



Auditory Tuning and Call Frequency Predict Population-Based Mating Preferences in the Cricket Frog, *Acris crepitans*

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AUDITORY TUNING AND CALL FREQUENCY PREDICT
POPULATION-BASED MATING PREFERENCES IN THE CRICKET
FROG, *ACRIS CREPITANS*

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Abstract.—We examined frequency tuning of the female's peripheral auditory system, the dominant frequency of the male's mating call, and population-based mating preferences in cricket frogs (*Acris crepitans*) to determine how the relationship between the mean call frequency and mean frequency sensitivity of the female's auditory system determines such preferences. Females could exhibit preferences for either local calls or foreign calls. In all instances in which there was a preference, females preferred lower-frequency calls, regardless of whether they were local or foreign. These patterns of female preference are consistent with data showing that females are tuned below the mean call frequency of their population. Tuning also explains differences in preference among females of the same population. Tuning is negatively correlated with body size, and within a population larger females preferred lower frequencies and smaller females preferred higher frequencies. Thus female preference will generate directional selection acting on male call frequency but will also contribute to variation in call frequency.

The relationship between male courtship signals and the sensory biases of females decoding these signals determines patterns of mating preferences. Studies in animal behavior and neuroethology have demonstrated how preferential responses of females to conspecific signals relative to heterospecific signals contribute to reproductive isolation (Gerhardt 1988; Walkowiak 1988; Huber 1990). Congruence between sender and receiver can also generate homotypic preferences among populations, in which females prefer local males to foreign males of the same species (Capranica et al. 1973; Baker and Cunningham 1985; Claridge et al. 1988; Ryan and Wilczynski 1988). However, a perfect match between the signal and receiver and the consequential homotypic mating preferences are not always the case. In sticklebacks (Moodie 1982) and swordtails (Ryan and Wagner 1987), some females prefer heterospecific to conspecific males, and in fruit flies (Kaneshiro 1980) females do not discriminate between closely related species. In these cases it is thought that females find the red nuptial colors in sticklebacks, larger size and courtship in swordtails, and more courtship elements in fruit flies more stimulating.

Studies of mate choice within populations often reveal preferences for males with traits that deviate from the population mean (Ryan and Keddy-Hector 1992).

This is true, for example, in the frog *Physalaemus pustulosus*; females prefer males with lower-than-average call frequencies. This preference might result from a slight mismatch between the sender and receiver; the female's auditory system is maximally sensitive to call frequencies below the population mean (Ryan et al. 1990b). The sensory basis of nonrandom mating within other species is not well-known, but it seems likely that in such cases some parameter of female preference does not best match the average male's signal.

In order to investigate the role of sender and receiver in mate preferences, we have been investigating variation among populations of the cricket frog, *Acris crepitans*. In this study we determine how the dominant frequency of the male's advertisement call and the tuning of the female's peripheral auditory system interact to yield female phonotactic preferences between male calls from different populations. Although there is substantial and important variation in temporal call characters and temporal properties of the auditory system, we restrict our analysis here to the spectral domain.

THE COMMUNICATION SYSTEM

Anurans produce advertisement calls that are used to attract females and repel males. The calls are species specific, and female preference for conspecific calls promotes mating between conspecifics; that is, it serves species recognition (Blair 1958; Gerhardt 1988). However, there is also significant variation in calls within a population, and female preferences based on variation in these characters can result in nonrandom mating success among males, that is, generate sexual selection (Ryan 1990b).

There is some understanding of the neural basis of call recognition in anurans. These animals have two inner-ear organs that are sensitive to sound and are differentially sensitive (or tuned) to different frequencies. The amphibian papilla is more sensitive to lower frequencies, whereas the basilar papilla is more sensitive to higher frequencies. The relationship between the tuning of these auditory end organs and the spectral properties of the advertisement calls accounts for some observed patterns of species recognition. These auditory organs are more sensitive to frequencies that characterize conspecific calls relative to frequencies that characterize heterospecific calls (Zakon and Wilczynski 1988).

Acris crepitans is distributed widely throughout much of eastern and central North America. The communication system of this species has been well studied in terms of geographical variation in the call (Nevo and Capranica 1985; Ryan and Wilczynski 1991), geographical variation in female preferences and auditory processing (Capranica et al. 1973; Nevo and Capranica 1985; Ryan and Wilczynski 1988; Keddy-Hector et al., in press; Wilczynski et al., in press), vocal interactions among males (Wagner 1989a, 1989b, 1989c), and environmental selection acting on call structure (Ryan et al. 1990a). We briefly summarize pertinent aspects of the communication system.

The call is a series of clicklike pulses (fig. 1). Pulses are combined to form calls, and calls are repeated in call groups. From the beginning to the end of the call group, calls tend to increase in both the number of pulses and note duration.

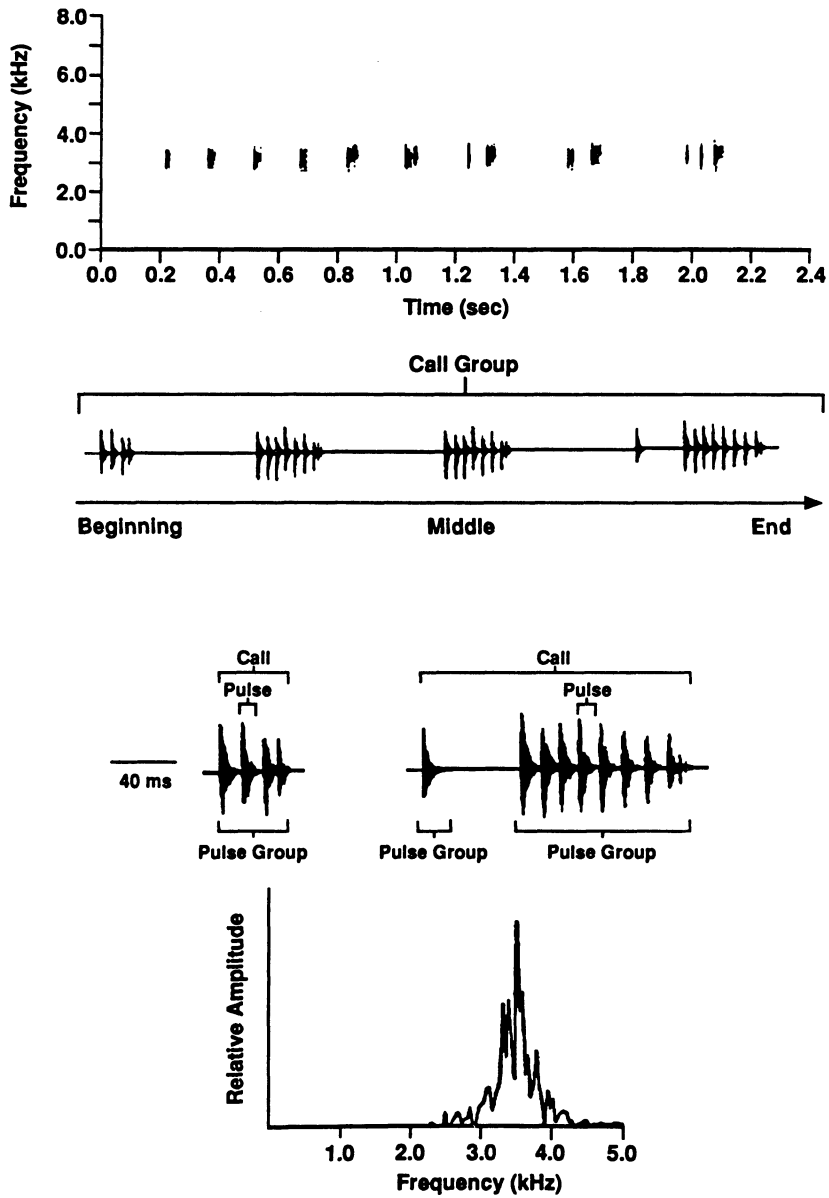


FIG. 1.—The advertisement call of the cricket frog *Acris crepitans*. From top to bottom, a sonogram of an entire call group, an oscillogram showing representative calls from different parts of the call group, oscillograms showing the pulse structure of a call with one pulse group and a call with two pulse groups, and a Fourier transform showing the relative amplitude of different frequencies in a single call (modified from Wagner 1989a).

The call has a dominant frequency of 2.7–4.0 kHz with sidebands that probably result from low-frequency amplitude modulation of the carrier frequency. The frequency remains constant throughout the call, although males sometimes lower their dominant frequency in response to the vocalizations of other males.

As with most animals, females prefer conspecifics to heterospecifics, but in cricket frogs there are also population-based mating preferences. Capranica et al. (1973) showed that females from New Jersey preferred the local call to the call of males from Nebraska (ca. 2,500 km away), and it was later shown that females from Austin, Texas, preferred local calls to calls of males from nearby (ca. 50 km) Bastrop, Texas (Ryan and Wilczynski 1988). In both studies the preferences appear to result from the basilar papilla's being more sensitive to the dominant frequency that characterizes the local call than to the dominant frequency of the foreign call. In a detailed analysis of 17 populations on a longitudinal transect through Texas, we showed that call dominant frequency exhibits strong clinal variation. In many frogs dominant frequency is negatively correlated with body size (Ryan 1988), but this clinal variation in call frequency persists even after the effects of variation in body size are removed statistically (Ryan and Wilczynski 1991). The purpose of this study is to determine how the relationship between call frequency and tuning influences population-based mating preferences.

METHODS

Basilar papilla tuning was determined by recording the responses of eighth cranial nerve afferent fibers to 300-ms tone bursts presented every 1.5 s in 12 female frogs from Bastrop, Texas, 7 female frogs from Indianapolis, Indiana, and 1 female frog from Austin, Texas. In addition, basilar papilla tuning was determined in four female frogs from Austin by recording neural activity in the mid-brain auditory center, the torus semicircularis (Wilczynski 1988), rather than the eighth cranial nerve. The data obtained by these two methods were combined. Although amphibian papilla fibers were also encountered during the recordings, their response properties are not described here, as call frequencies do not fall into the amphibian papilla's sensitivity range in this species (Capranica et al. 1973; Ryan and Wilczynski 1988; Wilczynski et al., in press).

The recording procedures are described in detail elsewhere (Wilczynski et al. 1984, in press; Ryan and Wilczynski 1988). In brief, frogs were anesthetized by immersion in 2.5% urethane, and the eighth cranial nerve or midbrain was surgically exposed. A frog then recovered for 1–3 d, at which time it was immobilized by an intramuscular injection of curare and locally anesthetized with a topical application of 2% lidocaine. An earphone was sealed over the tympanic membrane ipsilateral to the exposed nerve or contralateral to the exposed midbrain. Auditory responses to tonal stimuli were recorded through a 3M KCl-filled glass microelectrode. The best excitatory frequency (BEF: frequency at which neural activity is evoked at the lowest sound pressure level) for each basilar papilla afferent fiber or isolated midbrain activity was determined by standard techniques. The BEFs of basilar papilla afferents within an individual were usually identical, although occasional variation of ± 25 Hz in BEFs was encountered (see

also Zakon and Wilczynski 1988 for a discussion of basilar papilla tuning in frogs). For each individual frog, BEFs from all basilar papilla characterizations were averaged to yield a single mean basilar papilla BEF for that individual. These individual mean BEFs were averaged together to yield population means for basilar papilla tuning.

The dominant frequencies of calls from Austin and Bastrop were analyzed previously (Ryan and Wilczynski 1991). Calls from Indiana were recorded and analyzed in a similar manner. Calls of 10 males were recorded on a Uher 4400 Report recorder using a Sennheiser ME 80 microphone. For three calls of each male—one from the beginning, middle, and end of the call group—the dominant frequency was determined by fast Fourier transform using a DATA 6000 digital waveform analyzer. The sampling rate was 10 kHz and the maximum call frequency was 4 kHz, which is below the Nyquist frequency of 5 kHz for this sampling rate. The three calls were averaged to obtain the mean for each male, and the 10 means were averaged to obtain the population mean.

For the phonotaxis experiments, we synthesized calls in which the dominant frequency varied but temporal characters were held constant. We did this by modulating the amplitude of a sine wave for the duration of a single pulse of 5 ms on an Amiga 500 computer using a synthesis program provided by J. Schwartz and the Future Sound software package. Five pulses were combined to produce a call of 30 ms, and 10 calls were combined to produce a call group of 2 s. This resulted in a call with the dominant frequency, sideband frequencies, and number of pulses that resemble the model call. Calls with a dominant frequency of 3.5 kHz represented calls from Austin, Texas, and Indianapolis, Indiana, and the calls with a dominant frequency of 3.8 kHz represented calls from Bastrop, Texas. We also synthesized calls of dominant frequencies 300 Hz above and below these calls (i.e., 3.2 kHz, 3.8 kHz, and 4.1 kHz).

Female phonotaxis experiments were conducted in three localities, in two laboratories (Austin and Indiana) and in an acoustic chamber placed in the back of a Chevrolet Suburban truck at the breeding site in Bastrop. Except for the size of the testing arenas (Austin and Indianapolis, 2 m × 2 m; Suburban, 1.3 m × 2 m), similar procedures were followed. Females in amplexus were collected from natural populations. On this same night an individual female was placed under a small cone in the center of the arena between two speakers and allowed to acclimate. Stimuli were then presented antiphonally with a Sony TCD-5M or a Marantz PMD 420 tape recorder through ADS L200C or APM-007 AV Sony speakers at an intensity of ca. 75 dB SPL (in reference to 2×10^{-5} N/m²) at the center of the arena. The female was released, and a response was noted if she approached to within 10 cm of a speaker. More than 90% of the females tested responded, always in less than 20 min and usually in less than 10 min. Females were released into their home pond after testing. Data were analyzed by two-tailed exact binomial probabilities.

We will discuss the results of these phonotaxis experiments in relation to studies of population variation in the tuning of the basilar papilla. The females used for the neurophysiology and the females used in the female phonotaxis experiments were randomly sampled from the population. Since tuning of the basilar

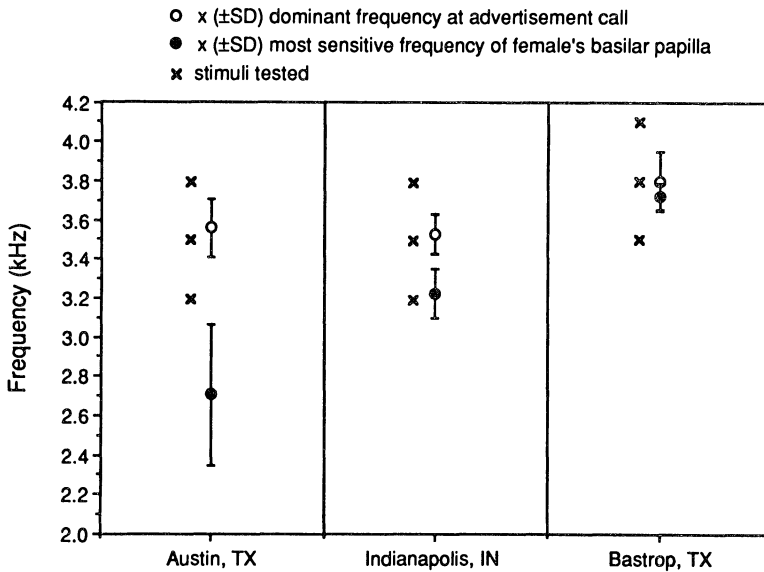


FIG. 2.—The means and standard deviations of the most sensitive frequency of the females' basilar papilla and the dominant frequency of the males' advertisement call for three populations of *Acris crepitans*. Also shown are the frequencies of the stimuli used in the phonotaxis experiments.

papilla is negatively correlated to body size within populations (Keddy-Hector et al., in press), if body size differed between samples (i.e., the females used for neurophysiology and phonotaxis), the tuning of the basilar papilla of the females used in the phonotaxis experiments would not be representative of the population mean. However, for all populations the mean body size of females used in the phonotaxis experiments was almost identical to the mean size in the neurophysiological studies.

RESULTS

Basilar papilla tuning differed among females from the three populations. Among females, mean basilar papilla tuning was highest in the Bastrop population at 3.72 kHz and lowest in the Austin population at 2.71 kHz. These differences in tuning were correlated to differences in the mean dominant frequency of the calls for each population; Bastrop was highest at 3.80 kHz, and Austin and Indiana were both between 3.50 and 3.60 kHz (fig. 2).

It has already been shown (Ryan and Wilczynski 1988) that when female cricket frogs from Austin were given a choice between stimuli with a dominant frequency of their own calls ("local" call, 3.5 kHz) and the frequency of calls from Bastrop, which is 300 Hz higher ("foreign" call, 3.8 kHz), females preferred the local call (fig. 3). However, this was not the case in the present study when Austin females were given a choice between a local call and foreign call that was 300 Hz lower

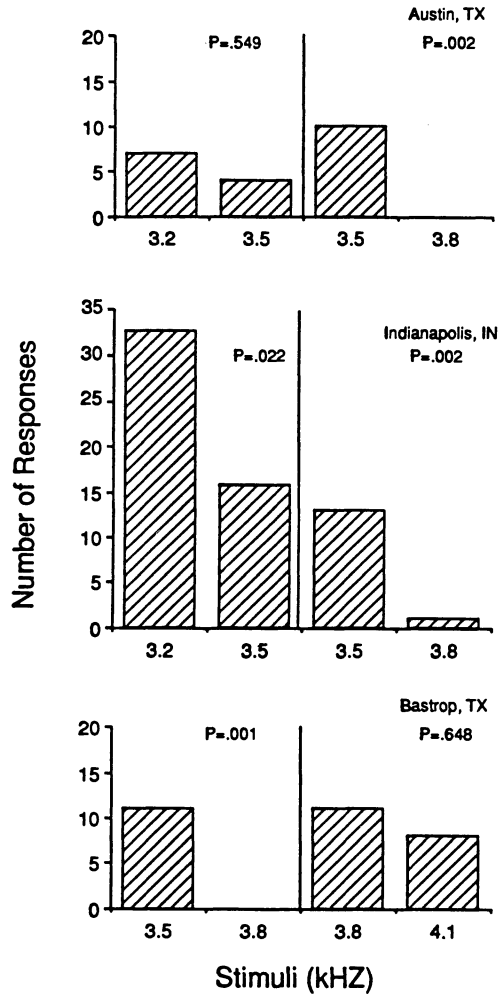


FIG. 3.—The responses of female *Acris crepitans* to various stimulus pairs in phonotaxis experiments.

in frequency. In this case females did not exhibit a significant preference, and the majority of responses was to the foreign call (fig. 3).

The mean dominant frequency of calls from Indiana is similar to that of Austin (fig. 2). In both experiments Indiana females exhibited significant preferences, one for the local call (3.5 kHz vs. 3.8 kHz) and one for the foreign call (3.2 kHz vs. 3.5 kHz). In both experiments females preferred the lower-frequency call (fig. 3). The preference for 3.2 kHz was robust over a substantial intensity range; when the peak amplitude of the lower frequency was reduced by 6 dB, it was still preferred (17 vs. 5; exact binomial probability, $P = .017$).

Females from Bastrop were also given a choice between the local call and a foreign call that was either 300 Hz lower or 300 Hz higher in frequency. In neither

case did the females prefer the local call. They preferred the foreign call of lower frequency (3.5 kHz) to the local call (3.8 kHz), and there was no significant discrimination between the local call and the higher-frequency foreign call (4.1 kHz), although the majority of responses was to the lower-frequency local call (fig. 3).

Each population exhibited a significant preference in at least one of the two choice tests. Two populations showed a preference for local calls to foreign calls, and two preferred foreign to local calls. In all four phonotaxis experiments in which there was a preference, females preferred lower-frequency calls to higher-frequency calls. Furthermore, in all of the six phonotaxis experiments, the females exhibited more responses to the lower-frequency call of the stimulus pair; this is a significantly nonrandom bias (exact binomial probability, $P = .031$). There was no analogous bias when comparing the majority of responses to local versus foreign calls (3:3, exact binomial probability, $P = 1.00$).

Lack of a significant preference between stimuli can result from two causes. Either female response could be random, or female response could be nonrandom; but if different females have different preferences, this would generate apparent random choice within the population. Although never before documented in anurans, it is possible that within a population females respond differentially to frequency. Since the tuning of the basilar papilla and female size are negatively correlated (Keddy-Hector et al., in press), we asked whether female size might predict responses within populations. We examined the results of the three phonotaxis experiments in which there were enough responses to each stimuli to justify statistical analysis. In the experiments with both the Austin and Bastrop females, the mean size of females that preferred the lower-frequency stimulus was larger than the mean size of females that preferred the higher-frequency stimulus, but these differences were not statistically significant (Austin: 3.2 kHz, size [snout-vent length, SVL] $\bar{X} = 29.0$ mm, $SD = 1.45$, $N = 7$; 3.5 kHz, $SVL \bar{X} = 28.4$, $SD = 1.97$, $N = 4$; $t = 0.54$, $P = .60$; Bastrop: 3.8 kHz, $SVL \bar{X} = 28.3$ mm, $SD = 1.79$, $N = 10$; 4.1 kHz, $SVL \bar{X} = 27.6$ mm, $SD = 1.42$, $N = 8$; $t = 0.89$, $P = .39$). Note that in these comparisons the sample sizes are small. However, in the experiments with females from Indiana, which have a much larger sample size, the size of females that preferred the lower-frequency stimulus (3.2 kHz: $SVL \bar{X} = 28.8$ mm, $SD = 1.62$, $N = 33$) was significantly larger than the size of females that preferred the higher-frequency stimulus (3.5 kHz: $SVL \bar{X} = 27.3$ mm, $SD = 1.60$, $N = 16$; $t = 2.93$, $P = .005$). In all three comparisons, the variances of the two groups being compared were not significantly different (Bartlett's test of homogeneity of variances, all P 's $> .05$).

DISCUSSION

Comparisons of population means of call dominant frequency and tuning of the basilar papilla in cricket frogs reveal two general patterns. There is correlated change in these two components of the communication system among populations, but within each population the females' basilar papilla is tuned lower than the mean call frequency (see also Keddy-Hector et al., in press; Wilczynski et

al., in press). The results of the female phonotaxis experiments parallel these two patterns.

In some cases the relationship between call frequency and tuning results in local mate preference, as would be expected from the correlated changes in call frequency and tuning among populations. Thus, population-based mating preferences can result from congruence between the sender and receiver in the spectral domain (as was shown for this species by Nevo and Capranica [1985] and Ryan and Wilczynski [1988]). But because the females' mean tuning is always lower than the males' mean call frequency, there is also a tendency for females to prefer lower-frequency calls. Females did not prefer the local call when it was higher in frequency than the foreign call; and in fact females from Bastrop and Indiana preferred the lower-frequency foreign calls. There was a significant trend across all experiments for preference for lower-frequency calls but not for local calls. Also, W. Wagner (personal communication) presented females from Austin with a choice between two stimuli with dominant frequencies within the population range (3.3 kHz and 3.7 kHz) that were 200 Hz below and above the population mean of 3.5 kHz; females preferred the lower-frequency call (16 vs. 5, exact binomial probability, $P = .027$). Therefore, the mismatch between the mean call frequency and the mean tuning of the basilar papilla generates predictable patterns of mate preference both between and within populations. Regardless of the calls' geographical origin, females prefer lower-frequency calls.

The absolute relationship between the call and tuning explains most but not all of the results of the phonotaxis experiments. In five of the six cases, females exhibited a greater number of responses to the stimulus that was closer in frequency to the mean tuning of the basilar papilla. When females from Bastrop were given a choice between the local call and the lower-frequency foreign call, the females preferred the foreign call although it deviated more from the mean tuning than did the higher-frequency, local call. Therefore, the absolute departure of the call frequency from the mean auditory tuning does not predict the female's response in this experiment; rather, there seems to be a bias toward lower frequencies. This might result from the precise form of the tuning curves; they usually are asymmetric around the most sensitive frequency, with the flanks on the lower-frequency end being more shallow than the flanks on the higher-frequency end (Lewis and Lombard 1988). Therefore, for the same absolute frequency departure from the most sensitive frequency, frequencies below the BEF would elicit greater neural stimulation and presumably be perceived as louder by the female. Such an asymmetry also has been shown in *Physalaemus pustulosus* (Ryan et al. 1990b).

It is not clear whether the slight mismatch between call frequency and tuning represents an adaptation for female mate choice or is the result of a developmental constraint. Larger frogs produce lower-frequency calls, and in several species females prefer these larger males with lower calls (Ryan 1980; Forester and Czarnowsky 1985; Robertson 1986; Morris and Yoon 1989), and females can also gain an immediate reproductive advantage by mating with larger males because they tend to fertilize more of the female's eggs (Ryan 1983, 1985; Robertson 1990).

Therefore, female preference for lower-frequency calls might be favored by direct selection.

The mismatch between tuning and call frequency, however, might be due to allometric constraints. Call dominant frequency decreases with size because it is negatively correlated to vocal cord mass. Similarly, the tuning of the basilar papilla is negatively correlated with size because its resonating properties are frequency-dependent (Zakon and Wilczynski 1988). In most species females are larger than males and thus their basilar papilla is tuned to lower frequencies than is the basilar papilla in males (although there are sexual differences in tuning after the effects of body size are removed statistically; Keddy-Hector et al., in press). This results in a persistent mismatch between male and female basilar papilla tuning. This mismatch in tuning does not explain why females should be tuned lower than the calls of males. But one possibility is that males need to communicate effectively with both sexes, and therefore the male's dominant frequency might be a compromise between the tuning of both sexes and by necessity higher than the female's tuning. In two other frogs, *P. pustulosus* (Ryan et al. 1990b) and *Hyla versicolor* (Gerhardt and Doherty 1988), females prefer calls with lower-than-average frequencies, and this preference coincides with tuning properties of the female's peripheral auditory system. However, in *Hyla crucifer* males are tuned higher than females, but the male call closely matches the female's tuning (Wilczynski et al. 1984). Thus it is not clear whether the mismatch between female tuning and male call frequency that exists in *Acris crepitans*, *P. pustulosus*, and *H. versicolor* is a general phenomenon. If so, it would suggest that female choice in frogs would generally favor characters (i.e., lower frequencies) deviating from the population mean (Ryan 1990a).

An advantage of species-specific mate preference is the promotion of syngamy between complimentary genomes. A similar argument has been advanced for population-based mate preferences (Shields 1982; Baker and Cunningham 1985). However, there are cases of asymmetries in species-specific mating preferences. In fruit flies (Kaneshiro 1980) and in two fishes, swordtails (Ryan and Wagner 1987) and sticklebacks (Moodie 1982), preference for heterospecifics results from females' preferring more elaborate courtship signals. In all of these cases the authors suggested that the more elaborate signals are more stimulating to the females. This applies to our results as well. The preference of the female cricket frogs between populations is a function of the relationship between the female's tuning and the male's call. Calls that are closer to the most sensitive regions of the female auditory system are preferred. Whether the preference be for local or foreign calls in cricket frogs, the population-level preference is clearly not an adaptation to promote syngamy between genetically more similar individuals, since females can prefer foreign calls; instead, it appears to be an epiphenomenon of the allometric relationships of female tuning and male call frequency.

Not only does the tuning-call relationship determine female responses to different frequency calls, it also explains how variation in female call preferences is maintained. Larger females are more sensitive to lower frequencies, and with sufficiently large sample sizes it can be shown that larger females prefer lower

frequencies and smaller females prefer higher frequencies. Therefore, although the mismatch between the average females' tuning and males' call could generate directional selection on call frequency, the size-based variation in female tuning could also contribute to the maintenance of variation in the male trait. A similar phenomenon also has been demonstrated in *Colias* butterflies (Sappington and Taylor 1990).

Many models of sexual selection, whether they be direct selection, good genes, or runaway, assume heritable variation in female mating preferences and also predict correlated evolution of mate traits and preferences (Bradbury and Andersson 1987; Houde and Endler 1990; Kirkpatrick and Ryan 1991). Both of these factors can be initially addressed by documenting phenotypic variation in female preferences, but such studies are not common. Some studies have shown that mating preferences within a species vary, that there can be a heritable component to this variation (e.g., Majerus et al. 1982, 1986; Sappington and Taylor 1990), and that preferences and traits can covary among populations (e.g., Stoner and Breden 1988; Houde and Endler 1990). In our study, we have concentrated on the neural mechanisms that might underlie variation in female preferences. In the cricket frogs, it seems possible that variation of preferences, at least within a population, need not have a heritable component but instead can arise from the effect of body size on tuning of the basilar papilla. If so, none of the models of sexual selection need contribute to our understanding of how this form of preference variation is maintained. However, we also find correlated differences in male call and female tuning frequencies among populations, and these differences are not due to differences in body size alone and thus are not simple epiphenomena of a call-tuning allometry (Ryan and Wilczynski 1991; Wilczynski et al., in press).

Studies of mate preferences at different levels often have resulted in different conclusions (Ryan 1990*b*). Most studies at the species and the population levels find a tight match between sender and receiver that results in homotypic matings, and these studies emphasize the importance of species recognition and stabilizing selection. Many studies of mate preferences within populations, however, show that females prefer males that are not average but deviate from the mean, which suggests that at some level there should be a mismatch between the average sender and receiver (Ryan and Keddy-Hector 1992). These studies emphasize the role of sexual selection in the directional evolution of male traits. There are exceptions to both generalizations (Gerhardt 1988; Kodric-Brown and Hohmann 1990), and there are arguments as to which, if any, of these mate discrimination tasks is the evolved function and which is an incidental consequence (Littlejohn 1981; Paterson 1982; Claridge et al. 1988; Ryan 1990*b*).

We suggest that the degree of concordance between the sender and receiver predicts the type of mate preference but that this concordance is relative, depending on whether it is being compared among species, populations, or individuals within populations. When compared to the calls of other species, the auditory periphery of *Acris crepitans* closely matches the conspecific call properties, but there are significant mismatches between sender and receiver among and within populations. At least in this study, a knowledge of the sensory mechanisms has

provided a better understanding of the origin and maintenance of variation in mate preferences.

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