

# Sexual selection, sensory systems and sensory exploitation

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## 1. INTRODUCTION

Sexual selection by female choice is a process involving communication. The male is the sender and his courtship display is the signal, whereas the female is the receiver, with both her sensory and endocrine systems responding to the signal. To the extent that variation in signals differentially influences receivers, there is the opportunity for sexual selection. Understanding the mechanisms of this communication process reveals how sexual selection by female choice operates. It can suggest how females might evolve preferences that result in adaptive mate choice, how sensory biases could determine the direction of the runaway process, and how males might evolve traits that exploit pre-existing sensory biases of the female (sensory exploitation). When combined with appropriate phylogenetic data, an understanding of the sensory basis of female choice can allow the test of hypotheses for the evolution of female choice. The purpose of this chapter is to consider sensory mechanisms in sexual selection.

## 2. FEMALE MATE CHOICE AS COMMUNICATION

In sexually reproducing species, mating rarely takes place without some form of communication between the two partners. In many mating systems, this communication takes place in the form of courtship, usually males courting females. Most studies of mate choice have dealt with species recognition. The early ethologists discovered that one of the most important functions of courtship was to communicate information about species identity; thus species-typical aspects of courtship behavior were documented extensively (e.g. Lorenz 1950; Tinbergen 1951; Morris 1956). However, in order to recognize conspecifics, not only must species differ in their displays, but females must be able to discriminate these differences; neuroethologists have been successful in demonstrating that sensory systems are biased towards species-specific information (e.g. Huber 1978; Capranica 1976; Hoy 1978; Kendrick and Baldwin 1987; Walkowiak 1988).

Studies of species recognition also have played an important role in studies of evolution. Speciation theory was the cornerstone of the Modern Synthesis in evolutionary biology (Dobzhansky 1937; Mayr 1942, 1963, 1982), and the role of courtship as an ethological isolating mechanism was the most important contribution of animal behavior to evolutionary theory (Blair 1964; Littlejohn 1965; Walker 1974; Alexander 1975). The value of considering interspecific mate choice as a problem in communication is apparent in the success of delineating this behavior at three levels of analysis: mechanism, current function and evolution.

Since the seminal work of Williams (1966) and the influential collection of contributed papers assembled by Campbell (1972), the choice of mates within a species (i.e. sexual selection by female choice) has become an important topic of research, attracting interest from behavioral ecologists and population geneticists. The parallels between species recognition and sexual selection by female choice are more obvious than are the distinctions. The two phenomena are similar in that both involve discrimination among potential mates (usually) by females, there is an obvious effect of the female's behavior on the mating success of males, and a possible influence of the female's choice on her own reproductive success. However, the process of male courtship and female choice as a problem in communication has been less appreciated in sexual selection studies than in studies of species recognition (but see Morris 1956; Barlow 1977; West-Eberhard 1979; Arak 1983; Burley 1985; Endler 1989; Rowland 1989*a*, 1989*b*). It is hoped that this chapter will convince readers of the value of considering sexual selection by female choice in the context of communication, especially regarding mechanisms of the receiver.

### 3. MECHANISMS OF FEMALE CHOICE

#### 3.1 Mate choice based on male traits

Studies of female mate choice in the past two decades have helped resurrect an important aspect of sexual selection ignored or rejected for more than a century. The immediate reception of Darwin's theory of sexual selection (1859, 1871) was ambivalent. He suggested that sexual selection could operate in two modes: males could differ in their ability to gain access to females through direct competition, and males could differ in their attraction to females. Although willing to accept the role of male competition, many authors, including steadfast Darwinians such as Wallace (1905) and Huxley (1938), doubted the efficacy of female choice. Darwin himself seemed skeptical of the ability to actually demonstrate female choice: 'What the attractions may be which give an advantage to certain males in wooing . . . can rarely have been conjectured' (Darwin

1882). Sexual selection by female choice lay dormant for more than a century.

One of the first issues to receive rigorous attention in recent studies of sexual selection was that of female choice based on male traits. These studies of mechanisms of mate choice often required the combination of quantitative field observations and controlled experiments. Such studies have shown, for example, the importance of acoustic (crickets: Hedrick 1986; fish: Myrberg *et al.* 1986; frogs: Ryan 1980; Sullivan 1983; Gerhardt 1988; Morris and Yoon 1989; birds: Searcy and Marler 1981; Payne 1983; Searcy 1984; Gibson and Bradbury 1985), visual (crabs: Christy 1988; fish: Semler 1971; Kodric-Brown 1985; Houde 1987, 1988; Ryan and Wagner 1987; birds: Andersson 1982; Burley 1985) and chemical signals (moths: Conner *et al.* 1981; Boppré and Schneider 1985) of males that influence female mate choice.

Searcy and Andersson (1986) have argued that to demonstrate female mate choice based on male traits, studies must show a significant relationship between male traits and male mating success, and then demonstrate experimentally that the traits in question influence female mating decisions. Regarding the first criterion, there have been recent developments of statistical techniques to estimate the strength of direct and indirect selection on male traits, and these have greatly improved our resolution in estimating selection (reviewed in Endler 1986; Wade 1987). However, the current emphasis on measuring selection has sometimes resulted in ignoring the second criterion suggested by Searcy and Andersson (1986), that is, understanding the processes that generate selection (Endler 1986; Graffen 1987; Ryan 1988*b*). In fact, Endler (1986) states: 'A highly accurate measure of selection differentials or coefficients, combined with a lack of knowledge of the reasons for and the mechanisms of selection, is little more than refined alchemy.'

There are some cases in which experimental studies of female mate choice are informative even in the absence of data showing that mating preferences generate selection. For example, Forester and Czarnowsky (1985) showed that in a frog, *Hyla crucifer*, larger males produced calls with lower frequencies and females preferred lower frequency calls. However, in nature there was not a large-male mating advantage. The reason for this disparity, the authors suggested, is that smaller males adopt non-calling, satellite mating strategies and ambush females en route to calling males. Therefore, the lack of size-based variance in male mating success is due to opposition of two mechanisms of sexual selection, female choice and male interactions, rather than to the lack of selection. Andersson (1982) provides another motivation for probing female preferences without evidence of selection. Male widowbirds have long tails that might appear to have evolved under the influence of sexual selection by female mate choice. Andersson did not find a significant correlation in the field

between male mating success and tail length, but when he artificially altered tail length such a relationship became apparent. This study makes two important points. First, examining a female preference in relation to only the extant variation in male traits informs us about current mechanisms generating (or not generating) selection, but does not tell us the potential for female choice to influence variation in male traits that might arise. Secondly, this study highlights the problem of addressing an historical question (why do males have long tails?) by studying only current effects (how does the current variation in the male trait affect female mate choice?). We will return to this issue later.

General conclusions from more than a decade of studies of sexual selection by female choice are that: in many systems there is significant variation among males in their courtship behavior; females are responsive to this variation; and, as a result, females generate sexual selection on male traits by their differential choice of mates. Although there are many systems in which sexual selection by female mate choice has little or no importance, there are now enough data to generally confirm Darwin's intuition regarding the efficacy of female mate choice.

### 3.2 Sensory systems and mate choice

Studies of mechanisms of female mate choice have established the importance of female choice, but such studies can offer much more. For example, understanding how signals used in male courtship influence a female's perception of potential mates can reveal much about the evolution of male traits under sexual selection. A trivial example is how the sensory modality that guides mate choice determines those aspects of the male's phenotype subject to selection. In nocturnally breeding animals such as many frogs and moths, visual signals are of limited value, and thus vocal or chemical cues are used in mate attraction, whereas in diurnally breeding animals, such as dart-poison frogs and butterflies, males are strikingly colored. Although the acoustic and chemical channels still play some role in mate choice in the diurnal species, visual signals have become elaborated under sexual selection. It is an obvious observation that only those aspects of the male's phenotype perceived by the female can be subject to sexual selection by female choice.

Although the sensory modality used in communication defines the type of signals used in sexual selection, the sensory system can be permissive about the precise form of the signal favored by selection. In bower birds, it has been suggested that there is a trade-off between elaboration of the bower and elaboration of male plumage; species with dull plumage have elaborate bowers and those with elaborate male plumage are characterized by less extravagant bowers (Gilliard 1956; Borgia 1986). Some studies have shown such permissiveness by presenting females with male pheno-

types that do not exist in nature. For example, Burley (1986) has shown that female zebra finches favor males with orange beaks, and that the preference for orange can be transferred to the color of artificial leg bands. A similar phenomenon occurs in anuran mate recognition. Many examples upon which I will draw come from this literature, and thus I will quickly review some of the basic aspects of call recognition in anurans (for detailed discussions of mechanisms, function and evolution of anuran acoustic systems, see reviews in Fritzsche *et al.* 1988).

All frogs have two inner ear organs with distinct ranges of frequency sensitivity. The amphibian papilla is most sensitive to low-frequency sounds. Individual fibers emanating from this end organ are each most sensitive to one of a variety of frequencies below *c.* 1200 Hz, and as a population these fibers show one or two peaks of frequency sensitivity at threshold intensities. The basilar papilla is sensitive to higher frequencies, all the fibers from this end organ are tuned to the same frequency, and this best excitatory frequency is usually above 1500 Hz (Zakon and Wilczynski 1988). In the male's advertisement call, those frequencies that contain the most energy match the tuning of the peripheral auditory system. If the call has two frequency peaks of energy, they usually match the tuning of both the amphibian and basilar papillae. If the call has only one frequency peak, then it matches the tuning of either the amphibian or basilar papillae. At higher levels of the brain (e.g. the midbrain and thalamus) information from separate frequency channels is integrated to result in a synergistic neural response to stimuli from the conspecific mating call (Gerhardt 1988; Fuzessery 1988; Walkowiak 1988). Therefore, an important initial step in the processing of spectral information takes place in the auditory periphery, even before this information reaches the brain. Less is known about how temporal aspects of the mating call are processed, but it has been shown that neurons in the brainstem are similarly tuned to temporal properties of the call (Rose and Capranica 1983; Walkowiak 1988).

Most experimental studies of female mate choice that use synthetic stimuli restrict the form and the range of the stimulus to that observed in nature. However, such experiments can also provide an opportunity to probe the female's response properties for hypothetical male traits, and thus to determine how sexual selection might act if certain male variants were to arise. In studies of natural selection, such opportunities are rarely available and evaluation of the performance of hypothetical variants, such as changes in functional-morphological relationships, can only be evaluated by models (Hildebrand *et al.* 1985; Radinsky 1987). It seems that researchers have been too conservative in exploiting experimental methods available in studies of mate choice.

Sexual selection and communication have been investigated extensively in the túngara frog, *Physalaemus pustulosus* (e.g. Ryan 1985). Recently,

we investigated how signal variants that are not part of the male's repertoire might influence female choice if these traits were to evolve.

Males of *P. pustulosus* can add a 'chuck' to the initial 'whine' portion of their call. This makes the call more attractive to females (Fig. 1). A natural chuck has a broad frequency range that includes the frequencies to which each of the inner ear organs is most sensitive. Ryan and Rand (1990) have shown that synthetic chucks with either only the lower frequency portion or only the higher frequency portion of the chuck, and thus matching the most sensitive frequencies of only one of the two inner ear organs, are as effective in eliciting preferential female phonotaxis as the natural chuck with the full frequency range, as long as all the stimuli contain the same total amount of energy. This is despite the fact that the

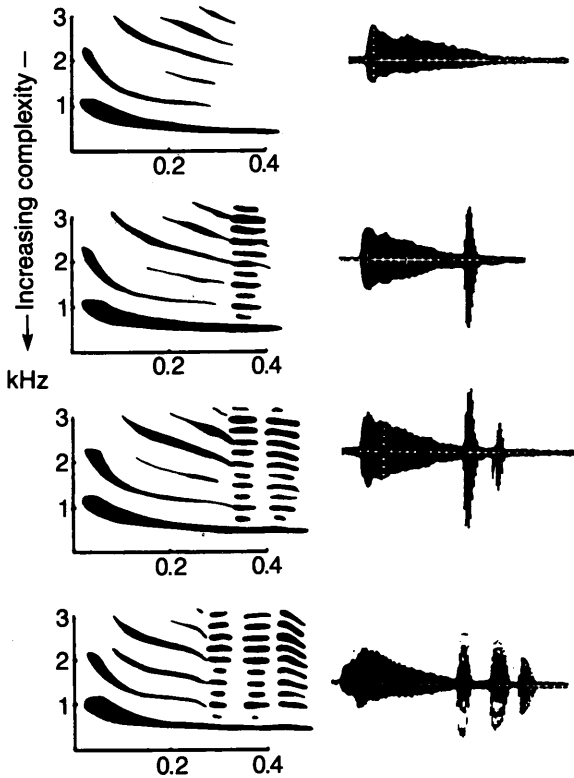


Fig. 1. Advertisement calls of the frog *Physalaemus pustulosus*. Calls increase in complexity from a whine with no chucks (top) to a whine with three chucks (bottom). Sonograms (left) exhibit how frequency (kHz) changes as a function of time (sec). Oscillograms (right) exhibit how amplitude of the same calls change with time.

low-frequency portion of the chuck has only 10 per cent of the total energy in natural calls.

The studies by both Burley (1986) and Ryan and Rand (1990) indicate that the sensory system might define a wide range of signals that could be favored by sexual selection. A female preference for a particular variant of a male trait might be due to a general preference for a certain kind of stimulation. Understanding preferences at this more general level would greatly enhance our understanding of the dynamics of sexual selection. In such cases, morphological constraints on signal evolution probably determine which of the favored forms of the signal evolve (Ryan and Drewes 1990).

I have discussed sexual selection acting in only a single modality, but many biologically relevant tasks facing an animal involve the potential use of more than one sensory modality, such as homing in pigeons (Keeton 1979) and foraging in bats (Ryan and Tuttle 1987). In both these examples there is a hierarchy of cues. Pigeons rely first on the sun and only switch to cues such as polarized light and magnetism if the sun is not visible, and the African bat, *Cardioderma cor*, ignores information from echolocation signals if the sound made by its prey is sufficient for localization.

The interaction of sensory modalities has hardly been explored in mate choice. In one example, cues in different modalities might be redundant. Conner (1987) showed that an arctiid moth uses both chemical and acoustic signals in courtship. Ablation experiments showed that the lack of one of the cues did not reduce the male's mating success, but he was unable to mate if he lost the ability to produce both signals.

Another example of multiple cues is conspecific mate choice in sword-tails. Ryan and Wagner (1987) showed that when exposed only to visual cues, female *Xiphophorus pygmaeus* preferred larger, courting males of their allopatric, sister species, *X. nigrensis*, to their own smaller males which do not court. However, if exposed only to chemical cues, the females preferred the conspecific stimulus to that of the heterospecific. When female *X. pygmaeus* were simultaneously presented with both stimuli they showed neither a conspecific nor a heterospecific preference (Crapon de Caprona and Ryan 1990). In this case, the conflicting preferences from the two sensory modalities cancelled. It is not known if these cues are used simultaneously in nature or, for example, if females use chemical cues to locate areas with males and then base their final mate choice on visual cues. But this study shows that cues in different sensory modalities can result in different female preferences, and that the interaction of two modalities produces different results than when only one is considered. In general, these kinds of studies both define the signal modalities subject to selection, and allow investigations as to the fate of hypothetical traits that might be subject to sexual selection.

### 3.3 Sensory limits on signal divergence and the opportunity for speciation

The range of stimuli to which the sensory system is capable of responding will define the limits of signal evolution; this is more apparent in among-species comparisons. Because the divergence of courtship signals is often an important component of the speciation process (e.g. Mayr 1963), Ryan (1986) suggested that sensory constraints on signal divergence could also limit the opportunity for speciation. In many frogs, the amphibian papilla, which is sensitive to low-frequency sounds, is critically involved in the perception of the species-specific advertisement call. In primitive frogs, this organ consists of only a single, small patch of sensory epithelium that is sensitive to a fairly narrow range of frequencies. In advanced frogs, an embryonically distinct patch of sensory epithelium joins the homologous patch present in primitive frogs; the sensory epithelium is much longer, and the frequency range to which this inner ear organ is sensitive is much larger.

There are four character states for this inner ear organ, from small to greatly elongated. Because the length of the sensory epithelium is directly related to the frequency range of hearing, then it also determines the variation in call frequencies that can be perceived by females. Therefore, the state of the amphibian papilla imposes sensory limits on signal evolution. In primitive frogs, the sensory constraints are more severe and the number of species is smaller, whereas in advanced frogs the sensory constraints are most relaxed and the number of species is greatest. This relation holds for the two intermediate character states as well (Fig. 2). This is consistent with the notion that sensory constraints influence the opportunity for speciation.

A similar explanation involving morphological rather than sensory constraints on signal divergence may apply to the age-old question of why there are so many species of passerine birds. An obvious response is that there are many passerines because there are lots of oscines (song birds, a group within the passerines: Raikow 1986). This group has a complicated syrinx capable of producing internal duetting and thus an overwhelming diversity of song. It has been suggested that divergence of songs among populations can give rise to local mate preferences and thus genetic structuring of populations (Baker and Cunningham 1985; but see Baptista 1985; Brenowitz 1985; Chambers 1985). And it also has been suggested that the extreme ability of generating a variety of sounds in oscines might promote divergence of mate recognition signals and enhance the speciation process, in much the same way as was suggested for frogs (Fitzpatrick 1988; Vermeij 1988).

The assertion that constraints on signal divergence influence speciation rates in frogs and birds is difficult to evaluate because of the possibility



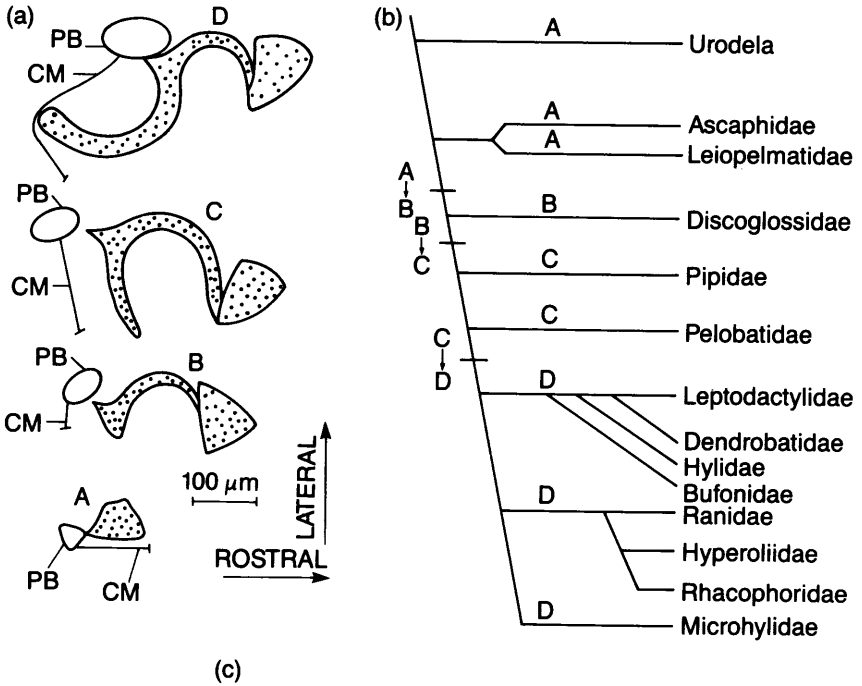


Fig. 2. (a) The size and complexity of various character states of the amphibian papilla. (b) The distribution of character states of the amphibian papilla across anuran taxa with hypothesized evolutionary transitions. (c) The number of taxa as a function of the character state of the amphibian papilla.

of confounding cause and effect, and because the sample sizes are too small for rigorous statistical evaluation, e.g. there are only four character states of the amphibian papilla and thus only four data points. But if sensory and morphological constraints on the divergence of male courtship signals is an important phenomenon, it should be found in other taxa using other sensory modalities for mate recognition.

### 3.4 Stabilizing sexual selection on male traits

Many studies of conspecific mate recognition were motivated by the knowledge that the cost to a female of mating with the wrong species can be severe. This suggests that mate recognition systems should have evolved to reject heterospecifics as potential mates, even if, in doing so, females were to make an occasional error of rejecting a conspecific mate. Therefore, the sensory system involved in mate recognition should be strongly biased toward the mean, and thus should exert strong stabilizing selection on the male trait. This assertion has been invoked by several authors to suggest that (directional) sexual selection is unlikely because it would favor male traits that deviated from the mean (Templeton 1979; Paterson 1982; Gerhardt 1982).

Several studies have shown that sensory biases in mate recognition systems can result in stabilizing selection. One of the better examples comes from Gerhardt's studies of mechanisms of mate choice in tree frogs of the genus *Hyla* (summarized in Gerhardt 1982).

The call of *H. cinerea* has a frequency spectrum with two energy peaks, each of which matches the tuning properties of either the amphibian papilla or basilar papilla. The most attractive synthetic stimulus for eliciting female phonotaxis is that which combines the two frequency peaks. Gerhardt showed that for the low-frequency peak, females preferred that frequency closer to the population average rather than one that was higher or lower. These results suggest that there should be stabilizing selection on the male trait in nature, and measures of male mating success in the field are consistent with this interpretation (Gerhardt *et al.* 1987).

Why do the females prefer males with call characters close to the population average? Or, asking the question at another level of analysis, why do females have auditory tuning properties that result in preference for average calls? Gerhardt suggests that it is in response to selection for conspecific mate recognition. The sympatric tree frogs *H. gratiiosa* and *H. squirella* have calls similar to that of *H. cinerea* but are slightly lower and higher, respectively, in frequency. Thus, if female *H. cinerea* chose calls that deviated substantially from the population mean, they would risk mating with a heterospecific. This study suggests that the mate recognition system evolved to effect conspecific matings. However, are selection for species recognition and sexual selection mutually exclusive phenomena?

The dichotomy between species recognition and sexual selection is a false one, as is evident from considering Gerhardt's study. For the green tree frogs it seems clear that the sensory biases of the female's auditory system and, by extension, the female choice behavior that it guides, enhance the female's chances of mating with conspecifics. This does not mean that the female preferences do not generate sexual selection on the male trait. Again, sexual selection by female choice refers to males' differential ability to attract mates. If females are more attracted to some males than to others, and if this differential attraction generates variance in male mating success, then sexual selection operates.

Sexual selection need not be directional, it can be stabilizing as in the green tree frog system in which sexual selection favors males with average call frequencies. In this example, and in others demonstrating stabilizing selection, there can be debate as to why females evolved preferences for average males. For the green tree frog the most logical argument is that females that avoid mating with conspecifics are favored by selection. The evolutionary forces responsible for the preference need not determine its current effects on male traits; even if the preference evolved for the benefit of mating with conspecifics, that does not mean that it cannot generate sexual selection.

There are many examples of female mate choice generating stabilizing selection on male traits. Many of these studies were conducted as investigations of species recognition and, because of the false dichotomy between species recognition and sexual selection, many of these studies have been cited as evidence for the lack of sexual selection. Understanding the processes of both species recognition and sexual selection will be enhanced if we abandon the notion that they are mutually exclusive.

### 3.5 Directional selection on male traits

Female preference for extreme, rather than mean, traits has received the most attention in the field of sexual selection. This is not surprising. It was the extreme elaboration of male traits and its obvious survival cost that led Darwin (1859, 1871) to consider sexual selection theory, and that motivated Fisher's (1958) hypothesis of runaway sexual selection. This also led to the controversy of the lek (Bradbury 1981; Beehler and Foster 1988; Höngstrum 1989): Why should females choose a male from whom they would accrue no immediate benefit, and why should they prefer a male whose own courtship promotes his early demise? It is perhaps in these instances that understanding the mechanism of female choice reveals the most about the operation of sexual selection.

The number of studies demonstrating that female preferences exert directional selection on male traits has increased dramatically in the last decade. There has not been a systematic review of the findings of such

studies, but a casual survey seems to reveal some pattern.

Among frogs alone, studies have shown that females prefer lower frequency calls (Ryan 1980, 1983; Forester and Czarnowsky 1985; Robertson 1986; Ryan and Wilczynski 1988; Morris and Yoon 1989), calls with more notes (Wells and Schwartz 1984; Rand and Ryan 1981; Littlejohn and Harrison 1985), faster call rates or more calls (Sullivan 1983; Forester and Czarnowsky 1985; Schwartz 1986; Klump and Gerhardt 1987; Wells 1988; Forester *et al.* 1989), longer calls (Straughn 1975; Klump and Gerhardt 1987) and more intense calls (Fellers 1979; Zelick and Narins 1983; many of these studies are reviewed in Gerhardt 1988). Female crickets prefer longer calling bouts (Hedrick 1986) and more intense calls (Latimer and Sippel 1987), and female birds prefer larger song repertoires (Catchpole 1980; Searcy and Marler 1981; McGregor and Krebs 1982; Payne 1983; Searcy 1984; Catchpole *et al.* 1984). There are analogous studies of systems in which courtship is primarily visual: female swordtails prefer males with longer swords (Basola 1990); female guppies prefer males with a greater area of brighter colors (Kodric-Brown 1985; Houde 1987) and larger tails (Bischoff *et al.* 1985); female sticklebacks prefer larger males (Moodie 1982; Rowland 1989*b*), with more color (Semler 1971) and higher display rates (Ridley 1986); male sticklebacks prefer more rotund females (Rowland 1989*a*); male butterflies prefer females with larger wings (Tinbergen *et al.* 1942; Rutowski 1982) and faster wing beat (Magnus 1958); and female widowbirds, swallows and pied flycatchers prefer longer tails on their males (Andersson 1982; Møller 1988; Lijfeld and Slagsvold 1988). There are fewer studies dealing with chemical communication. However, it has been shown that male newts prefer stronger concentrations of female pheromone (Verill 1985). Also, female moths prefer larger males, and size is correlated with the amount of pheromone (Phelan and Baker 1986, 1987; Conner *et al.* 1990; Conner, pers. comm.). Rowland (1989*a*) discusses many of these examples.

In some studies, the female preference extends beyond the population's phenotypic range; that is, there is preference for a supernormal stimulus (Tinbergen 1948). For example, Sullivan (1983) showed that female toads prefer call rates that exceed those produced by any males. Rowland (1989*a*) showed a male preference for female sticklebacks who were distended far beyond the normal range, and a female preference for males that were 25 per cent larger than normal (Rowland 1989*b*). Also, Magnus (1958) reported that male mate choice in a moth favored a wing beat rate that greatly exceeded that exhibited by any females. Andersson's (1982) study is particularly interesting because not only did female widowbirds prefer artificial tails that exceeded the maximum length in the population, but there was no evidence of female preference when it was based on the population's normal variation. However, in most studies, the traits tested do not extend into the supernormal range, and thus the generality of

preference for a supernormal stimulus cannot be evaluated.

Species recognition might sometimes generate directional selection. If two species are similar in a trait, females might be selected to prefer traits of conspecifics that differ most from those of heterospecifics (Trivers 1972). An example of just such an effect might be seen in the variation in dewlap color in the lizard *Anolis brevirostris* (Webster and Burns 1973). Dewlap color can be important in mate choice (Crews 1974), and populations of *A. brevirostris* vary in dewlap color. Those *A. brevirostris* that are nearest to a northern congeneric with light dewlaps have darker dewlaps, whereas those nearer to a southern congeneric characterized by darker dewlaps have lighter colored dewlaps. Unfortunately, the influence of dewlap-color variation on mate choice in this species has not been investigated.

As I emphasized in the previous section, there are many studies suggesting stabilizing selection. The disparity between the number of studies cited demonstrating stabilizing versus directional selection is not meant to reflect the relative frequency of these phenomena. However, the above review shows that in many cases females do not prefer the mean trait; females often exert directional rather than stabilizing selection.

When female choice generates directional selection, the direction is usually consistent, and it usually favors the more elaborate or greater quantity: longer tails, stronger odors, more intense calls, more complicated calls, larger song repertoires, brighter colors and more of them. It is unusual to find female preference for shorter tails, softer calls, simpler songs and duller colors. Thus there appears to be an inherent directionality in female preferences.

In Section 4.1, I will discuss in more detail competing hypotheses for the evolution of female preferences. One such hypothesis is Fisher's theory of runaway sexual selection. Unfortunately, there seems to be a common misconception among some behavioral ecologists that the continued exaggeration of a male trait is the necessary outcome of Fisher's hypothesis of runaway sexual selection (e.g. Alcock 1989). The essence of the runaway process is the genetic correlation of a male trait and a female preference through linkage disequilibrium. This causes an ever-accelerating increase in the frequency of the trait, due to selection by female choice, and the preference, as a correlated response to selection on the trait (see also Kirkpatrick 1987*b*). There is no inherent direction to the evolution of male traits under the runaway process alone, as many mathematical models have demonstrated (e.g. O'Donald 1983; Lande 1981; Kirkpatrick 1982). It is important to note that the runaway process applies to a specific mode of correlated evolution of trait and preference; this theory can accommodate, but does not predict, the exaggeration of male traits under sexual selection.

If the notion of an inherent directionality in female choice is true (i.e.

more, not less, elaborate), the runaway process by itself cannot account for patterns of male traits observed in nature. Population geneticists acknowledge this, and have suggested that biases in perceptual mechanisms can influence the direction in which the runaway sexual selection will proceed (e.g. O'Donald 1983; Kirkpatrick 1987a); thus the data are consistent with Fisher's hypothesis. Also, the directionality in female choice is consistent with hypotheses that suggest female choice is based on traits that indicate male quality (e.g. Zahavi 1975; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Andersson 1986; Pomiankowski 1988), if we assume that the more elaborate the trait, the better the male quality, and the stronger the preference. In fact, this directionality is consistent with several hypotheses. For example, there is evidence that male courtship might have such an important effect on the reproductive state of the female, that in an experimental situation the female's fecundity decreases if she is deprived of the mate she first chose (Bluhm 1985; Yamamoto *et al.* 1989). In Section 4.3, I will discuss in more detail competing theories of the evolution of female preferences, and ask how our knowledge of mechanisms can add to or even reject some of the competing hypotheses.

### 3.6 Sensory biases and directional selection

An understanding of any inherent property of sensory systems that causes preferences resulting in directional selection, and especially preferences for exaggerated stimuli, would be an important addition to sexual selection theory. Such an understanding could explain mechanisms underlying the evolution of elaborate male traits in many animals, and thus it would contribute to our understanding of patterns of organic diversity, which is one of the major goals of evolutionary biology. The beginnings of such a perspective is suggested in some of the following studies.

Magnus (1958) showed that male butterflies preferred females with faster rates of wing beat, even when it exceeded the normal rate of 8–10 Hz. Using a model, he showed that males preferred supernormal rates, and that this preference continued up to a wing beat rate of 140 Hz, which is also the flicker-fusion rate of the butterfly's eye (the rate at which the individual flaps blur into a single movement). Therefore, the preference increased as the rate of retinal stimulation increased, and then ceased when the maximum rate of stimulation was reached. Not only does this suggest the sensory mechanism of (male) mate preference, it also shows that if the female's wing beat rate were not constrained by morphology and physiology, it might eventually reach a point at which further elaboration would be limited by the male's perceptual abilities. This would produce a result similar to that proposed by Fisher (1958), in which the counter-selection force of predation halts the further elaboration of a

male's trait. Cohen (1984) has also discussed how sensory constraints on perceptual discrimination might impose an upper limit on the evolution of elaborate male traits under sexual selection.

Another indication of how retinal physiology can affect mate choice comes from crabs. In the fiddler crab, *Uca beebei*, some males construct pillars at the entrance to their burrows. Burrows with pillars are more likely to attract females, and Christy (1988) has suggested that the pillars are used by males to exploit the female's tendency to detect objects that project above the horizon (Zeil *et al.* 1986).

Rowland (1989a) also used animal models to investigate male choice based on a female trait. He had previously shown that male sticklebacks preferred larger, more gravid females, and suggested that the benefit to such a preference was due to the positive correlation between female size and female fecundity (Rowland 1982). In the more recent study, he showed that the male preference is elicited by the total projection area of the female, not just her volume due to distension with eggs. Males preferred a projectional area that greatly exceeded the normal range, suggesting that this preference is dictated by the amount of sensory stimulation of the retina. In addition, he pointed out that although in many cases this mechanism would result in males choosing more fecund females, it could also lead to males preferring to mate with females that were grossly distended with parasites.

The importance of red color in eliciting female sexual response in sticklebacks has been well known since Tinbergen (1953) reported interactions between these fish and red mail trucks. Semler (1971) showed female preference for males with more intense red. Interestingly, it is known that the female's sensitivity to red increases in the breeding season (Crounly-Dillon and Shama 1968). Also, Reimchen (1989) showed that a significant amount of the variation in the number of males with red nuptial coloration could be explained by the light transmission qualities of the environment; red nuptial colors were less common in water in which red wavelengths did not transmit well. In these fish, not only is the eye tuned toward red males, this tuning increases during the time of breeding but is susceptible to environmental noise that masks the signal.

The bright, polymorphic color patterns of male guppies are also well known, as are the studies of how predation and sexual selection act on these color patterns (Endler 1980, 1982, 1983; Kodric-Brown 1985; Breden and Stoner 1987; Houde 1987). Recent studies of the guppy's retina suggest how the variation in male color might be maintained. Archer *et al.* (1987) found that guppies exhibit a degree of polymorphism in visual pigments exceeding that reported for most vertebrates. They suggested that the pigment polymorphism might give rise to a perceptual polymorphism in females that could account for the maintenance of variation in the male trait.

Anurans have emerged as an especially good model for examining the neural bases of species-specific call preferences, and this approach is now being extended into the area of sexual selection. As suggested above, among species there is a good match between the frequencies in the advertisement call that contain the most energy and the tuning properties of the amphibian papilla and basilar papilla in the peripheral auditory system. I have discussed how male *P. pustulosus* increase the attractiveness of their call to females by adding chucks to the initial whine of the advertisement call. The chuck has a fundamental frequency of 200 Hz with 15 harmonics, and thus a frequency range of 200–3000 Hz. Besides preferring calls with chucks, females also show a more subtle call preference. They prefer chucks having a lower fundamental frequency. Larger males produce lower-frequency chucks, and in nature larger males have greater mating success because they are more likely to be chosen as mates by females. Thus the female preference for lower-frequency chucks exerts directional selection on the male trait (Ryan 1980, 1983, 1985).

Ryan *et al.* (1990) investigated the sensory basis of sexual selection in *P. pustulosus*. Because the chuck is harmonically structured, a preference for a lower fundamental frequency could be due to a preference based on any of the 15 harmonics. In this species, the frog's amphibian papilla is most sensitive to 700 Hz at threshold intensities and the basilar papilla is most sensitive to 2200 Hz. Although Ryan and Rand (1990) have shown that either the low or high half of the chuck is as attractive as the full chuck if the total amount of energy is the same, in nature more than 90 per cent of the energy is above 1500 Hz, falling in the frequency range to which the basilar papilla is most sensitive. Thus it would appear that the preference for the lower-frequency chucks might reside in the basilar papilla. The average dominant frequency from a random sample of 54 calls was 2500 Hz, higher than the average tuning of the female's basilar papilla (Fig. 3). This alone would suggest that calls with lower than average frequencies elicit greater neural stimulation in the females.

The amount of neural stimulation was quantified by determining the Fourier spectrum (frequency versus energy) of the chuck, and using a computer model to measure how much of this energy would pass through the tuning filter of the basilar papilla. Ryan *et al.* (1990) then asked if most chucks in the population would be more stimulatory if they were of lower frequency. To do this they multiplied all the frequencies in a chuck by a series of numbers (frequency multipliers) from 0.95 to 1.05. Frequency multipliers less than 1.0 would result in chucks with lower frequencies and frequency multipliers greater than 1.0 would produce higher-frequency chucks. They then determined the 'optimal' frequency multiplier; that is, the frequency multiplier that would result in the chuck that elicited the greatest amount of neural stimulation. The hypothesis that females prefer lower-frequency chucks because they elicit greater



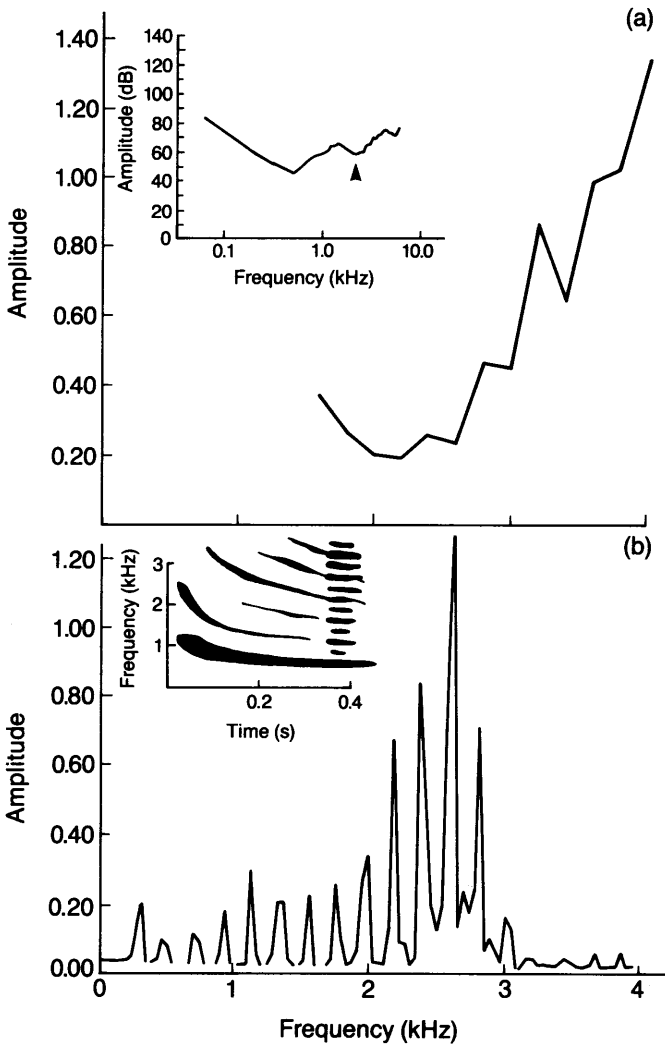


Fig. 3. (a) An average ( $N = 7$ ) audiogram derived from the hindbrain of the frog *Physalaemus pustulosus* truncated to represent only those frequencies to which the basilar papilla is most sensitive. The inset shows the complete audiogram. (b) A Fourier spectrum, showing the distribution of call energy as a function of frequency for a single chuck. The inset shows a sonogram of whine plus one chuck.

neural stimulation predicts an optimal frequency multiplier significantly less than 1.0. The results support that hypothesis (Fig. 4).

A second property of the sensory system also results in directional selection on call frequency. Ryan *et al.* (1990) determined the average amount of neural stimulation for all of the 54 calls as a function of the frequency multiplier (Fig. 4). As expected from the previous results, the maximum was less than 1.0 (i.e. the unmanipulated call). However, the distribution of the amount of neural stimulation was asymmetric around 1.0. A chuck that was slightly lower in frequency than the optimum showed only a slight decrement in the amount of stimulation, whereas a

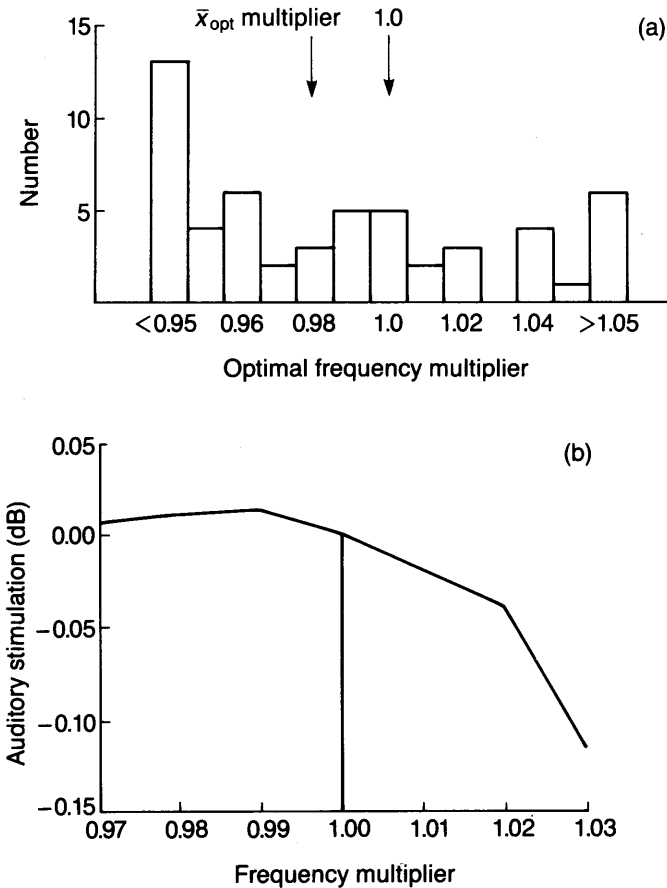


Fig. 4. (a) A frequency histogram of the optimal frequency multipliers of calls of 54 *Physalaemus pustulosus*. (b) The average amount of auditory stimulation elicited from the audiogram as a function of the frequency multiplier for all 54 calls.

chuck that was higher in frequency than the optimum showed a greater decrement in neural stimulation. Thus the disadvantage of producing a suboptimal chuck is more severe for higher-frequency chucks than lower-frequency chucks. Even if the peak tuning of the basilar papilla matched the mean dominant frequency of the chuck, the asymmetry in the tuning curve could still result in directional selection on chuck frequency by virtue of an asymmetric fitness function with respect to chuck frequency.

The cricket frog, *Acris crepitans*, offers another example of how female auditory tuning results in directional patterns of mate preferences. Ryan and Wilczynski (1988) showed that variation in the dominant frequency of calls among populations of cricket frogs (c. 3200–4000 Hz) resulted in different female preferences among populations. When presented with a choice between their own calls and calls from nearby Bastrop, female cricket frogs from Gill Ranch preferred the local call, because the tuning of the basilar papilla of the Gill Ranch females more closely matched the dominant frequency of the local call (3200 Hz) than the calls of the Bastrop males (3800 Hz).

The females did not always prefer the local call. For example, Bastrop females preferred calls from Gill Ranch to calls of their own males (Ryan and Wilczynski, unpublished data). In a series of studies of females from three populations in which the frequency differences were always c. 400 Hz, Ryan and Wilczynski (unpublished data) showed that over the range of frequencies tested, if there was a preference it was always for the call of the lower frequency, whether it was the local call or a foreign call. Large samples of tuning and calls from the same populations show that females usually are tuned slightly below the population's mean dominant call frequency. This can result in local mate preferences when the female is faced with the choice between the local call and a foreign call of higher frequency, or it can result in females preferring a foreign call of lower frequency to their own call. Furthermore, the slight mismatch between the mean female's tuning and the mean call's dominant frequency for the same population suggests the potential for sexual selection on call frequency. However, the 400 Hz differences that elicited preferences might be too large compared to the population variance in call frequency to have a significant effect within populations.

These studies of butterflies, crabs, fish and frogs all suggest that the total amount of stimulation received by the female is crucial in determining her mate preference. In the butterflies, it appears to be due to the rate at which the retina is stimulated, in the crabs by the orientation of the male's landmark, in the fish it is related to the area of the retina and photopigments that are stimulated, and in the frogs it is the result of the relationship between the call's dominant frequency and the tuning of the auditory system. Although these studies investigate very different signals in two sensory modalities, there seems to be a common theme: preference

for greater stimulation (see also Morris 1956; Barlow 1977; Arak 1983; O'Donald 1983; West-Eberhard 1979; Burley 1985; Endler 1989).

Preference for a supernormal stimulus is a special case of females preferring more stimulating traits within the population's normal range, only more extreme. Staddon (1975) has offered a general explanation as to why some animals evolve preferential responses to supernormal stimuli. He gives an example of discrimination learning in which an animal is rewarded for a positive response to a light of 550 nm wavelength and receives no reward or a punishment for a response to a 500-nm light. When the animal is later tested with a series of stimuli, the most intense response has been shifted in the positive direction away from the stimulus for which positive reinforcement occurred, say 560 nm instead of 550 nm. This change in response is called a peak shift, and it occurs because of an asymmetry around the initially favored peak. If the animal responds to the positive side there may be no added advantage (reward), but if it responds to the negative side it has the risk of no reward or of punishment.

The asymmetry that causes the peak shift could have population effects similar to the asymmetric tuning of the basilar papilla in *P. pustulosus*; that is, it could result in an asymmetric fitness function of the male trait under selection. Staddon suggested that selection might be analogous to the positive and negative reinforcement in a discrimination paradigm, and O'Donald (1983) argued that Staddon's model could provide the direction for Fisher's runaway model. The mechanism proposed by Staddon, however, is crucially different than the mechanism implied by many of the studies reviewed above – selection for greater sensory stimulation. Depending on the conditioning paradigm, the peak shift could occur in either direction. Thus, like Fisher's hypothesis, Staddon's model could result in directional evolution but the direction is indeterminate.

Although many patterns of mate choice can be explained by differences in the amount of stimulation delivered by the male signal, this does not initially seem to explain another general pattern of mate choice, i.e. selection for novelty. However, I suggest that this is only a special case of preference for increased stimulation.

Several authors have discussed selection for novelty in different contexts. In a striking example, Burley (cited in Trivers 1985) fitted zebra finches with hats decorated with feathers and showed that females preferred these bizarre males to the normal, less ostentatious males (as long as the hats were white). Ehrman and Prober (1978) showed that in fruit flies the male phenotype in the minority had a mating advantage, although the generality of the rare male effect in fruit flies has been questioned (e.g. Peterson and Merrell 1983). Farr (1977) also demonstrated female preferences for novel male traits in guppies, and he suggested that preference for rare males is a special case of novelty.

The importance of novelty has been considered in some detail in the

evolution of bird song, and discussions of the underlying mechanisms suggest that preference for novelty is a special case of preference for increased stimulation.

One of the most striking features of oscine birds is the diverse song repertoires of many species. The evolution of song repertoire has long been debated, and one of the seriously considered explanations is the monotony hypothesis (Hartshorne 1956). The crux of the argument is that animals habituate to repeated stimuli and novelty will be favored because it is most likely to 'draw attention', that is, to be perceived rather than merely detected.

Barlow (1977) pointed out that, in general, animal signals have to stand out against background noise, the source of which could originate in the environment or from conspecifics competing for the same communication channel. Novelty is one means by which an animal can become more apparent and thus increase its signal to noise ratio. If the receiver habituates, the novelty effect can increase the signal-to-noise ratio at the level of the receiver's sensory system. Hinde (1970) suggested that selection imposed by habituation might be an important force favoring both novelty and supernormal stimuli, and West-Eberhard (1979) argued that in sexual selection by female choice there might be a selective advantage to novelty *per se*, due to this release from habituation. If a selective advantage to novelty exists for the signaller, and if the mechanism responsible is an increase in the signal-to-noise ratio due to habituation, then selection for novelty is really only a special case of selection for greater sensory stimulation.

There are cases in which selection for novelty and familiarity might conflict. Bateson (1983) has shown that young Japanese quail imprint on birds with which they were raised, and then prefer mates that are similar to, but slightly deviant from, the model. He suggests that this results in an optimal balance between inbreeding and outbreeding. For example, first cousins are preferred over both siblings and more distantly related birds. Cate and Bateson (1988) suggested that within this preference there might be an asymmetry; among the mates that are slightly deviant from the model, individuals (in this case males) would prefer the mate that was more elaborately adorned. The reason for this asymmetry would be that more elaborate mates would also be more conspicuous. If this asymmetry existed, then mate selection would impose a directional bias on the evolution of male traits. Cate and Bateson (1989) provide evidence for such an effect. They showed that males imprinted to white birds with dots on the breast preferred white birds over birds with the wild, brown, dotless plumage. When given a choice among white birds, they preferred birds with the larger number of dots, regardless of the number of dots present on the model.

In summary, in this section I have reviewed studies showing that female

choice generates directional selection on male traits. Usually, the direction is not random. Females tend to prefer traits that are more stimulating; the preferred traits are usually larger, brighter, more energetic and more complex. This bias in directionality is not predicted, although is easily accommodated, by the runaway sexual selection hypothesis. It is also consistent with predictions of the good genes hypothesis, and other hypotheses such as sexual selection for sensory exploitation, which will be discussed in the next section. In a few cases, knowledge of the mechanisms reveals the physiological locus at which the greater stimulation is generated, as well as constraints on signal elaboration. Finally, several researchers have discussed models or data that might result in asymmetric or directional mating preferences. These biases could impart a directionality on other processes, such as runaway sexual selection, and, as discussed below, might by themselves explain some patterns of the evolution of male traits under sexual selection.

#### 4. EVOLUTION OF FEMALE PREFERENCES

In this section, I will discuss how mechanisms of mate choice can contribute to our understanding of the evolution of female preferences. Ever since Darwin, an important question in sexual selection has been if females choose males on the basis of male traits. That has now been well documented in a variety of studies. There is no doubt that female preferences can generate sexual selection. But why have these preferences evolved? This is now the most controversial question in sexual selection (e.g. Bradbury and Andersson 1987).

##### 4.1 Hypotheses for the evolution of female preferences

Several hypotheses have been posited to explain the evolution of female preferences. Natural selection hypotheses, such as the good genes hypothesis (e.g. Zahavi 1975; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Andersson 1986; Pomiankowski 1988), suggest that certain female preferences are favored by natural selection because they increase either the number or the quality (e.g. physical vigor) of offspring. There are many studies demonstrating adaptive mate choice. In most such cases, females receive an immediate natural selection advantage, such as more eggs fertilized and higher offspring survivorship due to superior territories or parental care (e.g. Thornhill 1976; Perrone 1978). However, there is currently little empirical evidence to suggest adaptive mate choice based on genetic benefits (Kirkpatrick 1987a), and genetic models have led to different interpretations of the internal validity of the good genes hypothesis (Kirkpatrick 1986; Andersson 1986; Pomiankowski 1988).

What is often viewed as the major alternative to natural selection hypotheses for the evolution of female preferences is runaway sexual selection (Fisher 1958). This hypothesis suggests that alleles for the female preference and the male trait genetically co-vary due to linkage disequilibrium. The preference evolves as a correlated response to selection on the trait. The interesting aspect of the runaway process is that it is the female preference that generates the selection on the male trait. Fisher referred to the runaway process as self-reinforcing choice, because when females prefer certain males, not only do their sons possess the trait but their daughters will mate with similarly endowed males. The stronger the preference, the stronger the selection on the trait, and thus the greater the correlated response in the preference.

In order for the runaway process to be initiated, the preference needs to be at a relatively high frequency. Fisher suggested that adaptive mate choice for good genes could confer an initial advantage on the preference by causing an increase in the frequency of the preference. Lande (1981) and Kirkpatrick (1982) have pointed out that stochastic processes such as drift could initiate the process. Another important factor could be the sensory biases discussed in the previous section. Sensory biases that might have evolved under selection pressures unrelated to mate choice could result in an increase in the frequency of a preference sufficient for the runaway process to be initiated.

The runaway hypothesis has been investigated extensively by population genetics models, its essential features validated, and some unexpected outcomes observed, but currently there is little empirical evidence to support the notion that runaway sexual selection has been an important process in the evolution of female preferences (see reviews by Kirkpatrick 1987a, 1987b).

Another hypothesis suggests that current preferences for traits have become established in the population for reasons not related to adaptive mate choice or sexual selection. In such instances, the current congruence between a preference and a trait is due to the male trait having evolved to exploit pre-existing biases in the female's sensory system. I refer to this hypothesis as sexual selection for sensory exploitation (Ryan and Rand 1990; Ryan *et al.* 1990). This hypothesis is evolutionary rather than mechanistic. As noted above, at some level the most preferred male traits exploit female sensory (including cognitive) biases. That fact says nothing about the evolutionary history of the preference and trait. Sensory exploitation states specifically that the male trait evolved to match a pre-existing sensory bias (see also Barlow 1977; West-Eberhard 1979; Arak 1983; Burley 1985; Kirkpatrick 1987a; Endler 1989).

I have discussed various patterns of mate choice and the underlying sensory mechanisms of mate choice that could favor the elaboration of male traits. Many evolutionary biologists might feel that these mechanistic

studies are worthwhile only if they reveal the evolutionary history of sexual selection. (Of course, some comparative physiologists feel that studies of behavior are only important if they reveal something about sensor processing.) Studies of mechanisms of mate choice are important in their own right because they reveal how selection operates. Because sexual selection by female choice is a problem in communication, it cannot be understood completely without a knowledge of the interaction of the signal and the receiver. The knowledge of mechanisms alone might be very helpful in determining the current effects of a preference, but by itself it often tells us nothing about why the preference evolved. That is an historical question that requires techniques used to investigate history.

#### 4.2 Passive and active mate choice

Not all researchers would agree with the assertion that knowledge of the mechanism alone cannot test evolutionary hypotheses. In fact, a great deal of attention has been given to just such an approach in sexual selection by female choice.

Parker (1983) made a distinction between two mechanistic categories of mate choice: active and passive. As an extreme example, consider two males vocalizing to attract mates. One male has a call of very low intensity, whereas the other has a much higher-intensity call. If the female is attracted to the call she first encounters, then she is likely to be attracted to the more intense call because of its larger active space. This is passive choice. In this case, there would be no need for conjecture as to the selective forces responsible for a female not choosing a male she never hears.

Passive choice also has been extended to cases in which the females perceive alternative signals but are attracted preferentially to the stimulus that is perceived as more intense; again, evidence of this type of passive choice is used to reject hypotheses of adaptive mate choice. The argument is that preference for the most intense signal reflects selection for females to mate with the closest male in order to decrease the costs (e.g. time and energy) of searching for a mate. If the male's signal indicated he was a better mate, then females would have been selected to endure these costs of searching. So, it is argued that because the female's behavior is not consistent with the adaptive hypothesis, that passive choice rejects such an explanation.

The more inclusive definition of passive choice seems parallel to the notion I attempted to document above; that is, females often are attracted to males with the most stimulating signals. However, it is important to understand that this is not the case. The passive/active dichotomy is not useful in cases in which the female actually perceives alternative stimuli, and in which the preference results from sensory biases enhancing the



perception of one of the stimuli. Again invoking anuran vocal signals as an example, many studies have shown that the spectral tuning of the peripheral auditory system tends to match the spectral characteristics of the species-specific advertisement call. Thus the conspecific call will be perceived as more intense than a heterospecific call, and this difference in perceived intensity contributes to the preference. Is this conspecific preference passive attraction? And, if so, at what neurological level must the preference arise to be classified as active choice: if not the peripheral nervous system, then the central nervous system? Must it be in the fore-brain rather than the hindbrain? Must it be cognitive rather than reflexive? Most neuroscientists assert that a preference among alternative stimuli results from enhanced neural stimulation at some level of the nervous system (e.g. Bullock 1986). Thus, except in some very obvious situations such as when the female is exposed only to the more intense stimuli, the classification of passive and active choice is difficult (see also Pomiankowski 1988; Sullivan 1989).

Besides operational problems, another difficulty arises when the mechanism of passive choice is used to reject hypotheses for the evolution of preferences. Returning to the example of peripheral tuning in a frog, many frequency preferences can be neutralized or reversed by changes in intensity (Gerhardt 1988). In fact, in some species preferences for conspecifics are intensity-dependent. This might be especially true for higher frequencies that overlap the most sensitive frequencies of the basilar papilla. This inner ear organ is thought not to be capable of pitch discrimination (Lewis and Lombard 1988), but the preference for different frequencies in this range is due to those that better match the peak tuning being perceived as more intense. In this case, should we then assume that a preference for conspecific calls is due to passive attraction, and conclude that selection for species recognition has had no role in the evolution of the preference? If calls are processed by only the basilar papilla, which is the case for many species, then the only option is intensity-dependent preferences, what Parker calls passive choice. Perhaps the intensity-dependence of the preference in this case tells us more about the sensory constraints on signal recognition in these animals than it does about the evolution of preferences.

The evolution of female preference is controversial because it has been difficult to gather the necessary empirical data to discriminate among hypotheses. The passive/active choice dichotomy seemed to offer a solution: if there is a preference, increase the intensity of the less preferred stimulus. If the preference is neutralized, then the curtain of time is torn and the evolutionary history of the preference is revealed. The controversy is solved. If only it were that simple! I suggest that as with the species recognition/sexual selection dichotomy, we also abandon the notion of passive versus active choice.

### 4.3 Sensory exploitation and history

Most studies of sexual selection by female choice address the current interactions and effects of the preference and the trait. It is often implied that if females prefer a certain trait, then the preference evolved under a (natural or sexual) selective advantage associated with that trait. Of course, most evolutionary biologists are aware of the critical difference between an evolved function and a current effect (Williams 1966), or an adaptation and an exaption (Gould and Vrba 1982). Both ideas remind us that current function, regardless of its fitness effects, does not always indicate the selective forces responsible for the evolution of the trait under consideration; this seems to have been forgotten in some research in behavioral ecology and sociobiology. Paraphrasing Kirkpatrick (1987a), the fact that females do not mate with dead males is not evidence for selection against necrophilia.

Despite the fact that animal behavior has its roots in a rich, comparative tradition (e.g. Lorenz 1950), the increased interest in behavioral ecology and sociobiology in the 1960s coincided with a decreased interest in phylogenetic (and mechanistic) aspects of animal behavior (Marler 1985). More recently, behaviorists have realized the necessity of using phylogenetic information to increase independence of data in testing hypotheses of adaptation (e.g. Harvey *et al.* 1978; Ridley 1983; Huey 1987; Pagel and Harvey 1988; Ryan 1988a). There are some cases in sexual selection when a knowledge of mechanisms, combined with meaningful phylogenetic information, can be used to examine hypotheses for the evolution of female preferences.

Although the natural selection and sexual selection hypotheses for the evolution of female choice make some critically different predictions, it has been difficult to collect empirical data to test these hypotheses (Kirkpatrick 1987a; Alcock 1989). However, there are some quite testable predictions when contrasting the natural and runaway sexual selection hypotheses with the sensory exploitation hypothesis. Both the natural selection and the runaway sexual selection hypotheses implicate the male trait as a causal agent in the evolution of the preference. The sensory exploitation hypothesis, on the other hand, predicts that the preference was established before the trait evolved. Therefore, appropriate phylogenetic data can produce a test of these hypotheses.

In Section 3.6, I reviewed data showing that female *Physalaemus pustulosus* preferred calls that contained lower-frequency chucks, that larger males produce lower-frequency chucks, and that this preference resulted in larger males having greater mating success in nature. The neurophysiological data suggest this preference might result from the tuning of the basilar papilla being lower than the mean dominant frequency of the population; that is, lower frequency calls are more stimulatory. The

question of the evolution of the preference can be reduced to the evolution of this tuning bias.

The *P. pustulosus* species group is a well corroborated monophyletic unit consisting of two species pairs (Cannatella and Duellman 1984; Fig. 5). *P. pustulosus* and *P. petersi* are sister species, and both can produce calls with chucks. *P. coloradorum* and *P. pustulatus* comprise the other species pair. Neither of these species produces chucks, and chucks have not been reported in any of the other 40+ species in the genus (Barrio 1965). Thus parsimony dictates that the chuck is the derived condition that evolved in the ancestor of the *P. pustulosus*-*P. petersi* species pair (Ryan and Drewes, 1990).

Ryan *et al.* (1990) have determined the tuning of the basilar papilla of *P. coloradorum* and found that its best excitatory frequency is not significantly different from that of *P. pustulosus*. Thus the sensory bias responsible for the preference for lower-frequency chucks existed prior to the chuck (Fig. 5). This suggests that the distribution of frequencies in the chuck evolved to exploit the already existing biases of the female's basilar papilla. Both *P. coloradorum* and *P. pustulatus* produce whine-like advertisement calls that have very little energy in the range to which the basilar papilla is most sensitive. Therefore, *P. coloradorum* probably

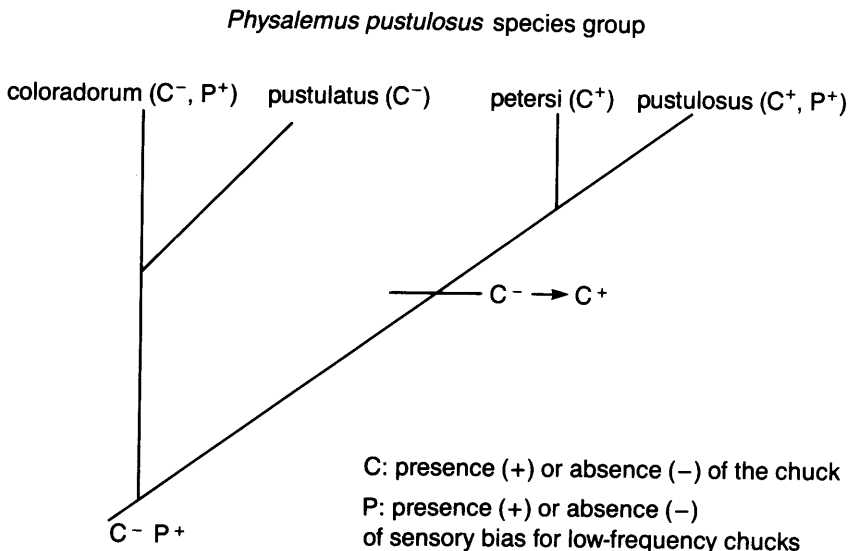


Fig. 5. The distribution of calls with chucks, the tuning of the basilar papilla that, in *P. pustulosus*, results in preference for low-frequency chucks, and the hypothesized evolutionary transitions among taxa of the *Physalaemus pustulosus* species group.

relies only, or at least primarily, on the amphibian papilla for call processing. However, even if the basilar papilla is not used in communication by *P. coloradorum*, all frogs have a basilar papilla and the basilar papilla is tuned to some frequency, often closely correlated to the frog's body size (Zakon and Wilczynski 1988). Thus it appears that the evolution of the chuck allowed stimulation of an inner ear receptor not used in communication in the earlier history of the species group.

An interesting aspect of the *P. pustulosus* study is that previous work has shown that females gain a reproductive advantage by choosing larger males, because they fertilize more of their eggs (Ryan 1983, 1985). These data could lead to the logical conclusion that this reproductive advantage generated selection for the preference. With the historical data now available, it seems that this is an incidental consequence, although certainly a selective advantage, and not the evolved function of the preference. Clearly a measure of current effects in this case does not accurately reflect historical processes.

One of the striking examples of an extremely sexually dimorphic male trait is the elaboration of the caudal fin in swordtails, as noted by Darwin (1871). Basolo (1990) demonstrated that the swordtail *Xiphophorus helleri* preferred males with longer tails. Swordtails constitute only one group of the genus *Xiphophorus*, the other group consists of the platyfish. Although the sword evolved in the swordtail clade, a recent study by Basolo (1989) suggests that the preference exists in the platy group as well. If artificial swords were attached to male platyfish, *X. maculatus*, females preferred the newly sworded males. As with the *Physalaemus* example, it appears that the preference was present in a common ancestor of species both with and without the male trait. This seems to be another case in which male swordtails evolved a trait that exploited already existing preferences.

Another example of pre-existing female preferences involves the species group of pygmy swordtails. *X. nigrensis* males span a size range of 18–40 mm in length, more than 90 per cent of the variation in body size is due to allelic variation at a single Y-linked locus (Kallman 1984, 1989), and only the larger males exhibit courtship behavior (Ryan and Causey 1989). Most populations of *X. pygmaeus*, however, consist almost entirely of males less than 25 mm in length, and never have males greater than 30 mm in length (Kallman 1984). Ryan and Wagner (1987) found that female *X. pygmaeus* preferred larger, courting *X. nigrensis* to their own smaller, non-courting males; when size was controlled, the heterospecific preference was based on courtship alone (Ryan and Wagner 1987). It is not clear if large size and courtship were secondarily lost in *X. pygmaeus*, or if *X. pygmaeus* retained the primitive condition and *X. nigrensis* evolved large size and courtship independent of the other swordtails; Kallman (1989) suggests the latter. Regardless, this study illustrates that the preference can exist independently of the trait. Furthermore, there is

a preference residing in *X. pygmaeus* for both large size and courtship behavior, a preference that could be exploited if the appropriate male variation were to arise.

There are not many other examples that argue strongly for sexual selection for sensory exploitation, but some cases are suggestive. Arctiid moths have evolved the ability to perceive ultrasonics in order to detect bats and thus reduce predation risk. Some moths within this group have further evolved the ability to produce ultrasonics themselves to either jam the bat's echolocation signals or to advertise to the bats that they are distasteful. Conner (1987) has shown that at least one arctiid uses ultrasonics in courting the female. Although not yet conclusive, it appears that in males of this species the production of ultrasonic sound has become secondarily adapted to exploit a sensory modality of females that evolved under selection for avoidance of predators.

Previously, I discussed Christy's (1988) study that showed female fiddler crabs (*Uca beebei*) are attracted to pillars built by males near the openings of burrows, and that these structures exploit the female's visual system, which is adapted for detecting objects that disrupt the horizon. Females of the closely related *U. stenodactylus* also prefer burrows with pillars even though their males do not build them (Christy, pers. comm.). This is yet another example of a preference existing independent of a trait. However, the necessary phylogenetic data are not available to make any conclusion about the historical relationships of preference and trait. Unfortunately, with the general lack of use of a phylogenetic framework by animal behaviorists, any understanding of history will be a slow process.

If a female preference for a male trait in any species is due to sensory exploitation, this need not imply that the sensory bias has never been under selection, even selection for mate choice. For instance, retinal sensitivities might evolve in response to available light, background colors in the environment or food colors. As an example, Ewert's (1980) classic studies of worm detectors in the toad's visual system shows that movements of a bar with the short edge perpendicular to the horizontal plane elicits approach, whereas movements of the same bar rotated 90 degrees elicits withdrawal. If these toads were to evolve visual courtship signals, the most effective form of the movement might be influenced by these motion detectors. Visual courtship signals are rare, but do exist, such as the foot-waving behavior of the Bornean frog (Harding 1982). An examination of the effectiveness of various types of movement in these species might be instructive. In another example, Fleischman (in press) pointed out that the eye of anoline lizards is exquisitely adapted for detecting fine movements of potential prey, and this sensitivity to movement is probably partly responsible for the evolution of the well-known push-up display of these lizards rather than a more static form of advertisement.

A sensory bias also could have resulted from selection for mate choice. Consider the preference for swords by the swordless platyfish (Basolo 1989). There might be a general preference in fish for larger males for adaptive reasons. The sword is one means by which a male could increase his apparent size, and the platyfish preference for the sworded males could result from a general preference for larger males. On the other hand, the pigmentation of the sword enhances the contrast of the fish against its background. There are several other possibilities and, encouragingly, most of them are testable.

Those of us who study female choice should be more explicit about the specificity of preferences. Is the preference for the sword directed only toward that specific morphological trait, or is it a more general, less-defined preference? And, clearly, we need to pay more attention to the phylogenetic distribution of traits and preferences, especially considering if the preference exists independent of the trait (e.g. Höngstrum 1989).

Sexual selection for sensory exploitation has been criticized because adaptationist theory predicts that female sensory biases should evolve to favor those male traits that are beneficial. Certainly, there are many examples of adaptive mate choice that bear out this prediction. However, there are also many examples of sensory exploitation in other social contexts, besides mate choice, that clearly are disadvantageous for the signal recipient. Inter- and intraspecific deception in communication is a general example (Lloyd 1984), and brood parasites in birds a specific one. Parents of the host species preferentially feed the brood parasites while their own young starve to death or are thrown from their nest and die. The parents respond preferentially to the parasite because the large young with its increased gape response and enlarged associated markings acts as a supernormal stimulus that releases the parent's feeding response (Lack 1968). If ever selection should override a sensory constraint this would be the case.

## 5. CONCLUSIONS

Sexual selection by female choice involves communication, and the intent of this chapter has been to suggest the importance of understanding the role of the receiver in this process. Such an approach can only increase our understanding of the fascinating process of sexual selection by showing how properties of the receiver exert selection on male traits, and how they are responsible for some of the most bizarre morphologies and behaviors in the animal kingdom. It certainly will inform us about how evolution operates, and thus can contribute to hypotheses of the evolution of female preferences. When an understanding of mechanisms is combined with appropriate phylogenetic information, it might sometimes support a

more parsimonious hypothesis of female preference – sexual selection for sensory exploitation. The main point of this chapter is that although behavioral ecology and population genetics have made important contributions to our understanding of sexual selection by female choice, we need to exploit the rich biology of this phenomenon and incorporate two additional levels of analysis, sensory mechanisms and phylogenetics. An integrative approach should enhance our understanding not only of sexual selection but of many problems in behavioral biology.

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