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Call Patterns and Basilar Papilla Tuning in Cricket Frogs.

I. Differences among Populations and between Sexes

Key Words

Acoustic communication
Amphibian
Audition
Basilar papilla
Geographic variation
Sex differences
Acris crepitans

Abstract

Male cricket frogs (*Acris crepitans*) produce a broad-band, high frequency advertisement call with a single spectral peak (the dominant frequency). We measured the dominant frequencies of male calls from six populations in central Texas and one from Indiana and compared them to the tuning of basilar papilla afferents in males and females. Averaging over all populations, mean call dominant frequency was 3.69 kHz, mean male basilar papilla tuning was 3.63 kHz, and mean female basilar papilla tuning was 3.17 kHz. Among populations, mean dominant frequency varied from 3.56 kHz to 3.82 kHz. Dominant frequencies were slightly higher in the more eastern Texas populations occupying pine forest habitats than in the more western populations occupying open grassland habitats. Changes in dominant frequency in a population coincided with changes in tuning of both male and female basilar papillae. Furthermore, within populations females were tuned on average lower than males and lower than the mean dominant frequency of calls in their own population. We suggest that the coincident changes in calls and basilar papilla tuning plus the sexual difference in tuning indicate that female mate choice would be directed toward males from her home population with low frequency calls or toward males from foreign populations with average calls lower in frequency than those in her home population. This in turn suggests that any gene flow between populations would be biased from east to west and from forest to open habitats.

Introduction

A fundamental principle of neuroethology is that properties of the sensory systems used for communication match species-specific characteristics of communication signals. Capranica's seminal studies of bullfrogs and subse-

quent studies of a variety of anurans have shown that a congruence between species-specific advertisement call properties and the auditory system begins at the periphery in the form of interspecific differences in the tuning of inner ear auditory receptors [Capranica, 1976; Capranica and Moffat, 1983; Zakon and Wilczynski, 1988; Feng et al., 1990].

In all anuran amphibians, auditory receptor organs are divided between two inner ear organs [Capranica, 1976; Wilczynski and Capranica, 1984; Lewis and Lombard, 1988; Zakon and Wilczynski, 1988], the amphibian papilla (AP) and the basilar papilla (BP). Within an individual, all BP afferents have approximately identical best excitatory frequencies [Ehret and Capranica, 1980; Capranica and Moffat, 1983; Wilczynski et al., 1984; Zakon and Wilczynski, 1988] while AP afferents are tuned to a range of lower frequencies. Both the AP and BP show interspecific differences [Capranica, 1976; Walkowiak, 1988; Zakon and Wilczynski, 1988], but interspecific variation associated specifically with call variation is much more apparent in the tuning of the BP. In many species, best excitatory frequencies (BEFs) of the VIIIth cranial nerve afferents innervating the BP match a spectral peak in the species-specific advertisement (or mating) call. Many small frogs have high frequency calls in which spectral energy overlaps only the BP's sensitivity band [Zakon and Wilczynski, 1988].

The match between the spectral characteristics of the call and the tuning of the auditory system is an important factor in maintaining reproductive isolation in a species by facilitating interspecific mate recognition [Blair, 1964]. In many anurans, females use the male advertisement call to locate and recognize conspecifics during the breeding season [Wells, 1977; Ryan, 1985; Gerhardt, 1988; Rand, 1988]. A match between the species-specific call and the ear's tuning maximizes the frog's sensitivity to its own species' call, thereby extending the distance over which the call can be detected [Brenowitz, 1986; Wilczynski, 1986] and biasing the female phonotaxis behavior toward it [Gerhardt, 1988].

The characteristics of the call can also be important determinants of intraspecific mate choice. In a variety of anurans, particular temporal or spectral call values bias female phonotaxis in two-choice experiments or correlate with enhanced mating success [Capranica et al., 1973; Ryan, 1985; Narins and Smith, 1986; Schwartz, 1986; Sullivan and Leek, 1987; Gerhardt, 1988; Wells, 1988]. The use of spectral cues for intraspecific mate choice suggests that, by analogy with interspecific mate choice, the relationship of the dominant frequency of a male's advertisement call to the tuning of a female's peripheral auditory system could bias her choice toward particular males [Ryan et al., 1990a]. In fact, in the cricket frog (*Acris crepitans*) and the tungara frog (*Physalaemus pustulosus*) the tuning of the female's BP predicts her phonotaxis behavior when she is given a choice between conspecific advertisement calls varying only in dominant frequency [Capranica et al., 1973; Ryan and Wilczynski, 1988; Ryan et al., 1990a, 1992].

Because the relationship between peripheral auditory tuning and the spectral characteristics of the call can influence mate choice, understanding the nature of variation in these parameters within a species becomes important for understanding the behavioral evolution of that species. This variation can take several forms. Calls and auditory characteristics can vary geographically among conspecific breeding populations [Nevo and Capranica, 1985; Narins and Smith, 1986; Littlejohn, 1988; Ryan and Wilczynski, 1991]. Variation in tuning has been studied less systematically. However, comparisons between isolated populations suggest that, on average, individuals are tuned more closely to their own population's calls than to those of a geographically separate conspecific population [Capranica et al., 1973; Ryan and Wilczynski, 1988]. Variation also occurs within populations. Again, patterns of call variation have been examined more closely than variations in tuning [Ryan, 1985; Robertson, 1986; Sullivan and Wagner, 1988; Wagner, 1989a]. Variation in call dominant frequency among conspecific males is often correlated with body size [Zweifel, 1968; Ramer et al., 1983; Ryan, 1985; Narins and Smith, 1986; Sullivan and Wagner, 1988; Wagner, 1989a]. One study has reported that female tuning also varies with body size [Wilczynski, 1986], but in most studies auditory characteristics are reduced to population or species means and compared against similar means for the call. Finally, calls and tuning may vary according to sex. Sex differences in tuning, and in call characteristics in species in which both sexes vocalize [Dixon, 1957; Rand, 1988; McClelland and Wilczynski, 1989], have been reported for several anuran species [Narins and Capranica, 1976; Wilczynski et al., 1984; Wilczynski, 1986].

Variation in calls and tuning provides the raw material for processes directing the evolution of acoustic communication in anurans. Because communication underlies reproductive behavior, such variation would dictate the presence and direction of sexual selection and might underlie processes as fundamental as speciation if, for example, interpopulational differences lead to reproductive isolation [Nevo and Capranica, 1985; Littlejohn, 1988; Ryan and Wilczynski, 1988]. In this paper and its companion, we therefore examined all three types of variation (interpopulational, interindividual, and sexual) in the dominant frequency of the advertisement call and the tuning of the basilar papilla, the auditory organ that receives it, in a single species, the cricket frog, *Acris crepitans*.

Acoustic Communication in Cricket Frogs

Cricket frogs are small hylids occupying a wide geographic range encompassing the eastern two-thirds of the

United States. An eastern subspecies, *Acris crepitans crepitans*, and a western subspecies, *Acris crepitans blanchardi*, are recognized. The boundary separating the geographic ranges of the subspecies runs through East Texas. The advertisement call produced by male cricket frogs is a relatively broad-band, pulsatile signal with a dominant frequency of about 3.5 kHz and a stereotypical temporal pattern [Wagner, 1989a; Ryan and Wilczynski, 1991]. All spectral and temporal call characteristics vary geographically among cricket frog populations [Nevo and Capranica, 1985; Ryan and Wilczynski, 1991]. Most of the variation is clinal; in general, eastern populations produce higher pitched, shorter, more rapid calls than western populations. Call characteristics also differ significantly between open and forest habitats [Ryan and Wilczynski, 1991; Ryan et al., 1990b]. As in other anuran species, body size correlates negatively with dominant frequency [Wagner, 1989a]. However, body size differences do not account for clinal or habitat differences in the call [Ryan and Wilczynski, 1991].

Capranica et al. [1973] and Ryan and Wilczynski [1988], each examined two cricket frog populations and found that the energy in the advertisement call was restricted to the sensitivity range of the basilar papilla and that BP tuning differences between populations resulted in each population being more closely tuned to its own population's calls. However, it should be noted that male and female tuning were not distinguished in either of these studies. This omission might mask sex differences in BP tuning, which have been reported in other anuran species [Wilczynski et al., 1984; Wilczynski, 1986; Zakon and Wilczynski, 1988].

We extended this previous work by examining the pattern of the dominant frequency of the male advertisement call and the tuning of the basilar papilla in males and females in a series of geographically separate, but closely spaced, populations of *A. c. blanchardi* in an east-west cline across central Texas and in an Indiana population located well north of that cline. In this paper we report on the pattern of interpopulational and intersexual differences in the call and BP tuning. In a second paper, we examine intrapopulational variation in these aspects of cricket frog acoustic communication [Keddy-Hector et al., 1992].

Materials and Methods

Advertisement calls were recorded from *Acris crepitans blanchardi* males in six populations in central Texas along a 100 km transect at 30.5° (+/- 0.5°) latitude and one population near Indianapolis, Indiana, northeast of the transect. The Indiana population was included to check whether the relationship between calls and tuning in

the Texas populations was idiosyncratic to that latitude. Calls were obtained during the breeding seasons (April–July) from 1986–1989. The three easternmost of the six Texas populations (identified as Stengel Ranch, Bastrop and South Lake Bastrop, with longitudes of 97.10°, 97.20°, and 97.21° respectively) are in the isolated pine forests in Bastrop County, Texas, while the other three (Nichols Ranch, Gill Ranch, and Wimberley, with longitudes of 97.50°, 98.08°, and 98.10°) occupy open grassland typifying the central Texas Hill Country. Ten to 15 calls of each of 10 males in the Texas populations were recorded, except for the Nichols Ranch site, where only four males were sampled due to the small size of that population. Nine males were sampled from the Indiana population. Calls were recorded from undisturbed, naturally vocalizing males in breeding choruses on metal tape using either a Sony TCD-5M cassette recorder, Marantz PMD 420 cassette recorder, or a Uher 4400 Report tape recorder and a Sennheiser ME80 microphone with K3U power module and M2W415 windscreen. The temperature at each male's calling site was recorded.

Call Analysis

Call dominant frequencies were determined by performing a fast Fourier transform on the call with a Data 6000 digital waveform analyzer at a sampling rate of 10 kHz and a resolution of 12 Hz. The dominant frequencies for each male's recorded calls were averaged to yield a mean dominant frequency for each male. The dominant frequency was defined as that frequency with the greatest amount of energy. Although male *Acris crepitans* are capable of changing the dominant frequency of their call during social interactions [Wagner, 1989b, c], the sample of calls we obtained for each male did not differ in dominant frequency. The resultant dominant frequency for each male was corrected for temperature at the call site according to equations derived by Wagner [1989a] for this subspecies. However, spectral characteristics change little with temperature, and the temperature variation at each call site was so small as to require little correction of this call parameter.

Neurophysiology

Successful, unambiguous characterization of BP tuning was obtained in a total of 66 frogs from the 7 populations. Animals from which no auditory activity could be isolated, from which only amphibian papilla fibers were isolated, or animals in which the best excitatory frequencies (BEFs) of isolated BP fibers could not be clearly characterized were not included in this study. Due to difficulties in collecting animals and performing the physiological experiments on such small animals (snout-vent lengths of approximately 19–24 mm and head widths of 7–10 mm), BP tuning was ultimately obtained from a variable number of animals from each population. The number of male (M) and female (F) frogs from each population was as follows: Stengel Ranch: 12F, 7M; Bastrop: 0F, 4M; South Lake Bastrop: 0F, 2M; Nichols Ranch: 2F; 0M; Gill Ranch: 5F, 6M; Wimberley: 15F, 9M; Indiana: 4F, 0M. That is, female tuning and male tuning were each determined in 5 of the populations from which call data were obtained, and both sexes were characterized in 3 of these populations.

With the exception of the 2 females from the Nichols Ranch and 6 of the Gill Ranch frogs, BP tuning was obtained by recording single unit activity in the VIIIth cranial nerve. For this procedure, frogs were anesthetized by immersion in 2.5% Urethane. The VIIIth nerve was exposed through the roof of the mouth by cutting a skin flap and drilling a small hole in the underlying skull with a dental drill. (The small head size of these frogs precluded using a dorsal approach through the top of the skull.) The skin flap was then repositioned over the expo-

sure and the frog was allowed to recover for 1–3 days. The frog was then immobilized by an intramuscular injection of curare and the roof of the mouth was locally anesthetized with 2% lidocaine. The frog was placed on its back on a cork platform inside an Industrial Acoustics audiometric room and an earphone was sealed over the tympanic membrane ipsilateral to the exposed nerve. A 3M KCl-filled glass microelectrode was lowered into the nerve using a hydraulic micro-drive. Once isolated, an auditory fiber's BEF and tuning curve was determined by standard techniques [Wilczynski et al., 1984; Ryan and Wilczynski, 1988] using 300 msec tone bursts presented every 1.5 seconds. The BEFs of BP fibers usually varied within an individual by no more than ± 25 Hz. For each individual frog, the BP BEFs were averaged together to yield a single mean BEF for that individual. Tuning curves of AP fibers were also taken, but as energy in the call does not overlap the best frequencies of AP fibers [Capranica et al., 1973; Ryan and Wilczynski, 1988], their characteristics are not reported here.

In the 8 frogs listed above as exceptions, BP tuning was derived from multiunit audiograms recorded from the torus semicircularis. These frogs were anesthetized as above. The dorsal surface of the mid-brain was exposed by incising and retracting the skin over the skull, drilling through the underlying bone with a dental drill, and removing the meninges over the optic tectum. The animal was allowed to recover for 1–3 days, then immobilized with curare and locally anesthetized with 2% lidocaine. The frog was then placed on the cork platform inside the audiometric room, an earphone was sealed over one tympanic membrane, and a low impedance (1–2 MOhms), 3M KCl-filled glass microelectrode was lowered through the optic tectum into the underlying torus semicircularis. Once robust auditory-evoked activity was found using a multi-tone search stimulus, an audiogram (threshold intensity as a function of frequency) was determined by standard techniques using 300 msec tone bursts repeated every 1.5 sec [Ryan et al., 1990a]. Recordings were made in multiple sites in the torus. No tonotopy was observed, probably due to the very small size of the torus in these frogs and the gross nature of the multi-unit recording procedure. As a result, every audiogram produced in an individual frog had sensitivity peaks at virtually the same frequency and at similar thresholds, and therefore summary audiograms for each frog were derived by averaging all the audiograms obtained from it.

The research procedures used in this study were approved by the University of Texas Institutional Animal Care and Use Committee.

Results

Call Characteristics

As reported previously [Nevo and Capranica, 1985; Ryan and Wilczynski, 1988, 1991; Wagner, 1989a], the species-typical advertisement call of *Acris crepitans* is a broadband (band width approximately 1.0 kHz) signal marked by a single, distinct spectral peak, the dominant frequency, in the middle of the frequency distribution (fig. 1). Across all populations, the mean dominant frequency was 3.69 kHz. Each population could be characterized by its own dominant frequency (table 1, fig. 2). The three populations occupying pine forest habitats had on average only slightly

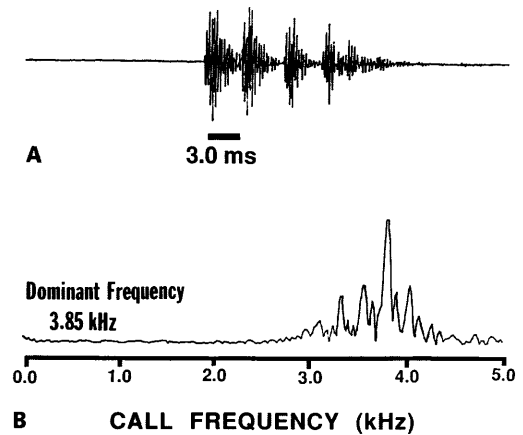


Fig. 1. Oscillogram (A) and power spectrum (B) of a typical call from a Stengel Ranch male *Acris crepitans*.

higher dominant frequencies (Stengel = 3.82, Bastrop = 3.77, South Lake Bastrop = 3.66 kHz) than those occupying the open grassland habitats (Nichols Ranch = 3.78, Gill Ranch = 3.56, Wimberley = 3.75 kHz). The Indianapolis population's call had a dominant frequency of 3.54 kHz.

An assessment of the east-west clinal variation across Texas [Ryan and Wilczynski, 1991; see also Nevo and Capranica, 1985] from high to low dominant frequencies is confounded by habitat effects in this sample because the eastern most populations all resided in pine forests, a habitat correlated with high frequency calls independent of longitude [Ryan and Wilczynski, 1991]. Furthermore, the distances between populations are so small relative to the slope of the clinal variation reported by Ryan and Wilczynski [1991] that strong statements about clinal changes can not be made here.

Basilar Papilla Tuning

Clearly defined BP tuning was obtained in 66 individuals (38 female, 28 male). For the VIIIth nerve recordings, multiple BP fibers were isolated in all but two frogs. Representative tuning curves from two populations are presented in figure 3.

Toral multiunit audiograms were obtained only from individuals from the Nichols and Gill Ranches. No single unit data were obtained from Nichols Ranch frogs, but such data were gathered from a separate set of Gill Ranch frogs.

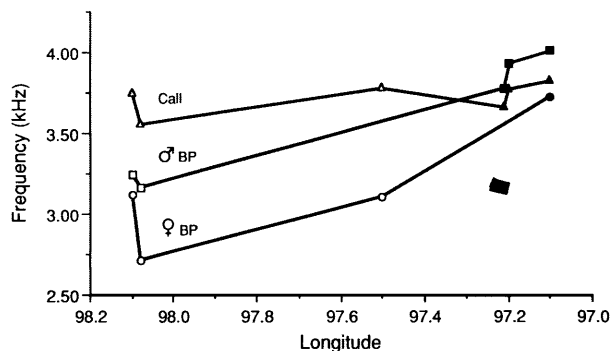


Fig. 2. Plot of mean values for call dominant frequency (triangles), female basilar papilla BEF (circles), and male basilar papilla BEF (squares) vs. longitude for the six Texas populations of *Acris crepitans blanchardi*. The three easternmost populations occupying pine forest habitats are at the right (filled symbols) and the three occupying open grassland habitats are at the left of the graph (open symbols). See also table 1.

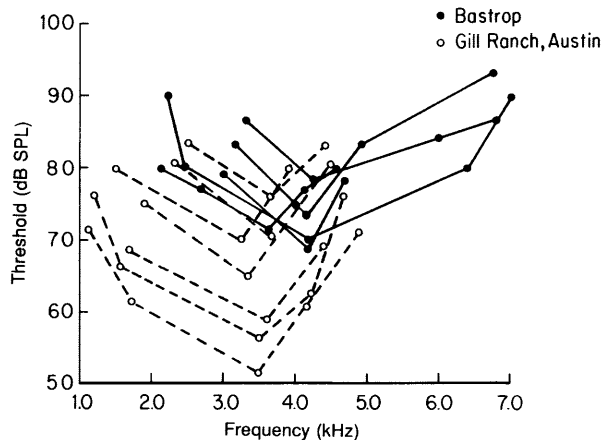


Fig. 3. Representative basilar papilla tuning curves for two Gill Ranch and two Bastrop male cricket frogs. Thresholds varied widely among frogs within a population and among units within a frog.

Table 1. Summary of means (plus standard error) for call dominant frequency, female basilar papilla tuning, and male basilar papilla tuning in *Acris crepitans* populations from open grassland and pine forest habitats in Texas and from a population in Indiana

Habitat	Open			Forest			
	West					East	North
Location	Wimberley	Gill	Nichols	S.L. Bastrop	Bastrop	Stengel	Indiana
Longitude	98°10"	98°08"	97°30"	97°21"	97°20"	97°10"	86°10"
Call DF (kHz)	3.75 (0.20)	3.56 (0.05)	3.78 (0.07)	3.66 (0.05)	3.77 (0.04)	3.82 (0.45)	3.54 (0.04)
Female tuning (kHz)	3.12 (0.17)	2.71 (0.16)	3.10 (0.50)	–	–	3.72 (0.17)	3.22 (0.04)
Male tuning (kHz)	3.24 (0.16)	3.19 (0.22)	–	3.77 (0.02)	3.93 (0.19)	4.01 (0.76)	–

A comparison between BEFs obtained by the two methods in the different Gill Ranch frogs suggested that the toral data yielded slightly lower estimates of BP tuning. However, use of the toral data does not alter the pattern of geographic or intersexual variation in tuning apparent from the single unit data, and therefore they were included in this study.

The mean BP BEFs for males and females in each population are listed in table 1. Averaging across all populations, male BP tuning was 3.63 kHz while mean female tuning was 3.17 kHz. The overall species sex difference in tuning was confirmed by inspecting the populations from

which both males and females were sampled. In each of these three populations, females were tuned lower than males (fig.4). A statistical analysis of these differences is presented in the following paper [Keddy-Hector et al., 1992].

Furthermore, in every population examined, the mean BP tuning of females was below the mean dominant frequency of the male calls (table 1, fig.2). By contrast, the relationship between male tuning and call dominant frequency within a population varied (table 1, fig.2). In three Texas pine forest habitats, males were tuned higher than the average calls produced in their population. In two open

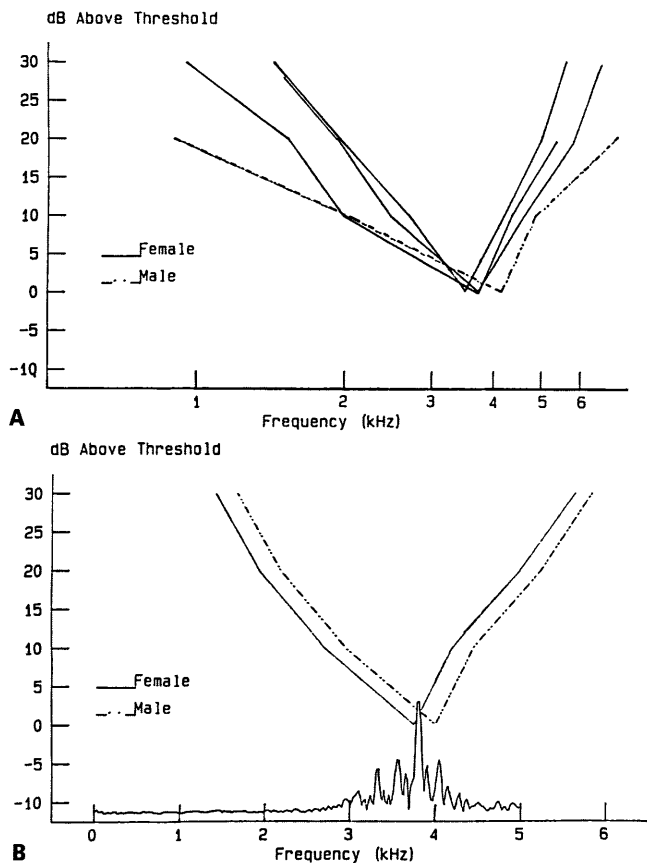


Fig. 4. **A** Basilar papilla tuning curves from a female and a male cricket frog from the Stengel Ranch population. **B** Diagrammatic representation of average Stengel Ranch male and female basilar papilla tuning curves and their relationship to an average power spectrum of a male advertisement call from the Stengel Ranch population. dB scale relates to the tuning curves only, not the power spectrum.

habitats, males were tuned lower than the average calls in their population, although not as low as the females. The net result is that, averaging across all populations, mean male BP tuning (3.63 kHz) is virtually identical to mean male call dominant frequency (3.69 kHz) while mean female BP tuning is considerably lower (3.17 kHz), although the statistical representation for males is deceiving, as call frequency and male BP tuning were not precisely matched in any population.

Geographic variation in BP tuning followed geographic variation in call dominant frequency in that an increase or decrease in call dominant frequency was coupled with a shift in both male and female tuning in the same direction

(table 1). However, calls and tuning did not shift between populations by an equal amount. Across the sampled populations BP tuning in both sexes changed much more than the call dominant frequency (fig. 2). This appears to reflect a pattern in which the western open habitat populations compared to the eastern forest habitat populations manifest a substantial lowering of both male and female BP tuning and a shift in both away from the mean call dominant frequency in their population. Geographic shifts of tuning and calls are much more nearly equal if one looks across populations within a habitat category.

Discussion

Different anuran species are characterized by species typical calls and species typical auditory systems whose response properties generally match the properties of the call [see reviews in Fritzsche et al., 1988]. While this is certainly true on average, our results in this and earlier studies [Ryan and Wilczynski, 1988; Ryan et al., 1991] demonstrate that neither the call nor the properties of the auditory system are static within a species even across relatively short geographic distances. Although calls and tuning generally shift in the same direction across populations, population variation in the quantitative relationship between them, in addition to a sex difference in BP tuning, indicates a more complicated, more dynamic communication system than implied by the concept of matching at the species level.

Males in each of the investigated populations produced the broad-band, high frequency pulsatile call characteristic of *Acris crepitans*. However, each population was marked by population-specific dominant frequencies and temporal features. This geographic variation is in part related to the habitat occupied by the population. As reported by Ryan and Wilczynski [1991], cricket frog populations in forest habitats have higher frequency, as well as faster and shorter, calls. An analysis of the transmission of calls through the different habitats in which cricket frogs are found [Ryan et al., 1990b] suggested that habitat selection on the call contributes to this difference. Higher frequency, faster calls degrade less than the lower frequency, slower calls in the forest habitat.

The current study shows that shifts in the call dominant frequency among populations coincide with shifts in BP tuning in both sexes. Sample sizes for the physiological data were small in several of the populations. The problem this represents for interpreting the data can be remedied to some extent by collapsing the population means across

habitats and examining how calls and tuning shift as one moves out of the pine forest habitat occupied by the Stengel, Bastrop, and South Lake Bastrop populations. Moving either west into the open habitat of the remaining Texas populations or northeast to the Indiana population yields a slight drop in the call dominant frequency and a larger drop in BP tuning in both males and females. A more thorough statistical analysis of two populations with adequate sample sizes of both males and females, Wimberley and Stengel Ranch, is presented in a companion paper [Keddy-Hector et al., 1992].

The physiological results show a sex difference in BP tuning. The average male cricket frog has a BP with a BEF of 3.63 kHz and the average female has a BP tuned to 3.17 kHz. The difference is confirmed in the three populations in which tuning in both sexes was assessed. In each, female BP tuning lies below male tuning. In the two populations, Wimberley and Stengel Ranch, with sample sizes for both sexes adequate to support a statistical test, the differences are significant [Keddy-Hector et al., 1992].

In two other anuran species in which a sex difference in BP tuning was observed, *Eleutherodactylus coqui* [Narins and Capranica, 1976] and *Hyla crucifer* [Wilczynski et al., 1984], females were also tuned lower than males. As BP tuning varies inversely with body size in frogs [Zakon and Wilczynski, 1988], and as females are generally larger than males, Wilczynski [Wilczynski et al., 1984; Wilczynski, 1986] hypothesized that an anuran sex difference in BP tuning may simply be due to the sex difference in body size. However, a careful allometric analysis of BP tuning and body or head size, discussed in detail in the following paper [Keddy-Hector et al., 1992], shows that this simple explanation does not hold for cricket frogs. Similarly, body size differences among populations are not sufficient to explain the differences in either calls or tuning [Ryan and Wilczynski, 1988, 1991; Keddy-Hector et al., 1992].

Although the difference between male and female BP tuning is consistent with previous findings, the relationship between BP tuning in the sexes and the call dominant frequency is somewhat surprising. In both *Hyla crucifer* [Brenowitz et al., 1984; Wilczynski et al., 1984] and *Eleutherodactylus coqui* [Narins and Capranica, 1976] the sex difference in BP tuning results in female auditory systems being matched to the dominant frequency of male calls while the males are tuned higher than the call. By contrast, in *Acris crepitans* mean female tuning is consistently lower than the mean dominant frequency of the male call in each of the five populations examined. The relationship between male BP tuning and the call is more variable. In each of the pine forest populations, males are tuned higher than the call,

while in the open habitat they are tuned considerably lower (table 1, fig.2). Within a population, neither sex may be tuned precisely to the peak energy in the advertisement call. One difference between *Acris crepitans* and either *H. crucifer* or *E. coqui* is that in the latter two species the call, or in the case of *E. coqui* the 'qui' note, stimulating the BP is virtually a pure tone [Narins and Capranica, 1976; Wilczynski et al., 1984], whereas the cricket frog call has energy spread over a 1.0 kHz band [Wagner, 1989a; Ryan and Wilczynski, 1991]. Perhaps this difference means that the need to exact a precise match between the call and BP tuning is relaxed in this species because the broad-band nature of the call ensures some stimulation of the BP receptors even when the call dominant frequency and the BP BEF are not precisely matched (fig.4B).

However, even though the band-width of the call may be large, cricket frogs can still discriminate among calls when dominant frequencies differ by a few hundred Hz [Nevo and Capranica, 1985; Ryan and Wilczynski, 1988; Wagner, 1989b, c]. As in several other species, frequency differences can bias the phonotaxis of reproductively-ready females toward the stimulus that most closely matches the BEF of her BP [Ryan and Wilczynski, 1988; Ryan et al., 1990a]. While frequency resolution by the BP may be limited [Zakon and Wilczynski, 1988], the differences that can be resolved by frogs in the populations we studied [Ryan and Wilczynski, 1988; Wagner, 1989b, c; Ryan et al., 1992] are sufficient to distinguish differences in the average call dominant frequencies among populations.

Given that population differences in the calls exist [Nevo and Capranica, 1985] and that cricket frogs may be able to discriminate them [Ryan and Wilczynski, 1988; Wagner, 1989b, c], the coincident shifts in male calls and female BP tuning suggests that mate choice would often, but not always, be biased toward males in the population in which the female resides, particularly towards males with lower than average calls. However, because females are on average tuned to frequencies lower than those used by the average male in her population, the strength of the bias should differ among populations. Females from open habitats should discriminate against calls from forest populations more strongly than forest females should discriminate against calls from open habitats. This is because open habitat females are tuned much further away from forest calls than forest females are from open habitat calls. Female choice tests [Ryan and Wilczynski, 1988; Ryan et al., 1992] support this. Females from the open habitat Gill Ranch population preferentially move toward synthetic calls with a dominant frequency like the mean of their own population's calls over a synthetic call with a higher dominant fre-

quency like that seen in the forest population at the Bastrop site. By contrast, Stengel Ranch females prefer the lower frequency Gill Ranch call over the higher calls produced by males in their own population.

Over the geographic range inhabited by *Acris crepitans*, calls decrease in dominant frequency from east to west [Ryan and Wilczynski, 1991]. Because females are generally tuned lower than their own populations, they should on average discriminate more strongly against calls from more easterly populations than more westerly populations. The clinal trend in call dominant frequency [Nevo and Capranica, 1985; Ryan and Wilczynski, 1991] and the consistent tuning of female BPs below the average call of their own population therefore predicts an asymmetric gene flow from the eastern subspecies *Acris crepitans crepitans* to the western subspecies *Acris crepitans blanchardi*. Similarly, within *Acris crepitans blanchardi* there may be asymmetric gene flow from east to west and from forest to open habitats.

An examination of population means, like an examination of species means, is not sufficient to fully

understand the dynamics of acoustic communication within a species. An examination of geographic variation in both vocal and auditory characters does provide insights into such processes as the pattern of gene flow, habitat effects, and the potential for speciation due to population-based mate choice. However, to gain insight into how characters might shift between populations and how mate choice could yield sexual selection, an examination of variation within a population, the true breeding unit of the species, is necessary. The following paper [Keddy-Hector et al., 1992] therefore analyzes intrapopulation variation in call dominant frequency and male and female BP tuning in two populations of *Acris crepitans blanchardi*.

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