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American Naturalist, Volume 139, Issue Supplement: Sensory Drive. Does Sensory Drive Biology Bias or Constrain the Direction of Evolution? (Mar., 1992), S4-S35.

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American Naturalist
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DIRECTIONAL PATTERNS OF FEMALE MATE CHOICE AND THE ROLE OF SENSORY BIASES

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Abstract.—A review of the literature reveals that, if females prefer traits that deviate from the population mean, they usually prefer traits of greater quantity. In cases in which the sensory bases of these preferences are identified, females prefer traits of greater quantity because these traits elicit greater sensory stimulation. However, two caveats apply. First, the studies surveyed might not represent an unbiased sample of mate choice, because researchers usually study systems characterized by exaggerated traits. Second, a preference for traits of greater quantity does not suggest that preference for average traits is unimportant; it might be more usual than preference for exaggerated traits. Phylogenetic comparisons sometimes allow one to distinguish among competing hypotheses for the evolution of female mating preferences. Two hypotheses, Fisher's theory of "runaway" sexual selection and the "good genes" hypothesis, predict that traits and preferences coevolve, whereas the "sensory exploitation" hypothesis predicts that males evolve traits to exploit preexisting female biases. Some studies of frogs and fish support the sensory exploitation hypothesis, although this does not exclude the role of other factors in establishing the preexisting bias or in the subsequent elaboration of the preference. It is suggested that studies of mate choice will benefit by a more integrative approach, especially one that combines knowledge of sensory mechanisms with appropriate phylogenetic comparisons.

The various behaviors and morphologies that males use in courting females have long been a source of interest to evolutionary biologists, a target of selection for animal breeders, and even a source of entertainment for the general public. The extreme and bizarre courtship traits have drawn the most attention, and, at least for biologists, this has raised the question of how traits that so obviously diminish survival could evolve. Darwin resolved this paradox with his theory of sexual selection (1871).

Female choice as an agent of sexual selection was disputed until recently (see, e.g., Halliday 1983), despite the fact that the interest in speciation that preoccupied much of the Modern Synthesis of evolutionary biology generated many proofs that females are preferentially attracted to conspecific courtship relative to heterospecific courtship (Mayr 1982). However, these proofs usually compared the average signals of the two species, and they concluded that there should be strong stabilizing selection for the average species-specific signal. If female choice within species were to promote the evolution of exaggerated traits, then females might not prefer the average male trait but rather traits that deviate from the population mean.

A large number of studies that demonstrate the efficacy of female choice are now available. As a result, there is a general consensus among evolutionary biologists that females often compare traits among conspecific males when choos-

ing mates (Bradbury and Andersson 1987). Unfortunately, this literature provides few other insights, especially with regard to the evolution of these preferences (Kirkpatrick and Ryan 1991).

We begin by reviewing studies that show females select male traits that deviate from the population mean. Because this literature is so vast, employs methods ranging from purely observational to totally experimental, varies substantially in quality, and is fraught with pitfalls of interpretation, our goals are modest. First, we feel it would be a service to compile this literature and to discover how much evidence for directional female preferences is available. (Given all the reviews of sexual selection [Bradbury and Andersson 1987], it is surprising that this has not been done before.) Second, we ask whether there is a directional bias to female preferences. We are especially interested in cases in which females choose male traits that deviate from the population mean, because these are the cases in which female choice most obviously generates sexual selection. Therefore, we intentionally do not review studies that discuss female preference based on average traits (e.g., Kodric-Brown and Hohmann 1990); many of these studies address problems of species recognition. This review, then, is not an unbiased sample of all studies addressing all aspects of female mate choice; also, the studies themselves are biased, because they favor systems in which male traits are especially elaborate.

After reviewing the literature, we relate the observed patterns of mate choice revealed therein to recent discussions of the role of sensory systems in sexual selection (Ryan 1990*b*). Finally, we consider how such biases might be important in the evolution of female mating preferences by reviewing studies we and our colleagues have been conducting in frog mate recognition.

FEMALE MATE CHOICE WITHOUT SEXUAL SELECTION

Searcy and Andersson (1986) suggested that, to demonstrate song-based female mate choice, two criteria must be met (these criteria can be extended to other male traits as well): (1) females should exhibit a preference for a trait when all other traits are controlled, either experimentally or statistically, and (2) male mating success in nature is correlated with that trait. These criteria are appropriate for a consideration of how female mate choice generates variation in male mating success; however, there are at least two important reasons to document female preference for male traits even if these preferences do not generate variation in male mating success (criterion 2). First, sometimes random male mating success is actually due to the presence rather than the absence of female mating preferences. For example, in the frog *Pseudacris* (= *Hyla*) *crucifer*, larger males produce calls with lower frequencies and, while phonotaxis experiments show that females are attracted preferentially to these calls of larger males, there is no size-biased male mating success (Forester and Czarnowsky 1985; but see Doherty and Gerhardt 1984). This might suggest that female frequency preference plays no role in the mating system. However, smaller males adopt noncalling mating strategies and intercept females that are attracted to larger males. Therefore, mating preferences for larger males might result in the adoption of alternative mating strategies by smaller males, and the two strategies appear to result in equal

average mating success (Forester and Czarnowsky 1985). Female preference that promotes the evolution of alternative mating strategies is clearly different from having no preference at all, although the outcome, the absence of size-biased mating success, is the same.

The second reason for exploring female preferences in the absence of biases in male mating success is perhaps best exemplified by the work of M. B. Andersson (1982). Male widowbirds are distinguished by their extremely long tails. Andersson found that, in nature, there was no correlation between male tail length and male mating success. However, when he artificially changed tail length, he found that females prefer to mate with the longer-tailed males, including males with tail lengths that exceeded those in the population (supernormal tails). His finding suggests that although female mate choice did not generate selection for male tail length in the population studied at that particular time, the preference still exists and could exert directional selection for tail length if the appropriate variation were to occur. Although the importance of supernormal stimuli in animal behavior has had a long and distinguished history (Tinbergen 1951), this concept has only recently been integrated into studies of sexual selection (e.g., West-Eberhard 1979; Burley 1985; Rowland 1989*a*, 1989*b*; Ryan 1990*b*; Ryan and Rand 1990). Therefore, in our review we also consider studies that do not qualify under the normal criteria (e.g., Searcy and Andersson 1986) for demonstrating female mate choice that is based on male traits.

In our review we indicate the range over which most stimuli were varied. Typically, the stimulus range is restricted to within-population or within-species variation; we refer to this range as "normal." In some cases, however, the researchers specifically contrast different populations or different species, and this is noted. Finally, some studies test the response of females to novel stimuli. Both novel stimuli and heterospecific stimuli may also be supernormal; that is, they extend the continuous range of a stimulus beyond what is normally exhibited. All of these categories are somewhat arbitrary, but the classification of any individual study does not change any of our general conclusions.

We restrict our review to acoustic and visual cues because the data are more plentiful and thus allow us to draw more valid conclusions. Alberts (1992) reviews much of the literature on the role of chemical sex attractants.

DIRECTIONAL PATTERNS OF MATE CHOICE BASED ON ACOUSTIC CUES

There is a rich literature on the role of acoustic signals in female mating preferences, especially the calls and songs of insects, frogs, and birds. Although calls of conspecifics are more similar to one another than they are to calls of heterospecifics, there can be substantial variation within a species. In our review we categorize female mate choice on the basis of five general types of acoustic variation: intensity, rate, duration, complexity, and frequency. Our categories are not meant to suggest homology. For example, large song repertoires in birds usually contain many different notes, whereas frogs often increase their call complexity by adding one different note and, perhaps, repeating it.

We review approximately 60 studies (table 1). Studies of insects and frogs have

TABLE 1
SOME EXAMPLES OF DIRECTIONAL FEMALE PREFERENCES BASED ON MALE ACOUSTIC TRAITS

Taxon	Preference	Range of Trait	Reference
Call intensity:			
Insects:			
<i>Acheta domestica</i>	> Intensity	Normal	Stout and McGhee 1988
<i>Conocephalus nigropleurum</i>	> Intensity	Normal	Morris et al. 1978
<i>C. upobvensis</i>	> Intensity	Normal	Bailey 1985
<i>Cystoma saundersii</i>	> Intensity	Normal	Doolan 1981
<i>Palmaricoria nana</i>	> Intensity	Normal	Aiken 1982
<i>Requina verticalis</i>	> Intensity	Normal	Bailey 1985
<i>Scapteriscus acletus</i>	> Intensity	Normal	Forrest 1980
<i>Tettigonia cantans</i>	> Intensity	Normal	Latimer and Sippel 1987
<i>Teleogryllus oceanicus</i>	> Intensity	Normal	Doolan and Pollack 1985
Anurans:			
<i>H. cinerea</i>	> Intensity	Normal	Gerhardt 1987
<i>H. crucifer</i>	> Intensity	Normal	Forester and Czarnowsky 1985
<i>H. microcephala</i>	> Intensity	Normal	Schwartz 1986
<i>Hyperolius marmoratus</i>	> Intensity	Normal	Dyson 1985
<i>Physalaemus pustulosus</i>	> Intensity	Supernormal	Ryan and Rand 1990
Calling rate:			
Insects:			
<i>A. domestica</i>	> Calling rate	Normal	Stout and McGhee 1988
<i>Anastrepha suspensa</i>	> Calling rate	Normal	Burk and Webb 1983
<i>Chorthippus brunneus</i>	> Calling rate	Normal	Butlin et al. 1985
<i>Conocephalus nigropleurum</i>	> Calling rate	Supernormal and/or heterospecific	Morris and Fullard 1978
<i>Gryllodinus kerkerinensis</i>	> Calling rate	Normal	Popov and Shuvalov 1977
<i>P. nana</i>	> Calling rate	Normal	Aiken 1982
<i>T. oceanicus</i>	> Chirp rate	Normal and supernormal	Pollack and Hoy 1981

(continued)

TABLE 1 (Continued)

Taxon	Preference	Range of Trait	Reference
Anurans:			
<i>Bufo americanus</i>	> Calling rate	Normal	Howard 1988
<i>B. woodhousei</i>	> Calling rate	Normal and supernormal	Sullivan 1983
<i>Hyla cadaverina</i>	> Calling rate	Normal	Straughan 1975
<i>H. cinerea</i>	> Calling rate	Normal	Gerhardt 1987
<i>H. chrysoscelis</i>	> Calling rate	Normal	Morris and Yoon 1989
<i>H. crucifer</i>	> Calling rate	Normal	Forester and Czarnowsky 1985
<i>H. crucifer</i>	> Calling persistence	Normal	Forester et al. 1989
<i>H. ebraccata</i>	> Calling rate	Normal	Wells and Bard 1987
<i>H. meridionalis</i>	> Calling rate	Normal	Schneider 1982
<i>H. microcephala</i>	> Calling rate	Normal	Schwartz 1986
<i>H. regilla</i>	> Calling rate	Normal	Straughan 1975; Whitney and Krebs 1975
<i>H. versicolor</i>	> Calling rate	Normal	Klump and Gerhardt 1987
Birds:			
<i>Phylloscopus trochilus</i>	> Song rate	Normal	Radesäter et al. 1987
<i>Vidua chalybeata</i>	> Song activity	Normal	Payne and Payne 1977
Call length:			
Insects:			
<i>Gryllus integer</i>	> Call bout length	Normal	Hedrick 1986
Anurans:			
<i>H. cinerea</i>	> Call duration	Normal	Gerhardt 1987
<i>H. crucifer</i>	> Call duration	Normal	Doherty and Gerhardt 1984
<i>H. versicolor</i>	> Call length	Normal and supernormal	Klump and Gerhardt 1987
Birds:			
<i>Acrocephalus arundinaceus</i>	> Song length	Normal	Catchpole et al. 1986
<i>Taeniopygia guttata</i>	> Song phrase length	Normal	Clayton and Prove 1989
Complexity:			
Anurans:			
<i>H. ebraccata</i>	> Complexity	Normal	Wells and Schwartz 1984; Wells and Bard 1987
<i>H. microcephala</i>	> Complexity	Normal	Schwartz 1986
<i>Physalaemus coloradorum</i>	> Complexity	Novel	M. J. Ryan and A. S. Rand, unpublished data
<i>P. pustulosus</i>	> Complexity	Normal	Rand and Ryan 1981
<i>P. pustulosus</i>	> Complexity	Novel	Ryan and Rand 1990

Birds:				
<i>Acrocephalus schoenobaenus</i>	> Repertoire size	Normal	Catchpole et al. 1984	
<i>A. arundinaceus</i>	> Repertoire size	Normal	Catchpole et al. 1986	
<i>A. arundinaceus</i>	> Repertoire size	Normal	Catchpole 1986	
<i>Agelaius phoeniceus</i>	> Repertoire size	Normal	Searcy, in press	
<i>Melospiza georgiana</i>	> Repertoire size	Normal	Searcy and Marler 1984	
<i>M. melodia</i>	> Repertoire size	Normal	Searcy and Marler 1981; Searcy 1984	
<i>Mimus polyglottus</i>	> Repertoire size	Normal	Howard 1974	
<i>Passer major</i>	> Repertoire size	Normal	Baker et al. 1986	
<i>Taeniopygia guttata</i>	> Repertoire size	Normal	Clayton and Prove 1989	
<i>Quiscalus quiscula</i>	> Repertoire size	Supernormal	Searcy, in press	
Insects:				
<i>T. cantans</i>	< Frequency	Normal	Latimer and Sippel 1987	
Fish:				
<i>Pomacentrus paritius</i>	< Frequency	Normal	Myrberg et al. 1986	
Anurans:				
<i>Acris crepitans</i>	< Frequency	Normal	W. E. Wagner, Jr., unpublished data	
<i>A. crepitans</i>	< Frequency	Among populations	Ryan and Wilczynski 1988; Ryan et al., in press	
<i>H. chrysocephalus</i>	< Frequency	Normal	Morris and Yoon 1989	
<i>H. crucifer</i>	< Frequency	Normal	Forester and Czarnowsky 1985	
<i>H. versicolor</i>	< Frequency	Normal	Gerhardt and Doherty 1988	
<i>Hyperolius marmoratus</i>	< Frequency	Normal	Dyson and Passmore 1988	
<i>P. pustulosus</i>	< Frequency	Normal	Ryan 1980, 1983, 1985	
<i>Uperoleia rugosa</i>	< Frequency	Normal	Robertson 1986, 1990	

NOTE.—For an explanation of terms, see text, Directional Patterns of Mate Choice Based on Acoustic Cues. >, High; <, low.

all investigated the role of call intensity in mating preferences. (Different studies use different measures of the amount of signal energy, but sound power, pressure, and intensity are all interrelated.) The studies we review show that if a preference exists on the basis of intensity differences, the females prefer the more intense call. Some studies have also shown that intensity can cancel or even reverse a preference that is based on other call characters, such as call frequency or call complexity preferences in frogs (e.g., Gerhardt 1982, 1988; Ryan and Rand 1990). However, the intensity dependence of preferences for other traits decreases the magnitude of selection but does not necessarily remove its effect, unless intensity is inversely correlated with the degree of attractiveness of the other traits (see Gerhardt 1988).

Female choice is also influenced by call rate, and the results of these studies parallel the intensity results: females prefer calls delivered at a greater rate. In two insects and a toad, females also prefer supernormal call rates, even though, in one of the insects, the meadow katydid (*Conocephalus nigropleurum*), this call rate puts the stimulus within the range of another species (table 1). Analogous results are seen for call length. In many species, females prefer the average call length, perhaps because of its importance in species recognition (Butlin et al. 1985; Gerhardt 1988), but, when there is a preference, it is for longer calls rather than for shorter calls.

A great deal of research has been directed toward understanding the evolution of acoustic signal complexity, especially the significance of repertoire size in birds. Several experiments have shown that repertoire size need not influence female preferences (Searcy and Marler 1984; Catchpole 1987); Irwin (1990) came to a similar conclusion when she analyzed phylogenetic patterns of repertoire size. However, in cases in which there is a preference on the basis of repertoire size it is for the larger repertoire; we found no studies in which females preferred smaller repertoires (table 1). This preference can exist in species in which males do not have repertoires but instead sing only a single call type, as Searcy (in press) observed in the common grackle.

Frogs can also add different components or syllables to their calls. In the túngara frog (*Physalaemus pustulosus*) males produce calls consisting of a whine that can be followed by up to six chucks (fig. 1). Only the whine is needed to attract females, but females prefer calls with chucks. This is true even though the males increase their risk of bat predation when they increase their call complexity (Ryan et al. 1982). Also, there can be preference for novel complexity. In one case, it was shown that the structure of the chuck can be altered considerably and can even be replaced by white noise (Rand et al., in press), and it will still elicit preferential phonotaxis from females (Ryan and Rand 1990). In another example, *Physalaemus coloradorum*, the close relative of *P. pustulosus*, does not produce complex calls. However, when chucks of the *P. pustulosus* call are added to the call of *P. coloradorum*, *P. coloradorum* females prefer this call of novel complexity to the normal call of their conspecific males (fig. 2; table 1).

Directional mate choice for frequency is possible, but perhaps the most consistent pattern is that females prefer the average dominant frequency of their species to the average dominant frequency of a heterospecific; this preference for average

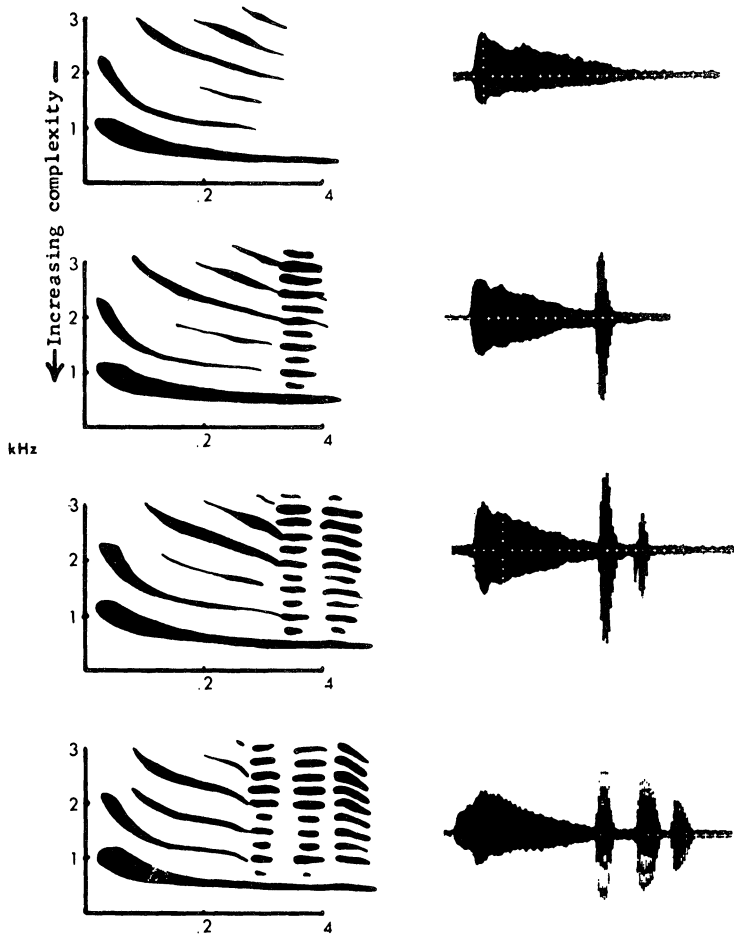


FIG. 1.—The call complexity series of the frog *Physalaemus pustulosus*. Calls consisting of a whistle alone and a whistle followed by zero (*top*) to three (*bottom*) chucks are shown. *Left*, sonograms representing changes in frequency as a function of time; *right*, oscillograms representing changes in amplitude as a function of time.

call frequency has also been demonstrated in many frogs for variation within a species (Gerhardt 1988). In three taxa (insects, fish, and frogs), however, females prefer call frequencies that deviate from the mean. In all cases, females prefer lower-frequency calls, which usually indicate larger body size; we do not know of studies in which females preferred calls that were higher than the population's average dominant frequency (table 1). In some cases, such as the gray tree frog (*Hyla chrysoscelis*), females prefer lower to higher frequencies, but they do not exhibit a preference between lower and average frequencies. Still, such preferences could generate selection favoring lower-frequency calls in the population, as the estimates of mating success in this study suggest (Morris and Yoon 1989).

We have also investigated call-frequency preferences among conspecific popu-

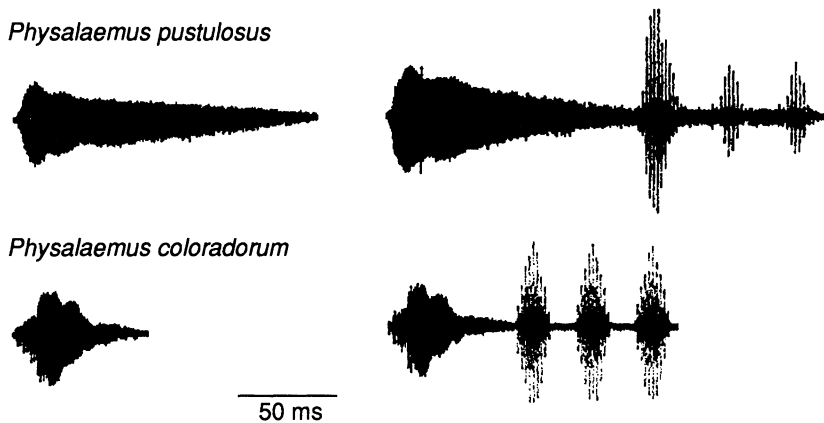


FIG. 2.—*Top*, advertisement calls consisting of a whine (*left*) and a whine followed by three chucks (*right*) of *Physalaemus pustulosus*; *bottom*, the whinelike call of *Physalaemus coloradorum* (*left*) to which three chucks from a *P. pustulosus* call have been added (*right*).

lations. For example, cricket frogs (*Acris crepitans*) exhibit geographical variation in body size, and although female preference for low-frequency calls can result in local mate preferences (Ryan and Wilczynski 1988), in some cases this preference can also lead females to choose males from foreign populations if their calls are of lower frequency (table 1). Because females are tuned to frequencies below the average male call, lower-frequency calls might be perceived as more intense; we discuss this below. We also reemphasize that frequency preference is one of many types of preferences that can be reversed by intensity differences. Thus the ability of this and other intensity-dependent preferences to generate selection might be less than implied by intensity-controlled phonotaxis experiments.

There seems to be some misunderstanding about the potential for certain frequency preferences to generate sexual selection. Halliday (1983) criticized studies that implicated frequency preferences in sexual selection on the basis of preferences between low and high frequencies; he stated that it is necessary to demonstrate that females prefer low frequencies to average frequencies. This is clearly not the case because, if females do not discriminate between low and average frequencies, then the low-frequency preference generates directional selection. Also, even if females prefer average to low frequencies, the low- versus high-frequency preference could still shift the population mean toward lower frequencies, although the magnitude of the effect would be less than in the situation in which females did not discriminate between low and average frequencies. This fallacy is important to recognize because it is applied to all types of preferences, not only those that are based on call frequency.

The studies we review (table 1) reveal a clear trend: whenever there is a preference that is based on male acoustic cues, females prefer those calls that are of greater intensity, delivered at a greater rate, longer, more complex, and of lower frequency. There is an obvious relation between call intensity, length, and repetition rate and the amount of stimulation perceived by the female. Females prefer

calls with more energy, which elicit greater stimulation, and, as we discuss below, the same principle might apply to preference for lower-frequency calls, given the relation between auditory tuning and average call frequency.

The relation between trait preference and amount of stimulation might also pertain to complexity, but the relation is more subtle. In *P. pustulosus*, for example, females prefer a whine plus a chuck to a whine only, even if the amplitude of the whine is increased so it contains more acoustic energy than the whine plus a chuck (table 1). In another example, Klump and Gerhardt (1987) showed that, in the tree frog (*Hyla versicolor*), males can increase total call energy either by increasing call rate or call length; females prefer faster to slower call rates and longer to shorter calls. If these two factors differ and total acoustic energy is the same, females prefer longer calls. Also, in studies of bird song, the number of different elements rather than the total number of elements is important (Catchpole 1987). Thus there might be a premium on call complexity that is independent of any effect of increased acoustic energy. However, in his discussion of Hartshorne's (1956) "monotony principle," Nottebohm (1972) suggested that larger repertoires might be favored by sexual selection by female choice because they reduce attendant habituation and thus elicit a stronger response from the auditory system. Searcy (in press) supported this hypothesis by showing that the rate of female courtship-solicitation displays increases with changes in call elements. Therefore, it appears that more complex acoustic signals also might increase the amount of stimulation, although not by increasing the total amount of energy.

Our review of female mate choice based on acoustic characters reveals general and consistent patterns. In general, we expect species recognition to define a multivariate signal space within which sexual selection can act, and thus sexual selection might have greater influence on signals not involved in species recognition (Ryan 1990a). However, if there is a preference, it is almost unanimously for the trait of greater quantity, and this pattern suggests a general motivating factor for preferences; namely, females prefer traits that elicit greater stimulation. This pattern also suggests that females might be predisposed to favor more exaggerated male traits, as well as traits that are not exhibited by their species. We emphasize again, however, that in many cases there might be preference for the average signal.

DIRECTIONAL PATTERNS OF MATE CHOICE BASED ON VISUAL CUES

As is the case with acoustic cues used in mate recognition, visual cues are more similar within than among species, but substantial and biologically meaningful intraspecific variation does exist. We review more than 50 studies of female mate choice (and a few studies of male mate choice) that were based on visual cues. These studies were categorized into female mate choice on the basis of variation in the amount of courtship, body size, ornaments, and color (table 2).

In fishes, salamanders, and birds there is evidence that variation in the amount of courtship influences female mate choice and that females prefer males that exhibit more courtship. Most of these studies concern cases in which the amount

TABLE 2
SOME EXAMPLES OF DIRECTIONAL FEMALE PREFERENCES BASED ON MALE VISUAL TRAITS

Taxon	Preference	Range of Trait	Reference
Amount of courtship:			
Insects:			
<i>Drosophila melanogaster</i>	> Courtship	Normal	Partridge et al. 1987
<i>D. pseudoobscura</i>	> Courtship	Normal	Partridge et al. 1987
Fish:			
<i>Poecilia reticulata</i>	> Display rate	Normal	Farr 1980; Bischoff et al. 1985; Kennedy et al. 1987; McMinn 1990
<i>Xiphophorus nigrensis</i>	> Courtship (courtship/sneak)	Normal	Ryan et al. 1990b
<i>X. pygmaeus</i>	> Courtship (courtship/sneak)	Heterospecific	Ryan and Wagner 1987
Salamanders:			
<i>Notophthalmus viridescens</i>	> Courtship	Normal	Verrell 1982
<i>Triturus cristatus</i>	> Time courting	Normal	Malacarne and Cortassa 1983
<i>T. vulgaris</i>	> Courtship	Normal	Teyssedre and Halliday 1986
Birds:			
<i>Anas platyrhynchos</i>	> Display rates	Normal	Holmberg et al. 1989
<i>Centrocercus urophasianus</i>	> Display rates	Normal	Gibson and Bradbury 1985
<i>Columba livia</i>	> Display rates	Normal	Clayton 1990
<i>Euplectes jacksoni</i>	> Display rates	Normal	S. Andersson 1989
<i>Gallinago media</i>	> Display rates	Normal	Höglund and Lundberg 1987
<i>Phasianus colchicus</i>	> Display rates	Normal	Hillgarth 1990
Body size:			
Insects:			
<i>Harpobitticus nigriceps</i>	> Size	Normal	Thornhill 1983
<i>Monochamus scutellatus</i>	> Size	Normal	Hughes and Hughes 1985
<i>Scatophaga stercoraria</i>	> Size	Normal	Borgia 1981
Crustaceans:			
<i>Uca rapax</i>	> Size correlated with female's size	Normal	Greenspan 1980
Fish:			
<i>Chichlosoma nigrofasciatum</i>	> Size	Normal	Noonan 1983
<i>Coralliozetus angelica</i>	> Size	Normal	Hastings 1988
<i>Cottus gobio</i>	> Size	Normal	Bisazza and Marconato 1988
<i>Gasterosteus aculeatus</i>	> Size (female)	Supernormal	Rowland 1989a, 1989b
<i>G. aculeatus</i>	> Size (heterospecific)	Normal and/or supernormal	Moodie 1982
<i>Salmo salar</i>	> Size	Normal	Jarvi 1990

Birds:					
<i>A. platyrhynchos</i>	< Size		Normal	Holmberg et al. 1989	
<i>Ficedula hypoleuca</i>	> Size		Normal	Lifeld and Slagsvold 1988	
<i>Gallinula chloropus</i>	> Fat; < Size		Normal	Petrie 1983	
<i>Geospiza fortis</i>	> Size		Normal	Price 1984	
Ornaments:					
Insects:					
<i>Cyrtodiopsis whitei</i>	> Antlers (no preference)		Normal and (supernormal)	Burkhardt and de la Motte 1988	
<i>Libellula luctuosa</i>	> Wing patch size		Normal	Moore 1990	
Crustaceans:					
<i>Uca beebei</i>	> Pillars (presence/absence)		Normal	Christy 1988	
Fish:					
<i>P. reticulata</i>	> Tail		Normal	Bischoff et al. 1985	
<i>Xiphophorus helleri</i>	> Tail		Normal	Basolo 1990a	
<i>X. maculatus</i>	> Tail heterospecific		Presence/ absence	A. Basolo, unpublished data	
<i>X. variatus</i>	> Tail heterospecific		Presence/ absence	Basolo 1990b	
Salamanders:					
<i>Triturus cristatus</i>	> Tail height		Normal	Malacarne and Cortassa 1983	
Birds:					
<i>Coturnix coturnix</i>	> Spots		Novel	ten Cate and Bateson 1989	
<i>E. jacksoni</i>	> Tail		Normal	S. Andersson 1989	
<i>E. progné</i>	> Tail		Supernormal	M. B. Andersson 1982	
<i>Gallus gallus</i>	> Feathers, comb		Normal	Zuk et al. 1990	
<i>Hirundo rustica</i>	> Tail		Supernormal	Møller 1988b	
<i>H. rustica</i>	> Tail		Normal	Møller 1990	
<i>Lagopus mutus</i>	> Comb size		Normal	Brodsky 1988	
<i>Passer domesticus</i>	> Badge size		Normal	Møller 1988a, 1989	
<i>P. major</i>	> Stripe size		Normal	Norris 1990	
<i>Ptilinorhynchus violaceus</i>	> Decorated bowers		Normal	Borgia 1985	
<i>Vidua regia</i>	> Tail		Supernormal	Barnard 1990	

(continued)

TABLE 2 (Continued)

Taxon	Preference	Range of Trait	Reference
Color:			
Fish:			
<i>Cyprinodon pecoensis</i>	> Brightness	Normal	Kodric-Brown 1983
<i>G. aculeatus</i>	> Color	Presence and/or absence	Semler 1971
<i>G. aculeatus</i>	> Brightness	Normal	Milinski and Bakker 1990
<i>P. reticulata</i>	> Color contrast with background	Normal	Endler 1980, 1983
<i>P. reticulata</i>	> Orange	Normal	Houde 1987; Long and Houde 1989
<i>P. reticulata</i>	> Brightness	Normal	Kodric-Brown 1985, 1989
<i>P. reticulata</i>	> Orange (population biased)	Normal	Houde 1988; Stoner and Breden 1988; Houde and Endler 1990
Birds:			
<i>A. platyrhynchos</i>	> Nuptial plumage	Normal	Holmberg et al. 1989
<i>Carpodacus mexicanus</i>	> Colorful plumage	Normal	Hill 1990
<i>C. coturnix</i>	> Spots	Novel	ten Cate and Bateson 1989
<i>F. hypoleuca</i>	> Darker plumage	Normal	Liffeld and Slagsvold 1988
<i>G. gallus</i>	> Brighter combs; > Brighter eyes	Normal	Zuk et al. 1990
<i>Geospiza conirostris</i>	> Darker plumage	Normal	Grant 1985
<i>G. fortis</i>	> Darker plumage	Normal	Price 1984
<i>Gymnorhinus cyanocephalus</i>	> Brighter plumage	Normal	Johnson 1988
<i>L. mutus</i>	> Color	Novel and/or leg band	Brodsky 1988
<i>Poephila bichenous</i>	> Color	Novel and/or leg band	Burley 1986
<i>P. guttata</i>	> Color	Novel and/or leg band	Burley et al. 1982; Burley 1988

NOTE.—For an explanation of terms, see text, Directional Patterns of Mate Choice Based on Visual Cues. >, High; <, low.

of courtship varies continuously among males. However, in studies of swordtails (*Xiphophorus* genus), females were presented with males that did and males that did not exhibit courtship behavior. In *Xiphophorus nigrensis*, this dichotomy is correlated with allelic variation at a single locus, as well as with body size, and females prefer larger courting males to smaller noncourting ones (table 2). It is clear from a variety of reports that females often avoid males exhibiting noncourting alternative mating behaviors (Van Den Berghe et al. 1989). More interesting is the case of *Xiphophorus pygmaeus*, the sister species of *X. nigrensis*. This species has only small, noncourting males. When given a choice between a conspecific male and a larger, courting *X. nigrensis* male, *X. pygmaeus* females prefer the heterospecific (table 2). This suggests that the preference for large, courting males occurs in the absence of the trait and could generate selection given the appropriate mutations at the single locus that correlates with size and behavior.

Although it is often not clear whether size per se is the cue or the preference is predicated on unidentified correlated traits, in many animals, females prefer larger males. Nevertheless, there are a few exceptions. In the moorhen *Gallinula chloropus*, females prefer smaller males, but it was suggested that perhaps this was because smaller males are also fatter and are thus better at incubating eggs (table 2). Also, in the duck *Anas platyrhynchos*, females prefer smaller males, but body weight did not influence mate preferences. However, if size is important, it is usually the larger males that are more successful. In some cases this can be an outcome of assortative mating by body size, as in the crab *Uca rapax* (table 2). There is a positive correlation between the size of paired males and females, but because females are larger than males, larger males are more successful at obtaining the larger, more fecund females. In sticklebacks, both female and male mate choice is influenced by supernormal-sized stimuli. Rowland (1989a, 1989b) showed that males prefer dummies whose size range greatly exceeds that of the females in the population, and Moodie (1982) showed that females can prefer males from other populations with body sizes that exceed those of local males. This general trend coincides with preferences that are based on call frequency in which female preference for lower frequencies also results in preference for larger body size.

Perhaps the most well known class of sexually dimorphic characters are ornaments, such as tails, badges, and antlers. The studies of ornaments show that females usually prefer the more exaggerated state. The ornament most studied is tail length. Previously, we mentioned M. B. Andersson's (1982) investigation of preference for manipulated tail length in widowbirds; this technique has now been duplicated with similar results in other bird species (table 2). An especially interesting set of experiments, however, addresses tail length in fish. Basolo (1990a) showed that female swordtails, *Xiphophorus helleri*, prefer males with longer swords. Platyfish are in the same genus as swordtails but lack any significant elaboration of the caudal fin. However, in the platyfish *Xiphophorus maculatus* females prefer males with artificially attached swords (Basolo 1990b). In many ways this is similar to the preference of *Physalaemus coloradorum* for calls with chucks. In both cases, females in the species lacking the male trait still exhibit a preference for the trait.

Another common sexually dimorphic trait is the brighter colors associated with many males. Not surprisingly, females usually prefer the more brightly colored males (table 2). This has been demonstrated especially clearly in several studies of guppies, *Poecilia reticulata*. These studies have also been among the few to examine population-based preferences. Endler (1980) has shown that conspicuous male color patterns evolve in response to the countervailing selection forces of predation and sexual selection and that the degree of color varies among populations and is correlated with the predation risk in natural streams and in laboratory populations. Furthermore, there is a preference for orange after effects of background contrast are removed (Endler 1983; table 2). Several studies have also shown that the degree of color preference is correlated with the average amount of color expressed by the males in that population (Houde 1988; Stoner and Breden 1988; Houde and Endler 1990). Females from low-predation (and colorful-male) populations have a strong preference for colorful males, whereas females from high-predation (and drab-male) populations have a weaker preference or a lack of preference for more colorful males. Interestingly, the females from the high-predation populations usually do not exhibit a significant preference for males with less color; rather, they only fail to exhibit a preference for males with more color. This preference is in accordance with mate choice that is based on other traits; if there is a preference, it is for the more exaggerated trait. Stoner and Breden (1988) do not show a preference for drab males in females from populations with drab males, only a lack of preference for males with more color.

There can also be preference for colors that occur on novel parts of the body. Female zebra finches prefer males with red leg bands (table 2). Beak color is an important species-recognition character in finches, and when comparing different species, Burley (1986) found that the color of the preferred leg band correlated with the color of the beak for that species. Also in another response to a novel stimulus, ten Cate and Bateson (1988, 1989) showed that young quail conditioned to models with spots on the breast later preferred mates with a greater number of spots.

Within each category of visual cues the results are fairly consistent: there is preference for more actively displaying, larger, and more colorful males. Rowland (1989*a*, 1989*b*) suggested that there might be a unifying theme to visual cue-based mate preference similar to that which we discussed in the preceding section for acoustic cues. He suggested that there is a preference for signals that stimulate a greater region of the retina because of their size or that stimulate more cone cells because of their brightness or area of color. Therefore, our review of visual cue-based mate choice reinforces the same conclusion we reached from the review of acoustic cue-based choice; namely, if females prefer traits that deviate from the mean, then they prefer traits of greater quantity, and these traits might increase the amount of neural stimulation elicited from the female. Also, on the basis of the response of females to supernormal and novel traits, it is clear that preferences can exist that precede the expression of the trait. Once more, we do not suggest that most traits are subject to directional preferences; preference for average traits might be more common. We only emphasize that when there is directional preference, there is some consistency in the direction.

SENSORY BASIS OF DIRECTIONAL MATE PREFERENCES

Depending on the system, greater neural stimulation could manifest itself in different ways—for example, greater firing rate of neurons, as suggested in the studies of fritillary butterflies discussed below; stimulation of a greater number of neurons, as Rowland (1989*a*, 1989*b*) suggested for preferences in sticklebacks; or the greater likelihood of eliciting a neural response from a feature detector, as Capranica (1976) suggested as the cause of conspecific call preferences in frogs.

The relation between mate preference and rate of sensory stimulation was exhibited clearly by Magnus's (1958) study of male mate choice in the fritillary butterfly. Females advertise to males by flapping their wings at a rate of 8–10 Hz. Magnus constructed a mechanical model to document the influence of flapping rate on mate preference. Within the normal range, males preferred the higher rate of flapping. Males also preferred supernormal rates up to 140 Hz, well above the rate at which females could possibly flap their wings. Independently, Magnus determined the flicker fusion rate for males; it was 140 Hz. Therefore, the males preferred greater rates of flapping until the rate of sensory stimulation no longer increased because males could no longer resolve individual wing movements.

Magnus's results indicate the value of studying the sensory system in order to understand how traits act on preferences. Studies of sensory filtering, in fact, compose the major thrust of research in neuroethology (e.g., Lettvin et al. 1959; Hubel and Wiesel 1962; Frishkopf et al. 1968; Ewert 1980; Wehner 1987; Pollack and Cassady 1989). As evolutionary biologists, we attempt to understand organic diversity, and, as we have just argued, female mate choice is responsible for generating considerable diversity in male courtship traits. Because female mate preferences are merely behavioral expressions of underlying sensory biases, we should examine the sensory mechanisms that ultimately generate the selection pressure on male traits. Although there have been many studies of the underlying sensory basis for conspecific versus heterospecific call recognition in insects (Huber 1990*a*, 1990*b*) and birds (Margoliash and Konishi 1985; Konishi 1989), these studies usually have not investigated preference among conspecific signals. However, we have begun to address this issue by examining frequency preferences in female frogs.

Capranica's (1965, 1976) approach to bullfrog hearing initiated an important series of studies whose ultimate aim was to understand how frogs extracted species-recognition information from the advertisement call. Frog calls are rich in potential spectral and temporal information, and both have been shown to be crucial in species recognition and sexual selection (Capranica 1976; Wilczynski and Capranica 1984; Fuzessery 1988; Gerhardt 1988; Rand 1988; Ryan 1988; Walkowiak 1988; Zakon and Wilczynski 1988). Spectral cues are first processed in the peripheral auditory system. This system acts as a matched filter that is biased toward the spectral components of the advertisement call. Anurans have two inner ear organs sensitive to airborne sound, the amphibian papilla (AP) and basilar papilla (BP; Zakon and Wilczynski 1988). The AP contains a tonotopic arrangement of hair cells coding low frequencies and midfrequencies from about 100 to 1,200 Hz (Feng et al. 1975; Lewis et al. 1982; Lewis and Lombard 1988).

A much smaller BP codes a narrower range of higher frequencies. The BP receptors appear to be tuned to approximately the same frequency in any individual (Capranica and Moffat 1983; Wilczynski and Capranica 1984; Wilczynski et al. 1984).

For all species studied to date, there is a general concordance between the spectral properties of the call and the tuning properties of the periphery. Some frogs have calls with bimodal frequency distributions, and these match the tuning of both the AP and BP (e.g., *Hyla cinerea*; Mudry and Capranica 1987). Others have only a single emphasized frequency, and this matches the tuning of either the AP (e.g., *Physalaemus coloradorum*; Ryan et al. 1990a) or the BP (e.g., *Acris crepitans*; Ryan and Wilczynski 1988). This congruence is evident in across-species comparisons, because neuroethological studies of call recognition in frogs have mostly concentrated on the problem of species recognition. Recently, we have extended this approach to examining the sensory biases underlying intra-specific mate choice (Ryan and Wilczynski 1988; Ryan et al. 1990a; Ryan and Rand 1990).

As discussed above, in several species of frogs, females prefer calls with frequencies lower than the population mean (table 1). In the túngara frog (*Physalaemus pustulosus*) females prefer lower-frequency chucks. The chuck is harmonically structured over a frequency range from about 200 to 3,000 Hz. More than 90% of the energy is above 1,500 Hz, and the mean dominant frequency is 2,550 Hz. This suggests the BP might be responsible for preference for lower-frequency chucks. We examined the tuning of the peripheral auditory system and showed that the most sensitive frequency of the BP is 2,130 Hz. Thus there is a slight mismatch between the average tuning of the BP and the average dominant frequency of the call (fig. 3). Computer simulations of the BP show that lower-frequency calls elicit greater neural stimulation. These results are consistent with the hypothesis that females prefer lower-frequency chucks because the sensory system is tuned to frequencies lower than the average call (Ryan et al. 1990a).

We also have obtained similar results from the cricket frog (*A. crepitans*). Ryan and Wilczynski (1988) examined call frequency, auditory tuning, and call preferences in three populations of *A. crepitans*: Austin, Texas; Bastrop, Texas; and Indianapolis, Indiana. We showed that females from the Austin population prefer the lower-frequency calls of local males to the higher-frequency calls of males from Bastrop; this is because the BP of the Austin females is tuned closer to the local calls than to the foreign calls. Similarly, we found that females from Indiana prefer the lower-frequency calls of their own males to the higher-frequency calls of Bastrop (Ryan et al., in press). However, Bastrop females prefer the lower-frequency calls from Austin to those of the higher frequency (fig. 4).

The above results suggest that there is not always a preference for the local call, but another pattern emerges. For each of the three populations (Austin, Bastrop, and Indianapolis), females were given a choice between a call of 300 Hz below the population mean and an average call and, in another test, a choice between an average call and one with a frequency of 300 Hz above the mean. Our results indicate that, whenever there is a preference, it is for the lower-

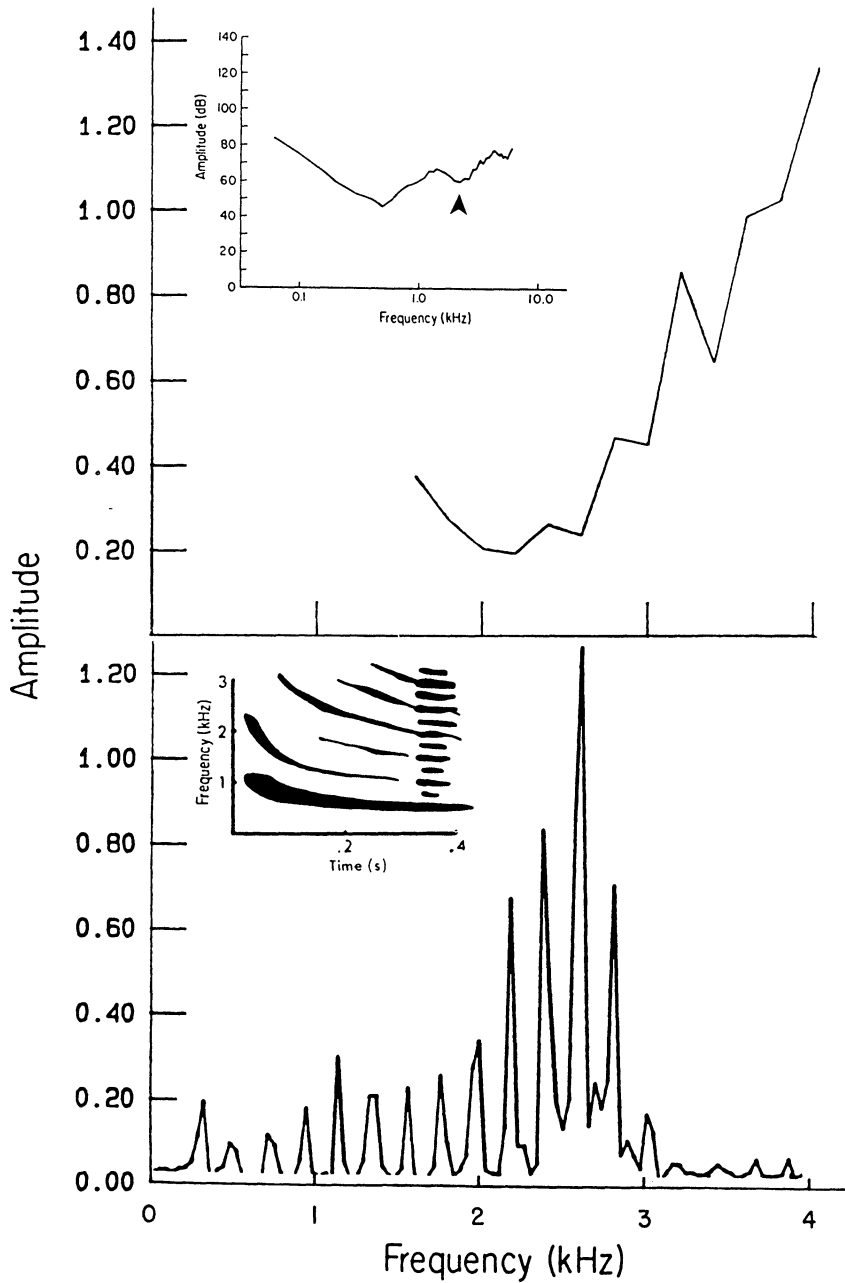


FIG. 3.—*a*, The frequency sensitivity of the basilar papilla of *Physalaemus pustulosus* derived from multiunit recordings from the torus semicircularis. *Inset*, the frequency sensitivity, including both the amphibian and basilar papillae. *b*, Fourier transform of a chuck showing the distribution of energy across frequencies. *Inset*, a sonogram of a whine and a chuck showing the distribution of frequency across time. (From Ryan et al. 1990a.)

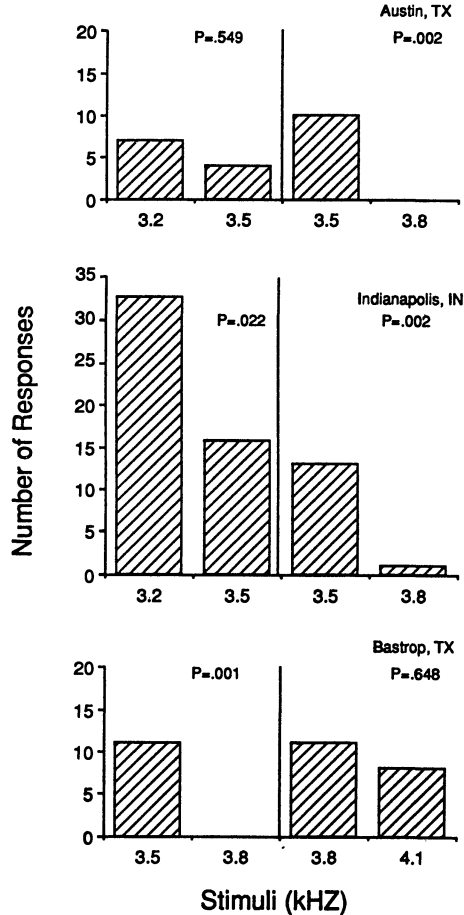


FIG. 4.—The number of responses of *Acris crepitans* females to calls from local (intermediate frequencies on each graph) and foreign (lower or higher frequencies on each graph) populations with different dominant frequencies.

frequency call; this included cases of preferences for local and foreign calls. Also, in all of the six sets of phonotaxis experiments, more females approach the lower-frequency calls (fig. 4). When we examined the mean tuning of the female's BP for these and other populations, we observed that the mean female tuning of the BP is always below the mean dominant frequency of the advertisement call for that population (fig. 5).

Gerhardt and Doherty (1988) report similar results for the gray tree frog (*Hyla versicolor*). In a series of phonotaxis experiments, they showed that the strongest preference is for a call with a dominant frequency of 1,900 Hz, below the standard call of 2,200 Hz. When this behavioral preference curve is compared to an auditory tuning curve, there is good congruence. Again, this suggests that the preference for calls with lower-than-average frequency derives from a slight mismatch

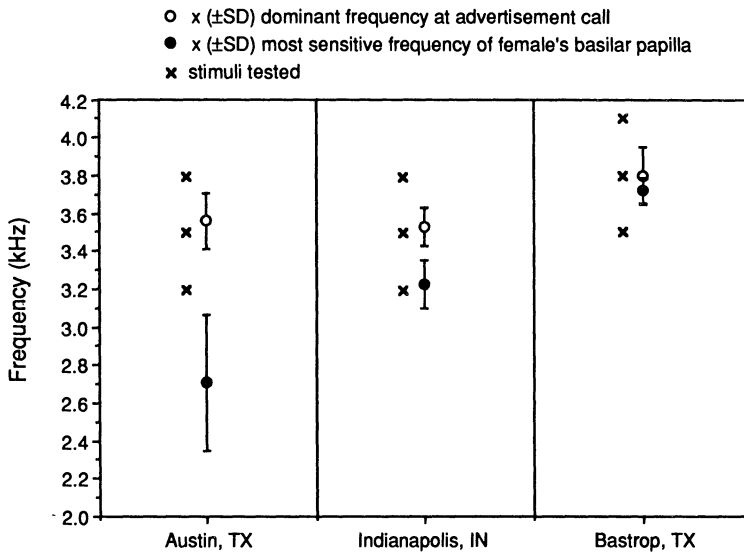


FIG. 5.—The relation of the average tuning of the basilar papilla of both sexes and the average dominant frequency of the male's advertisement call for three populations of *Acris crepitans*.

between the tuning of the auditory system and the average dominant frequency of calls.

These results do not contradict the general conclusion of neuroethological studies of specific mate recognition in frogs. At the species level there is good congruence between the tuning of the auditory system and the spectral properties of the advertisement call. However, in at least these three species (*P. pustulosus*, *A. crepitans*, and *H. versicolor*), the congruence is not perfect. It is biased toward lower frequencies, and this bias appears to be responsible for female preferences for lower-frequency calls.

These studies of the frequency preferences of female anurans show why, at the mechanistic level, females might prefer lower-frequency calls; these calls are more stimulating because of tuning biases in the auditory periphery. This is consistent with our conclusions from the review of the literature.

Studies of sensory biases in and of themselves do not address the question of how such biases evolved. However, they do contribute to our understanding of preferences because they reveal what evolutionary changes at the neural level must occur for preferences to evolve. In that sense, they reveal the neural target of selection under a "good genes," Fisherian "runaway," or "direct benefits" scenario for the evolution of preferences. These studies also raise the possibility that there might be inherent constraints that result from the design of sensory systems that give rise to certain biases. If so, these biases could determine the direction of the evolution of traits and preferences under various sexual selection hypotheses.

EVOLUTION OF FEMALE MATE PREFERENCES

The most controversial aspect of sexual selection today is how female preferences and their underlying sensory biases come into being (Bradbury and Andersson 1987; Kirkpatrick and Ryan 1991). There have been two widely debated groups of hypotheses for the evolution of female mate preferences. First, natural selection hypotheses suggest that preferences are under direct selection because they enhance the female's immediate reproductive success. This appears to be the case when females receive tangible resources from the male (Kirkpatrick and Ryan 1991). Other natural selection hypotheses are based on genetic quantity: good genes hypotheses, such as the "handicap principle" (Zahavi 1975) and the specific example of the parasite model (Hamilton and Zuk 1982), suggest that females evolve preferences that result in their mating with males of higher genetic quality. These preferences are favored because they increase the survival ability of their offspring. Second, Fisher's (1958) hypothesis of runaway sexual selection suggests that the female preference is genetically correlated with the male trait through linkage disequilibrium and that the preference evolves as a correlated response to evolution of the male trait. In this model, the preference is under indirect selection (see also Lande 1981; Kirkpatrick 1982; M. B. Andersson 1987). None of these hypotheses are mutually exclusive (M. B. Andersson 1987).

A third hypothesis, "sensory exploitation" (Ryan 1990*b*), is also not mutually exclusive with the above hypotheses and suggests that the signal value of the display is more important than its iconic value, for example, as an indicator of male health. This hypothesis, in various forms (Nottebohm 1972; Barlow 1977; West-Eberhard 1979; Burley 1985; Endler and McLellan 1988; ten Cate and Bateson 1988; Ryan 1990*b*; Ryan and Rand 1990; Ryan et al. 1990*a*; Endler 1992), suggests that females prefer male traits that elicit the greatest amount of stimulation from the sensory system. In other words, selection favors male traits that exploit sensory biases in females. These sensory biases may have evolved in response to selection in other contexts. For example, Fleishman (1992) has shown that the visual system of anoline lizards is exquisitely designed for prey detection and that this design dictates the form of male displays that are most effective in eliciting attention from females. Sensory biases also might exist for historical reasons associated with mate choice. For example, the good genes hypothesis would suggest that selection favors females whose sensory biases result in their being attracted to more energetic displays that indicate healthier males. The sensory exploitation hypothesis differs from the good genes hypothesis with regard to the explanation of the evolution of traits: in the sensory exploitation theory, the sensory biases already in place, regardless of the reason, explain the initial evolution of the trait in the species under study, whereas the good genes theory offers the explanation that good gene selection in the species under study causes females to prefer certain traits. The sensory exploitation hypothesis does not preclude other forces, such as good genes and runaway sexual selection, from initially establishing the preexisting bias or from maintaining or further modifying the preference and the trait.

PATTERNS OF FEMALE MATE CHOICE

How does the generalization of preference for exaggerated traits and greater sensory stimulation bear upon hypotheses for the evolution of female mating preferences?

The good genes hypothesis predicts that the male display should be an indicator of genes for health and vigor. Although there is not much direct evidence, it appears likely that healthier males will be brighter and larger, and they will produce more intense calls and display at more rapid rates. Some recent studies of parasites have shown that birds with brighter plumage also have fewer parasites (e.g., Hillgarth 1990; Zuk et al. 1990). The data we review are consistent with this expectation of the good genes hypothesis. With regard to our review of tuning biases in frogs, the good genes hypothesis would suggest that female frogs evolved tuning below the average call frequency because of the selective advantage obtained from mating with larger males.

The sensory exploitation hypothesis predicts that females should prefer more exaggerated male displays because of the display's signal value alone. This type of preference might be favored by selection because such displays have a greater signal-noise ratio, and they not only are more stimulatory to females but might also decrease search costs. Exaggerated displays have greater signal value because they elicit a stronger response from the female sensory system. Thus the data are also consistent with the sensory exploitation hypothesis. Although this hypothesis does not require the correlation between male health and exaggerated displays, this correlation is to be expected purely for reasons of behavioral physiology; more exaggerated displays require more energy, and healthier males are able to marshal more energy to support activity above and beyond that needed for maintenance.

The sensory exploitation hypothesis does not eliminate a role for selection pressure on mate choice in the historical establishment of biases, but it suggests that selection in other contexts can also cause the evolution of sensory biases. This is suggested by our studies of the frog's auditory periphery. In the *Acris crepitans* populations we have studied, on the average, females are tuned below the male's call (fig. 5), and they are always tuned lower than the males are tuned. The tuning of the BP is correlated with male body size; therefore, this sexual dimorphism in tuning is to be expected (Zakon and Wilczynski 1988). Although we have been discussing the fitness consequences of males communicating with females, male reproductive success is also influenced by male-male vocal competition; males must communicate effectively with other males (Wells 1988). Thus there might be two sexual selection optima for the call's dominant frequency. The female's tuning defines one optimum for female attraction, and the male's tuning defines a different optimum for male competition. The dominant frequency of the call might effect a compromise between these two optima. If so, females will always be tuned to frequencies below the average call and thus prefer lower-frequency calls and larger males. Another possibility is that the female's sensory system is under direct selection in contexts other than mate choice and that

certain mate preferences are pleiotropic effects of this direct selection (Kirkpatrick and Ryan 1991). We have already discussed such a possibility in terms of how the lizard's eye evolves to detect fine patterns of motion in order to increase foraging ability and how this evolution then has a pleiotropic effect on preference for certain aspects of the male's display (Fleishman 1992).

Fisher's hypothesis of runaway sexual selection does not, by itself, predict the evolution of more exaggerated traits (Fisher 1958; Lande 1981; Kirkpatrick 1982). The direction of evolution is indeterminate, and therefore less exaggerated traits should be as likely to evolve as more exaggerated traits. However, other processes, such as selection for greater signal value or good genes, could bias the direction of the runaway process toward more exaggeration. Therefore, the results of our review are also consistent with a runaway sexual selection process.

Although there is a fairly consistent pattern of female mate choice that can be generalized across taxa and sensory modalities, this generalization does not allow us to discriminate between competing hypotheses for the evolution of female preferences. This has been a general problem in the sexual selection theory; in most cases these hypotheses do not make mutually exclusive predictions (Kirkpatrick and Ryan 1991).

SEXUAL SELECTION FOR SENSORY EXPLOITATION: PHYLOGENETIC SUPPORT

There is one situation in which we can discriminate among some of the competing hypotheses for the evolution of female mating preferences. Both the good genes and the runaway sexual selection hypotheses implicate the male trait in the evolution of the preference, either because the trait indicates better males and the preference is favored by natural selection, or because the trait and the preference are genetically correlated and the preference evolves in response to the evolution of the trait.

The sensory exploitation hypothesis makes a unique testable prediction that allows it to be discriminated from the hypotheses of good genes and runaway sexual selection during a defined span of evolutionary history. The two latter hypotheses predict the coevolution of the trait and the preference, and thus the male trait is implicated in the evolution of the preference. In the sensory exploitation hypothesis, the preference exists before the evolution of the trait (fig. 6). Some support for this hypothesis comes from our comparative studies of mate recognition in the *Physalaemus pustulosus* species group.

As we have discussed, *P. pustulosus* males produce a two-component call (fig. 1). The whine is necessary and sufficient for species recognition, and males add chucks to their calls to increase their attractiveness to females. This species is a member of a group that is composed of four species (Cannatella and Duellman 1984) and a genus of about 40 species (Lynch 1970). Only *P. pustulosus* and its sister species, *Physalaemus petersi*, can add chucks to their whinelike call; this suggests that the chuck first evolved in the common ancestor of these two species (fig. 6; Ryan and Drewes 1990). When *Physalaemus coloradorum* females were given a choice between the normal call of their males, which resembles a whine, and this same call with chucks of *P. pustulosus* added, females preferred

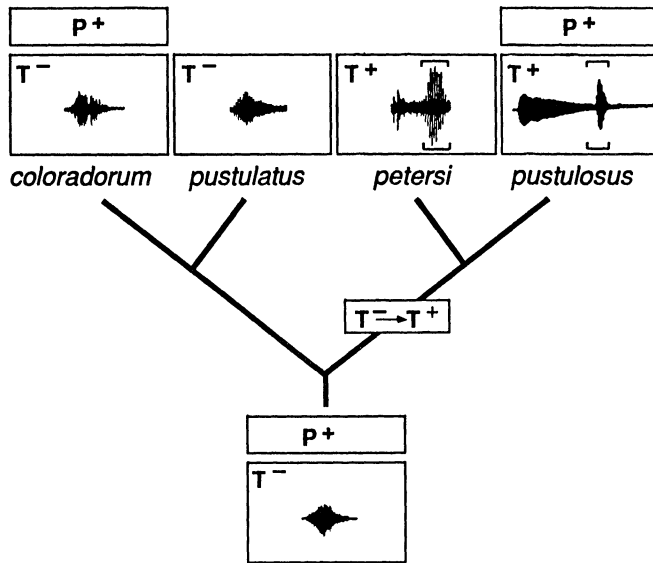


FIG. 6.—The phylogenetic relations of the *Physalaemus pustulosus* species group. Oscillograms of calls for each species are shown, as well as the call from a representative of the out-group (for scale, the *P. pustulosus* call is about 350 ms). Brackets indicate the chuck, the male trait under consideration. T, Male trait; P, female preference for chucks; +, presence; -, absence; →, hypothesized character transformation based on parsimony assumption.

chucks even though their males have not evolved the ability to produce this call (fig. 2). Therefore, it seems likely that the preference for calls with chucks existed in a common ancestor of all four species in the *P. pustulosus* species group. However, the chuck evolved after the divergence of *P. coloradorum* from the *P. pustulosus*–*P. petersi* species pair; thus the preference for chucks preceded the evolution of the chuck (fig. 6; Ryan and Rand, in press).

The same case can be made for the frequency tuning of the BP that in *P. pustulosus* gives rise to preference for calls with lower-frequency chucks. As reviewed previously, frogs use the band-pass characteristics of the peripheral auditory system for processing spectral information. Some species use both channels, whereas others use only either the AP or the BP. In the *P. pustulosus* species group and its closest relatives, all species probably use only the AP because most energy in the whinelike calls is below 1,200 Hz, well below those frequencies to which the BP is sensitive. In *P. coloradorum* (Ryan et al. 1990a) and *P. petersi* (W. Wilczynski, M. J. Ryan, and A. S. Rand, unpublished data) the dominant frequency of the call is generally matched to the most sensitive frequencies of the AP, yet these frogs still have a BP and all BPs are tuned. In *P. pustulosus*, on the other hand, the dominant frequency of the whine matches the tuning of the AP, and the dominant frequency of the chuck is generally matched to the tuning of the BP (Ryan et al. 1990a).

When we compared the peak sensitivity of the BPs of *P. pustulosus* and

P. coloradorum, they were statistically identical (Ryan et al. 1990a). Therefore, one cannot argue that *P. pustulosus* females evolved lower frequency tuning of the BP in order to select larger mates. The tuning was present before the chuck evolved. Therefore we can reject both good genes and runaway sexual selection as hypotheses for the evolution of preferences for the chuck and for chucks with lower frequencies in *P. pustulosus*.

Basolo (1990b) has demonstrated a similar phenomenon in her study of preference for swords in two groups of fish in the genus *Xiphophorus*, swordtails, which have swords, and platyfish, which lack swords. Swords are thought to have evolved at the origin of the swordtail clade, after this group diverged from the platyfish. However, female platyfish prefer conspecific males to which swords have been attached to their normal swordless males.

At least in these cases, it is clear that males evolved traits to exploit preexisting biases in the female sensory system. Coevolution of trait and preference, as required by the good genes and runaway sexual selection hypotheses, does not explain the presence of the sword and the preference for the sword in female swordtails. However, it is possible that these alternative explanations could have favored the preexisting preference for reasons unrelated to sword length (e.g., preference for large size in general) and also might have maintained or further elaborated the female preference.

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