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Call Patterns and Basilar Papilla Tuning in Cricket Frogs. II. Intrapopulation Variation and Allometry

Key Words

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Abstract

We determined the influence of body size on the male advertisement call's dominant frequency and basilar papilla's (BP) tuning in male and female cricket frogs (*Acris crepitans*) in two Texas populations (Wimberley and Stengel Ranch). In both populations, call and tuning characters correlated negatively with body size; females were larger than males and their BPs were tuned to a lower frequency. Analysis of covariance showed that neither the sex difference in tuning nor the population differences in calls or tuning were due to the difference in body size alone, but instead represented differences in the allometric relationships of each character with body size. The analysis implied that differences between sexes or populations were due more to shifts in the Y-intercept rather than the slope of the relationship with body size. This suggests a developmental model in which sexes or populations possess resonant structures in the ear or larynx with similar growth rates but different starting points or initial growth phases, resulting in different frequency characteristics as adults. The examination of the relationship between female BP tuning and male call dominant frequency predicts potentially different patterns of sexual selection in the two populations, with the Wimberley population males subject to much greater directional selection for low frequency calls.

Introduction

It has long been recognized that intraspecific communication often guides reproductive behavior and that the signals used for this purpose are species specific [Huxley, 1942; Mayr, 1942; Dobzhansky, 1951]. Males of different species give significantly different signals and females use those cues to recognize potential conspecific mates. Thus

interspecific variation in communication signals can result in reproductive isolation.

Variation in communication signals and sensory systems within a species can also be important. Because speciation results from the divergence of conspecific populations, intraspecific variation could drive the speciation process by creating ethological isolation between populations. One of the early conclusions to emerge from sexual selection the-

ory was that mating preferences which differ between populations could eventually lead to reproductive isolation [Tauber and Tauber, 1977a, b; Lande, 1981; West-Eberhard, 1982]. Ryan and Wilczynski [1988] supported this idea by showing that female cricket frogs (*Acris crepitans*) often prefer the advertisement calls of local males over neighboring conspecifics.

Intraspecific variation in signals and receivers exists not only between populations but within populations. Such variation can lead to variation in mate choice and reproductive success and thus generate sexual selection [Ryan, 1985; Ryan, 1990a, b; Ryan et al., 1990a, 1992]. As sexual selection can drive the evolution of signals, variation in signals and preferences for those signals could lead to divergence of signals within a species.

In this and the previous paper [Wilczynski et al., 1992] we use cricket frogs (*Acris crepitans*) as models to study patterns of intraspecific variation in acoustic communication. Cricket frogs are members of the family Hylidae. Their range extends over most of the eastern United States. Males produce broad-band, click-like advertisement calls that serve to attract females and repel other males [Nevo and Capranica, 1985; Ryan and Wilczynski, 1988; Wagner, 1989]. Previous work on acoustic communication in this species [Capranica et al., 1973; Nevo and Capranica, 1985; Ryan and Wilczynski, 1988; Ryan et al., 1990b] and anurans in general is summarized in the previous paper [Wilczynski et al., 1992]. In brief, like most other anurans [Geisler et al., 1964; Capranica, 1976; Wilczynski and Capranica, 1984; Zakon and Wilczynski, 1988], cricket frogs possess two auditory organs, the amphibian papilla (AP) and the basilar papilla (BP), each innervated by the VIIIth cranial nerve. Afferent fibers from these organs have distinctive auditory sensitivities. In anurans, the AP is most sensitive to low and mid-ranged frequencies while the BP is most sensitive to high frequencies [Wilczynski and Capranica, 1984; Zakon and Wilczynski, 1988; Feng et al., 1990]. Furthermore, BP afferent fibers are sensitive to approximately the same frequencies within an individual but vary between individuals [Capranica et al., 1973; Ehret and Capranica, 1980; Capranica and Moffat, 1983; Wilczynski et al., 1984]. Energy in the cricket frog advertisement call falls only in the sensitivity range of the BP [Capranica et al., 1973; Ryan and Wilczynski, 1988].

The previous paper [Wilczynski et al., 1992] demonstrated that the average best excitatory frequency (BEF) of the female cricket frog BP changes with changes in the average dominant frequency of the male call across populations. Moreover, females are tuned on average lower than the dominant frequency of male calls within their popula-

tion. The pattern of variation suggests the possibility of intrapopulation mate choice and sexual selection for lower than average frequency calls. This follows from results indicating that as a male's signal converges with the tuning of a female's receptor, the likelihood that she will mate with him increases [Ryan and Wilczynski, 1988; Ryan et al., 1992].

The possibilities for mate choice depend in part on the pattern of intrapopulation variation in the male call. Further, the strength and direction of selective pressure produced by female mate choice will depend upon the amount and nature of variation in female preferences, i.e. in female BP tuning. If females all prefer the lowest frequency call, female choice will culminate in strong directional selection for low frequency advertisement calls. If females exhibit variation in their preferences, however, this variation could result in stabilizing, disruptive, or directional selection depending upon how the variation in preferences interacts with variation in the male trait. Hence in order to examine the effect sexual selection will have on a given population of cricket frogs, one must examine the pattern of variation in male calls and female auditory tuning and how these communication parameters relate to each other.

A more proximate question is what generates the variation upon which selection might act. Several studies have shown that both within and between species body size correlates with the dominant frequency of a male's advertisement call. In many anuran species, as body size increases, the dominant frequency of calls decreases [Blair, 1958; Ryan, 1980, 1985; Nevo and Capranica, 1985; Wagner, 1989]. Body size differences do not account for interpopulation call differences in cricket frogs [Ryan and Wilczynski, 1988, 1991]. However, variation in male body size within a population might be important if it leads to variation in the dominant frequency of the call within it [Arak, 1983; Ryan, 1983, 1985].

Less is known about the correlates of variation in the tuning of the female auditory system. Wilczynski et al. [1984] suggested that in *Hyla crucifer* females body size was inversely correlated with the best excitatory frequency (BEF) of the BP. Since the BP may act as a simple resonating structure [Capranica and Moffat, 1977], it is reasonable to predict that an allometric relationship exists between body size and BP tuning in both males and females.

In the present study we examined variation in call characteristics and BP tuning within two populations of cricket frogs in central Texas. Specifically, we investigated: (1) if variation in female or male tuning exists within populations, and if so whether it varies as a function of body size; (2) how variation in the male calls and variation in female

tuning relate to each other within populations, and (3) if the patterns of communication characters differ between populations so as to suggest differences between populations in the intensity or direction of selection.

Materials and Methods

Male and female (*Acris crepitans*) were collected from two populations in central Texas. The first collection site, Wimberley, is a spring fed stream located on the Edwards Plateau 40 km southwest of Austin. The second site, Stengel Ranch, is a stockpond located in a loblolly pine woodland 50 km east of Austin.

Call Analysis

Recordings of advertisement calls of each male were made on metal tape using a Sennheiser ME80 microphone with a K3U power module and a M2W415 windscreen and a Sony TCD-5M or Marantz PMD 420 cassette tape recorder. Recordings were made as the male called spontaneously in its breeding chorus. Each male was then collected and its snout-vent length measured. Air temperatures were recorded from the calling substrate and males were either given a unique sequence of toe clippings (to prevent recapturing the same individual), and released, or retained for neurophysiological experiments. Calls were analyzed on a Data 6000 digital waveform analyzer in the same manner as described in the previous paper [Wilczynski et al., 1992]. Three calls were analyzed for each male: one each from the beginning, middle, and end of a call group. The dominant frequency was averaged over the three calls and corrected for temperature [see Wagner, 1989]. The calls of a total of 102 males were recorded from the two populations: 86 from the Wimberley population and 24 from the Stengel Ranch population.

Neurophysiology

Frogs were anesthetized by immersion in 2.5% urethane, and the VIIIth nerve was exposed through the roof of the mouth. The exposure was then covered with tissue paper and the animal allowed to recover. Two days later, individuals were immobilized with curare, locally anesthetized with 2% lidocaine, and an earphone was sealed over the tympanic membrane ipsilateral to the exposed nerve. The response of single auditory afferent fibers to tonal stimuli was recorded using 3M KCl filled glass electrodes. Stimulus generation and recording procedures are described in the previous paper [Wilczynski et al., 1992]. The best excitatory frequency (BEF) was determined for BP afferents of 27 females (Wimberley $n=15$, Stengel Ranch $n=12$) and 16 males (Wimberley $n=9$, Stengel Ranch $n=7$). All physiological procedures were performed at room temperature (22–24 °C). After the experiments, weight and snout-vent length measurements were recorded for each animal.

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

Statistical Analysis

We performed regression analyses to examine the relationship between body size, and both the dominant frequency of the male advertisement call and the BEF of the basilar papilla in each sex. Analysis of covariance was performed using body size as the covariate to determine whether differences between populations in BP tuning

Table 1. Comparison of mean (+ SE) of male and female body size and communication parameters for *Acris crepitans*

Population parameter	Female	N	Male	N	P
Wimberley					
Snout-vent length	23.7 mm (0.10)	15	21 mm (0.02)	86	0.001
BEF	3124 Hz (16.7)	15	3243 Hz (16.1)	9	0.02
Call Dom. Frequency	–		3746 Hz (20.3)	86	–
Stengel					
Snout-vent length	23.8 mm (0.12)	12	21.4 mm (0.04)	26	0.004
BEF	3720 Hz (17.6)	12	4006 Hz (76.3)	7	0.005
Call Dom. Frequency	–		3820 Hz (45.0)	26	–

BEF = Best Excitatory Frequency.

and call dominant frequency are dependent on body size differences. This analysis essentially asks whether the data sets being compared fall on the same regression line with respect to body size, and if not, considers any differences to be independent of body size differences.

Results

Table 1 presents mean body size and BP tuning for the Wimberley and Stengel Ranch populations. Females were significantly larger than males in both populations (Wimberley $t=6.6$, $df=1,99$, $p<0.001$; Stengel Ranch $t=4.30$, $df=1,36$, $p<0.004$) although male and female body size did not differ significantly between populations (Wimberley vs. Stengel females $t=0.98$, NS; Wimberley vs. Stengel males $t=0.66$, NS). The mean BP BEF of females was significantly lower than that of males in each population (Wimberley $t=5.50$, $df=1,22$, $p<0.001$; Stengel Ranch $t=3.59$, $df=1,17$, $p<0.005$). Females were on average tuned significantly lower than the dominant frequency in the Wimberley population ($t=6.70$, $df=1,87$, $p<0.001$), but the difference in the Stengel Ranch population was not significant ($t=1.62$, $p>0.05$). In addition, the average dominant frequency of male calls did not differ between the two populations ($t=0.54$, $df=1,107$, $p>0.05$).

A test of the homogeneity of variances revealed that the variance in the dominant frequency of male calls did not differ between populations ($F_{max}=1.51$, $df=2,25$,

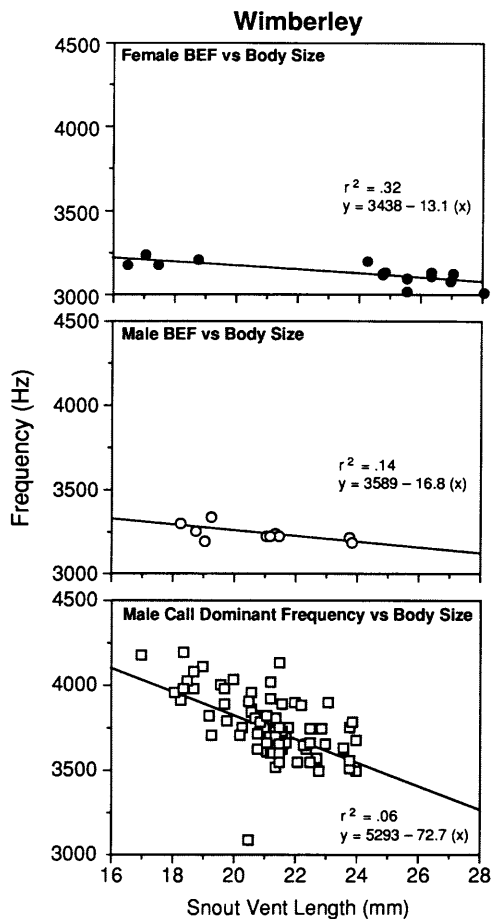


Fig. 1. From top to bottom, female basilar papilla BEF, male basilar papilla BEF, and dominant frequency of the male advertisement call plotted as a function of snout-vent length for cricket frogs from the Wimberley field site. The regression line and its equation is shown for each plot.

$p > 0.05$), nor did the variance in female tuning differ significantly between populations ($F_{\max} = 1.6$, $df = 2, 9$, $p > 0.05$). However, the variance in Stengel Ranch male tuning was significantly larger than in the Wimberley population ($F_{\max} = 14.2$, $df = 2, 7$, $p < 0.001$).

There was a significant inverse relationship between body size and the tuning of the male and female basilar papillae within both populations (Wimberley males $r = -0.38$, $p < 0.05$; females $r = -0.57$, $p < 0.009$; Stengel Ranch males $r = -0.64$, $p < 0.03$; females $r = -0.62$, $p < 0.009$; fig. 1, 2). Furthermore, an inverse relationship was found between body size and the dominant frequency of male calls in each population (Wimberley $r = -0.24$, $p < 0.0001$; Stengel Ranch $r = -0.18$, $p < 0.0001$).

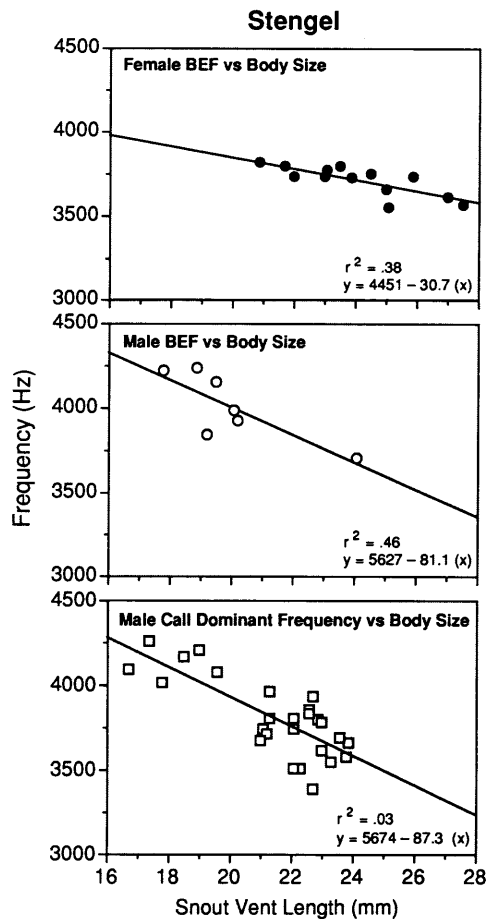


Fig. 2. From top to bottom, female basilar papilla BEF, male basilar papilla BEF, and dominant frequency of the male advertisement call plotted as a function of snout-vent length for cricket frogs from the Stengel Ranch field site. The regression line and its equation are shown for each plot.

An analysis of covariance was performed on each population using body size as the covariate (tables 2 and 3). In the Wimberley population, the adjusted means of male and female auditory tuning differed significantly ($F = 9.32$, $df = 1, 20$, $p < 0.05$). As the analysis also showed that the slopes of the male and female regression lines of tuning on body size did not differ, the result implies a greater difference in the Y-intercepts than the slopes of these lines. In contrast, the slopes of tuning vs. body size for both the sexes differed from the slope of call frequency vs. body size (female tuning vs. call: $F = 10.1$, $df = 1, 91$, $p < 0.001$; male tuning vs. call: $F = 4.76$, $df = 1, 88$, $p < 0.05$).

Analysis of the Stengel Ranch data revealed that the difference in slopes between male and female tuning vs.

Table 2. Wimberley ANCOVA results comparing communication parameters using body size as the covariate

Parameter comparisons	SS	Slope comparisons	Adjusted mean comparisons
Female BEF vs. Male BEF	40.4	F=0.181 (1,19)	F=9.32 (1,20)*
Female BEF vs. Call Dom. Freq.	1.8	F=10.1 (1,91)**	–
Male BEF vs. Call Dom. Freq.	1.8	F=4.76 (1,88)*	–

BEF=Best Excitatory Frequency.
 * p<0.05.
 ** p<0.001.

Table 3. Stengel ANCOVA results comparing communication parameters using body size as the covariate

Parameter comparisons	SS	Slope comparisons	Adjusted mean comparisons
Female BEF vs. Male BEF	1.20	F=4.50 (1,15)	F=1.77 (1,16)
Female BEF vs. Call Dom. Freq.	5.49	F=5.26 (1,34)*	–
Male BEF vs. Call Dom. Freq.	6.05	F=0.003 (1,29)	F=50.3 (1,30)**

BEF=Best Excitatory Frequency.
 * p<0.05.
 ** p<0.001.

body size approached significance ($F=4.50$, $df=1,15$, $p=0.0508$). However, the analysis of covariance (with body size as the covariate) did not indicate the adjusted male and female mean tuning to be significantly different ($F=1.77$, $df=1.16$) in this population. Nevertheless, an examination of the male and female regression lines of BP tuning on body size indicates that the Y-intercepts of these lines are very different and fall beyond each other's 95% confidence intervals (male Y-intercept=5627 Hz, 95% confidence interval=4925–6329; female Y-intercept=4451 Hz, 95% confidence interval=4056–4846). This suggests that the relationship of body size to BP tuning differs between males and females, as it does in the Wimberley population, but that the relatively larger variance and smaller sample size for male tuning in the Stengel population (table 1) prevented the analysis of covariance from identifying the adjusted male and female means as significantly different. The slopes of female tuning vs. body size and male calls vs. body size differed significantly ($F=5.26$, $df=1,34$, $p<0.05$). Finally, the slopes of male tuning vs. body size and male calls vs. body size were similar but the adjusted means differed significantly ($F=50.3$, $df=1,30$, $p<0.001$), suggesting a difference in the Y-intercept.

Statistical analysis within each population thus indicates that body size is a predictor of BP tuning in males and females, but male and female tuning remains different when body size is held constant. Calls and tuning relate to body size according to allometries that differ in either slope or Y-intercept.

Table 4 presents the analysis of covariance results using body size as the covariate to compare calls and tuning characteristics between the two populations. While the slopes of the female tuning vs. body size regression lines did not differ between populations ($F=3.19$, $df=1,21$), the adjusted

Table 4. ANCOVA results comparing Wimberley & Stengel populations, communication parameters using body size as the covariate

Parameter comparisons	SS	Slope comparisons	Adjusted mean comparisons
Female BEF Wimberley vs. Stengel	5534	F=3.19 (1,21)	F=72.8 (1,22)**
Male BEF Wimberley vs. Stengel	1.1	F=7.35 (1,13)*	–
Call Dom. Freq. Wimberley vs. Stengel	2.3	F=0.64 (1,104)	F=4.92 (1,105)*

BEF=Best Excitatory Frequency.
 * p<0.05.
 ** p<0.001.

means differed significantly ($F=72.8$, $df=1,22$, $p<0.001$), suggesting a difference in the Y-intercept. Similarly, the slopes of male call dominant frequency vs. body size did not differ significantly between the two populations ($F=0.64$, $df=1,104$), while the adjusted means did ($F=4.92$, $df=1,105$, $p<0.05$), indicating again a difference in Y-intercept between the regression lines. Thus there is a parallel shift in both the calls and female BP tuning between populations. In contrast, the slopes of the male tuning vs. body size regression lines differed significantly between the two populations ($F=7.35$, $df=1,13$, $p<0.05$). In summary, the analysis of covariance indicates that the populations differ in male call dominant frequency and male and female BP tuning when body size is held constant. Furthermore, as for the sex differences, most differences likely result from shifts in the Y-intercept rather than

Table 5. Summary of slopes and Y-intercepts for regression equations of female BEF, Male BEF, and male call dominant frequency (all in Hz) vs. body size (in mm) for Stengel and Wimberley populations

Parameter	Slope	95% Confidence interval	Y-intercept	95% Confidence interval
Stengel				
Female BEF	30.7	52.7– 8.7	4451	4846–4056
Male BEF	81.1	167.8–55.3	5627	6329–4925
Dominant Frequency	87.3	116.9–57.7	5674	6304–5036
Wimberley				
Female BEF	13.1	22.7– 3.6	3438	3672–3202
Male BEF	16.8	35.7– 2.0	3589	3949–3283
Dominant Frequency	72.7	94.6–50.9	5293	5758–4829

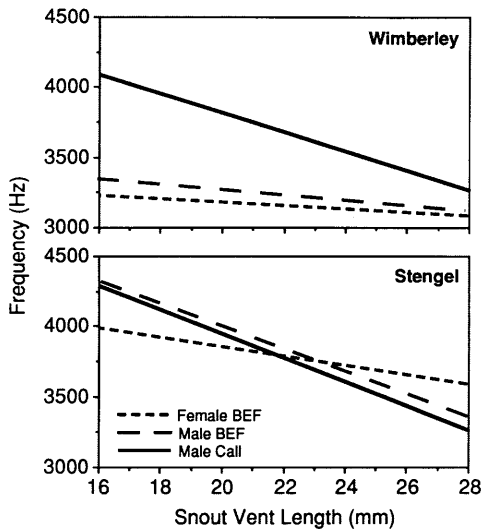


Fig. 3. Summary of the relationship of the dominant frequency of the male advertisement call, BEF of the female basilar papilla, and BEF of the male basilar papilla with body size (snout-vent length) for the Wimberley (top) and Stengel Ranch (bottom) populations showing the calculated regression lines for these data sets.

the slope of the allometric relationships. The relationships of these parameters in both populations are summarized in figure 3. The slopes and Y-intercepts for the regression lines are summarized in table 5.

Discussion

In the previous paper [Wilczynski et al., 1992] we described how male and female BP tuning and male call dominant frequencies varied across several populations of

cricket frogs [also see Nevo and Capranica, 1985; Ryan and Wilczynski, 1988, 1991]. Female BP tuning was, on average, lower than male BP tuning and lower than the average call dominant frequency in the female's local population. By carefully examining the pattern of variation in both BP tuning and male call dominant frequency within two populations, we can discern how allometric relationships influence both intra- and interpopulational variation, and speculate on how mate choice and sexual selection may operate within the populations.

Within both populations, male BP tuning, female BP tuning, and male dominant frequency correlate negatively with body size. A decrease in call dominant frequency with increasing body size has been reported previously for this [Nevo and Capranica, 1985; Wagner, 1989] and other species [Zweifel, 1968; Ramer et al., 1983; Ryan, 1985; Narins and Smith, 1986]. Presumably, the change derives from allometric enlargements of vocal cords and arytenoid cartilages as body size increases [Martin, 1972; Ryan, 1986, 1988; Schneider, 1988; McClelland et al., 1989].

It is less clear why tuning of the BP changes with body size. Capranica and Moffat [1977, 1983] argued that the BP functions as a simple resonator. Increasing size or mass lowers the resonant frequency of a resonator, and therefore such an allometric change could lower the tuning of the BP. Alternately, changes in the middle ear might change its resonance, this change being ultimately reflected in the BEFs of BP afferents [McClelland et al., 1988, 1989]. A negative correlation between BP tuning and body size holds across species [reviewed in Zakon and Wilczynski, 1988], as it does within the females of *Hyla crucifer*. However, a relationship between BP tuning and body size was not found in adult toads (*Bufo sp.*) [Capranica, 1976] or in one study examining adult bullfrogs (*Rana catesbeiana*) [Frischkopf et al., 1968], although Shofner [1988] showed that postmetamorphic growth in the latter species does coincide with a progressive decrease in BP tuning.

The present study is the first to examine the relationship between BP tuning and body size in both sexes within different populations of a single species. Our results show that in each cricket frog population body size is a determinant of BP tuning in both sexes. Interestingly, although females are, on average, larger than males, the sex difference in body size alone does not account for the sex differences in BP tuning manifest in lower tuning in females. This is contrary to the hypothesis advanced by Wilczynski [1986] to explain the sex difference in BP tuning observed in *Eleutherodactylus coqui* [Narins and Capranica, 1976] and *Hyla crucifer* [Wilczynski et al., 1984]. An analysis of covariance, with body size as the covariant, shows that the male and female BP tuning remain significantly different when body size is held constant. Furthermore, the allometric relationship between body size and BP tuning differs in the two sexes. In the Wimberley population, the Y-intercept of the relationship is lower for females vs. males, but the slopes are not significantly different, indicating that tuning changes with body size at similar rates in each sex, but at any given body size a female will be tuned lower than a male. In the Stengel Ranch population, both the Y-intercept and the slope of the allometry curve may differ between males and females, suggesting a more extensive difference between the sexes in the way morphological determinants of BP tuning change with body size.

Similarly, shifts in allometric relationships rather than body size *per se* are responsible for call and tuning differences between populations. Ryan and Wilczynski [1988, 1991] previously showed that geographic variation in the cricket frog's advertisement call was apparent even after controlling for variation in body size via an analysis of covariance. Although the mean dominant frequency did not differ between our samples of Wimberley and Stengel Ranch frogs, comparing the relationship of call dominant frequency and body size using regression analysis and analysis of covariance reveals that the allometric characteristics of tuning in the populations do differ. For similar changes in body size, males of both populations would show similar changes in call dominant frequency (i.e., the slopes of the regression lines are similar), but for a given body size, a Wimberley male would give a call with a lower dominant frequency than that of a Stengel Ranch male (i.e., the Y-intercept is lower in the Wimberley population).

As allometric shifts occur in the call dominant frequency of males, concomitant allometric shifts also occur in both sexes to yield population differences in BP tuning. As shown in the previous paper [Wilczynski et al., 1992], the direction of the change is constant for both call and tuning traits but the magnitude of the change can differ for each

trait and in each sex. This can be seen in the seven populations described in the previous paper [Wilczynski et al., 1992] and in the two populations described here. For example, a comparison of the Wimberley and Stengel Ranch populations shows that female tuning changes more rapidly with body size than does call dominant frequency.

The allometric changes between the investigated populations often appear to reflect changes in the Y-intercept of the trait's relationship with body size while the slopes of the relationship stay similar. This suggests a situation in which the general rules for growth are maintained after a shift in the initial values of the morphological features underlying the call dominant frequency or BP tuning. However, unlike female tuning, male BP tuning shifts between populations with a change in the slope of the tuning-body size relationship, suggesting a more fundamental allometric change in this trait. Of course, with only two populations examined, we can not determine whether slope changes or changes in the Y-intercept of the allometric relationships are more common for acoustic traits, or whether slope changes are restricted to male BP tuning. Nevertheless, the results show that, just as we [Wilczynski et al., 1992] and others [Nevo and Capranica, 1985; Ryan and Wilczynski, 1988, 1991] have argued that the features of communication signals and receivers can vary across populations within a species, so too can the manner in which body size influences these features.

Results presented here and in the companion article [Wilczynski et al., 1992] are part of a growing number of studies showing that coincident changes in communication signals and sensory systems mark variation within species as well [Littlejohn, 1981; Nevo and Capranica, 1985; Claridge et al., 1988; Ryan and Wilczynski, 1988]. At least two mechanisms have been proposed to explain coincident changes in mate recognition systems [Ryan, 1988]. The genetic coupling model assumes that both the signal and receiving systems are under the same genetic control [Alexander, 1962; Hoy et al., 1977; Doherty and Gerhardt, 1984; Kyriacou and Hall, 1986]. Alternatively, the coevolution model assumes that selection favors a match between senders and receivers, and therefore a change in one parameter results in a compensatory change in the other [Elsner and Popov, 1978; Butlin and Richie, 1989]. Currently we cannot distinguish between these two mechanisms, as that would require extensive cross-breeding experiments [Butlin and Richie, 1989] and an examination of allometric patterns in many more populations. However, the fact that the allometric relations for the call dominant frequency and male and female tuning do not all shift in the same manner between the Wimberley and Stengel

Ranch populations suggests a coevolutionary process of change, with at most a weak genetic coupling between these traits.

Coevolutionary changes between the call dominant frequency and BP tuning, especially in females, are to be expected given the importance of the call in guiding reproductive and other anuran social behavior [Wells, 1977, 1988; Gerhardt, 1982, 1988; Ryan, 1985; Rand, 1988; Ryan and Wilczynski, 1988]. Relationships between the frequencies of energy peaks in the call and the sensitivity peaks of the anuran auditory papillae can predict mate choice between species [Capranica, 1976; Capranica and Rose, 1983; Gerhardt, 1988], between populations [Capranica et al., 1973; Ryan and Wilczynski, 1988], and among individuals within a population [Ryan et al., 1990a]. Temporal processing features of the central nervous system also seem to coevolve with temporal features of the call [Capranica and Rose, 1983; Rose and Capranica, 1984; Walkowiak, 1988] and to predict mate choice [Gerhardt and Mudry, 1980], but we have not examined this aspect of call processing in cricket frogs.

Because the match between female BP tuning and male call dominant frequency is an important biasing influence on mate choice, the different allometric relationships in the Wimberley and Stengel Ranch populations predict some differences in the patterns of mate choice and sexual selection in the two populations. In the Wimberley population, the female BP tuning vs. body size regression line lies below and parallel to the male dominant frequency vs. body size regression line. In this case, female tuning, and presumably mate choice, would be biased toward the lower frequency range of the male call distribution. In such an

instance one would expect female choice to exert directional selection toward lower frequency calls and/or larger males. By contrast, in the Stengel Ranch population, the regression lines for male calls and female BP tuning intersect at a body size of 22 mm, at which size both calls and tuning are matched. In this population, one would predict female preferences to exert less directional selection and perhaps stabilizing selection on the males. Comparing the allometric relationship between calls and male body size in the two populations tends to support this interpretation: for a given body size, Wimberley males have a lower frequency call than Stengel males.

This scenario of sexual selection must still be considered a hypothesis addressing an ideal situation. The true effect female choice will have on the characteristics of the cricket frog communication system will depend upon additional factors such as the actual range of male size and call characteristics available on each night of the breeding season and the capacity of females to discriminate among males in the complex acoustic environment of a frog breeding chorus. Nevertheless, our results on geographic and individual variation in calls and tuning provide the necessary basis for exploring questions concerning the pattern and processes underlying the evolution of communication, reproductive patterns, and social behavior in this group of vertebrates.

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