# Trade-off in short- and long-distance communication in túngara (*Physalaemus pustulosus*) and cricket (*Acris crepitans*) frogs

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Female phonotaxis in túngara (*Physalaemus pustulosus*) and cricket (*Acris crepitans*) frogs is biased toward male advertisement calls or call components of lower frequency. This behavioral bias might result in part from a mismatch between the spectral characteristics of the advertisement call and the most sensitive frequency of the peripheral end organ implicated in reception of these sounds. In both species, females are tuned to frequencies lower than average for the calls in their population. This mismatch, however, represents the situation during short-distance communication. Female frogs can also use the call to detect choruses at long distances, and the spectral distribution of call energy can vary with transmission distance. We used computer simulations to test the hypothesis that there is a better match between tuning and call spectral energy at long distances from the calling male than at short distances by comparing the performance (sound energy received) of the natural tuning curve relative to an optimal tuning curve (i.e., one centered at the call's dominant frequency). The relative performance of the natural tuning curve increased with distance in túngara frogs. For the two subspecies of cricket frogs, however, the relative performance decreased at longer distances. The performance did not equal the optimal tuning curve at the distances tested. The results indicate that the relationship between calls and auditory tuning cannot be optimal for both long and short distance reception. The relationship between female tuning and call dominant frequency may represent a compromise between short and long distance communication, and the bias toward short or long distances may vary among species. *Key words: Acris crepitans, auditory system, communication, cricket frogs, Physalaemus pustulosus, sensory biases, sexual selection, túngara frogs. [Behav Ecol 11:102–109 (2000)]*

Female mating preferences are an important selection force influencing the evolution of male secondary sexual characters and are often influenced by male display traits that function as mating signals (Andersson, 1994; Darwin, 1871). Female preferences for different variants of these signals result from an interaction of the external signal with a set of internal physiological processes including neural, cognitive, and hormonal functions. Although these physiological systems mediate female mate choice at close distance, they serve a variety of other functions as well. Selection acting on these internal processes outside of the context of short-distance mate assessment might generate biases in female mating preferences as unintended consequences or pleiotropic effects; these biases, in turn, generate sexual selection on male signals (e.g., Christy, 1995; Dawkins and Guilford, 1996; Eberhard, 1993; Endler, 1992; Guilford and Dawkins, 1993; Kirkpatrick and Ryan, 1991; Ryan, 1990, 1997; Shaw, 1995; West-Eberhard, 1979). For example, signals might function as beacons for females to locate distant aggregates of calling males (i.e., choruses), as well as signals that females assess when choosing individual mates at short distances. In this study we tested the hypothesis that selection acting on aspects of the signal and receiver for long-distance communication might have unintended consequences on short-distance communication that generates sexual selection.

The courtship signals that males use to attract females for mating have played central roles in studies of speciation (Blair, 1958; Mayr, 1963) and sexual selection (Andersson, 1994; Darwin, 1871). Anurans have been a useful model system in these studies due to the relative stereotypy of male advertisement calls, the ability to assess female preferences using phonotaxis, and the potential to uncover the sensory bases for behavioral biases through neurophysiological studies of the auditory system (Capranica, 1976; Gerhardt, 1994a,b; Ryan, 1991). In all phonotaxis studies to date, females have shown preferences for a conspecific call versus a heterospecific call when they are presented with such a choice in a two-speaker, simultaneous-choice paradigm (Gerhardt, 1994b; Littlejohn and Michaud, 1959; Rand, 1988).

Call detection and recognition involve reception of the call by peripheral end organs in the inner ear for processing through a series of auditory centers in the central nervous system (Feng et al., 1990; Fritzsch et al., 1988; Hall, 1994; Wilczynski and Capranica, 1984). Two peripheral end organs can be involved in the initial reception of the call: the amphibian papilla (AP) and the basilar papilla (BP). These end organs differ in a variety of ways, including their frequency sensitivities. Within a species, the AP is always more sensitive to lower frequencies than is the BP. For most species, the AP is most sensitive to frequencies below 1500 Hz and the BP to frequencies above 1500 Hz (Wilczynski and Capranica, 1984; Zakon and Wilczynski, 1988; Fox, 1995). In some species the peak sensitivities of both the AP and the BP match concentrations of spectral energy in the call, whereas in other species most of the call energy lies within the most sensitive frequency
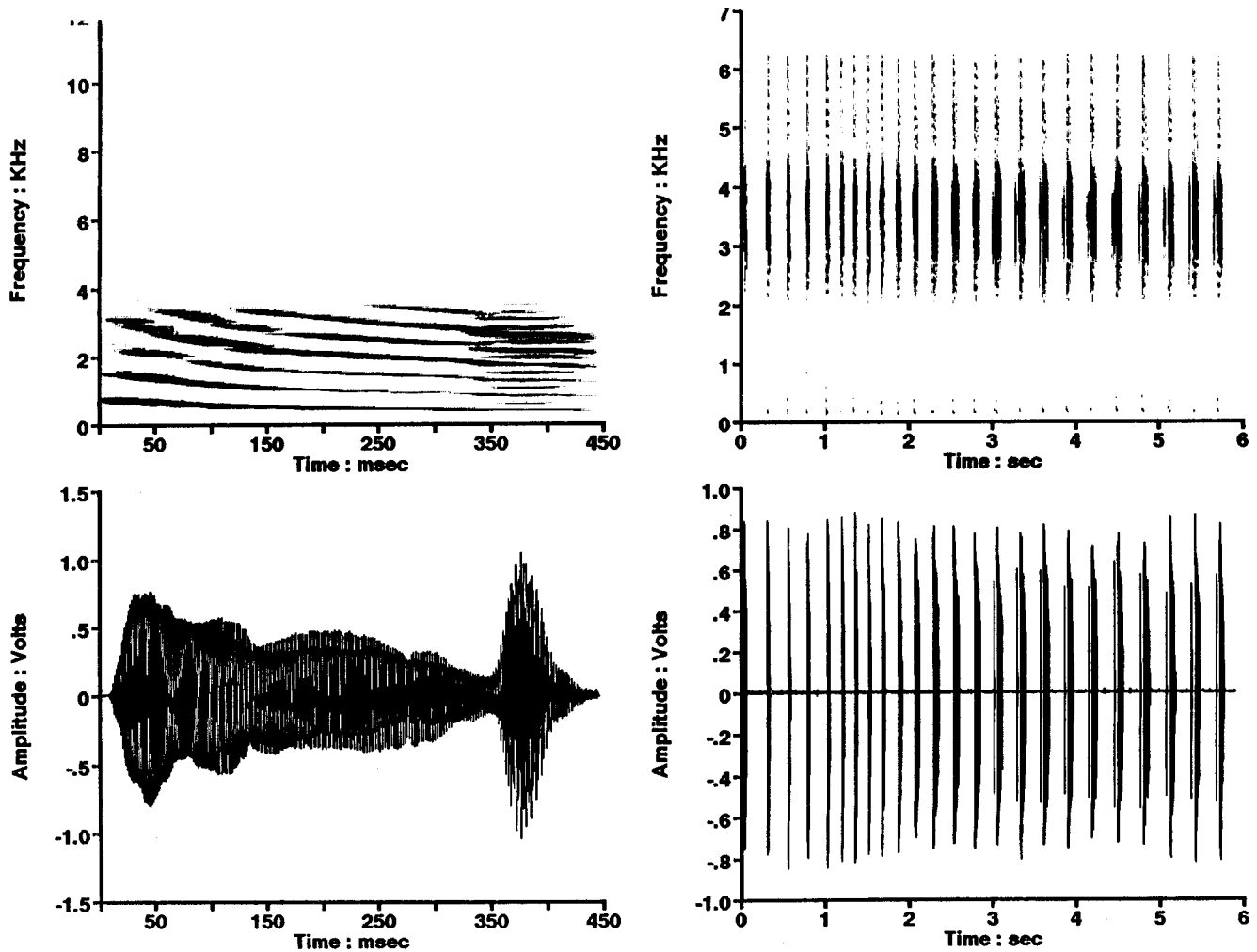
**Figure 1**
Sonograms (top) and oscillograms (bottom) of a whine-plus-chuck call of a túngara frog (*Physalaemus pustulosus*; left) and a call group of a cricket frog (*Acris crepitans*; right).

range of either the AP or the BP. The match between the tuning of the peripheral end organs and the calls' dominant frequencies is thought to be one of the characteristics of the communication system that facilitates female preferences for conspecific calls and for the calls of certain males within the species (e.g., Ryan, 1994).

### The systems

In the túngara frog, *Physalaemus pustulosus,* males produce a frequency-modulated call component, the whine, which consists of a fundamental frequency with substantial energy in the first four harmonics (Figure 1). In a typical call, the dominant frequency of the whine is 700 Hz, and most of the call energy is in the fundamental frequency, which sweeps from about 900 to 400 Hz in 300 ms. The whine can be produced alone, or it can be followed by additional components, chucks. A typical chuck is 35 ms in duration and has a fundamental frequency of 225 Hz with 14 harmonics that contain substantial energy. More than 90% of the chuck's energy lies above 1500 Hz, and the average dominant frequency of the chuck is 2500 Hz (Ryan et al., 1990b). Although females show phonotactic responses to the simple whine, they prefer whines with chucks (Rand and Ryan, 1981).

The most sensitive frequency of the AP in túngara frogs is

about 700 Hz, closely matching the dominant frequency of the whine (Ryan et al., 1990b), and phonotaxis experiments have shown that the portions of the fundamental frequency of the whine with energy close to 700 Hz are critical for call recognition (Rand et al., 1992; Wilczynski et al., 1995). The most sensitive frequency of the BP is 2200 Hz, which is in the range of most of the spectral energy in the chuck (Ryan et al., 1990b), although this tuning is below the average dominant frequency of the chuck in the population we studied (2500 Hz). Phonotaxis experiments show that the higher harmonics in the chuck (1600–2800 Hz) will increase call attractiveness, but this is not true for the lower harmonics (200–1400 Hz) at their normal amplitudes (Rand et al., 1992; Wilczynski et al., 1995).

Female túngara frogs tend to prefer calls with dominant frequencies in the lower end of the population's range to those at the higher end (Ryan, 1980, 1983; Wilczynski et al., 1995). We previously hypothesized that females prefer lower-frequency chucks because this effects a better match between call and BP tuning and thus increases the amount of neural stimulation of this peripheral end organ. Computer models that integrated natural chucks with the tuning function of an average BP were consistent with this hypothesis (Ryan et al., 1990b).

Cricket frogs, *Acris crepitans,* produce rapidly pulsed calls

with a dominant frequency of about 3500 Hz, depending on the population studied (Figure 1; Capranica et al., 1973; Nevo and Capranica, 1985; Ryan and Wilczynski, 1988; Wilczynski and Ryan, 1999). All of the call's energy falls within the range of the most sensitive frequencies of the BP, with little or no call energy below 1500 Hz (Capranica et al., 1973; Keddy-Hector et al., 1992; Wilczynski et al., 1992). Although call frequency and BP tuning tend to covary among populations, females are usually tuned below the average call dominant frequency in their population. When temporal properties of the calls are controlled, females often prefer calls with lower dominant frequencies (Ryan and Wilczynski, 1988; Ryan et al., 1992). Therefore, the mismatch of BP tuning and average call dominant frequency is in part responsible for the low frequency preference exhibited by females (Ryan et al., 1992), although the response of peripheral end organs may not be a good predictor of the behavior ultimately exhibited in nature (Schwartz and Gerhardt, 1998).

## The question

The slight mismatch between BP tuning and call dominant frequency could be explained by several hypotheses. One hypothesis is based on the fact that BP tuning can vary with body size within a species, as in cricket frogs (Keddy-Hector et al., 1992). Because females are larger than males in most species of frogs (Shine, 1979), females will tend to have a BP tuned to lower frequencies than the males' BP (McClelland et al., 1997; Wilczynski et al., 1984; Zakon and Wilczynski, 1988). If selection favors a male to be tuned to calls of other males, then, by default, females will be tuned lower than the male call. This might be a plausible explanation, as in some species the perceived intensity of the nearest neighbors' calls is thought to mediate nearest neighbor distances (Brenowitz et al., 1984; Wilczynski, 1986). A second hypothesis views this mismatch as an adaptation for choosing high-quality males. Larger males usually produce lower frequency calls; if females derived an advantage from mating with large males, selection might favor females being attracted to the lower frequency calls of larger males. In some frogs females gain increased fertilization success from mating with larger males (Bourne, 1993; Robertson, 1990; Ryan, 1985), but there is no evidence that such mating preferences increase the genetic quality of the offspring (Howard et al., 1994). Thus, other hypotheses are also likely.

Unlike many other animals, such as some insects, most frogs do not have different signals that are used in short- versus long-distance communication. The male's advertisement call typically acts as a beacon to attract females from long distances and as a courtship signal at short distances, but long and short-distance communication can act under different constraints. It is well known that sound degradation tends to be frequency dependent (Dusenbery, 1992). In general, higher frequencies degrade more rapidly due in part to the greater susceptibility to the scattering of shorter wavelengths (Forrest, 1994; Wiley and Richards, 1978). Therefore, lower frequencies lose less energy than the higher frequencies in the signal and so become relatively more prominent in long-distance communication. If the relative spectral distribution of call energy shifts to lower frequencies with distance from the source, then it would not be possible to optimize the match between tuning and call frequency at both long and short distances. Therefore, we tested a third hypothesis that the mismatch between BP tuning and call dominant frequency in short-distance communication is a trade-off for a better match between signal and receiver to facilitate long-distance communication.

This hypothesis makes two predictions. The first prediction is that there is a better match between tuning and call fre-

quency at long-distance interactions, but this necessitates a greater mismatch at short distances. If supported this suggests that the relationship between signal and receiver cannot be equally efficient at all distances, and the relationship thus results from compromises between short- and long-distance communication. The second prediction is that the match between tuning and call frequency is not only better at long than short distances, but that it is optimal. This would suggest that selection has maximized the signal–receiver match for long-distance communication despite its reduced efficiency in short-distance communication. This hypothesis might be especially appealing because, at its most sensitive frequencies, the BP has higher neural thresholds than the AP, i.e., it is less sensitive to sound. Because signals attenuate with distance, improving the match should improve sensitivity to low-amplitude calls. Thus optimizing the match between tuning and call frequency when the BP is involved might be more important for long-distance communication than for short-distance communication.

## METHODS

### General approach

We tested the hypothesis that the apparent mismatch between tuning and call frequency at short distances is a consequence of a better match between tuning and call frequency at long distances (Figure 2). We did this by constructing computer models of BP tuning based on the audiograms obtained in previous studies (Ryan et al., 1990; Wilczynski et al., 1992), then used these models as filters through which we passed digitized versions of natural calls tape recorded at different distances from a calling frog or a speaker broadcasting a call (see below). Two pairs of models were constructed for each taxon investigated. One filter model in the pair exhibited the tuning characteristics of the average female BP and thus was tuned to a frequency below the male call's average dominant frequency; we refer to this as the "natural filter." The second filter was similar to the first but was adjusted so that its peak tuning (or best excitatory frequency, BEF) matched the call's dominant frequency; we refer to this as the "optimal filter." We evaluated the performance of each filter by determining the amount of energy in the call after it was passed through each filter. We then calculated the relative performance, which is the ratio of the performance of the natural filter and the optimal filter. Finally, we used these data to test the prediction that the relative performance of the natural filter increased with distance from the source or, more specifically, that the difference in relative performance (DRP) at long and short distances was significantly different from zero.

### Degraded calls

*Physalaemus pustulosus*
We used calls of túngara frogs from a previous study of call degradation and attenuation (Ryan, 1986). Calls of male túngara frogs were recorded in a large, open field at ground level (the height of the sender and receiver in this communication system) in Gamboa, Republic of Panama. Two microphones (Sennheiser ME 80 with KU-3 power modules) were placed 1 m and 11.6 m away from calling frogs, and we recorded calls from at least three individuals on two channels of a stereo Sony TCD-5M tape recorder with metal tape. The frequency response of the recording system was flat (within 1 dB) for the frequency range (500–6000 Hz) of the frog calls (see Ryan, 1986, for more details). The spectra of all calls were close to the average of the species.
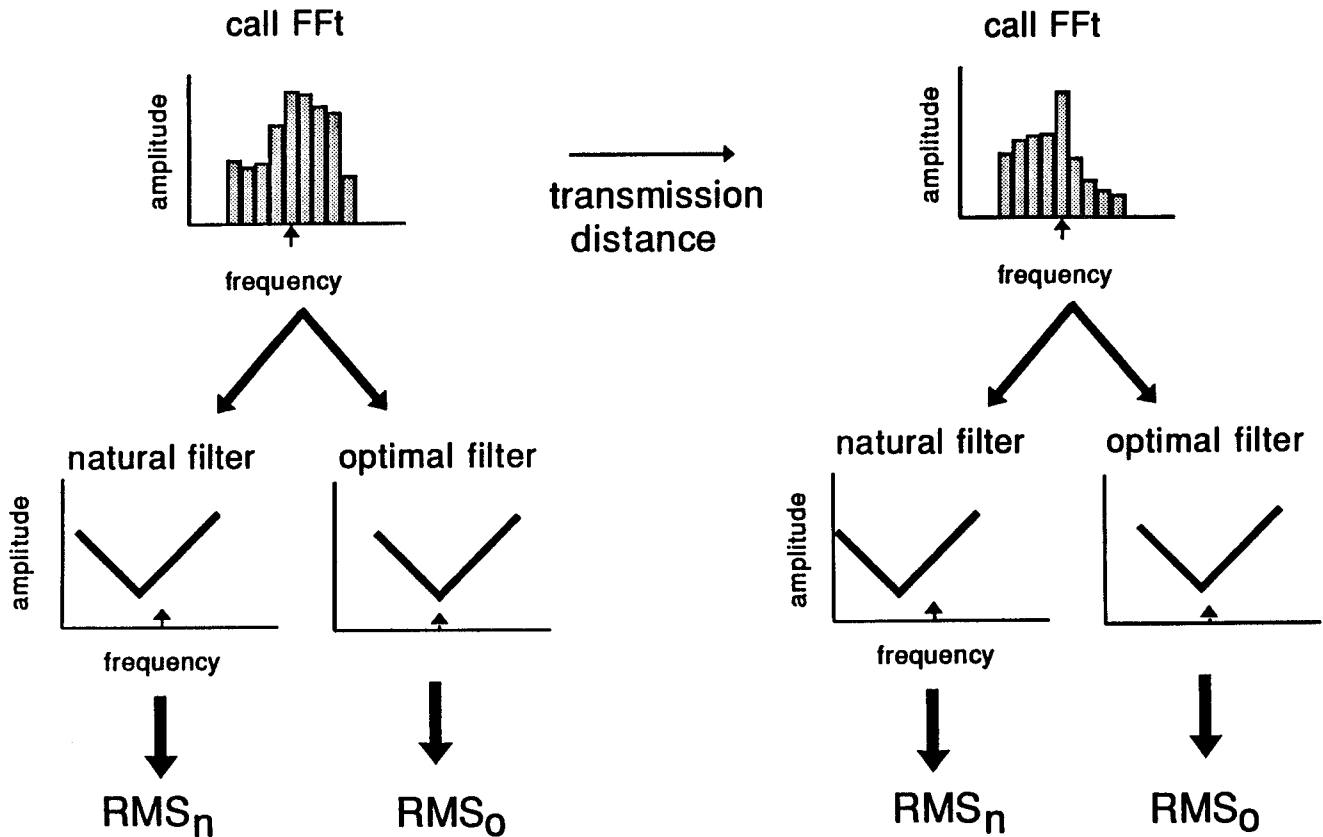
**call FFt**



**Figure 2**
Measures of performance for the natural and optimal filters. As a call transmits through the environment, its spectral features (call FFT), although not necessarily its dominant frequency ($\uparrow$), will change as a result of frequency-dependent attenuation. The performance of the natural filter ($RMS_n$), which models the filtering properties of the frog's basilar papilla, is the amount of energy in the call after it is passed through this filter. Note that the peak sensitivity of the filter does not match the call's dominant frequency. The hypothetical optimal filter, however, has its peak sensitivity centered on the call's dominant frequency. Its performance ($RMS_o$) is also determined by measuring the amount of energy in the call after it is passed through this filter. The performance of the natural filter is compared with the optimal filter to determine the natural filter's relative performance. This is done for both the short- and long-distance interaction.

*Acris crepitans*

We used calls of cricket frogs from a previous study of call degradation and attenuation (Ryan et al., 1990a). The calls were from six male cricket frogs (8–11 calls/frog) each from a population of *Acris crepitans crepitans* in Polk County, east Texas, USA, pine forest, which is characterized by relatively dense vegetation, and a population of *A. c. blanchardi* at Gill Ranch in Travis County, central Texas, USA, which is in juniper–oak woodland, a generally open habitat (see Ryan and Wilczynski, 1991, for details of geographic variation in calls). Because our purpose was to determine the influence of environmental factors on the performance of frog calls, the experimental unit was an individual call, rather than an individual frog. We broadcast the calls with a Sony TCD-5M tape recorder and a small extension speaker (Mineroff) at about 100 dB sound pressure level (SPL) (20 µPa) at 1 m from the source, which is within the range of the natural calling intensity of cricket frogs. We recorded calls simultaneously with stereo tape recorders (Marantz PMD 420) and two microphones (Sennheiser ME 80 with K3U power modules) placed at 1 m and 16 m from the source. An earlier study that extrapolated from recordings of neural thresholds and call attenuation suggested that females could detect a call of the same SPL from 18 m (Fox, 1988), although whether females use these calls to find choruses over this distance is unknown.

All experiments were conducted in early evening, the time when cricket frogs usually begin their calling. Degradation of

the *A. c. blanchardi* subspecies calls was measured in the open habitat at Gill Ranch in Austin, Texas, which is typical of this subspecies' environment. Degradation of calls of the *A. c. crepitans* subspecies was measured in a closed habitat of dense pine forest at Stengl Ranch in Bastrop County, Texas, which is the habitat type of this subspecies. To determine if any results obtained were a necessary consequence of frog calls and auditory systems independent of habitat characteristics, we also measured degradation for each subspecies call in the non-native habitat.

**Basilar papilla tuning**

Details about neurophysiological recordings of the response properties of the BP and the audiograms for túngara frogs from Panama and the two cricket frog subspecies from two populations in Texas are available elsewhere (Ryan et al., 1990a,b, 1992; Wilczynski et al., 1992). Data for the túngara frogs were obtained by recording acoustically evoked multi-unit activity from the midbrain. Data for the cricket frogs were obtained by recording acoustically evoked activity in individual VIIIth nerve afferent fibers. Data obtained from the two sources may provide different estimates of absolute threshold but generally agree well on basic tuning properties such as the best excitatory frequency (BEF) (Fox, 1995).

For each taxon, an average BP tuning function was first estimated. The audiograms for male and female túngara frogs

do not differ, and data from both sexes were used to determine the average audiogram (Ryan et al., 1990). BP tuning differed between the sexes in cricket frogs, thus only data from females were used. First, the average BEF (frequency with the lowest threshold) was calculated for each species and subspecies. Second, the average band widths of the tuning at 10 dB above threshold and at 20 dB above threshold were determined. Third, the asymmetry of natural tuning curves, for which the high-frequency slope is steeper than the low-frequency slope, was factored into the model by calculating the average frequency points on the high and low flanks of the physiologically recorded tuning curves at 10 and 20 dB above threshold, determining the relative displacements of each above and below the BEF, and adjusting the average curve accordingly while keeping the bandwidth at the average value. The resultant average BP tuning curve then served as a filter function, which we termed the "natural" tuning function of each of the three groups (the túngara frog and the two subspecies of cricket frogs, see Figure 2).

We obtained an optimal tuning curve for each of the three groups by shifting the natural tuning curve by a certain amount (by adding a constant: 420 Hz for *P. pustulosus,* 740 Hz for *A. crepitans blanchardi,* and 80 Hz for *A. c. crepitans*) such that the BEF of the shifted curve matched the dominant frequency of the average male call for that group. The natural and optimal tuning curves were then converted into fast Fourier transformation (FFT) files in the sound analysis-synthesis program Signal (Engineering Design; Beeman, 1994), where they could be used to filter the calls by convolving the filter function with the call spectrum.

## Data analysis

We used the Signal-RTS software to digitize the recorded calls (sampling rate: 12500 Hz for the túngara frogs, and 25000 Hz for the cricket frogs, higher than 1.5 times of the Nyquist frequency for all calls recorded). We analyzed the chuck of the túngara frog call and the entire call for the cricket frogs (see above).

Before analysis, calls were digitally band-pass filtered within Signal at frequencies of 500–4000 Hz for túngara frog calls and 1500–6000 Hz for cricket frog calls to minimize the effect that background noise had on the calls' spectral distribution. We then selected the same calls recorded from the short and long distances. We calculated the FFT size (1024 for the túngara frog and 2048 for the cricket frog) and compared the power spectra for each signal recorded at the two distances. The power spectra of short- and long-distance calls were then adjusted to the same average call energy, as measured by the root mean square (RMS) without equalizing energy level. We filtered the same calls recorded from the two distances with the two BP tuning functions, the natural and optimal filters. We calculated the relative performance (RP) of the natural and optimal filter for the same calls as:

$$RP = \frac{RMS_o - RMS_n}{(RMS_o + RMS_n)/2} \times 100\%, \qquad (1)$$

where $RMS_o$ and $RMS_n$ are the RMS values of a call passing through the optimal and natural filter, respectively, for the same distance (short or long). The above formula is an index showing how much the optimal filter outperforms the natural filter. The smaller the RP value, the better the performance of the natural filter relative to the optimal filter. We used the difference in the relative performances for long and short distances (DRP),

$$DRP = RP_{short} - RP_{long}, \qquad (2)$$

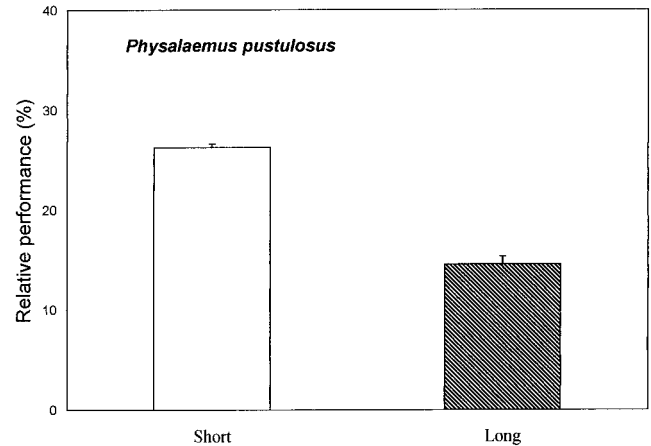to compare the performance of the natural and optimal tun-



**Figure 3**
The performance of the natural tuning curve relative to that of the optimal tuning curve in short- and long-distance communication in the túngara frog, *Physalaemus pustulosus.*

ing in relation to calling distance. Hence, a positive DRP indicates an increase in performance of the natural filter relative to the optimal filter as one moves from short- to long-distance communication. A negative DRP indicates that the natural filter's performance relative to the optimal filter is even worse at long distances than it is at short distances.

For túngara frogs, we tested the DRP using a *Z* test (two tailed) against the null hypothesis of DRP = 0, which indicates neither improvement nor deterioration in the performances between short- and long-distance communication. For cricket frogs, we used a factorial analysis of variance with habitat and subspecies as the 2 factors and 60 replications. If the interactions between the two main effects were significant, we used a *t* test (two tailed) to examine all simple effects. All tests were conducted after we had found that the normality assumption was not violated using the original data. The significance level for all tests was .05.

## RESULTS

The DRP between the optimal and natural filters for the túngara frog was 11.68% ± 9.50% (SD) between the short- and long-distance calls ($z = 13.70$, $df = 123$, $p < .001$; Figure 3). Thus the performance of the natural filter, when compared with that of the optimal filter, was greater at the longer distance than it was at the shorter distance. These results are consistent with the prediction that the tuning-call mismatch in short-distance communication is related to a better match in long-distance communication. For the long distance, the natural tuning curves consistently underperformed that of the optimal tuning curve (on average 0.47% worse in the túngara frog and 0.18% in the cricket frog, respectively). These data did not support the hypothesis that the natural tuning curve is optimized for maximizing long-distance communication.

The DRP was −2.39% ± 2.25% (SD) for *A. c. crepitans* and −7.21% ± 18.09% (SD) for *A. c. blanchardi* in their respective native habitat. In the non-native habitat, the DRP was −3.79% ± 1.72% (SD) for *A. c. crepitans* and 14.60% ± 11.33% (SD) for *A. c. blanchardi.* An analysis of variance showed that the main effects of habitat and subspecies were both significant ($F_{1,236} = 177.32$, $p < .001$ for habitat and $F_{1,236} = 78.43$, $p < .0001$ for subspecies), but the interaction between habitat and subspecies was also significant ($F_{1,236} = 229.19$, $p < .001$). We thus investigated the simple effect for the habitat factor. For both subspecies of cricket frogs, the RP increased with dis-
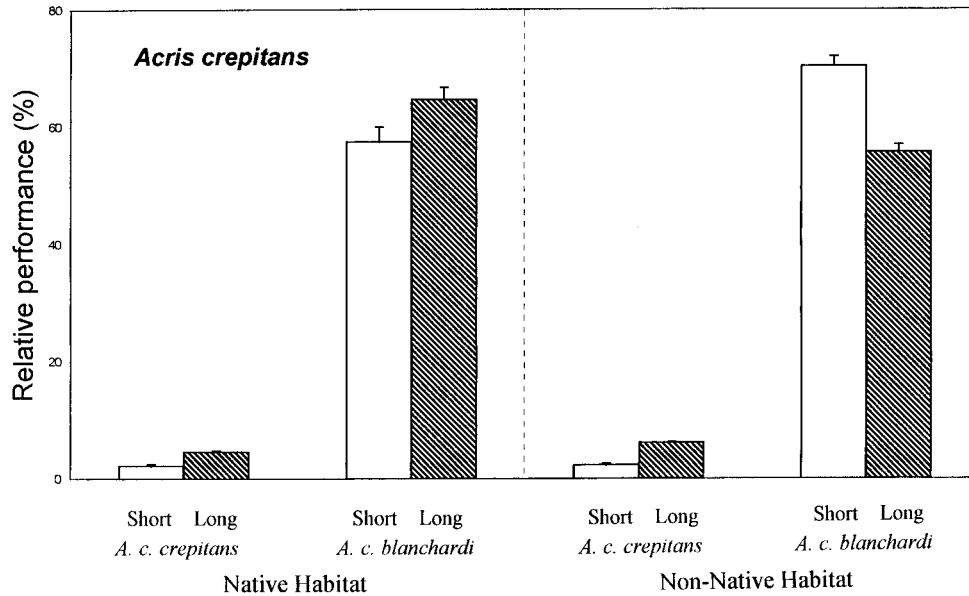
Figure 4
The performance of the natural tuning curve relative to that of the optimal tuning curve in short- and long-distance communication in the two subspecies of cricket frogs, *A. c. crepitans* and *A. c. blanchardi,* in their native and non-native habitats.

tance in their respective habitats (*A. c. blanchardi*: $t = 6.31$, $df = 59$, $p < .001$; *A. c. crepitans*: $t = 20.12$, $df = 59$, $p < .001$; Figure 4). Thus, for both subspecies in their native habitat, the performance of the natural filter was worse at the long distance than at the short distance. At neither distance did the natural filter perform as well as the optimal filter. In the non-native habitat, RP increased with distance for *A. c. crepitans* ($t = 10.82$, $df = 59$, $p < .001$), but decreased with distance for *A. c. blanchardi* ($t = 14.90$, $df = 59$, $p < .001$).

## DISCUSSION

We tested the hypothesis that the mismatch between BP tuning and call dominant frequency in túngara frogs and cricket frogs in short-distance communication is an epiphenomenon of a better match between signal and receiver to facilitate long-distance communication. We tested two predictions from this hypothesis: the relative performance of the tuning curves is better for long-distance than for short-distance communication, and the match between BP tuning and call frequency is optimal for long-distance communication. Our results from túngara frogs support the first prediction: the performance of the natural tuning curve relative to the optimal one increased with distance. In contrast, the relative performance of the natural filter in cricket frogs decreased as distance increased for both subspecies. These results are the opposite of the first prediction. In our analysis of both túngara frogs and cricket frogs, our results fail to support the more extreme optimization prediction because at both short and long distances the natural tuning curves performed worse than the theoretical optimum.

If the performance of the natural tuning curve relative to the optimal filter continued to increase with distance from the source, then at some distance the natural tuning curves' performance would equal that of the optimal for the túngara frog. We used only one estimate of a long distance in this study for each species, 11.6 m from the source for túngara frogs and 16 m for cricket frogs. Assume that incremental improvement in the performance of the natural filter is linear for simplicity in calculation. Extrapolating from the rate at which the relative performance of the natural tuning curve increases, the natural tuning curve would perform as well as the optimal tuning curve at about 94 m from the source for túngara frogs. This is far beyond the estimates of threshold

for response derived from neurophysiological data (Fox, 1988).

Our results lead us to conclude that selection for long-distance communication in certain circumstances might contribute to the mismatch between tuning and call frequency we observe in short-distance communication, but there is no evidence to support the notion that the signal–receiver match is optimized for long-distance communication. This lack of optimization might have several causes. We doubt that there are any nonselection constraints, in the sense of those discussed by Maynard Smith et al. (1985), that would prohibit the female's BP from being tuned to higher frequencies, as many small frogs are tuned to much higher frequencies than are túngara frogs (e.g., Wilczynski et al., 1993). But achieving an optimal match between tuning and call frequency for long-distance communication would result in an even larger mismatch between tuning and call frequency in short-distance communication than we already observe. This might be selectively disadvantageous for short-distance communication despite the fact that the absolute stimulus energy available to receivers is larger at short distances than long distances. The observed relationship between tuning and call frequency might have resulted from a compromise of contrasting selection forces to simultaneously increase efficiency for both short- and long-distance communication.

The notion that the relationship between peak call energy and tuning of the auditory system is a compromise between long- and short-distance communication is, in the most general sense, consistent with the results from both the túngara frog and both subspecies of the cricket frog. In no case was the natural filtering function of the auditory system as good as the theoretical optimum, suggesting that the relationship between the spectral composition of the call and the tuning properties of the auditory system is not optimal for communication over any distance (at least none of the distances measured here, which were all within the range over which frogs interact). For each species, however, the signal–receiver system was better at one distance than at another. For the túngara frog, the system performed better at long-distance communication, whereas for both cricket frog subspecies, the system performed better at short-distance communication.

At present, we cannot address the reason that the species adopt different strategies, as they differ in too many factors.

They are phylogenetically distinct, and one nonadaptive explanation would be the retention of an ancestral character in either the call or auditory properties that bias the responses. For *Physalaemus* at least, phylogeny does influence call recognition and preference (Ryan and Rand, 1995; Ryan et al., 1990). The species in this genus breed in different habitats, and the results testing the signal–receiver interaction of cricket frogs in non-native habitats shows that habitat and vegetation characteristics can play a pivotal role in the transmission and reception of sound measured by the performance of natural filters. In fact, the results from *A. c. blanchardi* in the non-native habitat demonstrate empirically that it is physically possible for cricket frog calls and tuning to be better matched at long distances than at short distances, but that the opposite specialization actually characterized the system in the habitat in which the calls are used. The behavioral ecology is different in the two species, with túngara frogs often calling from small, scattered ephemeral puddles or standing water in flooded fields, whereas cricket frogs call from larger and more permanent bodies of water such as ponds and streams. Examination of a much greater number of species, performed in a way that is sensitive to phylogenetic relationships, is necessary to extract the rules by which species become more specialized for long-distance or short-distance communication.

Although we cannot determine the evolutionary forces dictating the specializations of any one species, our results do address a neglected issue in the behavioral ecology and evolution of communication system—the tension between the requirements of long and short distance communication. We propose that an acoustic communication system using the same signal for communication over a variety of distances can be specialized for either long-distance or short-distance communication. It cannot, however, be equally sensitive to distant and to close calls in any environment in which there is noticeable signal degradation during transmission. Each species must therefore effect a compromise between long- and short-distance communication, and favoring one results in a disadvantage in the other.

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