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Sexual Selection and the Evolution of Animal Signals

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Introduction

Darwin defined sexual selection in *On the Origin of Species* as a mechanism that "depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring." Thus sexual selection is a form of selection in which variation in fitness is caused by variation in mating success, and which favors traits associated with enhanced mating success. Darwin's initial description of sexual selection – "a struggle between the males for possession of the females" – implies that he had in mind only aggressive competition among males, but the paragraphs that followed make it clear that Darwin recognized that the struggle "is often of a more peaceful character," with males competing through displays to attract females for mating. Darwin later expanded on these themes in *The Descent of Man, and Selection in Relation to Sex*, treating at length both of the major components of sexual selection: intrasexual selection through aggressive competition and intersexual selection through mate choice. Here we concentrate on the intersexual, mate choice component and its effects on animal communication.

Darwin thought that it was almost universally true that males are more eager to mate than are females and that as a consequence, females are the sex that exercises mate choice. This pattern is still considered the rule, though exceptions are now recognized, both cases in which males and females are almost equally selective and cases in which male choice of mates predominates. Theory successfully explains both the rule and the exceptions, either on the basis of the relative parental investment made by the two sexes or, almost equivalently, on the basis of maximal rates of reproduction. In brief, the sex that makes the greater investment in producing and rearing offspring, or that has the lower maximal rate of reproduction, limits reproduction in the other sex; consequently, the limited sex competes to mate, while the limiting sex exercises choice. Females typically provide greater parental investment than males do, whether in taxa in which both sexes invest only in gametes or in groups such as mammals and birds, with extensive parental care. Largely as a result of these parental investment patterns, females typically have lower maximal rates of reproduction. Thus sexual biases in both parental investment and maximal rates of reproduction predict the predominance of female choice.

Many of the greats of evolutionary biology who followed Darwin were skeptical of the importance of female choice as a selective mechanism. Alfred Russel Wallace, for example, thought "it almost inconceivable that female preference could have been effective in the way suggested," that is, in bringing about the evolution of male displays. Such skepticism may be attributed in part to unwary references by Darwin to an "aesthetic capacity" in female animals, allowing them "an appreciation of the beautiful in sound, colour or form. . . ." Attribution of an esthetic sense to animals, or even of simple choice, implied a higher level of cognition than many scientists were willing to accede to birds of paradise and peafowl, let alone to crickets and moths. Nowadays, however, evolutionary biologists realize that the kinds of mating preferences observed in many animals do not actually call for much in the way of cognitive ability. The words 'choice' and 'preference' currently are used to describe biases in the probability that females will mate with males having certain traits, without regard to whether these biases require cognitive processing. From an evolutionary perspective, what matters most is whether female mating behavior is biased in a way that affects male mating success, not the mechanism – cognitive or otherwise – that underlies the bias. Moreover, it is now realized that, though we may be tempted to label the preferences of nonhuman animals as esthetic, these preferences do not necessarily mesh with our own sense of what is beautiful, as should be conceded by anyone who observes such preferences as that of female common grackles for the songs of their own species.

Another reason for Wallace's skepticism about female choice was the lack of empirical evidence for the hypothesized preferences. One could in theory explain the evolution of the extravagant song of a nightingale or the brilliant coloration of a coral reef fish by positing the appropriate female preferences, but there was no evidence that the required preferences actually existed. Since Wallace's day, however, and in particular during the past 30 years, a great deal of evidence has supported the existence of female preferences in various animal groups. More often than

not, the female preference is for a male trait that we would label as a signal, and which is therefore an element of animal communication.

Evidence of Female Preferences Based on Male Signals

An excellent illustration of female preferences based on male signal characteristics is provided by the work of Michael Greenfield and colleagues on female choice in the lesser wax moth (*Achroia grisella*). Lesser wax moths are obligate symbionts of honeybees (*Apis mellifera*), feeding as larvae on honeycomb and other materials found in honeybee colonies. As adults, male lesser wax moths aggregate in the vicinity of a honeybee colony and produce sexual displays to attract females for mating. The primary display is an ultrasonic acoustic signal produced by fanning the wings. The sound-producing organs are a pair of tymbals located at the base of the forewings; these are hardened, platelike structures that produce sound when they buckle either in or out. A single stroke of the wings produces a pair of sound pulses, one from the left tymbal and one from the right, slightly offset in time (**Figure 1(a)**). Pairs of pulses are produced by both the downstroke and the upstroke of the wings. Males also release pheromones in conjunction with wing fanning, but playback of the sound from a loudspeaker is as effective in attracting females as is a live signaling male, indicating that the ultrasonic signal is the only cue essential for mate attraction.

Female lesser wax moths have been tested in the laboratory for preferences based on acoustic properties of male sounds, using phonotaxis to a loudspeaker playing a signal as a measure of preference for that signal. In each test, a female was given a choice between a standard stimulus, one having the average properties of a male signal, and a stimulus artificially modified along one dimension. Tested this way, females show a preference based on call amplitude, preferring louder calls across the entire range of amplitudes presented (**Figure 1(b)**). This preference should generate directional selection on males to produce signals of higher amplitude. Females also show a preference based on call rates, but here the shape of the preference function is different: instead of always preferring more-extreme signals, females most prefer signals of an intermediate rate, with response falling away for higher as well as lower rates (**Figure 1(c)**). The most preferred rate is higher than the mean rate in the male population (**Figure 1(c)**), however, so this preference should also impose directional selection, in this case for higher signal rates. Finally, females

show a preference based on 'asynchrony interval,' the time interval between the onsets of the two pulses in a pair. This preference function shows yet another shape, with females discriminating against signals with very short asynchrony intervals but treating all signals with higher intervals equivalently (**Figure 1(d)**).

Further experiments confirmed these preferences under more naturalistic conditions. Series of females were allowed to choose between sets of four males confined in separate cages. Approach was again assumed to indicate choice. Partial regression coefficients indicate that the number of females attracted by a male is significantly positively related to each of the three signal characteristics mentioned above: call amplitude, call rate, and asynchrony interval.

These results from lesser wax moths are typical of a large body of evidence from insects and anurans showing female preferences for male displays that have greater acoustic energy. In a review of results on several dozen species of frogs and insects, Gerhardt and Huber found that females prefer higher male call rates over lower in the great majority of the studied species. Similarly, females typically prefer male calls of longer duration to shorter ones. By contrast, preferences based on the rate of pulses within a call or on carrier frequency are most often stabilizing, with calls of average properties preferred over either extreme. Exceptions to all these generalizations have been found; in particular, females in several species of frogs show preferences for male calls of lower frequency than the population mean.

In birds, female preferences based on vocalization rates are again observed quite commonly, with females consistently preferring males that sing at higher rates. A second common preference in female birds is for local songs over foreign ones. An example is provided by our work on geographic preferences in female song sparrows (*Melospiza melodia*). We tested for preferences using the solicitation display assay, in which captive females are first treated with estradiol and then exposed to playback of male songs. Subjects respond to conspecific songs with a species-typical precopulation display, and the magnitude of this response is used to infer preferences. We tested females from a site in Pennsylvania for discrimination between a sample of local songs and songs recorded at various points along a transect leading away from the local site. Females showed no discrimination between local songs and songs from the first foreign site (at 18 km) but gave significantly more displays for local songs than for songs from the second foreign site, located 34 km from the start of the transect (**Figure 2(a)**). Females preferred local songs to songs from all sites
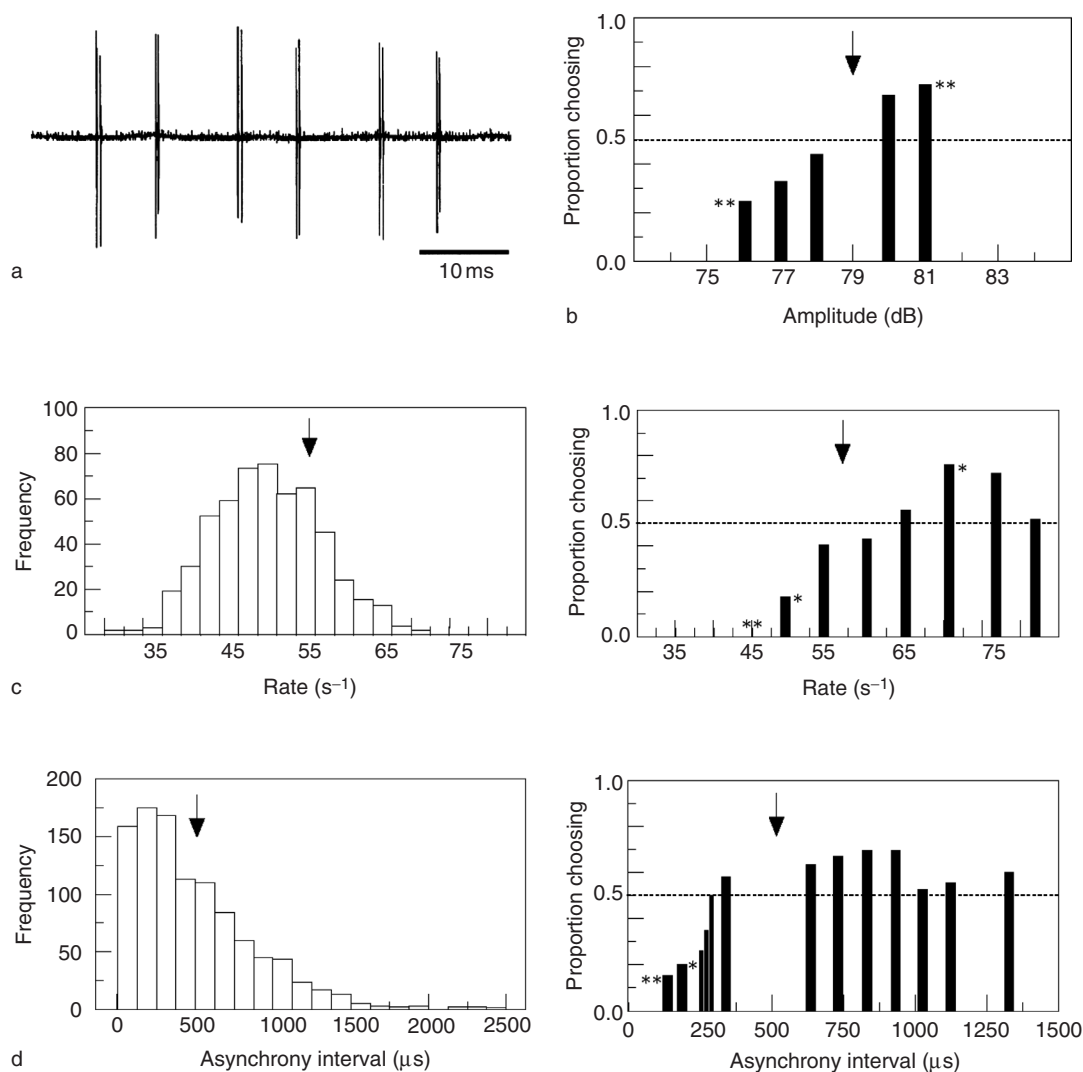
Figure 1 The shape of female preference functions for male ultrasonic signals in lesser wax moths (*Achroia grisella*), as measured by female orientation in two-speaker playback tests. (a) Oscillogram showing the temporal sequence of pulses produced by male wax moths. One pair of pulses is produced by each downstroke of the wings and the subsequent pair by the following upstroke. (b) Preferences of females for male calls differing in amplitude. Bars indicate the proportion of subjects choosing calls of specific amplitudes over a standard call in two speaker choice tests. The arrow indicates the amplitude of the standard call. (c) On the left is the frequency distribution of call rates in 529 calls of 33 males. Rate is the reciprocal of the time between one downstroke and the next. On the right are the preferences of females for calls differing in rate. Bars indicate the proportion of subjects choosing calls of specific rates over a standard rate. The arrow indicates the standard rate. Note that the most preferred call rate is well above the population mean. (d) On the left is the frequency distribution of asynchrony intervals in 1057 measurements of calls from 33 males. Asynchrony interval is the time between the beginning of the first pulse in a pair and the beginning of the second. On the right are the preferences of females for calls differing in asynchrony intervals. Bars indicate the proportion of subjects choosing specific intervals over a standard interval. The arrow indicates the standard interval. * indicates a significant preference ($p < 0.25$) for or against the indicated signal without correction for multiple tests. ** indicates a significant preference ($p < 0.05$) for or against the indicated signal after correction for multiple tests. Note that the only significant preferences are against especially short asynchrony intervals. Reprinted from Jang Y and Greenfield MD (1996) Ultrasonic communication and sexual selection in wax moths: Female choice based on energy and synchrony of male signals. *Animal Behaviour* 51: 1095–1106, with permission from Elsevier.

farther away than 34 km, and in general the strength of their preferences increased with increasing distance to the foreign site.

A third preference common in female birds is for more-complex song or more-complex song repertoires.

Song sparrows again provide an illustration. Male song sparrows possess repertoires of 5–13 song types, each of which is a discretely different version of the species song. Female song sparrows tested in captivity perform more courtship for 32 songs of four types than for
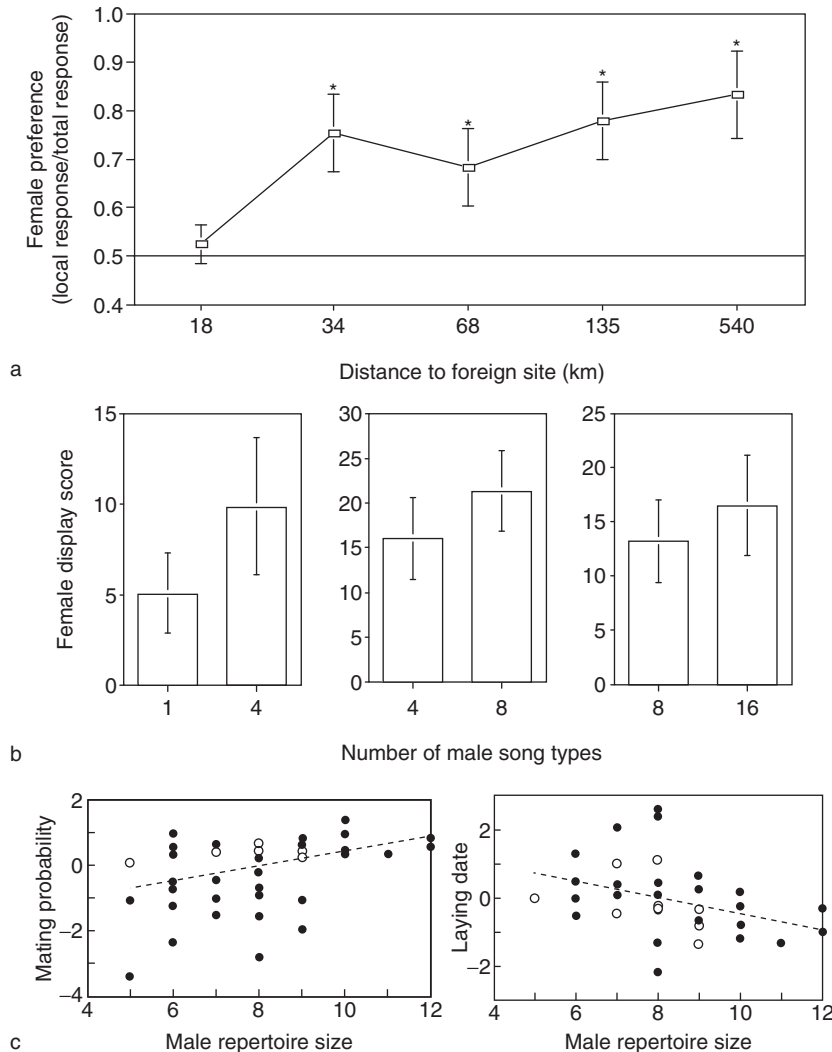
Figure 2 Female preferences based on song in song sparrows (*Melospiza melodia*). (a) Preferences based on geographic origin of song. Preference is measured as the number of courtship displays given by females in response to songs from their local site, as a proportion of the total given to songs from the local site plus the foreign site. An asterisk denotes a significant preference for the local songs over the foreign. Error bars indicate standard errors. Data are from Searcy WA, Nowicki S, Hughes M, and Peters S (2002) Geographic song discrimination in relation to dispersal distances in song sparrows. *American Naturalist* 159: 221–230. (b) Female preferences based on numbers of song types. Preferences are measured using display scores that combine the number and intensity of displays. Females were tested in single-speaker playbacks with (from left to right) 32 songs of one or four types; 64 songs of four or eight types; and 64 songs of eight or 16 types. Females in each test showed significantly higher response to the greater number of song types. Data are from Searcy WA (1984) Song repertoire size and female preferences in song sparrows. *Behavioral Ecology and Sociobiology* 14: 281–286; and Searcy WA and Marler P (1981) A test for responsiveness to song structure and programming in female sparrows. *Science* 213: 926–928. (c) Field measures of female preferences for males with larger repertoires in song sparrows. On the left, a male's residual probability of mating in his first year, after controlling for territory size and population sex ratio, increases with his repertoire size. On the right, a first-year male's residual laying date, after controlling for between-year variation in the timing of breeding, decreases as his repertoire size increases. Thus first-year males with large repertoires are more likely to mate and mate earlier than males with small repertoires. (c) Reproduced from Reid JM, Arcese P, Cassidy ALEV, et al., (2004) Song repertoire size predicts initial mating success in male song sparrows, *Melospiza melodia. Animal Behaviour* 68: 1055–1063, with permission from Elsevier.

32 songs of one type. Similarly, holding the number of songs constant, females perform more courtship for eight song types than for four, and more for 16 types than for eight (**Figure 2(b)**). In the field, Jane Reid and colleagues have shown that for male song sparrows holding territories for the first time, the probability of attracting a mate increases with repertoire size, holding the yearly sex ratio constant (**Figure 2(c)**). Among the males that do breed, laying date decreases as repertoire size increases, indicating that males with large repertoires are chosen before males with smaller repertoires (**Figure 2(c)**).

Female preferences can, of course, be based on signals other than acoustic ones. Preferences based

on color are common in both birds and fishes. In sticklebacks (*Gasterosteus aculeatus*), females prefer to lay eggs in the nest of males with red ventral coloration over males lacking red. Females show the same preference when the red is added experimentally as when the color is natural. Similarly, male house finches (*Carpodacus mexicanus*) are more likely to find a mate the redder their natural coloration, and their chances of being chosen by a female can be altered by manipulating their red coloration in either direction. Other visual ornaments known to be important to female preferences in birds include the exaggerated trains or tails of male common peafowl (*Pavo cristatus*), long-tailed widowbirds (*Euplectes progne*), and barn swallows (*Hirundo rustica*). In satin bowerbirds (*Ptilonorhynchus violaceus*), males decorate individual mating arenas ('bowers') with objects such as blue and yellow flowers, and the number of these external ornaments affects the likelihood that females will mate with a bower's owner.

In some animals, female preferences are based on olfactory signals rather than on visual or acoustic displays. In house mice (*Mus musculus*), females show preferences for the odors of healthy males over those of males experimentally infected with viral or protozoan parasites. Female house mice also show preferences for males whose major histocompatibility complex genotypes are dissimilar to their own, and these preferences are again thought to be based on odor. In Iberian rock lizards (*Lacerta monticola*), females prefer to associate with the odors of older males over those of younger males, and with the odors of males in good body condition over those of males in poor condition. In field crickets (*Gryllus integer*), females exhibit preferences based on male acoustic signals, but they also show preferences based on male odors, preferring odors of dominant males to odors of subordinates. Conversely, female cockroaches prefer the mix of pheromones produced by subordinate males to the mix produced by dominants.

Evolution of Female Preferences: Theory

If we accept the evidence for female preferences favoring such traits as the exaggerated tails of peacocks and the ultrasonic displays of male wax moths, we can explain the evolution of these traits in males; however, we have solved one difficulty only at the cost of creating another – explaining the evolution of female preferences. RA Fisher was the first to grapple with this problem, remarking that "the tastes of organisms, like their organs and faculties, must be regarded as the product of evolutionary change, governed by the relative advantage which such tastes may confer...." In other words, a female preference is a

trait that must have itself evolved, presumably in most cases in response to selection in one form or another. Understanding how selection works in such cases turns out to present considerable difficulties. Fisher stated his own solution concisely, perhaps too concisely given the subtlety of his proposal. Suppose females express a preference based on a male trait in a species in which female preferences have a considerable effect on the reproductive success of males. If the male trait has an initial selective advantage, for example, in promoting male survival, then the preference will begin to spread among the females because of the effect it has on the fitness of their sons. The increase in the preference among females then gives an additional advantage to the preferred trait in males, through increased mating success. As long as the sons of females exercising the preference have a net advantage, due to the combination of the initial natural selective advantage and the subsequent sexual selective advantage, the intensity of the preference will continue to increase. In this way, the male trait can be exaggerated past the point at which its initial natural selective advantage has been lost. The core idea expressed by Fisher – that the exaggeration of a female preference for a male trait leads to stronger selection on both the trait and the preference, leading to a further exaggeration of the preference and the preferred trait – is now termed the 'Fisher' or 'runaway' mechanism.

The Fisher mechanism may seem hopelessly circular, but its logic has been confirmed repeatedly during the past quarter century by mathematical models of various types. The gist of these models can be summarized as follows. We start with a female preference already existing at some low frequency, perhaps due to an initial advantage from securing mates of high viability. Females with the preference mate with males with the preferred trait, and their offspring therefore inherit both the genes for the preference and the genes for the male ornament. This creates a genetic correlation between trait and preference. Consequently, when sexual selection favors the male trait because of its advantage in mating, the preference is favored indirectly, because of the genetic correlation. As the preference increases, sexual selection in favor of the ornament strengthens, which in turn strengthens selection for the preference, and so on. Under certain conditions, such as weak genetic covariance between trait and preference, evolution proceeds toward a line of equilibria, at which the degree of exaggeration of the male trait balances the degree of strength of the preference. Under other conditions, such as stronger genetic covariance, the process can run away toward ever increasing levels of trait and preference. Even in the latter case, the process is

expected to stabilize eventually as the preferred trait becomes increasingly costly under natural selection. The benefit of increased mating success conferred by a bird's long tail, for example, may be outweighed at some point by the cost of poorer flight capabilities associated with having a long tail or the physiological cost of producing a long tail in the first place.

The Fisher mechanism is classified as an indirect selection hypothesis because selection acts on the preference only indirectly, through its genetic correlation with the preferred trait. A second indirect selection hypothesis is provided by the 'good genes' mechanism. Here the male ornamental trait is thought to serve as an 'indicator' of male viability because, for example, only males in good condition are able to develop the ornament fully. Mating between females with the preference and males with the preferred trait creates a genetic correlation between preference, preferred trait, and viability. Natural selection always favors high viability, and the preference and ornamental trait are consequently favored indirectly because of their genetic correlation with viability. A general problem with the good genes hypothesis is that it requires viability to be heritable; this is a problem because natural selection always favors high viability and thus tends to exhaust additive genetic variance for traits contributing to viability. Among several hypotheses for escaping this dilemma, the best known is that of William Hamilton and Marlene Zuk, who suggested that coevolutionary cycles between parasites and hosts ought to maintain additive genetic variance for resistance in hosts and thus the heritability of viability. A preference for males with good genes would then often manifest itself as a preference for males resistant to parasites.

Some theoreticians have considered the good genes mechanism to be a distinct alternative to the Fisher process – and a more parsimonious alternative by virtue of being both less circular and less arbitrary. Those taking this view have assumed that the fitness of offspring of preferred males is a test of these alternatives: under the good genes hypothesis, preferred males should have sons and daughters of superior viability, whereas under the Fisher hypothesis, only sons of preferred males would have an advantage, and the advantage would stem only from superior mating success. Recently, however, others have argued that Fisher effects – those in which sexual selection acts indirectly on the preference – are inevitable in a good genes process and that therefore the two mechanisms cannot be disentangled.

It is also possible for selection to act directly on a preference, because the preference affects the fitness of the female expressing the preference rather than the fitness of her offspring. Direct selection will occur if the preference affects the quality of material benefits provided by the male; such benefits might include nuptial gifts of food, a breeding territory, or resources passed to the offspring in parental care. If a female can observe something about a male, such as his size or vigor, that allows her to assess directly his potential for providing material benefits, then communication does not need to be invoked. If instead a female assesses a male through a signal that correlates with his ability to provide material benefits, then communication is involved. The signal can again be considered an 'indicator' of male quality, albeit of direct material benefits instead of indirect genetic benefits.

Another possibility is for the preference to affect the costs of mate choice to the female; for example, if searching for a mate exposes the female to predation risk, an appropriate preference shortens the search and thus reduces risk. Yet another possibility is that mating with preferred males may be harmful to females, as for example when male seminal fluids contain substances toxic to females, as occurs in *Drosophila*. In this case, females may evolve resistance to the preferred male display, in the sense of an increased threshold for response, which paradoxically may lead to selection for exaggeration of the display in order to overcome resistance.

A final possibility is for a preference to be the consequence of properties of the sensory or neural systems of the female that have evolved in contexts having nothing to do with mating. The preference is then said to represent a 'sensory bias,' and the evolution of a male signal in response to the preference is said to represent 'sensory exploitation.' Sensory bias is sometimes considered to fall in the category of direct selection hypotheses, as natural selection has presumably acted directly on the relevant sensory or neural properties in some other context, such as predator avoidance or food finding. Alternatively, sensory bias can be considered to be a case of no selection, because the mating preference *per se* has not affected either the female's fitness or that of her offspring and thus has not been acted on by selection.

Evolution of Female Preferences: Evidence

To a layperson, the simplest explanation of female preferences might seem to be the good genes hypothesis: a female prefers a male whose displays advertise his health and vigor, and she benefits when he passes those traits to her offspring. To a population geneticist, however, this explanation may seem the least parsimonious of the possibilities, depending as it does on a series of genetic correlations and heritabilities that are all likely to be low. Nevertheless, there is

evidence in some instances that females benefit from their preferences in ways predicted by the good genes hypothesis. In great reed warblers *(Acrocephalus arundinaceus)*, for example, females prefer males with larger syllable repertoires, and such males sire offspring that have superior postfledging survival. Similarly, peafowl females prefer males with larger trains, and those males sire offspring that experience higher survival. In gray treefrogs *(Hyla versicolor)*, females prefer calls of long duration, and males that give such calls sire offspring that grow at a faster rate and complete development in a shorter interval than the offspring of males giving shorter calls. This advantage, however, is seen only at low densities; at high densities, offspring of males of short call duration complete development faster. Similarly, in the lesser wax moths described above, the offspring of males with attractive ultrasonic signals develop faster under favorable environmental conditions but slower under unfavorable conditions. Thus support for the good genes mechanism must be considered equivocal for gray treefrogs and lesser wax moths.

A crucial prediction of the Fisher mechanism for the evolution of female preferences is that a genetic correlation ought to exist between the preference and the preferred trait. This prediction has been verified in several cases using two methods. In one, artificial selection is imposed on the preferred trait only; a genetic correlation between the two is demonstrated if the preference changes along with the preferred trait. In stalked-eyed flies *(Cyrtodiopsis dalmanni)*, for example, females normally prefer males with long eye spans. When males were selected for shorter eye spans for 13 generations, eye stalk length responded, and female preferences also changed, such that females in the selected population came to prefer males with short rather than long eye stalks. Similarly, when artificial selection was imposed on male guppies for greater or lesser area of orange, females in the selected lines also diverged in the strength of their preference for orange males. The second way to demonstrate a genetic correlation is by measuring the covariance of the trait and preference in genetic relatives, such as full sibs, half sibs, or parent and offspring. Using this method, a genetic correlation has been demonstrated in the field cricket *Gryllus texensis* between pulse rate in male calls and female preference for pulse rates, and in sticklebacks between area of red in males and female preference for red in their mates.

A second prediction of the Fisher mechanism is that the traits that make males attractive are heritable, so that attractive fathers produce attractive, or 'sexy,' sons. The predicted heritability has been demonstrated for pulse rate of male calls in the field cricket *G. texensis* mentioned above and for all three of the male call traits contributing to attractiveness in lesser wax moths. The prediction has been verified more directly in the lekking sandfly *Lutzomyia longipalpis*, through evidence of a positive relationship between mating success of fathers and mating success of sons. Pheromones are thought to mediate male attractiveness in this case. The most direct evidence confirming the prediction comes from guppies, in which it has been shown (through the resemblance of half-sibs) that male color pattern is heritable and that there is a genetic correlation between male color pattern and male attractiveness to females. Thus, a female choosing a male based on his attractive color pattern will acquire genes for her sons that enhance their attractiveness.

Although the good genes and Fisher mechanisms receive support in some cases, it is thought that the most parsimonious explanations for the evolution of female preferences are ones in which selection acts directly on a preference. In variable field crickets *(Gryllus lineaticeps)*, for example, females prefer males producing calling songs with higher chirp rates and longer chirp durations. Among females maintained on a restricted diet, longevity was positively associated with the chirp duration of the male to which they were mated, while the number of fertile eggs produced was positively associated with male chirp rate. Both effects seem likely to be due to nutrients passed in the seminal fluid, since neither effect occurred in females maintained on a better diet. Both aspects of the preference, for call rate and call duration, affect the female's own fitness, and thus selection acts directly on these preferences. Even in guppies, in which such a good case can be made that females benefit indirectly from mating with preferred males through the enhanced mating success of sons, it may be more important that the preferred males – those with a greater area of orange – have larger sperm stores and deliver more sperm to the female.

Sensory bias proposes that mating preferences are a consequence of properties of a female's sensory or neural systems that have evolved due to selection in some context other than mating. The hypothesis thus predicts that the preference existed before the preferred trait evolved, a prediction not made by other hypotheses for the evolution of preferences. Evidence supporting this prediction comes from the neotropical frog *Physalaemus pustulosus*. Here males produce calls consisting of a low-frequency whine plus one or more high-frequency chucks, and females prefer calls with chucks to calls without them. Females of a related species, *P. coloradorum*, also prefer conspecific calls to which chucks are added, even though males of this species never produce chucks. The preference can be explained by the organization of the anuran ear, which has two papillae, one tuned to low frequencies

and thus stimulated by a whine, and the other tuned to higher frequencies and thus stimulated by chucks. Phylogenetic analysis indicates that both the tuning properties of the ear and the preference for the chuck probably existed in an ancestor that lacked the preference; thus the preference seems to have evolved before the preferred trait. The same pattern of auditory tuning, however, also exists in another *Physalaemus* species that lacks the preference, arguing that the preference is not solely determined by the tuning pattern. Support for a sensory bias explanation has also been found in analyses of female preferences for swords in swordtail fish and for water vibrations in water mites.

Conclusions

Initial skepticism about the plausibility of female choice as a mechanism of sexual selection has given way in the face of overwhelming evidence that preferences for male traits do bias female mating patterns. The male traits on which female preferences act are most often male signal characteristics, and thus sexual selection plays a large role in shaping animal communication. Understanding why sexual selection shapes communication the way it does requires understanding the evolution of female preferences. Various theories have been elaborated on how and why female preferences evolve, including the Fisher mechanism, the good genes hypothesis, sensory bias, and various direct selection explanations. These hypotheses are not mutually exclusive, so it is not surprising that empirical support exists for multiple hypotheses, not only with respect to separate preferences in different species, but even with respect to a single preference in a single species.

See also: Kinship Signals in Animals; Multimodal Signaling in Animals; Pheromones in Mammals; Pheromones and other Chemical Communication in Animals; Signal Identification: Peripheral and Central Mechanisms; Visual Signaling in Animals.

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