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Multiple causation of the evolution of acoustic signals used in courtship

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ABSTRACT. *Multiple causation of the evolution of acoustic signals used in courtship.*- Female choice is an important selective force in the evolution of acoustic courtship signals. This paper focuses on the results of experiments using synthetic calls that have identified pertinent acoustic properties of the vocalizations of treefrogs. These studies show which values of the pertinent properties are preferred by females and thus generate predictions about patterns of mating success in males from the same populations. The generally stabilizing preference functions for dominant frequencies are discussed in terms of neural correlates such as audiograms; the directional preferences shown for dynamic properties, such as call duration, are shown to be based on more complex rules than merely the time and amount of acoustic stimulation. Because few phylogenetic data or techniques for estimating the survival and fitness of offspring are available, no single model of the evolution of male calls and female preferences can be singled out as superior.

KEY WORDS. Sexual selection, Female choice, Advertisement calls, Anurans, Preference functions, Audiograms, Stabilizing selection, Directional selection, Sensory exploitation

Introduction

We think of ornaments as elaborate, exaggerated structures that seem to be optional for day-to-day living. Ornaments are usually costly to obtain and maintain and sometimes get caught in machinery or attract thieves. However, such costs may be offset by the impressions that ornaments make on potential mates or rivals.

The acoustic signals of many animals qualify as ornaments because they are elaborate, attract potential mates, and affect the behavior of rivals. Such signals may also be energetically expensive and attract predators (e.g., Prestwich et al., 1989; Ryan, 1985). The enormously complex songs of some birds and marine mammals are certainly wonders of nature, but even the more modest signals of many other kinds of animals still qualify as exaggerated because simpler sounds or lower rates of repetition should be adequate. This paper will focus on the evolution of acoustic signals of frogs, with an emphasis on female choice as a major selective force. Many of the patterns and principles that emerge will apply to many species of insects and birds (e.g., Searcy & Andersson, 1986; Ewing, 1989).

Why study frogs?

There are several important advantages to studying vocal communication in frogs. First, unlike many songbirds, most species of anurans produce a relatively small set of acoustic signals. Each signal may be complex, but there are seldom more than two types of signals given at any one time. Some additional complexity can be generated by the production of graded signals (e.g., in *Hyla ebraccata*; Wells & Schwartz, 1984; Wells, 1989). For species producing multiple notes, the most unequivocal example of an acoustic ornament is the "chuck" note of *Physalaemus pustulosus* (Ryan, 1985). This sound by itself does not attract females, but enhances the attractive power of "whines" to which it is added. In other species that produce two-note calls, one type attracts females, whereas the other is used in male-male interactions (e.g., Narins & Capranica, 1978; Littlejohn & Harrison, 1985). Even if there is just one type of call, some of its acoustic characteristics (dynamic properties) may be complex and variable, within and between bouts of calling. Other acoustic characteristics (static properties) change relatively little from call to call or even over the course of a breeding season (Gerhardt, 1991).

Second, there is no evidence that male frogs learn their calls or that the preferences of females are affected by experience (Doherty & Gerhardt, 1984). Frogs thus provide an excellent model system for relating basic auditory function to acoustic communication, which is probably an important reason for the choice of frogs as the subjects of many neurophysiological studies of the auditory system.

Third, the diversity of closely related species invites phylogenetic comparisons of call structure, female preferences, and neural mechanisms. In the North American treefrogs I will discuss here, these comparisons involve species with a mating system in which the female only receives gametes from the male. However, extending comparisons to include treefrogs in tropical areas or other families of frogs would also allow us to assess the effects of direct male-male competition for mates, resource defense and parental care on the evolution of acoustic signaling (e.g., Wells, 1977; Howard, 1978; Kluge, 1981; Marquez, 1993).

Finally, the most important advantage of studying frogs is that the courtship behavior of many species is dominated by the acoustic modality. The female's approach to a speaker that plays back appropriate signals appears to be the same as her approach to a calling male in nature. Unlike many insects and birds, olfactory and visual stimuli play little, if any, role in mate choice. Speakers neither look nor smell like males.

Frogs are, however, not appropriate subjects for studying all aspects of acoustic communication and sexual selection. First, frogs are very resistant to conditioning to sounds. I consider this a disadvantage because we would very much like to be able to use psychoacoustical methods to estimate the resolving power of the auditory system with respect to differences in particular acoustic properties. In studying the unconditioned responses of frogs or other animals, we do not know if a failure to respond selectivity is caused by limitations of auditory resolution, by the reproductive condition of the animals, or by our failure to test the subjects in an appropriate setting.

Second, Frogs have a relatively long generation time and are difficult to breed in the lab. Thus, researchers interested in exploring the evolutionary consequences of mate choice through selection and breeding experiments should choose insects and not frogs. Third, It is difficult to obtain estimates of the survivorship and mating success of the offspring of individuals that may be especially good or poor at attracting males. Thus, researchers interested in estimating the fitness consequences of female choice should study barn swallows and not frogs.

Sources of selection on frog vocalizations

In figure 1 I provide an overview of some of the sources of selection on the call properties of acoustically signaling males. The first part of the tree is familiar enough, and here I define sexual selection as factors that affect the relative mating success of males independent of survivorship. The last part of the tree shows a dichotomy between models of sexual selection, which differ according to whether the consequences of mate choice are expected to feed back on the evolution of the

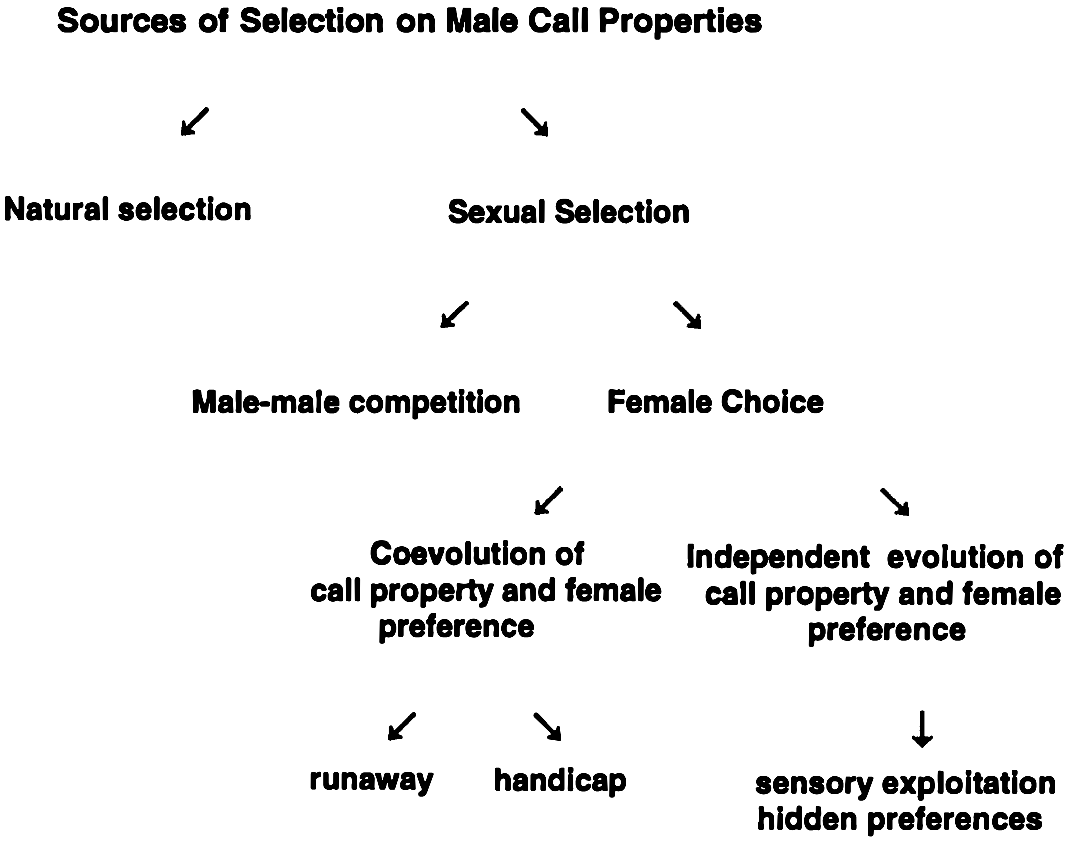

FIGURE 1. Diagram summarizing relationships between sources of selection on male signals and current models of sexual selection. Runaway and handicap (good genes) models require co-evolution of signals and preferences because the fitness consequences (direct or indirect) of mate choice affect the further evolution of the preference. Sensory exploitation and hidden preferences affect the evolution of male signals, but the consequences of mate choice for existing signal properties are unnecessary to explain the existence and form of the preference.

[Diagrama en el que se resumen las relaciones entre las fuerzas de selección sobre las señales de los machos y los modelos actuales de selección sexual.]

preference (Murphy, in preparation). That is, runaway and handicap (or good genes) models involve the co-evolution of signal structure (male traits) and female preferences. In the sensory exploitation and hidden preference-hypotheses, the preference pre-dates the appearance of the male trait (e.g. Ryan et al., 1990; Enquist & Arak, 1993), although once there is a fitness consequence of choice, then this may also affect the evolution of the preference (e.g. Pomiankowsky & Guilford,1990; Basalo, 1990; Ryan & Rand,1993).

Estimation and application of female preference functions

Preference functions provide estimates of the ranges of values of acoustic properties that are preferred by females. Because they are generated by many pairwise contrasts of synthetic calls, each of which is tested with a different sample of females, these preference functions are not the same as those defined by Lande (1981) in his models of the Fisher runaway process. Such functions would require obtaining data about the relative effectiveness of the entire range of signal values for each female and provide estimates of within- and between female variation in preference. The existence of variance in female preference is an assumption of several models of the evolution of female choice (e.g., Heisler et al., 1987). Multiple testing of females is discussed below.

Estimating female preference functions requires several steps. First, we identify the pertinent properties of the advertisement call by synthesizing a signal that has the features typical of conspecific males and that is as attractive to females as typical recorded calls. Usually the synthetic signals are simpler in structure than natural vocalizations, thus indicating that some properties of the call, although stereotyped and species-typical, may be irrelevant for eliciting selective phonotaxis (figure 2; review in Gerhardt, 1988). Second, we vary systematically the properties of another synthetic call and test it against the unaltered, "standard" call. When females fail to show a preference, then the altered property may be irrelevant for mate choice or it may not have been changed enough to elicit a preference. In the latter case, even if the alternative signals are discriminable, small differences in an acoustic property are probably not meaningful in the context of mate choice. Nelson & Marler (1990) use the term "just meaningful difference" to designate minimum differences in signals that elicit biologically significant responses in animals; these differences are typically larger than "just noticeable differences," which are estimates of auditory resolving power derived from tests of conditioned animals.

Third, we explore the intensity-independence of a preference by lowering the sound pressure level (SPL in decibels [dB] re 20 _Pa) of the preferred sound relative to that of the alternative stimulus until the preference disappears or reverses. One assumption, for which I will present data below, is that differences in SPL translate roughly into differences in distance.

A fourth and relatively new task is to test for possible variation in female preferences. Although I do not think that frogs are good subjects for obtaining data from many individuals for the entire range of values of call properties (as required for Lande-type preference functions), multiple testing of individuals in experiments in which a sample of females fails to show a preference is a first step. That is, such testing can tell us if some females in the population prefer one stimulus, and others, the alternative stimulus, or if most individual frogs do not have a preference (Gerhardt, 1991).

Finally, acoustic signals vary in a multi-dimensional way, and different properties are likely to encode different, biologically important information (Gerhardt, 1992). We are only

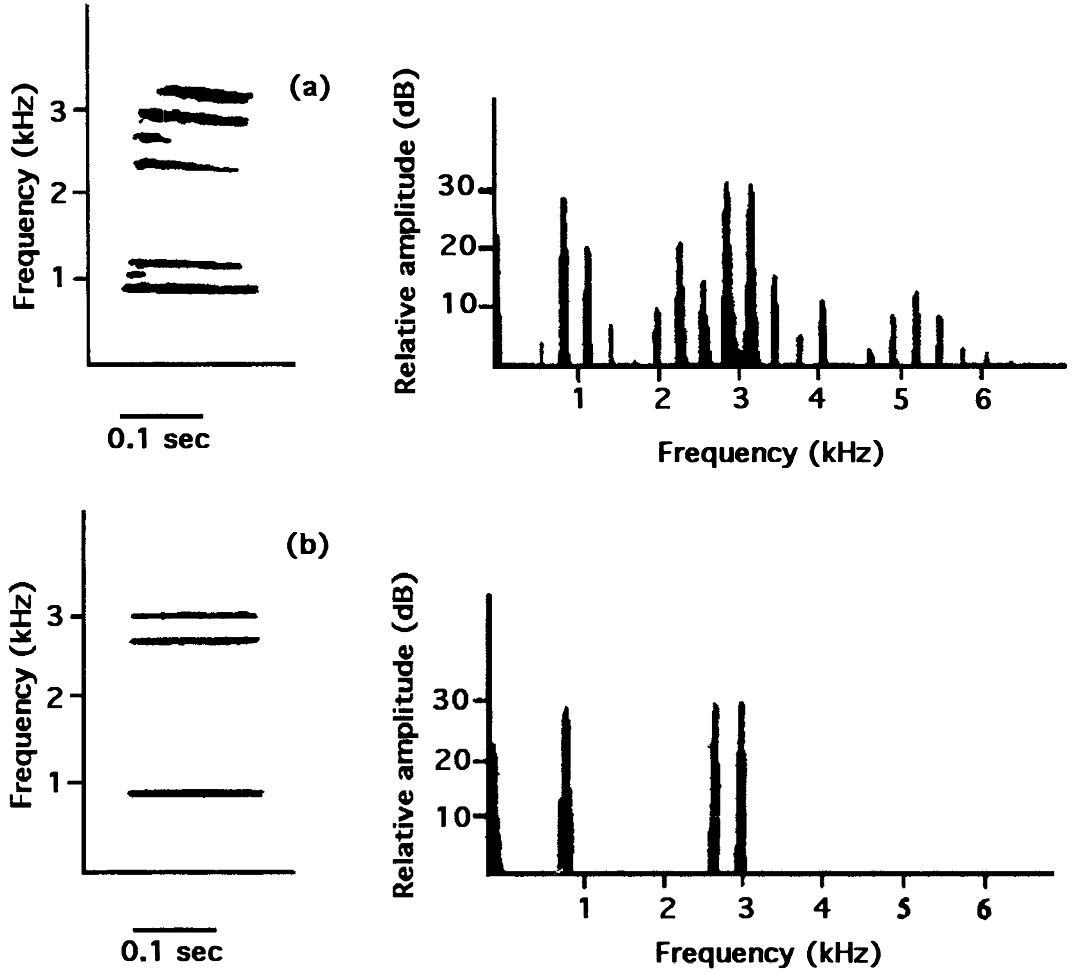

FIGURE 2. Sonagrams and spectra (amplitude-frequency) of (A) a typical advertisement call of *H. cinerea*; and (B) an equally attractive synthetic call. The two sounds both have a bimodal spectrum, but there are many components in the natural call that do not affect its relative attractiveness.

[Sonogramas y espectros (amplitud-frecuencia) de (A) una llamada típica de señalización de *H. cinerea*; y (B) una llamada sintética igualmente atractiva. Los dos sonidos tienen un espectro bimodal, pero hay muchos componentes en la llamada natural que no afectan a su atractivo relativo.]

beginning to explore the effects of varying two or more properties of signal. The questions that such experiments address include: Do females have an absolute hierarchy of acoustic criteria? Do females weight different criteria sequentially or simultaneously? It is too soon to make generalizations, but I will discuss one example below.

There are several applications of preference functions. First, we can visualize immediately the

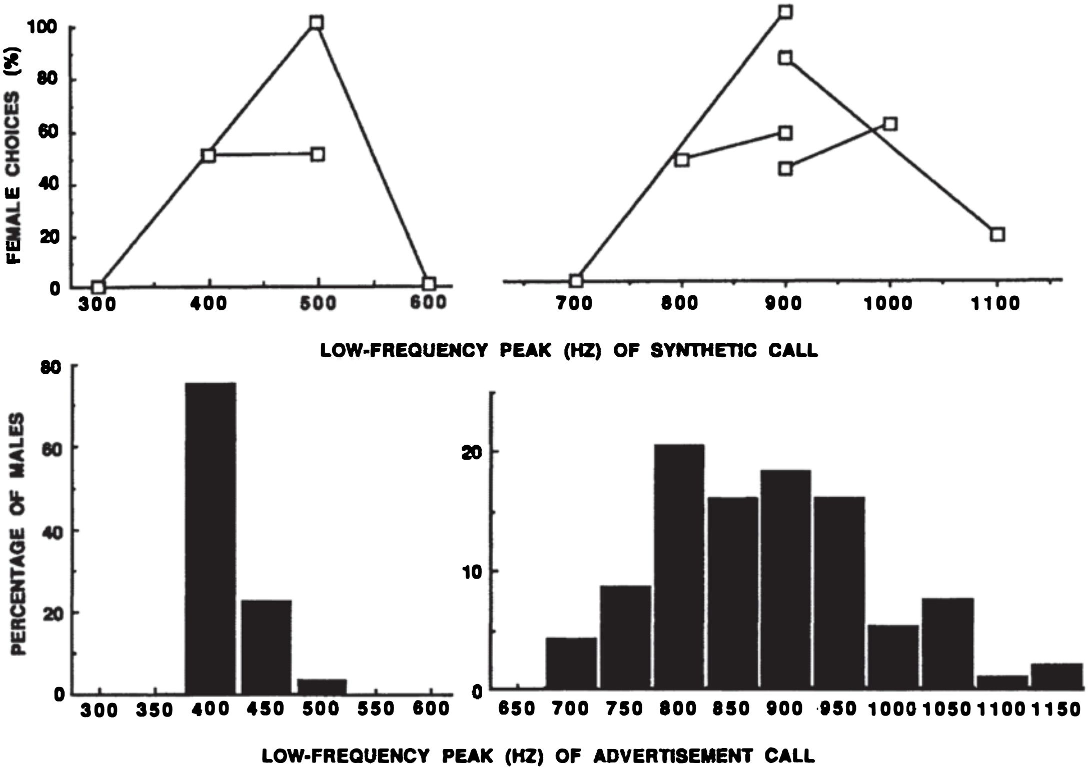

FIGURE 3. Preference functions for the low-frequency spectral peaks in the advertisement calls of (A) *Hyla gratiosa* (barking treefrog) ; and (B) *H. cinerea* (green treefrog). Each pair of symbols connected by a line in the top panels show the results of a two-stimulus preference test at a playback level of 75 dB (*H. cinerea*) or 80 dB (*H. gratiosa*). For example, all (100%) females of H. gratiosa that were offered a choice of synthetic calls with low-frequency peaks of 500 and 300 Hz chose the stimulus of 500 Hz. Equal proportions chose alternatives of 400 and 500 Hz. The distribution of the frequency (Hz) of the low-frequency peak in the calls of the two species are shown in the lower panels. Notice that calls with frequencies near the mean in the populations were more attractive than alternatives with frequencies at both ends of the distribution. These patterns represent stabilizing selection on this call property. The data are based on recordings from eastern Georgia and southern South Carolina, and females that were tested in playback experiments were collected in the same or nearby populations. Modified from Gerhardt & Schwartz (in press).

[Funciones de preferencia para los picos espectrales de baja frecuencia en las llamadas de señalizaci6n de (A) *Hyla gratiosa;* y (B) *H. cinerea.* Cada par de símbolos conectados por una línea en la parte superior representa los resultados de un test de preferencia a dos estímulos a un nivel de reproducci6n de 75 dB (*H. cinerea*) u 80 dB (*H. gratiosa*).]

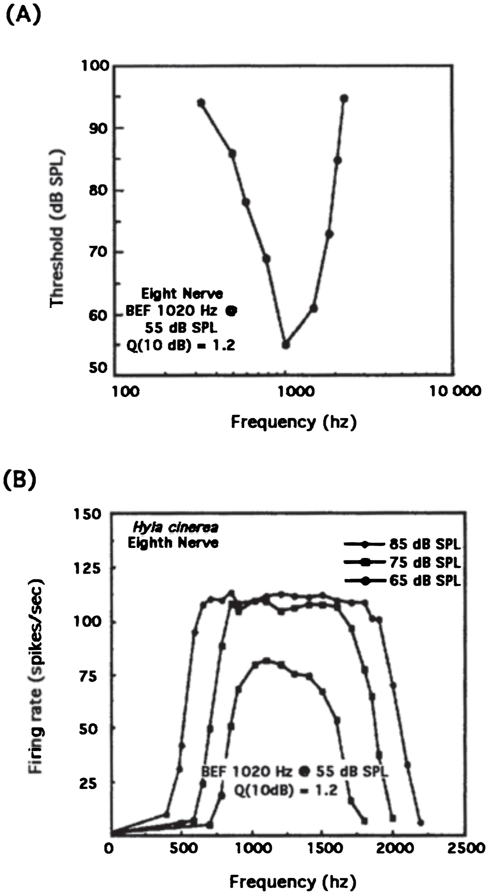

FIGURE 4. (A) Tuning curve of an auditory neuron from the eighth (auditory) nerve of a green treefrog, *H. cinerea.* The lowest point (threshold) is the neuron's characteristic (best) frequency. (B) Iso-intensity functions (spike rate versus frequency) at different stimulus levels for the same neuron as shown in (A). Note that at low levels, the iso-intensity function mirrors the tuning curve, but that at higher levels, the neuron shows little selectivity for frequency. Modified from Capranica (1992).

[(A) Curva de sintonización de una neurona auditiva del octavo nervio (auditivo) de *H. cinerea.* (B) Funciones de igual intensidad (tasa de picos *versus* frecuencia) a diferentes niveles de estímulos para la misma neurona mostrada en (A).]

form of selection that female choice may impose on the distribution of a call property. This serves as a working hypothesis about the past and future evolution of the property. Second, preference functions focus attention on attributes of the male that may be correlated with preferred values of the property. For example, do the values of a property relevant for mate choice vary with male size or condition or chorus density? Are these call properties heritable? What are the potential consequences (both direct and indirect) for the female that males with attractive values of the property? Third, female preference functions also provide a framework for studies of proximate mechanisms underlying female preferences. Fourth, preference functions can be used as characters in phylogenetic analyses.

Preference Functions for Call Frequency: Relationship to Audiograms and Other Neural Correlates of Frequency Selectivity

Some species of frogs alter the frequency of their calls somewhat (Lopez et al., 1988; Wagner, 1989), but most do not. The within-male coefficient of variation during a bout of calling is typically less than 1%, and the mean change in frequency from one recording of a male to another recording during the breeding season is usually less than 8% (Gerhardt, 1991). Studies of four species of treefrogs revealed stabilizing or weakly directional preference functions for call frequency (e. g., Gerhardt, 1981; Doherty & Gerhardt, 1984; Gerhardt, 1987; Gerhardt & Doherty, 1988). That is, frequencies near the mean of the population were seldom less attractive than alternatives with a different frequency and were usually more attractive than alternatives with frequencies at either one or both ends of the distribution. Two examples are shown in figure 3.

Robert Capranica was the first to emphasize that much of the frequency selectivity in frogs may be attributable to the tuning properties of the two auditory organs (e.g., Capranica, 1965; Capranica & Moffat, 1973). The amphibian papilla is the more

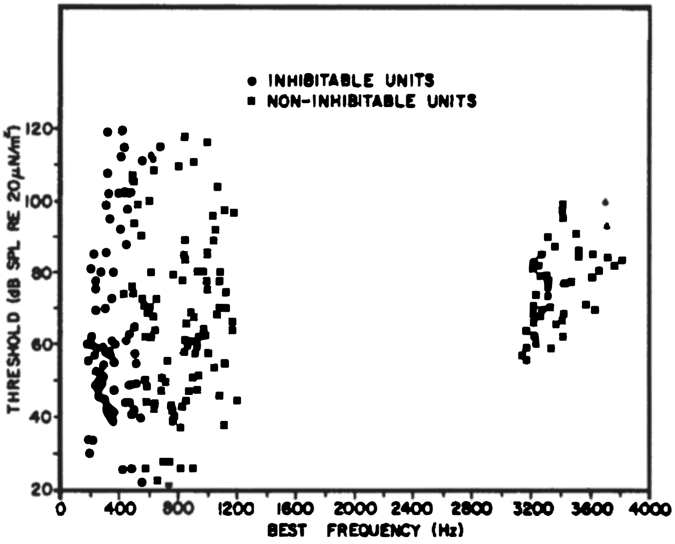

FIGURE 5. Scatter diagram showing the absolute thresholds of auditory neurons recorded from the eighth nerve of *H. cinerea.* Many of the neurons innervating the amphibian papilla (low- and mid-frequency neurons) have greater absolute sensitivity than the high-frequency neurons innervating the basilar papilla. These neurons are likely to be saturated by stimuli with frequencies at or near their best excitatory frequency at the sound pressure levels at which female frogs normally make choices among the calls of males. Modified from Capranica & Moffat (1983).

[Diagrama de dispersión mostrando los umbrales absolutos de neuronas auditivas tomadas del nervio octavo de *H. cinerea.*]

complex organ and has auditory neurons tuned to low and intermediate frequencies, whereas the basilar papilla, the homolog of the Organ of Corti in higher vertebrates, is tuned to high frequencies. Figure 4A shows a typical tuning curve of auditory nerve fiber. The lowest point on the curve indicates the best or characteristic frequency of the neruon, i.e. the sound frequency to which the neuron has its lowest threshold. Figure 5 shows a distribution of thresholds of auditory neurons at their characteristic frequency in the 8th nerve of the green treefrog, *H. cinerea.* There is a reasonably good match between the sensitivity of the mid- and high-frequency units and the low and high frequency peaks in the calls of green treefrogs (see figure 2A).

This bimodal pattern of threshold sensitivity is also seen in evoked potentials at the level of the midbrain - the torus semicircularis (figure 6). Here the curve of estimated sensitivity is continuous rather than discontinuous as might be predicted by the pattern seen in figure 5. This result is explained by the fact that auditory neurons in the 8th nerve and higher centers are not particularly sharp in their tuning. Thus, shifting the stimulus frequency away from the characteristic frequency of a neuron still excites it, provided that stimulus intensity is increased. An audiogram is thus based mainly on the responses of the most sensitive neurons, not only at their best frequencies but also at somewhat lower and higher frequencies.

However, vocal communication in nature and most playback studies take place at sound levels that would excite, for example, most of the neurons shown in figure 6 and not just the most sensitive

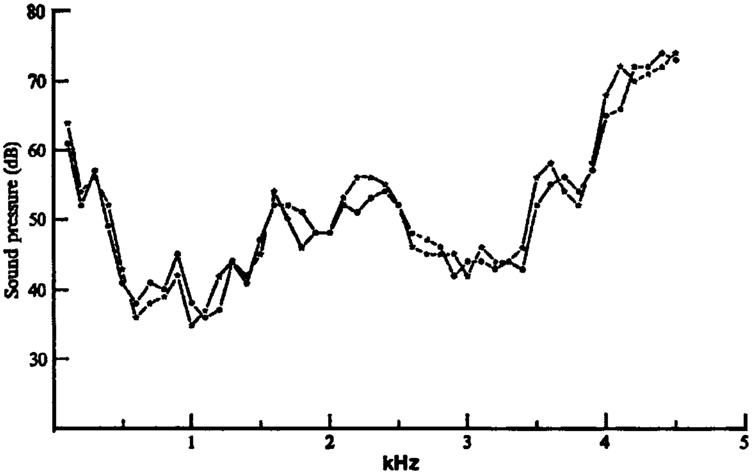

FIGURE 6. Audiogram based on multi-unit activity (evoked potentials) in the torus semicircularis (midbrain) of *H. cinerea*. Notice that the frog is still relatively sensitive in the mid-frequency region (1.5-2.8 kHz) to which very few single units (see figure 6) are tuned. Modified from Lombard & Straughan (1975).

[Audiograma basado en actividad multiunitaria (potenciales provocados) en el torus semicircularis (cerebro medio) de *H. cinerea.*]

ones. Furthermore, many of the more sensitive neurons will be saturated at these levels; that is, the neuron loses its frequency filtering characteristics because it fires at its maximal rate over a wide range of frequency. An example of saturation of an auditory neuron is shown in figure 4B. The question now arises: How well can we expect audiograms based on the summed responses (evoked potentials or multi-unit activity) to predict the relative frequency sensitivity and preferences of females at the sound levels at which mate choice occurs in nature?

In figure 7 I compare an audiogram and iso-intensity functions at two different sound pressure levels in the gray treefrog (H. versicolor); the data were derived from estimates of multi-unit activity in five females that were studied by Joshua Schwartz and me. There is a reasonably good match between the region of greatest threshold sensitivity in the audiogram and the dominant frequency of the advertisement call in males from the same population (about 2.1-2.2 kHz in both cases). Just as in the comparisons in the auditory neuron, however, the correlation between maximum sensitivity in the audiogram and the maximum level of multiunit activity depends strongly on SPL. At about 10 dB above threshold, the iso-intensity curve nicely mirrors the audiogram, with maximum activity being elicited by a frequency of 2.2 kHz. At 80 dB, however, there is a dramatic shift in the maximum response toward lower frequencies - frequencies that, in fact, correspond to the relatively weak, low-frequency peak in call of this species. Another feature of the iso-intensity function at 80 dB is that it is much flatter than that at 50 dB, suggesting that larger differences in frequency are necessary to elicit reliable differences in neural response.

Such intensity-dependent shifts in the frequency response of the auditory system are reflected at the behavioral level. The shapes of "behavioral tuning curves" in H. cinerea varied with the absolute SPL

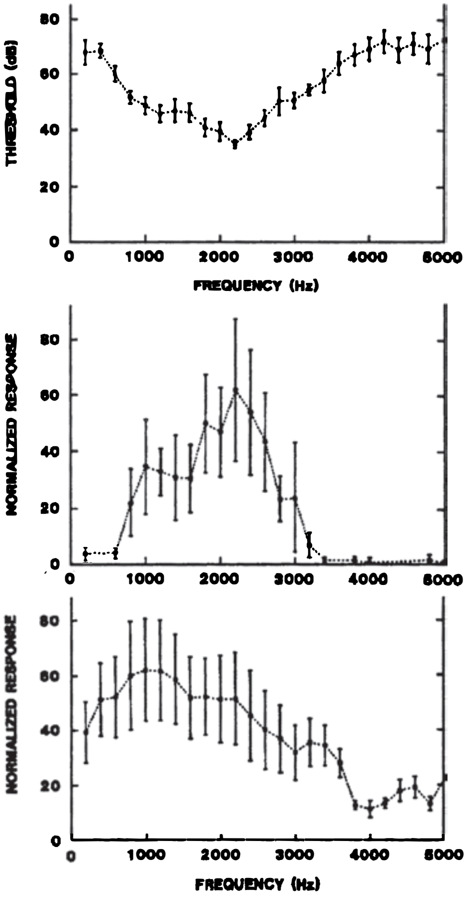

FIGURE 7. (A) Audiogram based on multi-unit activity in the mid-brain (torus semicircularis) of female gray treefrogs, *H. versicolor.* Notice that the most sensitive part of the curve is centered at about 2.1-2.2 kHz. (B) Iso-intensity function generated by plotting the magnitude of multi-unit activity as a function of stimulus frequency at a constant SPL of 50 dB. (C) Iso-intensity function at stimulus SPL of 80 dB, which is 5 dB less than the SPL at which the behavioral tests of frequency preferences were conducted.

[Audiograma basado en la actividad multiunitaria en el cerebro medio (torus semicircularis) de hembras de *H. versicolor.* (B) Función de igual intensidad generada por la representación de la magnitud de la actividad multiunitaria como una función de la frecuencia de estímulo a un SPL de 50 dB. (C) Función de igual intensidad a estímulo SPL de 80 dB.]

to which the two alternatives were equalized. For example, all females chose a call of 900 Hz to an alternative of 700 Hz at a playback level of 65 dB, but only 60% did so at a playback level of 85 dB (Gerhardt, 1987). Joshua Schwartz and I are in the process of obtaining and analyzing audiograms and iso-intensity functions from several species of treefrogs. We are also obtaining data on each individual's frequency preferences, with the aim of identifying measures of neural frequency sensitivity that best predict the animal's frequency preferences at various playback levels.

For the present, however, the results discussed above suggest that predictions about frequency preferences derived from such threshold measures of frequency sensitivity as audiograms are likely to be inaccurate at best and misleading at worst.

These problems are compounded because the neural data are highly variable from individual to individual and because physiological studies are typically based on small sample sizes of animals (e.g., Diekamp & Gerhardt, 1992). Thus, direct estimates of frequency preferences based on playback experiments conducted at appropriate playback levels are far superior to neural estimates of frequency biases that are presently available. Field observations of the distances and SPLs at which females make choices are critical for refining these playback experiments.

The importance of having appropriate quantitative data about frequency preferences is exemplified by the hypothesis of sensory exploitation, which predicts that there is no significant difference in the tuning biases of ancestral and derived species. The most widely cited example in frogs was initially supported by a failure to reject a null hypothesis with data based on audiograms from small samples of individuals (Ryan et al., 1990). Ryan & Rand (1993) provide behavioral data to support the hypothesis and acknowledge the problem of accepting null hypotheses when sample sizes are small.

Nevertheless the claim (Ryan & Rand, 1993) that there has been no further evolution of the female tuning bias in the derived species, *P. pustulosus* (since the evolution of the "chuck" call) requires a quantitative comparison of frequency preferences in P. coloradorum, the "ancestral" species, and P. pustulosus rather than just the demonstration that "chucks" enhance the attractive power of whines in *P. coloradorum.* The magnitude of differences in tuning that are still consistent with the judgment of "no further evolution" also needs to be stated.

Preference functions for dynamic properties

Preference functions for dynamic properties, such as call duration in the gray treefrog, are typically highly directional (figure 8), and there are many examples of studies showing that female frogs prefer extreme or even supernormal values of "gross" temporal properties (review in Gerhardt, 1991). These results are seemingly straightforward and could even be considered trivial. That is, perhaps any animal will prefer a stimulus that excites its auditory system to a greater extent in time or amplitude than another stimulus. Obviously, long calls or calls repeated at high rates should be more effective in the first respect than short calls, or calls repeated at slow rates; calls of greater SPL should be more effective in the second respect than calls of lower SPL. Indeed, this general idea was supported by an experiment in which a difference in call repetition rate was pitted against a difference in SPL. Schwartz (1986) found that the preference of females of H. microcephala for a stimulus with double the call rate of an alternative was abolished by a 3 dB (a factor of two in terms of sound power) reduction in the relative SPL of the call with the faster rate. Reduction of the relative SPL of the call with the high rate by 6 dB reversed the preference.

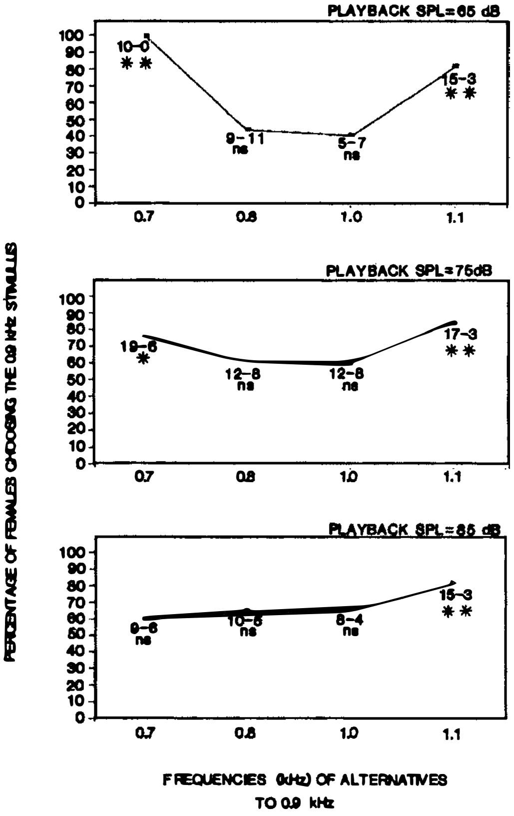

FIGURE 8. Frequency selectivity of females of *H. cinerea* for variants of the low-frequency peak as a function of the sound pressure level to which a standard call (Frequency = 900 Hz) and an alternative with a different frequency were equalized. From Gerhardt (1987).

[Selectividad de frecuencia de hembras de *H. cinerea.*]

More recently, however, my colleagues and I have found that females of the gray treefrog, H. versicolor, and its sibling species, the diploid H. chrysoscelis reliably choose calls with high repetition rates (2 times) or durations (2 times) even when the alternatives with slower rates and shorter

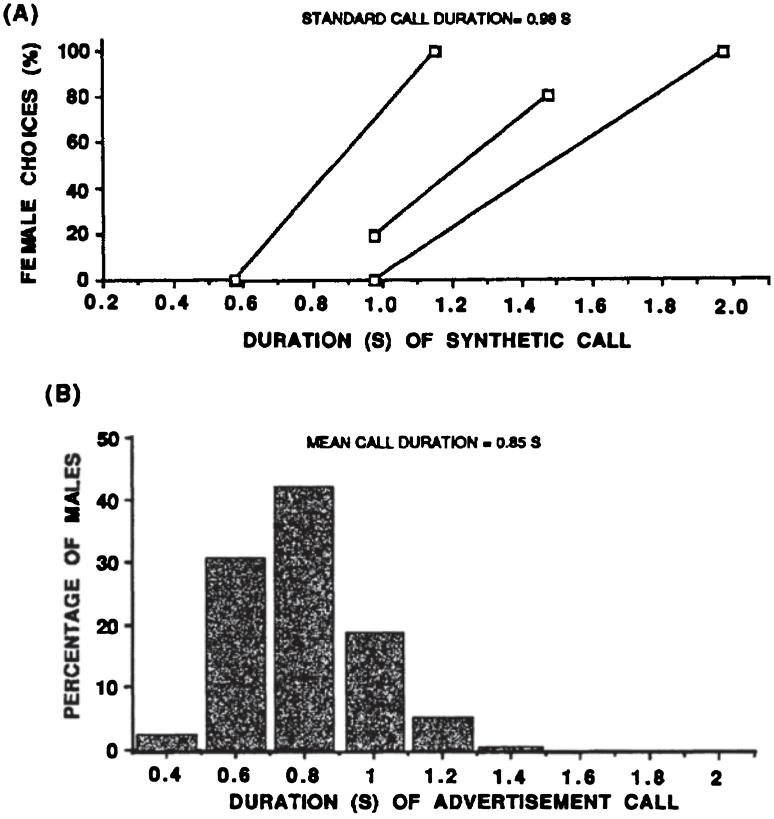

FIGURE 9. Female preference function for call duration in the gray treefrog, *H. versicolor*. See the legend of figure 3 for an explanation for how the preference data are plotted. Notice that female preferences for this dynamic property are highly directional. Modified from Gerhardt (1991).

[Función de preferencia de la hembra para la duración de la llamada en *H. versicolor*.]

durations, respectively, had relative SPLs that were 6 dB higher (Gerhardt, 1991; unpubl. data). These preferences were also maintained if the two-fold difference in SPL at the release point was achieved by changing the distances of the speakers (Gerhardt et al., unpublished data).

Klump and Gerhardt (1987) offered females of H. versicolor alternatives that provided the same total amount of acoustic stimulation because the longer calls (by a factor of two) had a call rate that was one-half of that of the alternative stimulus with short calls. If time of stimulation of the auditory system were the only criterion for mate choice, then females should not show a preference. However, females preferred the long calls with a slow repetition rate (Klump & Gerhardt, 1987), and similar studies with H. chrysoscelis yielded the same result (Gerhardt et al., unpubl. data). Call duration is directly correlated with chorus density and inversely correlated with the amount of time a male calls during a night or season (Wells & Taigen, 1986; Sullivan & Hinshaw, 1992), thus suggesting that the female's choice of long calls is not arbitrary (Klump & Gerhardt, 1987).

Miranda Dyson, Steven Tanner and I recently found that females will move considerable extra distances in order to choose the longer of two signals, even when the playback of the longer call is terminated for some period of time. More specifically, females were released at point midway between two speakers; long calls were broadcast from one speaker and short calls, from the other. The female moved toward the source of long calls, but when she arrived at a point half to that speaker, the playback of long calls is terminated. The females then moved back toward the source of short calls. When they were half-way between the original release point and the short call, the playback of long calls was resumed. If the speakers were separated by 2 m, females reversed their direction and returned to the source of long calls. If the speakers were separated by 4 m, they did not. Thus, there seems to be a limit to the amount of extra distance that a female will move to reach a source of longer calls. In nature, extra movements are probably inconsequential energetically, but females risk predation from bullfrogs and snakes, which use vision and tactile cues to locate prey. Additional experiments suggest that females are able to assess the absolute distance between speakers using the sound pressure gradient (Gerhardt et al., unpublished data).

Interaction between a dynamic and static property

Mean call duration is similar in the two species of gray treefrogs and usually varies over a three-fold range in a typical population (Gerhardt, 1991). By contrast, the mean temperature-corrected pulse rate, a static property, is 35 to 50% lower in H. versicolor than in H. chrysoscelis and varies little among males in a population (Gerhardt, 1982). To examine how females of H. chrysoscelis weight dynamic versus static properties of calls, I conducted playback experiments in which a difference of 300% in call duration was pitted against a difference of about 30% in pulse rate. The short call had a pulse rate typical of a local, conspecific male at the test temperature of 20_C, whereas the long call had a pulse rate that was about 30% lower (i.e., in the direction of H. versicolor) than the conspecific rate. This test thus represents something of a dilemma for the female: short calls may be produced by males of relatively lower physical or even genetic fitness, whereas the long calls may be produced by a genetically incompatible male of another species. The triploid hybrids that result from mismatings between the two species have low viability and are sterile.

How the females responded depended on whether or not H. versicolor occurred in the same or in a nearby area. In tests of females from sympatric populations, about 90% of the animals chose the short, conspecific call. Females from remote allopatric populations (>500 km from the nearest population of H. versicolor) did not show a preference (Gerhardt, in press). Thus, it appears that, in sympatry, selection has led to the development or maintenance of strong pulse rate selectivity that is not confounded by intraspecific differences in duration. This appears to be an example of reproductive character displacement of female mate choice (Gerhardt, in press).

Demonstrations of female choice in nature

Although sexual selection in the form of male-male competition and the defense of oviposition sites has been well-documented in some species of frogs and toads (Arak, 1983; Howard, 1978; Wells, 1977), there are relatively few unequivocal demonstrations of intraspecific female choice. Most studies have sought indirect evidence for female choice based on differences in call frequency. That is, rather than showing a relationship between mating success and call frequency, these studies have sought separate correlations between body size and call frequency and between body size and mating success. Only a handful of more than a dozen studies have demonstrated size-dependent mating in species in which females choose males freely (e.g., Ryan, 1985; Morris, 1989; Marquez de Orense & Tejedo Madueño, 1990; review in Gerhardt et al., 1987 and update in Gerhardt, 1991). In some studies small sample sizes have limited the statistical power to detect small size differences in mating success, but there have also been some negative results from studies with very large sample sizes (e.g., Ritke & Semlitsch, 1991; Dyson et al., 1992).

These negative results are not surprising, given the generally stabilizing preference functions for frequency, the relatively large differences in

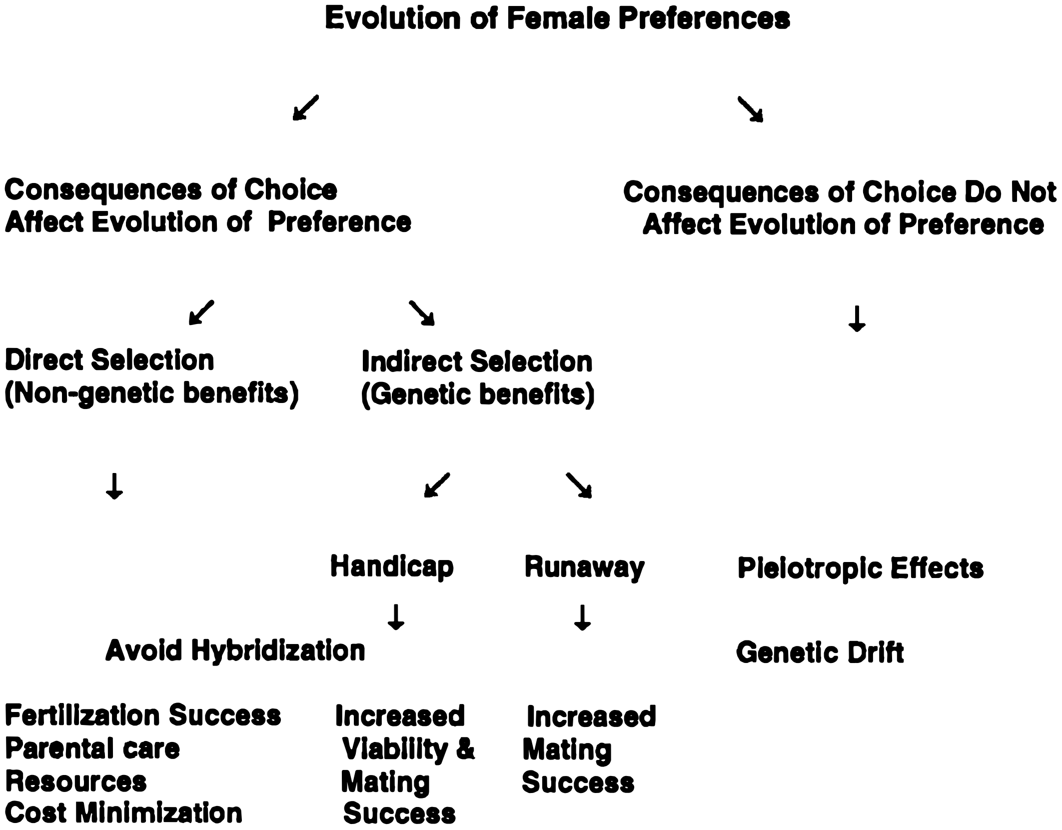

FIGURE10. Some models of the evolution of female preferences. See the text for discussion.
[Algunos modelos de evolución de las preferencias de la hembra.]

frequency necessary to elicit preferences, and the intensity-dependent nature of preferences based on frequency. These behavioral results, in turn, are consistent with the relatively weak frequency biases evident in most audiograms and with the reduction in frequency selectivity of other neural correlates, such as iso-intensity functions, at the high SPLs that are typical of natural communication.

In contrast to the rarity of studies demonstrating female choice for call frequency, several studies have demonstrated direct correlations between mating success and call rate, a dynamic property. In four of five studies mating success was positively correlated with some measure of call rate (e.g., Sullivan, 1983; Passmore et al., 1992; Cherry, 1993; Schwartz, unpubl. data). Similar results have been reported from a wide range of other taxa (review in Gerhardt, 1991). These results are consistent with the highly directional preference functions for dynamic properties (Gerhardt, 1991). Whereas differences in frequency are likely to be masked in dense chorus situations (e.g., Gerhardt & Klump, 1987), higher (preferred) values of dynamic properties make a male's calls conspicuous under these conditions. This effect would undoubtedly contribute to male mating success, even if high values of call rate were not preferred by the females. However, conspicuousness in noisy environment cannot be the proximate cause of the female preferences because the animals show these preferences in very quiet laboratory conditions.

Evolution of female preferences: multiple causation

In figure 9 I show one way of viewing some ideas about the evolution of female preferences. Notice that I have again emphasized that, in some models, there is a fitness consequence to female choice, and hence call properties and preferences should co-evolve. Of course other forces (natural selection, genetic drift, mutation, and pleiotropic effects) that are independent of the consequences of choice also influence the evolution of preferences. The benefits of choice are of two general kinds, direct selection, in which the female gains immediately from her preference, and indirect selection, in which the gains are genetic and must be assessed by measuring offspring fitness and mating success (e.g., Kirkpatrick & Ryan, 1991). Whether the negative consequences of mating with an individual of another species should be considered a genetic or direct consequence is a matter of opinion. I prefer to consider these indirect consequences because fertilization in crosses between different species of frogs can be as high as in control crosses, and the detrimental effects of genetic compatibility are often not manifest until the hybrids reach sexual maturity (e.g., Mecham, 1964).

The consequences of intraspecific choice in frogs are not easy to classify, mainly because we seldom have the necessary historical (phylogenetic) data or good information about the fate and fitness of offspring. Even when a consequence has been demonstrated, such as the differential fertilization of eggs by males of certain size classes, there may be other explanations for the preferences that lead to the choice of such males. For example, Ryan et al. (1990) argued that, in P. pustulosus the female preference for large males became established before the appearance of the chuck component of the male call, which contains information about the size of a male. Thus, the increased fertilization success of mating with large males (Ryan, 1985), a direct benefit of female choice, may not been a selective force in the evolution of the female preference for chucks of low frequency.

Preferences in frogs and other animals for males that display vigorously have been observed in many species (review in Gerhardt, 1991), and as I argued above, females may incur assessment costs to mate with such males or to avoid weak callers. How can these results be interpreted? Perhaps males that display vigorously are in good physical condition (e.g., Wells & Taigen, 1986) and can thus fertilize eggs more effectively than males in poor condition. If so, then preferences for vigorous display would be an example of direct selection. This hypothesis can be tested rather easily. In the absence of data, my own bias is toward the hypothesis suggested by Maynard Smith (1991): females may be using displays of physical fitness to assess directly a component of genetic fitness, which is likely to be correlated at least to some degree with total fitness. Another hypothesis is that preferences for large values of dynamic properties evolved as a correlated response to selection on males for conspicuous calling in dense chorus situations. We can test these last two hypotheses only by developing new techniques for assessing the fitness consequences of mate choice in nature and by interpreting these data in the light of comparative (phylogenetic) data.

Finally, I emphasize the value of phylogenetic data by giving an example in which selection may not have been a major causative factor in the evolution of call structure. A maximum parsimony analysis, based mitochondrial DNA sequences from diploid and tetraploid gray treefrogs from throughout the eastern U.S., indicates that the tetraploid has arisen independently at least three separate times (Ptacek et al., in press). If the pulse rate of the advertisement calls of males of the three lineages are corrected to a common temperature, then the mean pulse rate of the individuals of one of the lineages is only slightly higher than those of the other two lineages, which are indistinguishable in this respect. Possibly selection in the form of female choice could have driven pulse rate to the similar values observed in all three lineages. However, I favor the hypothesis proposed by Bogart & Wasserman (1974). These authors suggested that differences in cellular dimensions, which accompany speciation by polyploidy, may lead to mechanical differences in the vocal apparatus, which in turn results in different pulse rates. Thus, the larger cells of the tetraploids (*H. versicolor*) are responsible for the lower pulse rates (than *H. chrysoscelis*) of their advertisement calls. Similarly, the preferences of females of the tetraploid species for pulse rates lower than those of the diploid species could also be a by-product of polyploidization. We are currently testing these ideas by producing polyploids of H. chrysoscelis; we can record the calls of males and test the pulse-rate preferences of females.

Resumen

Causación multiple de la evolución de las señales acústicas usadas en el cortejo.

La eleccion de hembra es una importante fuerza selectiva en la evolución de las señales acústicas de cortejo. Este artículo se centra sobre los resultados de experimentos usando llamadas sintéticas que han identificado las propiedades acústicas pertinentes de las vocalizaciones de *Hyla cinerea*. Estos estudios muestran que los valores de las propiedades pertinentes son preferidas por las hembras y así generan predicciones sobre pautas de éxito de apareamiento en machos de la misma población. Las funciones preferentes generalmente estabilizantes para las frecuencias dominantes se discuten en términos de correlaciones neuronales tales como audiogramas; las preferencias direccionales mostradas por propiedades dinámicas, tales como la duracion de la llamada parece se basan en reglas mas complejas que el tiempo y cantidad de estimulación acústica. Debido a los pocos datos filogenéticos o a las técnicas para estimar la supervivencia y eficacia de los descendientes que llegan a término, no pueden escogerse como mejores modelos simples de la evolución de las llamadas de

los machos y de la preferencia de las hembras.

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