

8 Cognitive Mate Choice

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8.1 Introduction

One of the most important decisions an animal makes is choosing an appropriate mate, and females often do this by assessing male sexual displays. Sometimes the females discriminate between conspecific and heterospecific males, and sometimes they choose from among a pool of conspecifics. Although these two processes result in species recognition and sexual selection, they are essentially the same behavioral process (M. Ryan and Rand 1993; Phelps et al. 2006). Here we primarily address mate choice among conspecifics, but the basic concepts extend to mate choice among species. We will also consider the canonical case of displaying males and choosing females, but the same principles apply when there is male choice of females and when both sexes choose simultaneously.

Mate choice can generate sexual selection and it genetically isolates species from one another; thus, mate choice is an intricate part of several fields in evolution and behavior. Mate choice can also be viewed as a problem in animal communication (M. Ryan and Rand 1993); senders transmit signals that have a probabilistic influence on the behavior of the receiver. Here we more generally consider mate choice in the context of interactions between signalers and receivers. Mate choice is a function of the receiver but is inextricably linked to the signal. Thus, our discussion of mate choice addresses issues relevant to both sender and receiver.

Mate choice is a cognitive process. Receivers perceive signals in the environment through the lens of their sensory processing machinery and then evaluate this information using a set of decision-making rules before acting upon it. Each point along the path of a mate choice is governed by a receiver's cognitive abilities and constraints. We follow this course of events as it occurs during a mate choice, beginning with detection and perception, and then moving to evaluating information and acting on it. Detection and perception are the initial steps in managing the information that could influence a mate choice decision. An individual's sensory system filters what information

is available in the environment, and how that sensory information is then perceived sets off a chain of cognitive processing that makes up a female's evaluation of the information. We will consider intervening variables in this deceptively simple linear chain of reactions. We do not thoroughly review each of these components, but instead we consider topics that seem relevant, have not received sufficient attention, and might be ripe for integration into more mainstream studies of mate choice.

We will illustrate some of these issues with examples from the acoustic domain and others from the visual domain, using whichever data sets are most compelling. It should be obvious, however, that these principles are general to all modalities of communication and could influence mate choice based on acoustic, visual, olfactory, electrical, or tactile cues.

8.2. Detection and perception

Let us begin by considering mate choice in its simplest situation, a two-way interaction between a sender and a receiver. In his study that launched information theory, Claude Shannon (1948, 379) stated: "the fundamental problem of communication is that of reproducing at one point either exactly or approximately a message selected at another point." In mate choice, as in all communication, information transmitted between the sender and receiver must traverse a noisy channel where information can be lost (fig. 8.1). A fundamental problem for all communication is to enhance information transfer in a noisy world. This problem is solved by adaptations of both the sender and the receiver, and both must be considered to understand the interaction. We will illustrate these issues with examples in the acoustic domain, as did Shannon, as they are more numerous and detailed. More recently, analogous studies in the visual domain have become available (e.g., Seehausen et al. 1997; Persons et al. 1999; Endler et al. 2005; Cummings et al. 2006; G. Rosenthal 2007).

A female must perceive and detect a male's sexual display against an environmental background: noise in a forest, colors on a reef, and odors in the air. Male display traits should be conspicuous to the female in the relevant environment. The degree to which a signal is conspicuous is a product of the signal's contrast against the environment and the biases in the female's sensory system. We also expect females to have sensory and cognitive tools to detect and perceive these signals in that same environment. These general expectations apply to every mate choice: how do senders make their signals conspicuous and how do receivers increase their ability to perceive and detect them?

In a variety of animals, most notably many insects, frogs, and birds, mate choice decisions are based on acoustic signals. In most cases this occurs in a

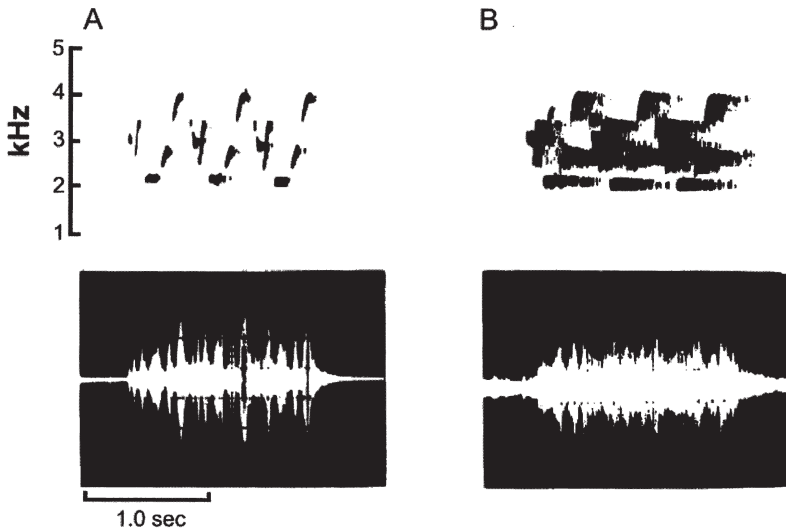


FIGURE 8.1. The song of a Carolina wren (top, sonograms; bottom, oscillograms) recorded (A) 10 m and (B) 50 m from the singing birds. Redrawn from D. Richards and Wiley 1980.

world where sound is degraded and attenuated by the habitat, and in which signals compete with abiotic noise and sound generated by both heterospecifics and conspecifics. It is a formidable challenge for senders to transmit signals that are salient to receivers over socially significant distances and for receivers to be able to parse these signals from the noise. The perception and detection of signals that are critical to mate choice do not occur unimpeded.

8.2.1. ENHANCING SIGNAL CONTRAST

Adaptations to enhance acoustic signal transmission are well known (Marler 1955; Morton 1975; Wiley and Richards 1978; Slabbekoorn and Peet 2003; Brumm and Slabbekoorn 2005). Habitats vary in how they affect signals, which results in some general patterns of signal evolution. For example, birds calling on the forest floor use lower-frequency calls than birds calling in the canopy; birds in open fields are more likely to use amplitude-modulated signals, whereas forest birds tend to use tonal signals (Morton 1975; see also Hunter and Krebs 1979). Birds can also use frequencies that avoid noise from insects (M. Ryan and Brenowitz 1985; Wiley 1991) or anthropogenic sources (Slabbekoorn and Peet 2003). In many taxa background noise influences a facultative shift in signal amplitude, known as the Lombard Effect (Lombard 1911; e.g., fish: Zelick et al. 1999; birds: Brumm and Todt 2002; Brumm 2004; Cynx et al. 1998; monkeys: Sinnott et al. 1975; whales: Scheifele et al. 2005;

humans: Tonkinson 1994; Winkworth and Davis 1997). Noise might also inhibit acoustic signaling in birds (Lengagne and Slater 2002), and some frogs have the ability to call in small gaps of silence between bursts of noise (Zelick and Narins 1985).

Interspecific competition can cause a diel shift in calling activity in some insects (Greenfield 1988, 2005), and intraspecific competition can cause some birds (e.g., Ficken et al. 1985) and frogs (e.g., Schwartz 1987) to interleave call notes with those of neighbors. Thus, there is a considerable amount of data allowing some understanding of how acoustic signals evolve to enhance detection and perception by the receiver. All of these general principles should apply specifically to sexual signals, and indeed, much of the empirical support is from studies of these types of acoustic signals. As mentioned above, there are analogous studies in the visual domain (reviewed in G. Rosenthal 2007).

8.2.2. ENHANCING SIGNAL DETECTION

Evolution of adaptations to noisy environments is not restricted to signals. There is also a suite of receiver adaptations that enhance detection and perception of acoustic signals. This begins with the transduction of the sexual display into a neural code that can be evaluated by the receiver during a mate choice. The simplest mechanism to enhance signal detection is when the tuning of the peripheral auditory systems matches the frequencies that characterize the species' mating signal, as is common in insects and frogs (Gerhardt and Huber 2002; Brumm and Slabbekoorn 2005). The more tuned the system, the more noise it rejects. The tuning can also be influenced by the environment. Witte et al. (2005) showed that the "noise reject" features of a cricket frog's peripheral auditory system are enhanced in populations in which signal detection is more difficult due to habitat acoustics.

Even with the most precisely tuned filters, noise will overlap signals. Noise can prevent a signal from being detected and perceived by a receiver due to signal masking (reviewed in Brumm and Slabbekoorn 2005); thus, mate choice can be obscured under noisy conditions. A more interesting phenomenon is when noise changes the rules of choice, as it does in female hourglass frogs (*Hyla ebracatta*). Wollerman and Wiley (2002) showed that in the absence of noise females preferred lower-frequency mating calls; at moderate noise levels they did not discriminate between call frequencies; and at higher noise levels they preferred the modal frequency of the population. Thus, it appears that, as the task of call discrimination becomes more difficult, the females switch from evaluating the quality of conspecific males to the more conservative task of ensuring choice of the correct species.

Noise need not be an insurmountable barrier to mate choice. If a signal is loud enough, it is released from masking. How loud it needs to be, in birds at least, depends on its frequency: higher frequencies need to be louder to be emancipated from masking. But exceptions to this general rule suggest that there are adaptations for perception and detection of social signals. In the parrot *Aratinga canicularis*, for example, release from masking for frequencies in social calls occurs at a lower amplitude than it does in other birds (T. Wright et al. 2003). Although these are not sexual signals in parrots, this finding identifies a fruitful area of investigation for cognitive adaptations for mate choice.

Another form of noise is the acoustic signals from other conspecifics. Sexual signaling in the acoustic domain often occurs in social aggregations or choruses; thus, animals must be able to parse signals of specific individuals from a complex acoustic background. In reference to human psychoacoustics, Bregman (1990) speaks of this general problem as auditory scene analysis, and Cherry (1953) refers to the specific challenge of assigning an auditory stream to a single individual as the “cocktail party effect.” Although social aggregations of signaling animals share some of these same challenges with humans at cocktail parties, only recently has the concept of auditory scene been applied to animal choruses (reviewed in Hulse 2002; Bee and Micheyl 2008).

There have been some detailed studies of mechanisms that allow animals to assign acoustic signals to specific individuals (i.e., auditory streaming), especially in birds and monkeys (Bee and Klump 2004, 2005; Fishman et al. 2004). Studies show, for example, that emperor penguins can identify calls of offspring when mixed with other penguin calls (Aubin and Jouventin 1998), and finches can parse the songs of conspecifics mixed with heterospecific songs (Benney and Braaten 2000). In addition, Schwartz and Gerhardt (1989) suggested that the spatial origin of the calls of gray treefrogs (*Hyla versicolor*) can facilitate auditory streaming. On the other hand, H. Farris et al. (2002, 2005) showed that túngara frogs (*Physalaemus pustulosus*) are not able to correctly assign components of the same call to individuals using only spatial cues, and Bishop showed that in painted reed frogs (*Hyperolius marmoratus*) preferences for call parameters that emerge in two-choice tests are not exhibited in four-choice tests (e.g., Bishop et al. 1995). These last two studies suggest that social communication imposes serious constraints on a receiver; we cannot assume that adaptations always arise to allow receivers to successfully parse signals. On the other hand, there could be context-dependent use of information, such that as density of signalers, complexity of the chorus, and distance to the source change so does the relevancy of different types of information. Although there have been numerous studies of mate choice in

acoustically chorusing species (Andersson 1994; Greenfield 2005), there has been little analysis of how this occurs in complex auditory scenes.

8.2.3. CATEGORICAL PERCEPTION

Once the sexual display is encoded by the receiver's sensory system, the neural code needs to be interpreted. In most cases it appears that stimuli can vary continuously and are usually perceived as such: louder-softer, brighter-darker, hotter-colder. There are, however, well-known exceptions in humans in which continuous variation in stimuli, especially in color, speech, and faces, is perceived categorically (Harnad 1987). Categorical perception can be identified by two components, labeling and discrimination. In the first, continuously variable stimuli on the same side of a border are labeled as being in the same category. In the second, the ability of receivers to discriminate between stimuli on different sides of the border, in different categories, is strong, while the ability to discriminate between stimuli of the same magnitude of difference on the same side of the border, within a category, is weak.

In a few cases, animals have been shown to exhibit categorical perception of human phonemes (e.g., Kuhl 1981; Kluender et al. 1987). There are several cases in which animals are known to show categorization of their own signals: syllables in songbirds (D. Nelson and Marler 1989), ultrasonic vocalizations in rat pups (Ehret and Haack 1981), and mating calls and bat echolocation calls in crickets (Wytttenbach et al. 1996).

We do not know if categorical perception of signals used in mate choice is common. Preference functions for simple signal parameters, such as pulse number (Ritchie 1996), call duration (Gerhardt et al. 2000), and tail length (Basolo 1990), or for suites of signal traits (M. Ryan et al. 2003) do not suggest categories of preferences. But data from studies of evoked calling in bullfrogs (Capranica 1966) and trill duration in red-winged blackbirds (Beletsky et al. 1980; reviewed in Ehret 1987) suggest that there are categories (i.e., that there is labeling), but discrimination within and between categories was not tested in these studies. A recent study of túngara frogs, however, demonstrates both criteria of categorical perception: labeling (fig. 8.2a) and discrimination (fig. 8.2; Baugh et al. 2008). Thus, categorical perception of variation in mating signals can occur. Evidence might be rare because few experiments have been designed specifically to test that hypothesis. The use of categorical perception of mating signals may be important in simplifying the processing of signals to make mating decisions. Assigning signals to categorical groups where each group triggers a different response, rather than determining a response to a signal that lies on a continuous scale, could be an effective way to reduce the time required to make a mating decision.

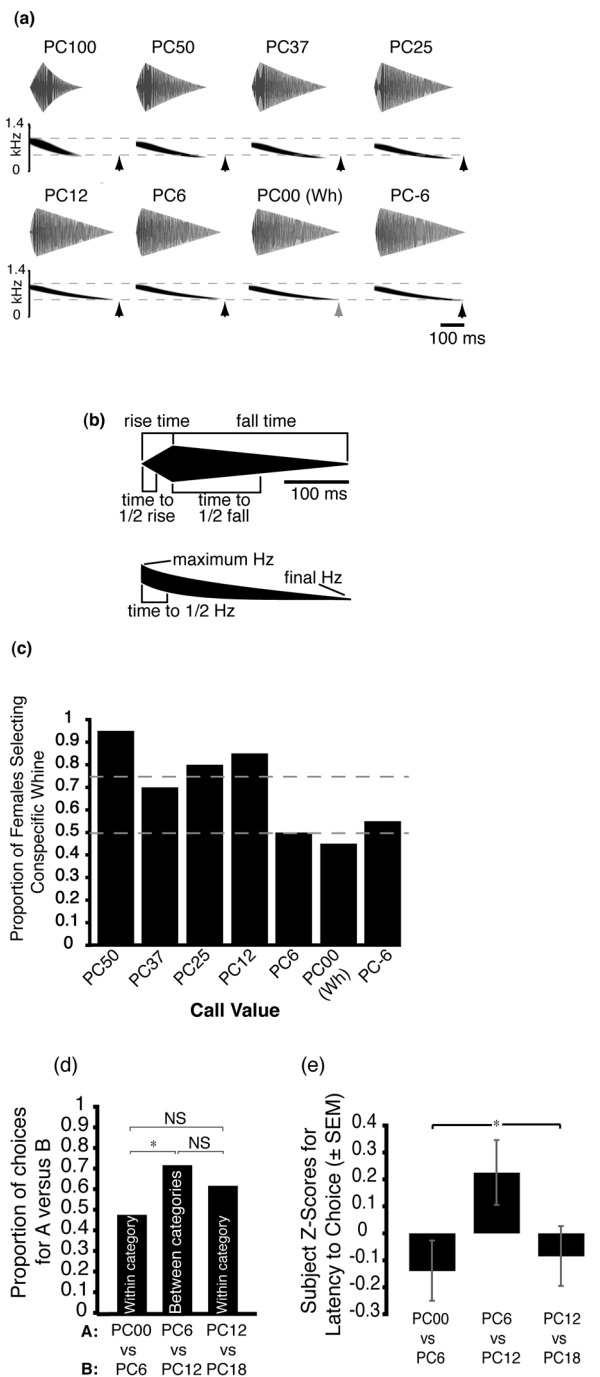


FIGURE 8.2. Categorical perception of mating signals in the túngara frog, *Physalaemus pustulosus*. a. Oscillograms and spectrograms of the seven synthetic stimuli used in the labeling component of the study. The heterospecific call, *Physalaemus coloradorum* (PC100), is presented for comparison. Dashed lines indicate the beginning and ending frequencies of the conspecific call, *P. pustulosus* (PC00), and arrowheads indicate the duration of the PC00. b. A stylized oscillogram (upper) and a spectrogram (lower) of the synthetic túngara whine are shown along with the seven acoustic parameters used to construct stimuli in this study. c. The number of túngara frog females (N for each experiment is 20) that prefer the conspecific call to each call variant shows that females label the calls PC - 0.06 through PC 0.06 as conspecific (they do not prefer the conspecific call to these variants), and PC 0.12 through PC 0.50 as not conspecific (they prefer the conspecific call to each of these variants). The dashed lines indicate the null expectation (bottom line) and the critical value for a significant preference (top line). d. Females were tested with pairs of stimuli in which one stimulus (row A on abscissa) was more similar to the conspecific call than the alternative was (row B). Females do not show a preference between a pair of calls that differ by 6% within the category that is labeled as conspecific (whine vs. PC6), whereas they do show a preference between calls that differ by 6% between the categories that are labeled as conspecific and not conspecific (PC6 vs. PC12). The difference in the strength of preference between the within-category and the between-category is statistically significant. There is, however, discrimination between calls that differ by 6% within the not-conspecific category (PC12 vs. PC18), but the strength of this discrimination between categories was not statistically significant (NS = not significant). e. The z -scores of the latency to respond from the same phonotaxis tests shown in fig. 8.2a show that females take significantly more time to make a choice in the between-category comparison than in either of the within-category comparisons (Baugh et al. 2008).

We caution that, if categorical perception occurs, it need not be present in perception of all stimuli. For example, in humans there is categorical perception of /ba/-/pa/ phonemes that is based on continuous variation in voice-onset time, but there are numerous other stimulus sets that are not perceived categorically (Harnad 1987). If categorical perception of mating signals were common, it would require that we seriously reevaluate how we examine mate choice rules that are based on continuously varying preference functions (section 8.3).

This abbreviated review clarifies where we are in our understandings of sexual communication and mate choice in naturalistic scenes, at least in the acoustic domain. Signal degradation and attenuation, a variety of noises, and animals signaling simultaneously are the rule rather than the exception in the wild. There is substantial knowledge of how senders have overcome these challenges in the acoustic domain, and there are analogous, although fewer, studies showing similar results in the visual domain (reviewed in G. Rosenthal 2007). On the receiver end of the equation, numerous studies show how peripheral tuning can increase signal-to-noise ratios prior to analysis in the central nervous system. We know very little, however, about how signal detection and perception might be enhanced or compromised in complex auditory scenes. It seems that studies of this aspect of mate choice should take their lead from studies of auditory (e.g., Bregman 1990) and visual scene analysis in humans (Bar 2004), which have made considerably more progress than have analogous studies in animals. The available data suggest that perception of sexual signals is usually continuous rather than categorical, but there are some exceptions and there has been little effort to directly assess the use of categorical perception in mate choice.

8.3. Evaluation and decision

Once a mating signal is perceived and detected, females use the information to make mate choice decisions. Much of the research on this part of the mate choice process is aimed at deducing the rules of mate choice without concern for the internal mechanisms involved. But even treating preferences as a black box has hidden subtleties.

8.3.1. RATIONAL MATE CHOICE

Almost all work on mate choice implicitly assumes that females act rationally. “Rational” here is a technical term borrowed from microeconomics and political science, and rational mate choice follows automatically if choice follows a simple two-step process (Samuelson 1947; Tversky 1969; Tversky and

Simonson 1993; M. Kirkpatrick et al. 2006). In the first step, all the signals and cues from a male are transduced into a single preference score that is independent of the scores of other potential mates. In the second step, the female chooses from among the males in such a way that males with higher scores are chosen more often than those with lower scores.

This paradigm leads to the idea of a “preference function” that shows the relation between a stimulus value (say, the fundamental frequency of an acoustic signal) and a female’s preference (Lande 1981). Researchers have estimated the preference function in several species (e.g., Basolo 1990; Diekamp and Gerhardt 1992; Ritchie 1996). The most common procedure is to measure how often a female chooses a focal stimulus when it is paired with a reference stimulus (either real or simulated). We then plot the probability that a focal stimulus is chosen over the reference as a function of the value of the focal stimulus. Figure 8.3 shows Ritchie’s (1996) results from estimating the preference functions of *Ephippiger* cricket females based on the number of syllables in the male call.

This approach seems so conceptually straightforward that it may be hard to believe that there could be a serious pitfall. But consider a case where a female chooses stimulus A twice as often as the reference display, and stimulus B four times as often. Does that guarantee that, when choosing between A and B, she will choose B exactly twice as often? Does it even guarantee that she will choose B more often than A? While both predictions seem plausible, in fact they are not experimentally tested in most studies. It is even possible that mating preferences are intransitive, such that a female prefers stimulus A over B, B over C, but C over A. Intransitive choice has been found in animal foraging (Shafir 1994) and human economic decisions (Tversky 1969), so it seems plausible that it also occurs in mate choice.

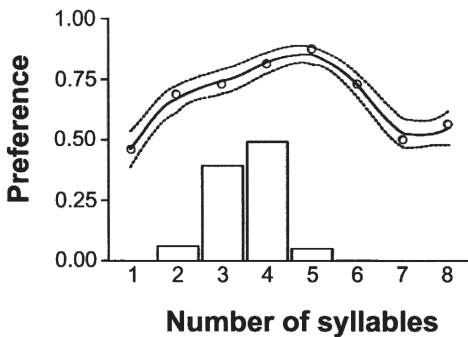


FIGURE 8.3. Preference function of *Ephippiger* cricket females based on the number of syllables in the male call. The reference stimulus was a call from a different population with a single syllable. The circles show the proportion of females preferring the test stimulus to the reference stimulus. The solid curve is fitted to the data with a cubic spline, and the dashed lines show ± 1 standard errors from bootstrapped replicates. The bar graph shows the distribution of syllable number in the females’ native population. Redrawn from Ritchie 1996.

A recent study of túngara frogs explicitly tested whether females use strict preferences or show evidence of intransitive choice (M. Kirkpatrick et al. 2006). We analyzed results from an earlier study in which females' choice was tested for all possible pairs of nine stimuli (M. Ryan and Rand 2003). Figure 8.4 shows how the data compare with the expectations based on strict preferences. If females did follow strict preferences, then the proportions of times they chose the focal male call (shown by the circles) would tend to fall on the curved surface. Statistical analysis shows that the deviations from that prediction are much greater than what sampling error alone would produce, and so we can say that females are not using strict preferences. Do they have intransitive preferences? A separate analysis gives an ambiguous answer: we cannot prove that these frogs have intransitive preferences, but we cannot reject the possibility either. In sum, there has been only one test to date of the near-universal assumption of strict mating preferences. The data reject that assumption, but unfortunately do not give a clear alternative paradigm that we can use for thinking about mate choice.

Understanding mate choice rules becomes yet more complex when there are more than two potential mates. If mate choice meets the test of rationality, then a female's preference for one male over another should not be reversed by the presence or absence of other males. Yet these kinds of reversals do in fact happen in foraging decisions. The quantity and quality of two sucrose awards can be matched to result in an equal preference by foraging hummingbirds. The presence of a third award of inferior value to the original two influences

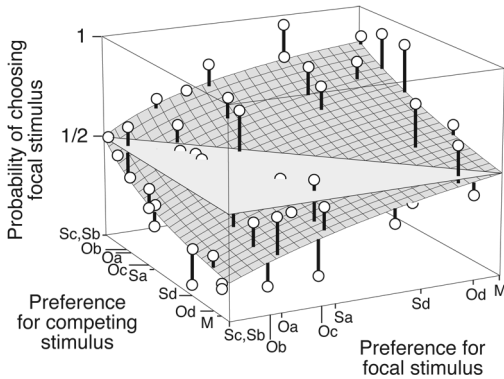


FIGURE 8.4. Fraction of times that females chose the focal male call (shown on the *x*-axis) for all possible pairs of nine call stimuli in the túngara frog. The curved surface shows the results expected if females follow the simple two-step rational preference rule described in the text. Relative preference scores for each stimulus (corresponding to positions on the horizontal axes) are assigned so that the data best fit the curve. The deviations are statistically significant, and so the simple preference rule is rejected. If females did follow strict preferences, then the proportions of times they chose the focal call (shown by the circles) would tend to fall on the curved surface. Redrawn from M. Kirkpatrick et al. 2006.

the preferences between the two superior awards (Bateson et al. 2002, 2003; Schuck-Paim et al. 2004). This principle of context-dependent choice is used to create “competitive decoys” in human marketing schemes. When there are two products equally preferred by consumers, placing a less-preferred object on the shelf can cause a preference for one of the original two products (M. Ryan et al. 2007).

We do not know of any demonstrations of irrational mate choice resulting from any of these mechanisms (M. Ryan et al. 2007). The possibility calls for investigation, however. If it occurs in foraging, it seems plausible that it occurs in mate choice. If it is a domain-specific phenomenon in animals (e.g., foraging but not mate choice), it would be important to know why.

8.3.2. THE SOCIAL CONTEXT

Mate choice often happens in an environment where there are several or many potential mates. When animals gather in groups to advertise and choose mates, receivers are faced with an enormous amount of potential information (Valone 2007). This situation poses challenges for both the sender and the receiver: the sender must compete with conspecific signals, and the receiver must parse individual signals from the conglomerate. In that sense, the social group is a source of noise, as we discussed earlier in section 8.2. But the group setting offers advantages as well as difficulties to mating systems. Females choosing a mate in a group environment are able to use information about both the general mating environment and individual potential mates in their mate choice decision.

Females can modify their receptivity to potential mates of different levels of attractiveness when given experience with variable mating conditions. Research in fruit flies (*Drosophila melanogaster*; Dukas 2005b), zebra finches (*Taeniopygia guttata*; Collins 1995), variable field crickets (*Gryllus lineaticeps*; Wagner et al. 2001), and painted reed frogs (*H. marmoratus*; Passmore and Telford 1981), among others, shows that, when females are exposed to groups of males that differ in the attractiveness of individuals, females modify their receptivity (fig. 8.5). In most of these cases, the females are always receptive to highly attractive mates, but experience influences how permissive they are to mating with less attractive males. One possible interpretation is that, in situations where highly attractive mates are uncommon, the cost of search time required to find highly attractive mates outweighs the benefits of passing up males of low attractiveness in order to mate with highly attractive individuals. This situation demonstrates one way that social context introduces more complexity to the dynamics of mate choice than is suggested by results of simple two-choice experiments.

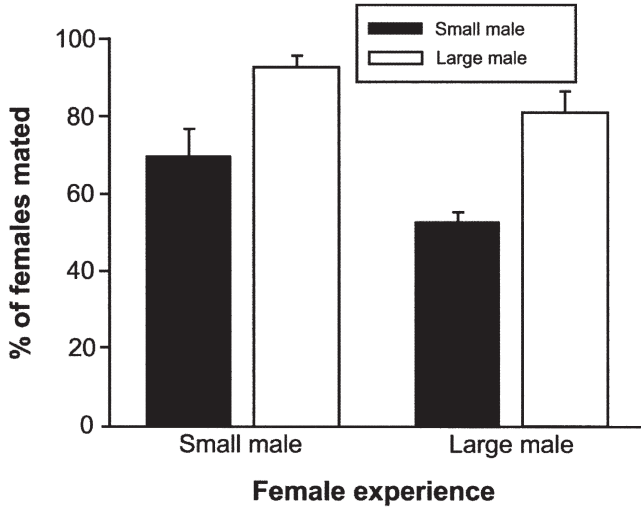


FIGURE 8.5. The mating behavior of female fruit flies depends upon previous experience with courtship by small (less attractive) or large (more attractive) males. Females that have been courted by small males mate more frequently with both small and large males. Redrawn from Dukas 2005b.

Mate assessment in a social group allows females to consider more information about potential mates than what can be gathered from a male's signal alone. A clear example of this use of social information is mate choice copying, which occurs when the choice of a mate is influenced by mating decisions of others. Male mating success on bird leks, where female choice reigns supreme, is sometimes too skewed to be explained by variation in male phenotypes alone. In sage grouse (*Aratinga canicularis*) leks, R. Gibson et al. (1991) suggested that skews emerge in part because females copy the mate choice of others (see also R. Gibson and Höglund 1992; D. White and Galef 2000). Strong support for this hypothesis came when Dugatkin (1992) showed experimentally that female guppies (*Poecilia reticulata*) show mate choice copying. In the standard experiment, versions of which have been repeated in numerous studies (e.g., Dugatkin and Godin 1992; Dugatkin 1992, 2007; Schlupp et al. 1994; Briggs et al. 1995; Grant and Green 1996; Schlupp and Ryan 1997; Witte and Ryan 1998, 2002; Witte and Noltemeier 2002), the focal female fish is in the center of a tank with only visual access to two potential mates, each one on the opposite side of the tank. The female's time spent associating with each male is used as a proxy for preference. The focal female is then allowed to see the less preferred male interact with a model female. The model female is removed, the mate choice experiment is repeated, and if mate copying oc-

curs, the female increases the amount of time she now spends with what had been the less preferred male. Mate choice copying has been demonstrated in other taxa besides fish, mostly birds and humans (e.g., birds: Höglund et al. 1995; Galef and White 1998; D. White and Galef 1999; Ophir and Galef 2004; humans: B. Jones et al. 2007). Although there are few published studies of negative data, mate choice copying is not universal (e.g., Clutton-Brock and McComb 1993).

We can make some generalizations from studies of mate choice copying. It can be exhibited by both males and females (e.g., male and female mollies, *Poecilia latipinna*: Schlupp and Ryan 1997 and Witte and Noltemeier 2002 respectively). Females can copy mate choices of heterospecifics as well as conspecifics (Schlupp et al. 1994), and younger females are more likely to copy older females (Amlacher and Dugatkin 2005). The effects of mate copying are more pronounced when the difference between potential mates is greater (Dugatkin 1996) and when the perceived utility of the model female is higher (S. Hill and Ryan 2006). The effects of copying can be long lasting, persisting up to five weeks in one study (Witte and Noltemeier 2002). And, importantly, it has been shown in the field as well as in the lab (Witte and Ryan 2002). Some of the evolutionary dynamics of copying have been modeled, and it has been shown that copying can even spread through a population when there is mild direct selection against the copying allele (Servedio and Kirkpatrick 1996).

There is no question that mate choice copying occurs. Although further empirical research is necessary, especially to determine more clearly why females exhibit this behavior, there needs to be some method for including this phenomenon into a formal model of mate choice rules, such as a preference function.

8.3.3. LEARNING AND MEMORY

Mating in a social group is one way that females can increase the information they use in mate choice decisions. Increasing the amount of information available for use in decision making can improve one's ability to make the "best" decision, or the decision that maximizes fitness, so many females draw upon learning and memory to inform their evaluation of potential mates. Learning and memory are two cognitive tools that can increase the amount of information available to females that are making mate choice decisions. Learning allows females to use experience to inform their decisions, and memory allows females to store, retain, and recall information for use in decisions that are made after there is no trace of that information in the environment. Processing too much information in a decision, however, can make the decision process time-consuming and inefficient, such that at some point more

information becomes costly rather than helpful (Bernays and Wcislo 1994; M. Sullivan 1994). Thus, learning and memory work together with the opposing forces of selective attention and forgetting to control the amount of information available to females for mate choice decisions.

The influence of learning and memory on natural decision making has been explored extensively with respect to foraging decisions (Guilford and Dawkins 1991; Speed 2000). This work has shown incredible variation in how animals learn and remember information related to food acquisition. Predators learn to avoid poisonous prey by recognizing conspicuous aposematic coloring (T. Roper and Redston 1987), while frog-eating bats use social learning to shape their response to potential prey (R. A. Page and Ryan 2006). Food-storing birds can remember specific cache sites for many months (Shettleworth 1990), and honeybees remember not only how to get to their food sources but also what kind of reward a flower produces and when the reward is produced (Boisvert et al. 2007). Learning and memory could have a dramatic influence on mate choice as well, but until recently research on mate choice has not focused on this question (Jennions and Petrie 1997; Bateson and Healy 2005). Mate choice decisions differ substantially from foraging decisions in three key ways that predict that learning and memory play different roles in these two domains.

(i) Most animals forage repeatedly, often for many hours of every day of their lives, but an animal's opportunity to mate is much less frequent, and some individuals mate only once in a lifetime. In these extreme semelparous cases, individuals have no opportunity to learn from actual mating experience. In these cases, individuals may learn information from social experiences other than mating itself, and short-term, or working, memory over the course of mate assessment may be more useful than long-term memory.

(ii) Many of the costs and benefits that result from a mate choice decision are more difficult to judge than those that result from a foraging decision, and so mating-related experiences may not be as easily learned. For individuals who mate multiple times, learning from previous mating experience may occur, but they can learn only about immediate costs and benefits rather than long-term costs and benefits such as the health of offspring resulting from a mate choice, which is apparent only long after the decision is made. In many species, males especially have the opportunity to learn from experience with multiple matings, because they mate or court more often than females do. Immediate costs and benefits of mate choice include factors such as time spent courting different kinds of females that vary in receptivity, as demonstrated in male fruit flies that learn from experience to modify their courtship behavior (Dukas 2004b, 2005a).

(iii) Many mate choice decisions are based on information received from communication signals. Communication related to foraging does occur but is less frequently critical to a foraging decision than to a mating decision. Signals used in mate choice are often ephemeral male advertisement signals—acoustic vocalizations or visual display behaviors that can influence a female's choice only if they persist in her decision process temporally beyond the moment of signal production to the moment of choice. This could occur through working memory. Thus, working memory of signals may be an important factor in mate choice decisions that is less relevant in foraging decisions.

Learning can influence both males (senders) and females (receivers) of a mating system. Males may learn what signals to produce, as has been demonstrated extensively in some birds and mammals (Janik and Slater 1997; Beecher and Brenowitz 2005; Searcy and Nowicki, chapter 5 in this volume), and they may learn which individuals to court, as mentioned above for fruit flies that learned about female receptivity (Dukas 2004b, 2005a). Females can apply learning to inform both preference and receptivity. The influence of early experience on female preference has been demonstrated in songbirds (reviewed in Riebel 2003) and also in invertebrates, as female wolf spiders' (*Schizocosa uetzi*) mate choice is dependent upon experience as a subadult (fig. 8.6; Hebets 2003). Not all learning about which mates are preferable occurs at an early age. As discussed above (section 8.3.2), once displaying males aggregate in groups, females can use short-term learning to inform their assessment of individuals that are potential mates.

The role of memory in mate choice has been less explored than that of learning. Each case of learning demonstrates some kind of memory, as the learned information must be retained in some form for animals to be able to use it. A study of memory, though, also considers when animals forget, shedding

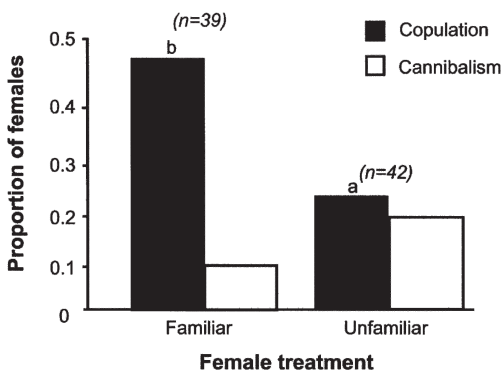


FIGURE 8.6. Mate choice is influenced by experience as a subadult in wolf spiders. Females mate more frequently with males of a familiar phenotype than with males of an unfamiliar phenotype, and they cannibalize males of an unfamiliar phenotype more frequently than males of a familiar phenotype. Redrawn from Hebets 2003.

the information they have stored. In a dynamic environment, memory of a temporary condition could become misleading once conditions have changed, so discarding memories at the appropriate time is adaptive, and an animal's performance is often enhanced by the ability to forget information that is no longer needed (West-Eberhard 2003). In social systems where individuals recognize each other and interact repeatedly, memories about a certain individual could influence the willingness to mate with that individual over a long period of time. For species that do not recognize individuals or encounter the same individuals repeatedly, remembering an evaluation of a potential mate over a long period would not be helpful. Retaining memories could even be costly due to mechanistic requirements of the physical process of memory (Dukas 1998b; Dukas, chapter 2 in this volume), such as the energy required for protein synthesis (Mery and Kawecki 2005), and out-of-date memories could clutter future mate choice decisions with irrelevant information that increases processing time (Bernays and Wcislo 1994; M. Sullivan 1994). These costs are especially relevant to working memory of an individual's signals because these signals rarely apply to future mate choice decisions and should be forgotten at some point.

Understanding the limits to working memory of mate choice-related information could help us understand mate choice strategies in general, because some mate choice strategies depend more than others upon working memory (Janetos 1980; Real 1990). For example, female gray treefrogs assess potential mates over a period of about 2 minutes, and an understanding of their memory capacity would help inform us about what occurs during this assessment period (Schwartz et al. 2004). During an assessment period, females could use a best-of- n strategy to compare males actively and then choose the most attractive one. This would require memory of the previous males that were assessed. If the memory capacity for this information is limited, it would impose a constraint on how long females could spend assessing each male or on how many males they could assess. As an alternative to simultaneous comparison of potential mates, a female could spend an assessment period attending sequentially to individual males until her attraction reaches a threshold sufficient to act upon, and then she would choose whichever male she is attending to. This sequential-search threshold model could operate without any working memory system, and in cases where memory is costly this threshold model may be favored. Figure 8.7 shows how mate search costs influence the expected fitness of the best-of- n versus the sequential-search strategies. Given the impact of mate search costs, females may even switch between strategies depending on what other factors demand usage of a limited memory capacity, such as when predators are present or when environmental conditions are especially treacherous.

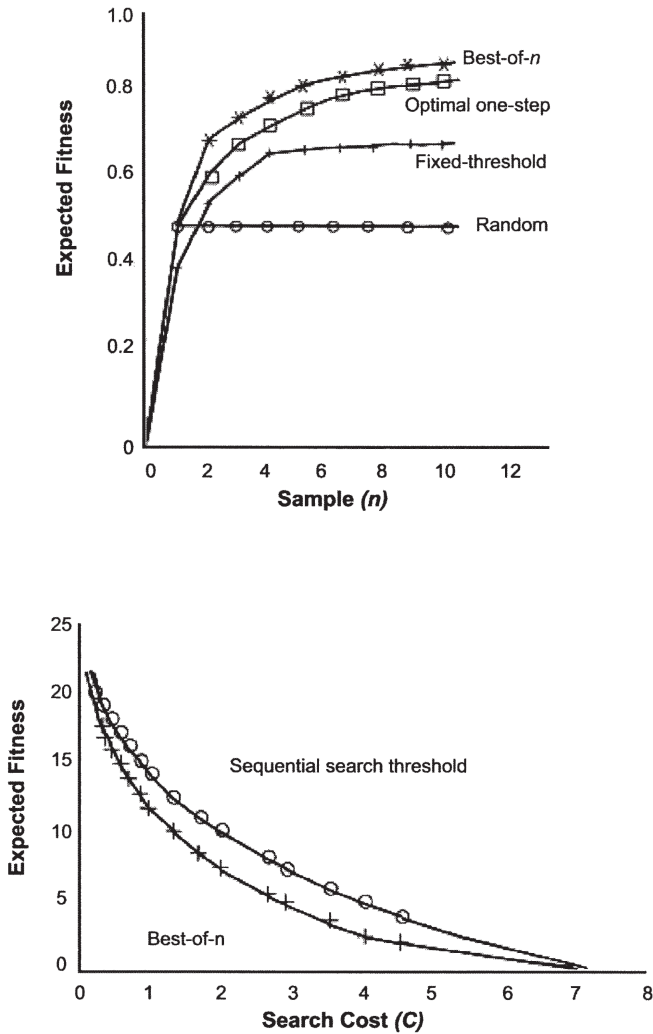


FIGURE 8.7. The costs of mate search influence the expected fitness of a mate choice strategy. Top: Initial models of mate choice strategy showed that a best-of- n comparison strategy would always be the strategy that resulted in the highest fitness for females, for any n number of males available to females. Redrawn from Janetos 1980. Bottom: But when the costs of searching for a mate are considered, models predict highest fitness for a sequential-search strategy, where the difference in expected fitness varies with the degree of cost entailed by mate search. Redrawn from Real 1990.

As mate choice research begins to address questions related to working memory, it will be helpful to consider when one would expect memory about potential mates to be beneficial to females. One relevant issue is whether an attractive signal indicates a potential mate that would increase a female's fitness. In cases where mating with the particular male whose signal is most attractive improves a female's fitness, she would benefit from the ability to remember the association between that male and his signal until she actually chooses her mate. In cases where females are attracted to a signal that does not relate to a male's quality—signals that reduce female search time, for example—there would be no selective force for her to remember which male makes an attractive signal, and signal memory would not be critical. Another relevant issue is whether signals are constant or variable through the course of a mate assessment, approach, and pairing. Females would benefit from remembering attractive signals that are patchy and variable through time, such as when attractive signals are rare and costly due to increased predation risk. Females would have no need to remember signals, though, when they are constant and uniform through time.

Exploring the influence of memory on mate choice could inform our understanding of sexual selection, as females' cognitive abilities and constraints pose yet another selective pressure on male advertisers. Given that certain stimulus configurations can be better remembered, this should guide the evolution of male display traits. Guilford and Dawkins (1991) broach this idea, arguing that how signals are remembered influences the evolution of warning coloration signals. The same process could occur in the evolution of mating signals, so research emphasizing how females' cognitive adaptations for learning and memory can bias display evolution would be valuable, akin to studies of pre-existing sensory biases in auditory tuning and photopigment sensitivity.

8.4. Conclusions and future directions

In this review we have considered some of the mechanistic aspects of mate choice. Our main goal was to review topics addressing how the animal's cognitive biology contributes to the patterns of mate choice in the wild.

We know a lot about mate choice. It is clear that female choice generates sexual selection that is responsible for the evolution of many of the details of male mating signals. Simple two-choice experiments show that females exercise preferences and have allowed researchers to understand the details of what makes signals attractive to females.

For example, we know that males can increase the attractiveness of their signals by making them contrast more with the environment and by matching

them to the sensory biases of females (M. Ryan 1998). On the other hand, females can evolve mechanisms to detect and perceive signals better at both the peripheral and the central nervous system. A popular approach to quantifying preferences has been the construction of preference functions.

But the principles of mate choice that have been established through all this research become less clear when we consider mate choice under conditions that approach the real world. Preferences exhibited in simple comparisons sometimes break down in more complicated ones, and we do not really know why. Preference functions need not be continuously variable but can be step functions, as when categorical perception takes place. Social groups can provide females with an enormous amount of information to consider in mate choice, as demonstrated by mate choice copying; thus, a male's utility is defined not only by his phenotype but by how others in the social group, besides the choosing female, react to his phenotype. To further complicate matters, the social group can also act as noise: male signals must compete to contrast against conspecifics, and females must parse signals from a complex social background.

As this review shows, a cognitive perspective on mate choice reveals some critical issues that have been virtually ignored. When female preferences change in social groups, is this adaptive plasticity or cognitive constraint? We have little idea as to the degree to which females' sensory and cognitive abilities are either adaptations to or constraints on mate choice. These abilities include auditory and visual scene analysis, auditory streaming, learning, and memory. When adaptations seem apparent, we must ask if these are domain specific or domain general. Have these adaptations arisen for mate choice specifically, or have they been co-opted from other domains such as foraging? Other major questions need to be addressed: Is female choice always rational? Do simple female preference functions really predict mate choice? Are preferences sometimes intransitive, and might choice be influenced by competitive decoys? Furthermore, we caution that there are other complicating factors in mate choice that we have not reviewed but have barely been probed, such as state-dependent (age, hormonal) changes in mate choice (e.g., K. Lynch et al. 2005), multimodal communication (e.g., Partan and Marler 1999), and the relationship between recognition and discrimination (Phelps et al. 2006.). Early studies of sexual selection and mate choice concentrated on demonstrating that they occurred and their potential adaptive significance. Given numerous insights into phenotypic plasticity, neural bases of signal decoding, and the cognitive biology of decision making, there are new frontiers in mate choice that will not only inform us more deeply about how it occurs but also give us a more realistic understanding of how and why it evolves.