Indirect Mate Choice*

Depending on the females' behavior, which sets the conditions for male competition, males might compete in either of two ways: by direct physical interaction (interference competition in ecology) or by scrambling or endurance (exploitation competition in ecology). Female tree and ground squirrels appear to set conditions for a scramble competition among males (Schwagmeyer and Woontner 1986). In many frogs with prolonged mating seasons, females appear at appointed places at irregular intervals. Males with the endurance to display for a larger proportion of the time stand to gain more matings (interaction-free sexual selection,

#### 5.2. *Competition versus Choice: the Importance of Limiting Resources*

Females usually exercise choice and males compete for mates because a female's reproductive success is usually limited by her ability to nourish and protect her gametes and a male's success by his ability to fertilize females' gametes. As ecologists have long recognized, competition requires a limiting resource. For females it is often shelter or nutrients for her gametes; for males it is usually females' gametes (sometimes in combination with direct contributions to his progeny).

Usually it is the nature of gametes that determines the nature of limitations on reproduction and thus whether individuals choose mates or compete for access to them (Wiley and Poston 1996). An individual producing nutritive gametes (ova) is likely to be limited by access to nutrients; an individual producing mobile gametes (sperm) is likely to be limited by access to ova. Although these individuals might invest similar levels of energy, time, and risk in production of gametes, the differences in the limitations on reproduction can explain careful choice of mates by the first individual and escalated competition for mates by the second. This focus on sexual differences in the limitations on reproduction clarifies previous proposals for the evolution of sexual differences as a result of differences in the numbers of gametes produced (Bateman 1948) or differences in parental investment (Trivers 1972, Wilson 1975). It also clarifies conditions under which both sexes might compete for access to preferred mates.

#### 5.3. *Two Proximate Mechanisms for Mate Choice*

This perspective alters the traditional view of the proximate mechanisms of sexual selection. A female can choose a mate (behave in a way that makes it more likely that she will mate with certain males rather than others) in two fundamentally different ways. She can attend to discernible differences between males and show a preference for mating with those that have certain traits. She thus discriminates between potential mates in a direct way. Discrimination, in this sense, requires a preferential response to cues with particular characteristics. This form of mate choice has received intensive investigation for two decades and in a more limited way for even longer. We know, for instance, that females

Murphy 1998). Female boat-tailed grackles copulate in their nesting colonies. Although they mate indiscriminately with any male that approaches them, they nevertheless copulate almost exclusively with the one male able to defend the vicinity of the colony from rivals (Poston 1997). In each of these cases, the females' behavior sets the conditions under which males compete.

Indirect mate choice can result from widely different sorts of female behavior. Especially clear examples are various signals advertising receptivity or fertility. This behavior has long been interpreted as incitement of male competition (Cox and LeBoeuf 1977, Clutton-Brock and Harvey 1976). Another possibility involves mating in particular places that are identifiable in advance by males, either because they are traditional sites or because they have special features (tops of hills or particular microhabitats). Temporal and spatial coordination with other females also sets conditions for male competition by affecting the "defendability" of females. Even fleeing or appearing at unpredictable times can increase the chance that persistent males will succeed. Making conspicuous signals before or during copulation, or mating only with males that make themselves conspicuous, assures that only those males able to repel rivals can mate successfully (Wiley and Poston 1996).

## 6. Consequences of an Expanded View of Mate Choice

There are five important consequences of this expanded view of mate choice.

(1) It is clear that much more of the behavior of females constitutes mate choice than is currently investigated. In particular, preferences for mating in specific places (arbitrary sites or special microhabitats) are often forms of indirect mate choice. In addition to whatever consequences these preferences have for survival or reproductive success, they also often affect with whom a female mates.

(2) Indirect mate choice might often provide a more reliable method for assessing potential mates than could direct discrimination. It often takes months or years of sustained effort for a male to achieve and to defend his dominance over rivals. Females with indirect choices for dominant males would thus obtain the advantage of a prolonged

assessment of potential mates. Direct discrimination of males' qualities might often require difficult snap judgments.

(3) Many aspects of female behavior not now usually considered mate choice must actually coevolve with male behavior as a result of sexual selection. Choice of microhabitats for nesting, for instance, affects both a female's prospects for reproductive success and also the traits of her probable mate. A decision by a female red-winged blackbird *Agelaius phoeniceus* to choose a particular microhabitat must evolve in response both to the consequences for her immediate reproductive success (as in the "polygyny threshold" model, Searcy and Yasukawa 1997) and to her prospects for indirect benefits or good genes from her mate or neighboring males (Westneat 1992). Note also that both indirect and direct mate choice can produce correlations between mating success and particular features of males.

(4) Indirect female choice evolves in conjunction with male traits that contribute to competitive success in just the same way that direct mate choice coevolves with male traits. Genetic correlation develops between female behavior (including any behavior that sets conditions for male competition for access to her) and male traits (including those that result in success in such competition). Thus the prospects for accelerating coevolution of female and male traits apply to indirect mate choice just as well as to direct mate choice. This expanded view of female mate choice, to include both direct and indirect choice, suggests that sexual selection results in pervasive coevolution of male and female behavior.

(5) The possibility of indirect mate choice complicates our understanding of mating systems in natural circumstances. In efforts to bring the study of mate choice under experimental control, many studies have focused on direct mate choice (reviewed by Andersson 1994). Subjects in controlled laboratory conditions often reveal preferential responses to particular cues. These preferences are rarely confirmed in the field, and, when such an attempt is made, it sometimes turns out that preferences in the laboratory differ from those in more natural situations (Marchetti 1998). Such discrepancies would be expected if the natural social context provided the conditions for indirect mate choice. Because indirect mate choice works by one sex setting the context for competition among members of the other sex, it is often strongly dependent on intact

social groups in their natural environment. In the future, experiments on mate choice must identify and incorporate the crucial elements of natural situations.

## 7. Indirect and Direct Mate Choice in the Evolution of Leks

Much field work on mating systems in the past two decades has failed to consider the possibilities for indirect choice. Instead the focus has been on identification of those traits of males that females might discriminate in direct mate choice. We are probably missing fundamental aspects of many mating systems. This is a case in which hypotheses too narrowly defined might lead us astray.

Lekking behavior provides an example. Many studies in recent decades have interpreted correlations between male success on leks and behavioral or morphological traits as evidence for direct preferences of females for these traits. Some models of the evolution of leks are based entirely on direct choice of males by females. For instance, the "hotshot" model proposes that females prefer certain males and that other males congregate to obtain matings with confused or impatient females ("spatial spillover") (Höglund and Alatalo 1995). Related proposals suggest that females prefer those males that can defend themselves and protect females from interference by rivals (Beehler and Foster 1988, Clutton-Brock et al. 1992).

"Hotspot" models of lekking likewise ignore the possibility of indirect female choice. In these models males select display sites that maximize their exposure to female traffic, while females' movements are unrelated to males (Bradbury and Gibson 1983, Apollonio et al. 1998). Females in short choose mates by running into them. We have seen, however, that females' behavior is likely to evolve in response both to ecological influences on their movements and to consequences for choice of mates. Many studies of the locations of leks in relation to females' movements have not separated the possible influences of mate choice and ecological factors on females.

An alternative, which has received less attention, is that leks result at least in part from indirect mate choice by females. If females choose particular sites for mating, which then become the objects of competition

for males, then males able to defend positions at these sites become most likely to mate. Females might benefit even if mating sites were chosen arbitrarily, because a brief investment of time by females could promote mating with vigorous, dominant males as assessed in male-male competition over many weeks or months.

Traditional mating sites in at least partly arbitrary locations might develop if inexperienced females copied the behavior of experienced ones. The clearest evidence for such behavior comes from bluehead wrasse *Thalassoma bifasciatum* (Warner 1987), but some evidence is also available for lekking birds and mammals (Apollonio et al. 1990, Wiley 1991, Gibson et al. 1991, Carranza 1995). Some studies show that females tend to mate at specific sites along routes used by many females (Apollonio et al. 1998, Westcott 1997) or at sites visited and marked by many previous females (Deutsch and Nefdt 1992). Other studies show strong competition among males to attain central positions on leks, together with preferences by females for mating in central territories (Rintamaki et al. 1995, Hovi et al. 1994).

## 8. Assessment of Mates: Reliable Signaling Systems and Honest Signals

If females receive either net direct benefits or good genes from matings with high-quality males, it should pay for females to adopt behavior that increases their chances of mating with these males. Selection should favor females that accurately assess the qualities of prospective mates. Indirect choice might sometimes provide the most reliable method for assessment. If, on the other hand, females use direct mate choice, they face the problem of assessing cues that can discriminate high- and low-quality males.

Over two decades ago, Zahavi (1975) suggested that females should focus on costly male traits as a way to identify high-quality males. He has since suggested that "wasteful" traits, those with "unnecessary" costs, are the most reliable (Zahavi 1998). Grafen (1990a,b) subsequently developed a model of this process, in which females benefit from mating with high-quality males but cannot directly assess male quality. Males produce signals, which affect their chances that females will accept them

as mates. Grafen showed that, in the first place, females should respond only to reliable signals (those that in fact indicate male quality) and that, in the second place, only costly traits are reliable (the cost of a trait increases with its size or amplitude). The latter conclusion requires an assumption of "continuity in everything". In other words, the effect of a male trait is a continuously increasing function of its cost -- there are no cheap imitations.

In thinking about these conclusions it is important to distinguish between a reliable *signaling system* (all signals produced in a particular context) and a reliable (honest) *signal* (one instance of signaling). An honest signal (an honest instance) is one that accurately reflects the signaler's state (for instance, large amplitude for high quality). A reliable signaling system is one in which most signals are honest. Grafen's results show that females should evolve to attend only to a reliable signaling system but not necessarily that all signals are honest. "Errors" (responses to signals that do not accurately reflect the signaler's state) change the expected advantages to responding females, but so long as there remains a net advantage when all signals are considered then female responses should still evolve (Johnstone and Grafen 1993). Below we shall see how female responses might evolve in response to errors in communication.

It is also important to realize that the most conspicuous result of this model, that assessment signals should evolve to reflect their costs, is not a strong inference, because there is no clear alternative hypothesis. It is difficult to imagine that any signal would not incur costs, in terms of energy, time, or risk, or that these costs would not increase with amplitude or duration of the signal. In fact, we shall see below that there are good reasons to think that all signals in natural, noisy circumstances should evolve some, often substantial, exaggeration and hence cost. How to think clearly about the "wastefulness" of signals is an enduring perplexity.

## 9. Inevitable Trade-offs in the Evolution of Displays

The focus on costs of male display suggest that the real issue is the nature of the trade-off between decreased survival and increased mating as a consequence of signaling. This approach is much more in line with a well-developed body of theory about life-history trade-offs (Stearns 1992).

In this approach, "fitness" is usually taken as the product of expected survival and fecundity. The propagation of alleles in a population requires that phenotypes carrying those alleles survive and reproduce in succession; the appropriate expression for combining the consequences of successive events is thus multiplication. The terms in a life table, for instance, combine age-specific survivorship and age-specific fecundity by multiplication. For any behavioral phenotype (strategy), we can use the product of current fecundity and survivorship as a measure of the current contribution to the overall net reproductive rate of that phenotype (we thus ignore for simplicity any consequences of the current trade-off for future survival and reproduction) (see Andersson 1982, Nur and Hasson 1984).

Simple graphic examples can show that costly signals will in general be reliable. We make assumptions similar to Grafen's: females cannot directly assess male quality, but instead choose mates based solely on the signals they produce; male survival decreases with the amplitude of the signal he produces (signals are costly); high-quality males can produce more signal for any given level of survival. Each male should thus choose an amplitude of signal that maximizes his own "fitness" (reproduction  $\times$  survival), in accordance with the trade-off between survival and mating for his particular quality (Fig. 2). If the lines for survival as a function of signal level for high- and low-quality males do not cross, high-quality males will produce larger signals than low-quality males (Fig. 3).

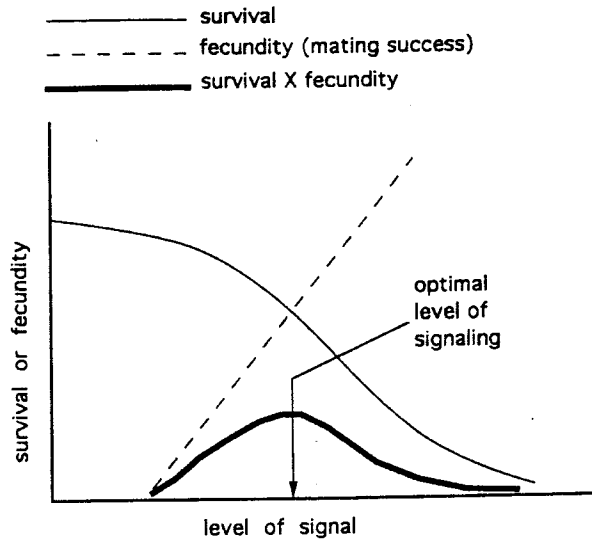


Figure 2. The level of signaling that optimizes survival X fecundity. In this general case, we assume that a male's survival decreases steadily as his level of signaling increases (in other words, signaling has costs). His success in mating increases with the level of signaling. Survival X fecundity is thus optimized at an intermediate level of signaling.

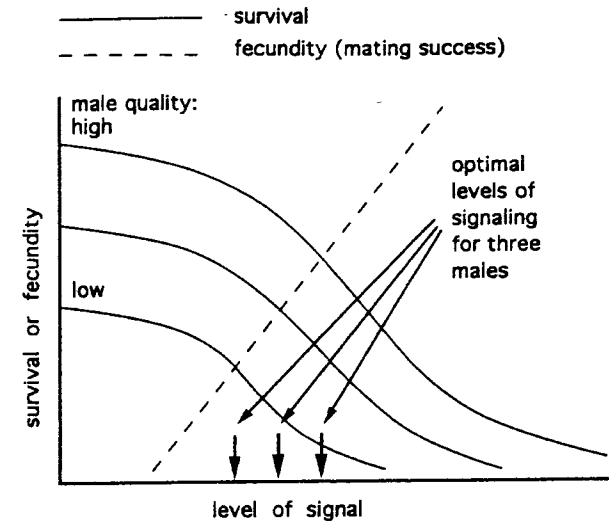


Figure 3. The trade-off between survival and reproductive success for males displaying to attract females. For each male the level of signal produced determines his survival. Males differ in survival as a function of signal level because some are of higher quality than others. The level of signal determines the probability of attracting a female. Each male should then optimize his fitness (survival X reproduction) according to his survival function and the mating function. If males' survival functions do not cross, males of higher quality will optimize their fitness at a higher level of signaling (and consequently at greater success in mating) than will males of lower quality.

Notice that the absolute cost of a signal to a particular male is the difference between the male's survival when he produces no signal and his survival when he produces an optimal signal. There is also a relative cost, the proportion of his maximal survival lost as a result of signalling. For neither measure of cost is it true that high-quality males necessarily have either higher or lower costs of optimal signalling than do low-quality males. The only general conclusion is that high-quality males always have a greater increase in "fitness" for any increase in signalling than do low-quality males (Getty 1998a,b).

## 10. Errors in Responses to Signals

### 10.1 Communication Requires Decisions by Receivers

Mate choice, direct or indirect, requires responses to signals. It is thus a special case of communication, and the evolution of mate choice encounters some general problems in the evolution of communication. To see the implications for mate choice, we first need to consider these general issues (Wiley 1994).

Signals are never sent and received in isolation. Background energy, to a greater or lesser degree, mixes with any signal as it impinges on a receiver. Furthermore, no signal passes from the emitter to the receiver without change. The structure and composition of signals are altered, to a greater or lesser degree, by the physical processes of transmission. These two factors, background energy and physical alteration, make it unlikely that receivers can ever expect to operate under ideal conditions, with certainty about what signal was emitted and when.

The problem receivers face is inherent in the nature of signals. Signals provide information on the basis of which a receiver can alter its behavior, but signals do not provide all of the power necessary for this alternation. Instead the receiver must provide some (usually nearly all) of the power for the response. Consequently, the receiver must decide both whether or not a particular signal has occurred and what an appropriate response is. This framework applies to all communication, whether between electronic instruments by means of electrons, between cells by means of molecules, or between animals, including humans, by means of acoustic, visual, olfactory, or any other signals.

### 10.2. Four Outcomes Are Possible for Each Decision by a Receiver

To conceptualize the general problem facing a receiver, we can think of the receiver responding to input that exceeds some threshold. Any receiver (or one of its receptors) is subject to fluctuating stimulation from background energy (probably often with an approximately random or Gaussian distribution of intensities); when a signal occurs, its intensity is added to that of the background energy (Fig. 4). As a result, the receiver is then subject to stimulation with a higher average intensity but with the same random fluctuations. Unless the distribution of stimulation with the

signal present is completely distinct from that with the signal absent, the receptor cannot completely separate the two situations. Wherever its threshold for response is set, it will make some errors (Fig. 5).

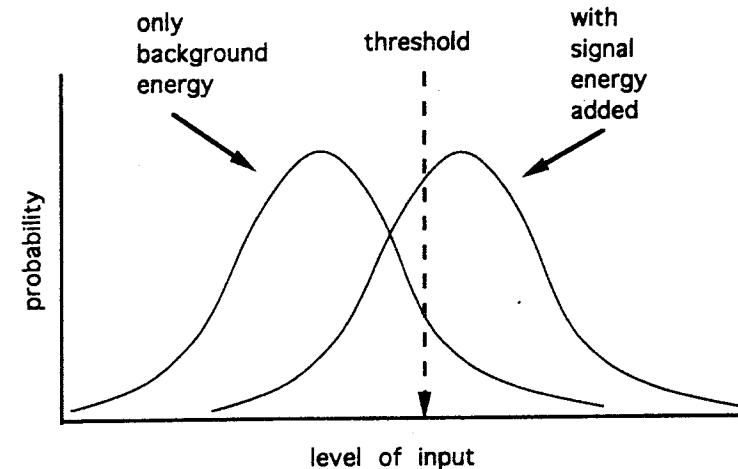


Figure 4. The trade-off between false alarms and missed detections for any receiver. A receiver monitors the level of input to its receptors. In the presence of background energy alone, this level fluctuates with a normal probability distribution. Depending on the level of input, the receiver must decide whether to respond as if a signal had occurred or not. This decision requires that the receiver set a threshold for response.

It is important to emphasize how general this simple model of communication is. It applies both to receptors with thresholds and to tuned receptors. The definition of error is also straightforward when we are considering the evolution of communication. A response (or failure to respond) is an error when it reduces the receiving individual's "fitness" (its reproduction or survival as these affect the rate at which its alleles spread in a population). These issues are treated in more detail elsewhere (Wiley 1994).

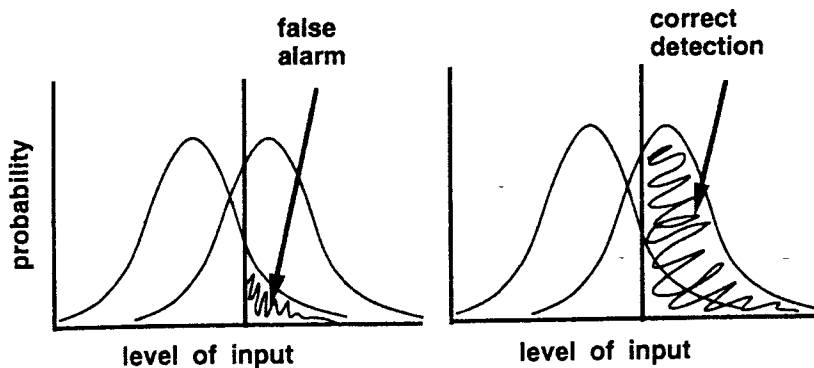


Figure 5. The trade-off between false alarms and missed detections for any receiver (continued). The threshold, together with the probability distributions for input with and without a signal present (see Figure 4), determine the probabilities of each of four outcomes. For instance, the probability of a **false alarm** is the area under the probability distribution from infinity to the threshold for response when a signal is absent. The probability of a **correct detection** is the area under the probability distribution from infinity to the threshold for response when a signal is present. A receiver can adjust its probabilities of false alarm or correct detection by adjusting its threshold – but it **cannot adjust these probabilities independently**.

Each time a receiver samples its input and decides to respond or not, four outcomes are possible. It might respond when in fact an appropriate signal has occurred (a *correct detection*); it might respond when no signal had occurred (because background energy was mistaken for a signal) (a *false alarm*); it might fail to respond when in fact no signal had occurred (a *correct rejection*); or it might fail to respond when a signal had occurred (because it was mistaken for background energy) (a *missed detection*).

### 11. Inevitable Trade-offs in the Evolution of Responses

A receiver can affect the probability of these four outcomes by setting its threshold for response higher or lower. A high threshold will

reduce the chances of false alarms; a low threshold will reduce the chances of missed detections. Yet the *four outcomes cannot all be adjusted independently*. A high threshold reduces false alarms but also inevitably increases missed detections; a low threshold reduces missed detections but also inevitably increases false alarms. The most important insight from this general model of communication is that a receiver cannot independently adjust the probabilities of the four outcomes of a decision to respond or not to respond. Instead a receiver must optimize the trade-offs between the four outcomes.

The general solution to this optimization problem consists of maximizing the expected utility  $E(U)$  of the threshold.  $E(U)$  equals the sum of the probability of each outcome times the expected payoff for this outcome:

$$E(U) = \sum (probability\ of\ outcome\ i)(payoff\ for\ outcome\ i)$$

The expected payoff for each outcome is its contribution to "fitness" (a change, either positive or negative, in reproduction  $\times$  survival). The mathematics is reviewed in detail elsewhere (Wiley 1994).

Consider two contrasting cases: a small bird listening for alarm calls from flockmates; and a female bird seeking a vigorous mate. In the first case, the small bird's ears provide input about the intensity of a particular, relatively high frequency that characterizes the alarm calls of conspecifics. Some part of the bird's brain decides, based on the input from the auditory receptors, whether or not to terminate feeding and to initiate a dive into cover. In this case, a correct detection might save the bird's life, a missed detection might risk its life, and a false alarm might involve the loss of food for a few minutes. A correct rejection might represent the alternative to which the others were compared (no change in fitness).

Our subject might face a situation in which errors were likely. Its ears might often report high tones when in fact no real alarm call had occurred (perhaps another species in the habitat produced false alarm calls in order to gain access to food or perhaps windy weather resulted in high levels of background energy from vegetation). Nevertheless, our subject is unlikely to raise its threshold very high in order to avoid frequent false



alarms. Instead, the consequences of missed detections of real alarm calls might make it optimal to keep a low threshold for response. Our subject's optimal behavior then is to accept the consequences of frequent false alarms -- it should evolve *adaptive gullibility*.

A female seeking a vigorous mate is often in the diametrically opposite situation. A correct detection might result in progeny with good (above average) genes, a missed detection would usually result in additional time searching, a false alarm might result in progeny with bad (below average) genes, and a correct rejection would (like a missed detection) result in additional time searching.

As before, our subject might face a situation in which error was likely. The features of males might correlate with but not completely reveal the quality of males; females might have to make snap judgments (particularly if there were high costs to continued searching); or background sound and visual patterns might interfere. A gravid female frog seeking a mate in a large multispecies chorus, for instance, must choose a mate on the basis of a call detected in the presence of high levels of background sound (Wollerman 1999).

If choosing an optimal mate had major consequences for the spread of the female's genes (because of direct benefits from the male on her reproductive success or because of good genes for her progeny) but searching had comparatively little cost, a female is unlikely to lower her threshold to avoid frequent missed detections. Instead, the high cost of false alarms will make it optimal to set a high threshold for response. Our subject should then accept the consequences of frequent missed detections -- she should evolve *adaptive fastidiousness*.

Mathematical justification for these two extremes in receivers' behavior is presented elsewhere (Wiley 1994).

## 12. Co-evolution of Signals and Responses for Mate Choice

### 12.1. Evolution of Signals

How might males evolve in response to high thresholds for response -- adaptive fastidiousness -- in prospective mates? Clearly individual males that can escalate the intensity, persistence, or amplitude of their displays will evoke more responses from females. These attributes

of display normally increase their costs, in terms of male survival, because display inevitably entails some risk or requires some energy or time. As we have seen, males must make trade-offs between survival and display, so high thresholds for response in females lead to costly displays by males that reliably indicate male vigor.

A number of studies have shown that males with more exaggerated displays survive as well, or even better, than those with less display. In some of these cases, artificial exaggeration of displays (such as lengths of tail feathers) has confirmed that increased display results in decreased survival for any males. These two results clearly show that some males can support more display than others.

These results are sufficient but not necessary to demonstrate that male display is a reliable signaling system. If males evolve to produce an individually optimal level of display, as suggested above, it is not true that optimal levels of display must always vary inversely with either absolute or relative costs to survival in order to have a reliable signaling system. It is only necessary that male "fitness" (reproduction  $\times$  survival) vary inversely with level of display. (Getty 1998a,b).

The level of display by males should also depend on the "fastidiousness" of preferences by females (Fig. 6). Few studies have attempted to compare the levels of preference and display in related species. Searcy (198), however, showed that female Common Grackles *Quiscalus quiscula* have less pronounced preference for large song repertoires than do female Red-winged Blackbirds, in accordance with the sizes of repertoires sung by males of these species. Nevertheless, females of both species prefer larger repertoires than conspecific males actually sing. Other cases of discordance between preference and trait are discussed below. More comparative studies could illuminate the coevolution of preferences and traits.

### 12.2. Evolution of Responses

If we approach mate choice as a problem in decision-making, as proposed above, we must face three issues.

(1) To understand the evolution of female choice, preferences must be studied under natural conditions. We know little about the influence of background energy or alternative signals on mate choice, because nearly

all experimental studies of females' response to males' signals have striven for ideal "quiet" conditions rather than natural "noisy" conditions.

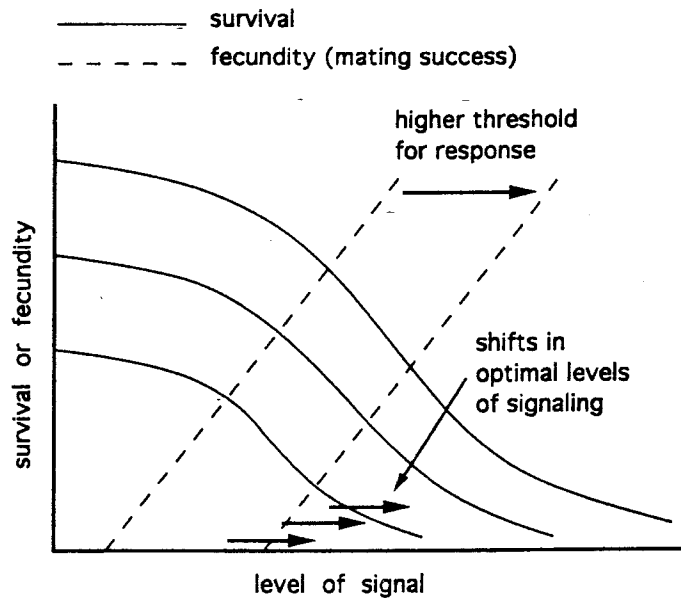


Figure 6. Evolutionary response of males when females evolve adaptive fastidiousness (higher thresholds for response to potential mates). The males face trade-off between survival and mating success as in Figure 2. When females raise their thresholds, the males' expected success in mating as a function of signal level shifts to the right. As a consequence, the level of signaling escalates, the costs of optimal signaling increase for all males, but mating success remains correlated with male quality.

Several such studies have confirmed basic predictions from signal detection theory. Background energy limits a female treefrog's ability to detect conspecific signals in natural choruses (Gerhardt and Klump 1988, Wollerman 1999). Furthermore, females cannot make discriminations between two conspecific signals in the presence of natural chorus sounds

despite their ability to do so in quiet conditions (Wollerman and Wiley MS). These results challenge our understanding of the evolution of mate choice.

(2) Females' thresholds or, in more general terms, their criteria for response to complex signals, are not likely to evolve to match the properties of actual signals. Recent studies of discrimination by neural nets make this point clearly. For instance, a neural net trained to recognize one of two stimuli that differ in one parameter (such as length) does not usually develop into a matched filter for the target stimulus. For instance, they usually perform poorly when asked to discriminate the target stimulus from a still longer stimulus. Evolution might well produce similarly "opened" preferences as a result of unidirectional selection on discrimination of signals (Enquist and Arak 1993). Receivers thus evolve to optimize discrimination between signals actually encountered, rather than to become matched filters for signals.

(3) Models of mate choice, indeed models of any behavioral decision, must consider the consequences of all four possible outcomes. Correct detections, missed detection, false alarms, and correct rejections have analogues in every decision. The expected utility of an individual's criteria for a response should take the probabilities and consequences of all four into account. Consider the decision of a monogamously mated female to desert her mate and seek another. If she leaves, she might choose a better mate (correct detection) or a poorer mate (false alarm); if she stays she might miss an opportunity to choose a better mate (missed detection) or not (correct rejection). The probability and consequences of all four options must be evaluated to understand the evolution of mate desertion.

Other decisions are similar. Should a female accept an extra-pair fertilization? Should a cuckolded male desert his mate and seek another? These questions need more thorough analysis than they have yet received.

### 13. Constraints on Evolution of Signals and Responses

The evolution of females' responses are also subject to "sensory biases" (Ryan 1990, Endler 1992, Ryan and Keddy-Hector 1992). Discussions of these issues have invoked several separate aspects of evolution.

### 13.1. Multiple Functions of Sense Organs

Sensory systems often have several different functions: feeding, avoiding predators, choosing mates, and so forth. It is sometimes possible to argue that sensory systems evolved primarily as adaptations for feeding or avoiding predators and that males then evolved signals to take advantage of the female's responses to food or predators. On the other hand, it is possible that females' have evolved to choose both mates and food (or to avoid predators) by focusing on the most reliable kinds of signals available.

Female hermit crabs of the species *Uca beebei* choose males by the size of the pillars males build beside their burrows. They, as well as females of many other species of *Uca*, retreat to such structures when chased by a predatory bird (Christy 1995). Have male *Uca beebei* evolved to build pillars in order to take advantage of females' adaptations for escaping from predators?

This case invites analysis by signal detection and decision theory. It seems probable that males' pillars create conspicuous signals against the horizon. Pillars are no doubt costly to construct and apparently indicate male quality (Blackwell et al. 1995). Thus female's responses to pillars might well have evolved both for mate choice and for predator avoidance.

### 13.2. Physical Constraints on Communication Imposed by the Environment

Physical features of the environment place constraints on any communication, so communication for different purposes in the same environment might well evolve some similarities as a result of similar constraints. For lizards inhabiting dense vegetation, the swaying of branches and leaves have characteristic frequencies which constitute background visual "noise" (Fleishman 1992). Prey attempting to avoid detection often adopt similar movements to blend with the background. Predatory lizards have visual systems adapted to filter out these visual frequencies, and conspecific social signals evolve to contrast with these frequencies.

### 13.3. Interactions of Phylogeny and Adaptation

Finally all evolution encounters phylogenetic or developmental constraints on possible directions of change. If multiple random mutations are less likely than single mutations to provide advantages to progeny, lineages would tend to change one mutation at a time. Organisms diverge progressively from their ancestors, so those with close phylogenetic relationships are more likely to share similarities than are those with distant relationships. Any current population is thus inevitably a result of both its previous evolutionary history and its adaptation to its current environment. Tinbergen and Lorenz made the study of phylogenetic constraints on the evolution of displays one of their primary interests; it is not surprising that sensory systems also show their phylogenetic heritage.

The interpretation of specific cases is, however, often problematic. Consider the case of elongated tails in *Xiphophorus* fishes. If we accept the most recent phylogenetic hypothesis, based on parsimony, short tails were ancestral and swords derived. Yet in some species with the ancestral condition of tail, females prefer elongated tails (Basolo 1990, 1995). One interpretation is that preferences evolved before elongated tails, for one of the reasons discussed in the preceding sections. Another interpretation is that parsimony is violated in this case. Although parsimony provides the best basis for a null hypothesis, it could be violated in specific instances. Thus the short-tailed species with discordant female preferences might actually have resulted from unparsimonious evolution (male swordtails evolved together with matched female preferences but were secondarily lost in some clades). Nevertheless, we are left with the discordance between signal and preference, regardless of the sequence of evolution.

The discordance might arise from the evolution of open-ended preferences, as described above, in combination with strong selection against elongated tails in some populations. If the absence of sword tails is an adaptation to a population's current environment, rather than the result of a phylogenetic constraint, then the sequence of evolution becomes moot. It is clear that we must determine current selection on preferences and traits, as well as their phylogenetic association, if we are to understand the evolution of these discordances. It will take field work along with phylogenetic work to develop the full picture.

#### 14. Pending Issues in the Study of Mating Systems and Sexual Selection

In the past decade, our understanding of sexual selection and mate choice has expanded considerably. One consequence, as I have tried to show, is an expanding series of connections with other branches of animal behavior and evolutionary biology. Nevertheless, the present review suggests that we have yet to reach a clear conclusions about at least the following features of sexual selection and mate choice:

1. the importance of arbitrary female preferences for the evolution of male traits;
2. the nature of accelerating coevolution of males and females;
3. the possibilities for indirect as well as direct mate choice by females;
4. the scope for coevolution of male and female behavior by sexual selection;
5. the evolution of males' trade-offs between survival and mating;
6. the scope for deception in assessment;
7. the limitations on discriminations of males by females in natural conditions;
8. the evolution of female choice as a consequence of decisions with four possible outcomes;
9. the role of phylogenetic constraints on current adaptations of female responses;
10. the evolution of mismatches between female responses and male traits.

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