

Primer

Mate choice

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If you are interested in the diversity of life, you can not ignore the plethora of striking behaviors and morphologies that have been the handiwork of sexual selection. The peacock's tail is one emblematic result, but a compendium would also include: the songs of birds, frogs, and crickets, the brilliant colors of fishes and corals, the complex odors of moths and mustelids, and the differences between the human sexes that have led many to embrace the suggestion that men are from Mars and women are from Venus.

That is what sexual selection does. How does it do it? Sexual selection occurs when some individuals in the population have more offspring because they are better at getting mates. This often happens because one sex selects mates from a pool in which members of the opposite sex vary in their attractiveness, a process known as 'mate choice'. Mate choice can be exercised by both sexes, but it is usually the female's domain and her influence on males is apparent as they evolve elaborate traits that make them more attractive. Despite some recent cries to the contrary, sexual selection does occur and there is overwhelming evidence for the efficacy of mate choice. Many studies, for example, have manipulated male traits experimentally and demonstrated that this treatment influences the male's probability of being chosen as a mate in a manner predicted by patterns of male variation and mating success in nature (Figure 1).

Knowing that mate choice occurs, however, does not mean we understand the rules that govern it, and uncovering these rules is a formidable challenge. 'Choice' is a behavioral outcome that results from females using internal rules to assess males,

but our assumptions about the basic properties of those rules have rarely been tested. Also, the well-controlled experiments that are necessary to document choice are often characterized by experimental controls that insulate the study subjects from problems they would encounter in the wild. For example, in the laboratory, stimuli are often presented to females continuously and are often binary. Both of these conditions could reduce the importance of memory and attention, which are critical when choosing among a larger number of simultaneously signaling animals. Internal factors of the female — such as her reproductive state — are usually standardized, and external factors — such as noise and predation risk — are usually minimized. Yet, these factors are known to skew mating decisions. In addition, when females apply a preference function to the task of assessing males, several factors can introduce error to the process, such that the female assigns preference values incorrectly and makes the 'wrong choice'. Furthermore, not all females are the same, and variation among female preferences adds another level of complexity to understanding mate choice rules.

Here, we review some of the factors that influence how the female's inherent preferences are translated into mate choice. We sort these points into three categories: uncertainty about basic properties of the preference function, factors that introduce variability to these preferences and factors that influence the ability to accurately assess potential mates.

Rules of the mate choice game

Virtually all studies of mate choice start with the unspoken assumption that females choose mates rationally. But do they? 'Rational' here means that females assign prospective mates a preference value and then choose more preferred males more often than less preferred males (Figure 2). This is a simple and plausible assumption, but

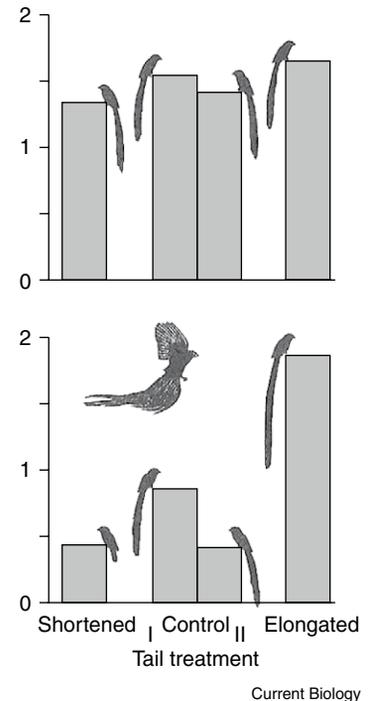


Figure 1. Tail length and mating success in widowbirds.

Experimental changes in tail length of male long-tailed widow birds influence their attraction to females. The tail is expanded into a deep keel during the advertising song flight of the male, performed in the presence of females. Bars show the mean number of active nests per territory in each of four groups of males, before the changes in tail length (top), and the number of new nests after the changes (bottom). Before the experiment, success was approximately equal in the four groups. After tail treatment, the attraction of females to the territory increased with the manipulated tail length of the male. With permission from Andersson (1982).

surprisingly it has not been tested seriously. A recent analysis of mate choice in lek-breeding túngara frogs did not support the idea that females choose based on an underlying preference value that they assign to prospective mates, calling into question this basic assumption about mate choice.

There are fascinating implications if mate choice is sometimes irrational. One is that preferences could be intransitive: if male A is preferred over male B, and male B over male C, then it is not certain that male A will be preferred over male C. Transitivity of mate

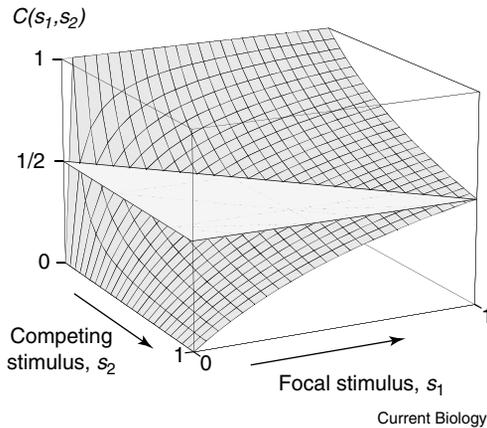


Figure 2. A choice function. An example of a simple choice function based on a single parameter. The X axis and Y axis give the values of the focal and competing stimuli, s_1 and s_2 , while the Z axis gives the probability C that the focal stimulus is chosen. The horizontal surface shows the plane at which the two choices are equally likely. The focal stimulus with value s_1 is more likely to be chosen than the competing stimulus with value s_2 when the gridded surface lies above this plane. With permission from Kirkpatrick *et al.*, (2006).

choice has been little studied, but there is ample evidence that humans sometimes make intransitive economic decisions, and there are suggestions that animals might do the same when making foraging decisions. A demonstration of intransitivity in mate choice would force us to rethink most current experimental approaches to studying mate choice, and a new approach would have important evolutionary implications. A second key implication of rationality in mate

choice involves the question of what happens when females choose between more than two males. With rational choice, the relative preferences for two males should not be altered by the presence of a third. Such 'irrelevant stimuli' or 'competitive decoys' are the basis of ploys in product marketing. The shelf placement of a less preferred product in the vicinity of a more preferred product can enhance consumer preference for the latter. This also seems to happen during foraging decisions of

hummingbirds. Quality and quantity of sucrose awards can be balanced such that each of two sources is equally attractive. But the introduction of a third, lower-quality source disrupts the symmetry between the original two. We know that females often choose mates from numerous males. If a female's fundamental ranking of two males is changed by the presence of others, then we need to rethink how to measure, interpret and think about mating preferences.

A flexible preference

Humans seem fickle in many aspects of life, and perhaps this is most apparent in their unstable evaluation of and dedication to their mates. One reason for such fickle behavior is that mate choice rules can be dependent on the internal state of the chooser such that optimal choice varies with state. The individual's state is not always transparent to an observer, therefore these state-dependent changes may appear to be problematic artifacts of 'raging hormones' when in fact they are optimal decisions. In animals, a female's internal physiology is a major source of variability in translating a preference into a choice. Mate choice decisions clearly vary with the hormonal changes in a single reproductive bout (Figure 3), but they also change at greater scales — over the course of a female's lifetime and throughout the breeding season. Each scale of change follows the same general prediction: as the need to reproduce becomes more urgent — because the female is approaching the end of her reproductive career, the end of her breeding season, or the brief window of opportunity for fertilizing her eggs — her threshold for male attractiveness is lowered, increasing the pool of acceptable males.

Mate choice can be strongly influenced by experience. This has been well demonstrated for half a century in the context of song learning and imprinting in birds. Many song birds have a sensitive period early in life during which exposure to song

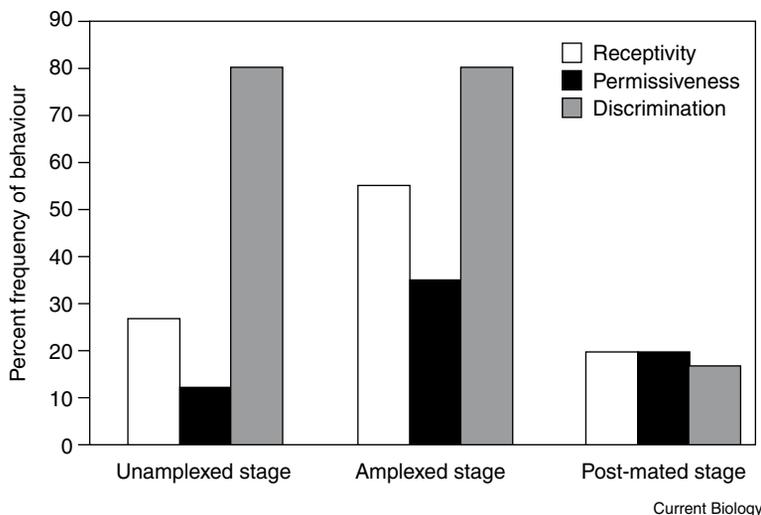


Figure 3. Mate choice and reproductive state.

Female túngara frogs were collected at the breeding site in one of three reproductive states: before they chose a male (unamplexed; left), after they chose a male (amplexed, i.e., clasped by a male; center) and after their eggs were fertilized (post-mating; right). They were then tested in binary phonotaxis tests to determine different aspects of mate choice. Receptivity is when females exhibit phonotaxis to a conspecific signal, permissiveness is when they respond to a typically unattractive signal, and discrimination is when they prefer the complex conspecific signal to the simple one. With permission from Lynch *et al.* (2005).

influences the details of song that a male later produces and that a female later prefers. In another example, Konrad Lorenz famously demonstrated that greylag geese imprint upon traits from those who raise them, and that these traits become part of a template for a range of social decisions. The opposite effect is apparent in quail as a sort of oedipal avoidance; associates during early life, such as parents and siblings, are later avoided as potential mates. Although the majority of these cases are known from observations of birds and mammals, recently similar effects have been demonstrated in fish and even spiders, suggesting that more research on the influence of experience on mate choice outside birds and mammals would be valuable.

The social context in which mate choice occurs can greatly influence a female's preference. It is usually assumed that females assign absolute utilities to male attractiveness, but the presence of other females in the environment can drastically influence the preference value assigned to a male. A number of studies shows that females exhibit mate choice copying. A female guppy, for example, usually prefers the male with more orange coloration in a binary choice. If she then observes the previously less attractive male consorting with a female, her assessment of that male's attractiveness increases. She will not copy the other female, however, if the original mate she preferred has 40% more orange than the male who is consorting with another female. Thus a full description of how guppies choose mates must consider how females rank males independently, how other females rank them, and the situations in which a female will copy the mate choices of other females.

Another major extrinsic influence on mate choice is the ecological context for that choice. For example, perceived predation risk has been shown to influence female receptivity to mating and even to reverse initial choice decisions. A recent study

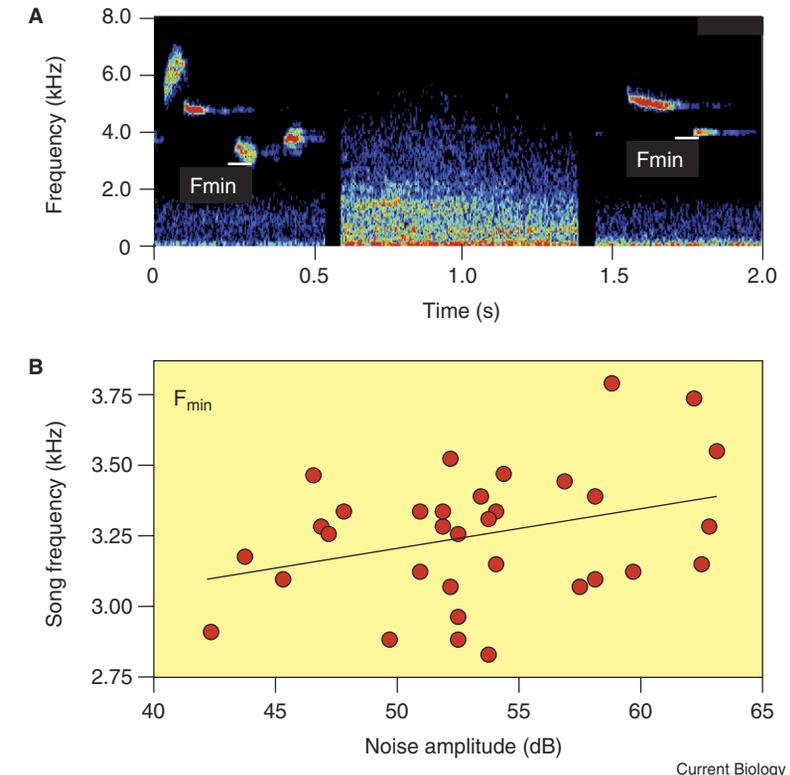


Figure 4. Singing in noise.

Ambient noise increases song frequency in urban great tits. (A) Two song types, one with low minimum frequency (F_{\min}) from a low-noise territory (left) and one with a high minimum frequency from a high-noise territory (right), recorded at a quiet moment. At the centre a typical spectrum of urban noise is shown. (B) Relationship between average noise amplitude in a territory and average minimum frequency of the territory owner's song. From Slabbekoorn and Peet (2003).

showed that female swordtails switch their preference from males with longer swords to males with shortened swords after watching a video of a predator eating another male with a long sword. Also habitat can influence female preference when males are displaying from locations with variable resources such as food or protection from predators. Males often fight fiercely to protect territories or even small temporary display sites, so habitat cues may provide valuable information about a male's quality as well.

Accurate assessment

Most people have experienced the frustrations of trying to listen to someone speak in a crowded, noisy room. These conditions can make it difficult to hear what is being said and hard to distinguish that particular speaker from all

the other voices in the room. This problem, known as the 'cocktail party effect' for humans, can be a challenge for females surveying potential mates as well. Such difficulties can introduce error into a female's assessment of males. Much of the potential for error in assessing males comes from limitations in an animal's cognitive tools. For example, females can only consider a given male's traits in their mate choice decision for as long as they can remember that information. When ephemeral traits such as vocalizations or behavioral displays are used to assess mates, a working memory of those traits must be important; yet, memory storage is limited, and we don't know how this affects mate choice. In addition, habituation may influence mate choice by gradually reducing the responsiveness of a female's



Figure 5. Mate choice in the field.

A male sage grouse (*Centrocercus urophasianus*) during courtship (left). Females chose from several males based on their display (right). (Photograph: Marc Dantzker.)

nervous system. This common effect could keep females from attending to important information in advertisement displays.

The processing of sensory information is another aspect of mate assessment during which error could occur. An animal's ability to discriminate between male traits will be greatly constrained by both the peripheral sensory organs that transduce physical stimuli — such as photoreceptor sensitivity — and high level processing of signals — such as opponency coding in vision. Because of this, females may not perceive the difference between the signals of two males; alternatively, the difference may be noticed, but mean nothing to the female. This distinction is an important concept in the study of mate choice and is referred to as just noticeable differences (JND, the difference necessary for discrimination) versus just meaningful differences (JMD, the difference necessary to influence a choice). If the JMD is larger than the JND, females are not making as fine discriminations between males as they could, and thus small variation in male traits are perceived as meaningless and are not important in indicating male quality. If the JND and JMD are the same, then small variation in male traits is informative and females might be perceptually constrained to make even finer discriminations.

Mate choice often takes place in chaotic environments which abound with additional sensory stimulation that acts as noise,

confusing sensory systems and introducing more error to female assessment. Heterospecific signals and abiotic sounds such as wind can mask a male's advertisement calls, and similar effects can occur in a complex visual environment (Figure 4). A common challenge in signal design is to contrast the signal with this noisy environment. Although there are more subtle solutions, for most signals this is accomplished by increasing signal strength: louder, brighter, bigger, longer and faster signals usually show a better contrast against a chaotic background. Although there are many exceptions, there is a strong trend for females to choose males with signals of greater quantity (Figure 5). One possible explanation is that such signals are more likely to be perceived, remembered, and located; in general, they are more salient to the receiver. Sometimes signals become even more conspicuous as males evolve through competition with other signaling conspecifics. Because the individual male's signal is the target of mate choice, noise generated by fellow males is perhaps the biggest challenge to be overcome by males trying to attract a females' attention. This competition may result in a sort of 'Red Queen' race to stand out from the other males to capture and hold a female's attention. Success in evolving conspicuous traits relative to conspecifics would be rewarded with sex, and what could be a more potent reinforcer? The result then can be a directional increase in male trait

quantity driven by the pre-existing biases in the females' perceptual systems.

Conclusions

There is overwhelming evidence for mate choice in a wide variety of animals, but there is no clear picture of the rules that females use when they make these choices. Those rules seem to be much more complex than the current experimental and theoretical studies assume. Simple binary choice tests have played an important role in uncovering the stimulus properties that mediate choice. More sophisticated paradigms are needed, however, if we are to understand how sensory, neural and cognitive constraints affect mate preferences, and to elucidate the effects of internal and external factors on mate choice. And then there is the intriguing possibility that mate choice might not even be rational. But perhaps human experience has already told us that.

Further reading

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