

The transmission of advertisement calls in Central American frogs

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Acoustic communication signals change over distance due to loss of amplitude and fidelity, and it is assumed that signal degradation influences the receiver's ability to detect and decode signals. The degree of degradation depends on the signal's structure and the environment through which it transmits. We broadcast the advertisement calls of 22 species of Central American frogs at two heights within forested and open environments in Panama. We recorded these calls at five distances from the source and estimated signal degradation with a cross-correlation analysis, a measure that combines the effects of decrement in signal amplitude and fidelity. Calls degraded less when broadcast higher above the ground compared to on the ground, and less in open habitat compared to forested habitat; there was an additional interaction between height and environment. Furthermore, calls with low dominant frequencies experienced less degradation than calls with high dominant frequencies. There was no evidence, however, that the calls of these frogs have evolved to maximize habitat-specific transmission. *Key words*: animal communication, anuran, attenuation, degradation, environmental acoustics, frog. [*Behav Ecol* 11:71–83 (2000)]

Animals often use acoustic signals for communication over long distances (e.g., Brown, 1989; Langbauer et al., 1991; Stebbins and Cohen, 1995). As these signals travel from sender to receiver, they are altered in a manner that can reduce the signal's ability to elicit a response from a receiver. Signal amplitude usually decreases at a minimum of 6 dB per doubling of distance due to spherical spreading, and additional or "excess" attenuation results from absorption and scattering of sound waves by the air, ground, and surrounding vegetation (Wiley and Richards, 1978). Additionally, the signal's temporal and spectral fidelity is disrupted by frequency-dependent attenuation, reverberations, and irregular amplitude fluctuations (Michelsen and Larsen, 1983; Richards and Wiley, 1980; Wiley and Richards, 1978).

Changes in both signal amplitude and fidelity over distance can degrade signal efficacy. Sufficient loss of amplitude can decrease signal-to-noise ratio to a level at which the receiver cannot detect the signal. Sufficient change in signal fidelity can make the signal unrecognizable to the receiver. There can also be important interaction effects; a certain decrease in fidelity might result in an effective signal at a high but not a low signal-to-noise ratio. Many studies partition the effects of attenuation and fidelity (the latter often referred to as degradation). We address degradation of signal efficacy over distance, which is dependent on changes in both amplitude and fidelity. Thus we analyze their combined effects in our measure of signal degradation. Throughout, we use the term "degradation" to refer to this combined effect of signal attenuation and loss of fidelity.

Signal degradation can be influenced by spectral and temporal characteristics of the signal, broadcast height, characteristics of the habitat through which the sound propagates, background noise, and meteorological conditions (Bradbury and Vehrencamp, 1998; Wiley and Richards, 1978). The effect of each of these factors on sound attenuation and degradation has been examined using transmission experiments. Some

generalizations can be drawn from these studies. Attenuation and degradation are affected by both the height from which the signal is broadcast or received (Brenowitz et al., 1984; Dabelsteen et al., 1993; Henwood and Fabrick, 1979; Marten and Marler, 1977; Mathevon et al., 1996; Waser and Waser, 1977) and the environment through which the signal travels (Brown and Gomez, 1992; Marten and Marler, 1977; Morton, 1975; Ryan et al., 1990; Waser and Brown, 1986).

Not all effects on signal degradation are external to the signal; various sounds are more or less susceptible to degradation. For example, signal degradation can vary with dominant frequency (Brown and Gomez, 1992; Marten and Marler, 1977; Marten et al., 1977; Morton, 1975; Ryan, 1986; Waser and Brown, 1986; Waser and Waser, 1977) or temporal characteristics (e.g., Mathevon et al., 1996; Ryan and Sullivan, 1989). Furthermore, the effects of call structure on degradation can differ among environments. Thus, for long distance communication, selection should favor signal characteristics that degrade less in their local transmission habitat (e.g., Endler, 1992; Morton, 1975; Ryan and Brenowitz, 1985; Sorjonen, 1986; Wiley, 1991).

Differences in call structure among species that call in different environments were first identified in comparative studies of bird song morphology (Bowman, 1979; Hunter and Krebs, 1979; Gish and Morton, 1981; Morton, 1975; Sorjonen, 1986; Wiley, 1991). In these studies, the observed differences in song structure supported predictions based on the acoustics of the local signaling habitat. A few studies in birds, primates, and frogs have also demonstrated differences within a species between calls that are used for long- and short-distance communication (Brown and Gomez, 1992; Ryan, 1986; Sorjonen, 1983; Waser and Waser, 1977). In contrast, some recent studies on anurans have failed to find the predicted differences in call structure among species that call in different environments (e.g., Penna and Solis, 1998; but see Ryan et al., 1990). In addition, some authors suggest that factors such as body size, phylogenetic constraints, and background noise can also contribute to habitat-specific differences in signal structure (Ryan and Brenowitz, 1985; Zimmerman, 1983).

In this study, we measured advertisement call degradation for 22 species of frogs. The advertisement call is usually a loud, conspicuous signal used by males to advertise their pres-

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ence to other males and to attract females over long distances. Only a few studies have investigated the role of habitat acoustics in the evolution of frog call structure (Penna and Solis, 1998; Ryan, 1986; Ryan et al., 1990; Zimmerman, 1983). We first asked to what extent transmission height and habitat type influence the amount of call degradation across species. We then investigated how the dominant frequency of advertisement calls influences the amount of degradation a call experiences. Finally, we tested the hypothesis that advertisement calls have evolved in response to selection generated by the acoustic properties of a species' calling habitat.

METHODS

Transmission experiments

Exemplars of the advertisement calls of 22 species of Panamanian frogs, including representatives from 11 genera, were selected from the call libraries of A. S. Rand and M. J. Ryan (Figure 1). Several calls were selected from each species and copied onto a single metal audio tape. All calls were recorded at the maximum amplitude without clipping. Thus, the relative peak amplitudes of the calls were similar; because the natural call amplitudes of most of these species are unknown, no attempt was made to scale them to their relative amplitudes in nature. We created two synthetic sounds using an Eico analog pulse generator (model 377) and transferred them to the same tape; these were a continuous tone with a fundamental frequency of 300 Hz and 10 harmonics (dominant frequency 900 Hz) and a 250-ms pulse with a dominant frequency of 1000 Hz (Figure 1). This master tape, which we used for all subsequent transmission studies, thus consisted of a sequence of different frog calls and sounds approximately 30 min in length.

M.J.R. conducted transmission experiments 3 June–27 July 1983 in Soberania National Park near Gamboa, Panama. All experiments were performed at night in one of two environments within the park, a field of tall grass or forest. The master tape was played from a Sony TCD 5M tape recorder through a 5-inch, full-range dynamic speaker packed in a plastic box and backed with a sound-absorbing medium. The sound pressure level (SPL; re. 20 μ Pa) of the pure tone stimulus measured at 50 cm in front of the speaker was adjusted to 90 dB SPL at the beginning of each experiment. Each broadcast was subsequently recorded at a distance from the source on one channel of metal tape using a Sennheiser ME80 microphone with a K3U power module and a second Sony TCD 5M recorder. Calls were broadcast and recorded at two heights within each of the two environments, at ground level and at 1.5 m above the ground, with both the speaker and the microphone at the same height. There were thus a total of four transmission locations. Recordings of the transmitted calls were made at distances of 1, 2, 3, 10, and 20 m from the broadcast source.

Cross-correlation analysis

We digitized recordings of transmitted calls at a sampling rate of 25 kHz with Signal (Engineering Design, 1997). We then saved up to four calls from each of the 22 frog species ($n = 82$ calls) for later analysis, using both the sonogram and amplitude envelope plotted on the same time axis. The same calls were systematically saved from each transmission tape so that subsequent analyses could be conducted on identical calls across all distances and locations. Only single calls were analyzed; for species that arrange their calls in groups, we took four individual calls from a variety of groups. In addition, we chose two 500-ms segments of the tone and two synthetic puls-

es haphazardly from the digitized transmission recordings and saved them in separate files. Some calls could not be discerned from the background noise at 10 and 20 m. We classified these as missing data for analysis. In addition, if another species of frog or insect was calling loudly during the target call, we also regarded it as missing data because the random presence of these individuals interfered with subsequent data analysis.

We digitally band-pass filtered the individual calls to decrease the amount of noise outside the frequency range of the signal. For calls with energy in frequencies <625 Hz, we applied only a low-pass filter due to a mathematical constraint of digital filtering functions. Filter ranges varied from species to species; they were determined from visual evaluation of the sonogram and power spectrum of undegraded calls transmitted over a short distance (1 m) at a height of 1.5 m in an open environment.

We made sonograms of identical calls from each of the five transmission distances (10.2 ms time resolution, 97.7 Hz frequency resolution). If necessary, we additionally trimmed the sound files so that all five sonograms were approximately the same length and contained the same call segment from the master tape. We then calculated the amplitude-normalized covariances between the sonograms of two signals as a function of the time offset between them. Sonogram cross-correlations were performed over a frequency range of 200 Hz–10 kHz. Four cross-correlations were performed for each call exemplar within each of the transmission locations; these were between a call recorded at the 1 m transmission distance (a relatively undegraded control) and the same call recorded at a transmission distance of 2, 3, 10, or 20 m in the same location. The maximum cross-correlation coefficient from each comparison was saved for statistical analyses.

In a sonogram cross-correlation analysis, two stimuli are slid past one another along the time axis. The cross-correlation coefficient is recorded for each point in time. The maximum cross-correlation coefficient for two sonograms should thus occur at the point at which the two signals are time-aligned. Cross-correlation coefficients are interpreted in the same way as other correlation coefficients; they vary between -1 and $+1$, where -1 signifies antisimilarity, 0 signifies no similarity, and $+1$ indicates that the two signals are indistinguishable. Cross-correlation coefficients computed from comparisons of sonograms reflect differences in the spectral and temporal characteristics of the call, as well as differences in signal-to-noise ratio. They are therefore indicators of both attenuation (change in call amplitude) and loss of fidelity (change in call structure). These two types of signal change cannot be distinguished from one another using this technique, but both contribute to the degradation of signal efficacy over distance, which is the goal of our analysis. Thus we analyzed their combined effects in our measure of signal degradation.

There are two methodological limitations of the sonogram cross-correlation procedure. Cross-correlation coefficients are calculated from the entire range of the digitized sound. Consequently, the cross-correlation coefficient does not reflect changes in the call alone; any random disturbance present in one transmission but not another can affect the correlation. We partially addressed this problem by filtering sound outside the frequency range of each call, as well as by using several call exemplars from each species. Second, as noted above, cross-correlation coefficients reflect differences between the control and degraded signal with respect to both attenuation and fidelity. Cross-correlation coefficients decrease as signal-to-noise ratio decreases and as the fidelity of the signal's temporal and spectral structure decreases. The effects of these two signal changes on the cross-correlation coefficients are not equal, but their combined effect will influence the deg-

radation of signal efficacy. Thus, this procedural limitation can be viewed as an advantage for the question we address: How does signal efficacy degrade with distance?

Statistical analyses

We used the mean values of the maximum cross-correlation coefficients for each species to assess differences in call degradation between transmission heights, between habitats, among species grouped by call dominant frequency, and among species grouped by natural calling location. Each of the 22 species was thus represented only once in each comparison. Separate analyses were conducted for each of the four transmission distances. We used nonparametric methods for all statistical tests, as unequal variances between groups and non-normal data distributions violated the assumptions of analysis of variance. In accordance with these nonparametric analyses, median values of the cross-correlation coefficients from each location or group are reported as indicators of the general tendencies within groups.

We also used a second method of analysis to investigate differences in call degradation among locations and species. For each species, we calculated the regression of cross-correlation coefficients plotted with respect to transmission distance within a single location. We used a linear regression as the simplest model, although degradation with distance was not linear for some of the species included in this study. In most (80 out of 95) cases, there was a significantly negative correlation between cross-correlation coefficients and transmission distance (Pearson product moment correlation, $p < .05$ for 12 cases, $p < .005$ for the remaining 68 cases). We used the slopes of those regressions for which the correlation was significant to estimate the rate of degradation with distance; highly negative slopes indicated high rates of degradation. Each species was again represented only once in the comparisons among locations and species, although the slopes were computed from all of the analyzed call exemplars from that species. We compared slopes among locations or species using nonparametric statistical tests.

RESULTS

Call degradation with distance

We first examined changes in cross-correlation coefficients over distance in order to test the validity of the cross-correlation technique in measuring call degradation. Cross-correlation coefficients decreased with distance in all four transmission locations (Table 1, Figure 2). At a recording distance of 2 m, cross-correlation coefficients for all species were high. At the 10 and 20 m recording distances, however, cross-correlation coefficients diverged among species; some calls remained similar to the 1 m control, and others became highly masked or degraded. Sample variance generally increased over distance (Table 1, Figure 3).

We compared cross-correlation coefficients between all possible pairs of transmission distances; there were thus six comparisons within each of the four transmission locations. In all 24 comparisons, the median cross-correlation coefficient was higher for the shorter transmission distance (Table 1, Figure 2). The difference between distances was significant in 20 out of these 24 comparisons (Mann-Whitney, $p < .05$ for 6 comparisons, $p < .005$ for the remaining 14 comparisons). Although increasing degradation with distance is certainly not surprising, our results are critically important because they indicate that the cross-correlation coefficients used in the following analyses are a useful measure of call degradation.

Differences in call degradation among locations

We investigated the effects of transmission height and habitat type on call degradation. Statistical analyses were conducted across all species and included the synthetic tone and pulse. Removing the tone and pulse from these analyses did not change the interpretation of any of the results. The following comparisons thus provide indications of how transmission height and environment affect signal degradation, without consideration of the structure of the sound.

We compared cross-correlation coefficients between the two heights from which calls were broadcast and recorded. Analyses were conducted separately for each of the two transmission environments as well as for each of the four transmission distances; eight height comparisons were made. Calls generally experienced less degradation when transmitted at a height of 1.5 m than when transmitted at ground level, but the effect of height was more notable in the tall grass environment than in the forest environment. In tall grass, cross-correlation coefficients from the 1.5 m transmission height were significantly higher, or nearly so, than those from ground level transmission at the 3, 10, and 20 m transmission distances (Mann-Whitney, $p < .001$, $p < .06$, $p < .005$ for the 3, 10, and 20 m transmission distances, respectively; Table 1, Figure 2A,B). In the forest environment, median cross-correlation coefficients from the 1.5 m transmission height were again higher than those from ground level at the three longer transmission distances, but the differences between the heights were not significant in this environment (Mann-Whitney, $p = .40$, $p = .07$, and $p = .11$ for the 3, 10, and 20 m transmission distances, respectively; Table 1, Figure 2C,D). At the 2 m distance within the forest environment, cross-correlation coefficients from calls transmitted at ground level were significantly higher than those of calls transmitted at a height of 1.5 m (Mann-Whitney, $p < .05$).

Comparisons of the regressions of cross-correlation coefficients over distance complemented the above direct comparisons of cross-correlation coefficients. Calls transmitted at ground level experienced a greater rate of degradation than calls transmitted at a height of 1.5 m (Mann-Whitney, $p < .001$ in the tall grass environment, $p < .05$ in the forest environment; Table 2, Figure 3). As above, the effect of height was much more pronounced in tall grass; median slopes differed between the two heights in tall grass more than in forest (Table 2, Figure 3).

We next compared cross-correlation coefficients between the two environments through which calls were transmitted. Separate analyses were conducted for each of the two transmission heights, as well as for each of the four transmission distances. At ground level, calls transmitted through forest and tall grass fared equally well at three of the four transmission distances. There were significant differences between the two environments at only the 3 m transmission distance, where the cross-correlation coefficients of calls transmitted through the forest environment were higher than those of calls transmitted through tall grass (Mann-Whitney, $p < .05$, Table 1, Figure 2B,D). The influence of environment on call degradation was slightly more pronounced at a transmission height of 1.5 m. Above the ground, cross-correlation coefficients from the tall grass environment were significantly higher than cross-correlation coefficients from forest for both the 2 m and 20 m transmission distances (Mann-Whitney, $p < .01$ for the 2 m transmission distance, $p < .005$ for the 20 m transmission distance; Table 1, Figure 2A,C).

Comparisons of the regressions of cross-correlation coefficients over distance again complemented the direct comparisons of cross-correlation coefficients outlined above. The rate of call degradation did not significantly differ between the two

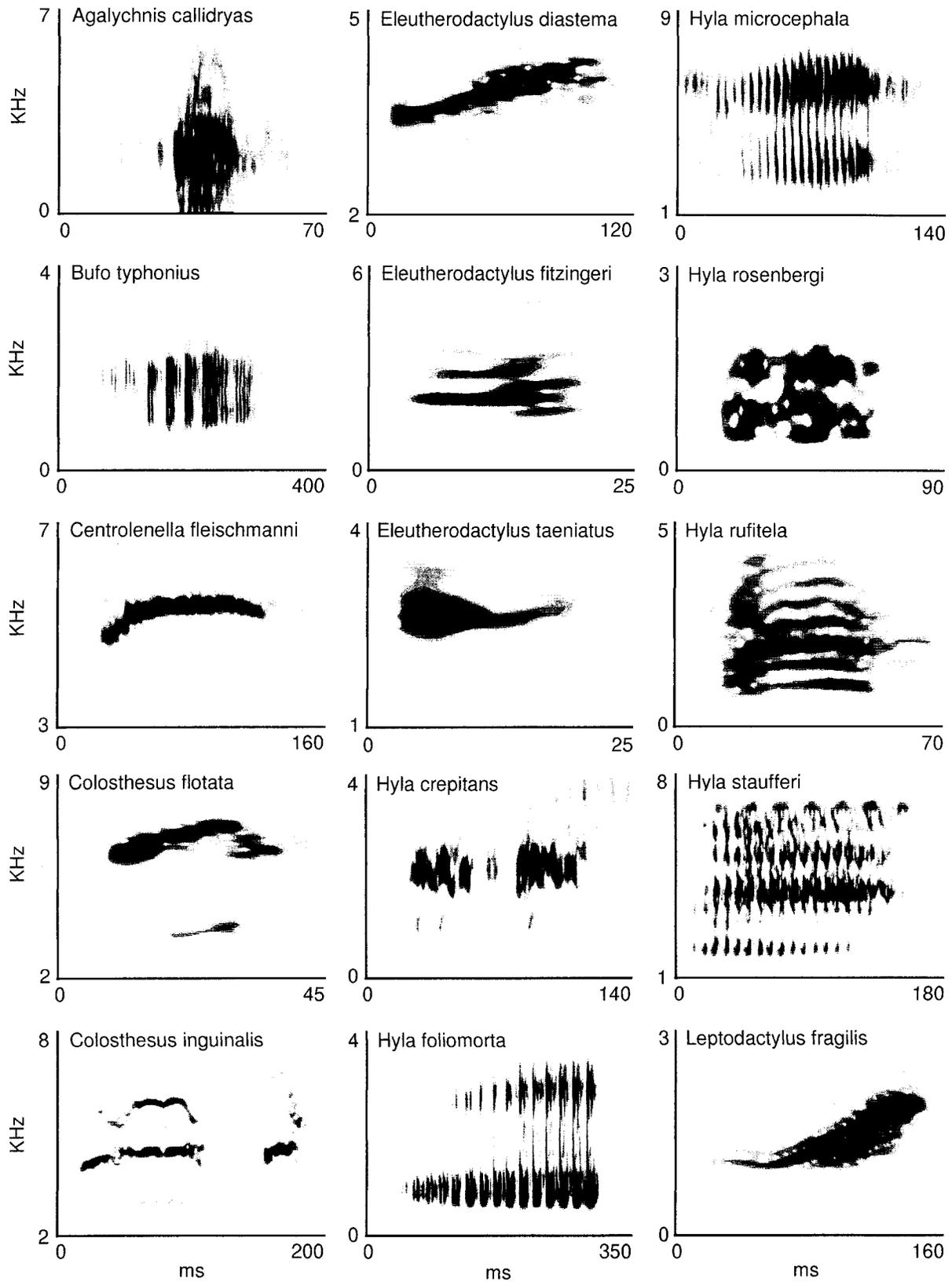


Figure 1

Sonograms of one call from each of the 22 frog species used in transmission experiments. The sonograms are not on identical time or frequency scales. Also included are sonograms of two synthetic sounds, a pulse and a continuous tone, which were used in some of the experiments.

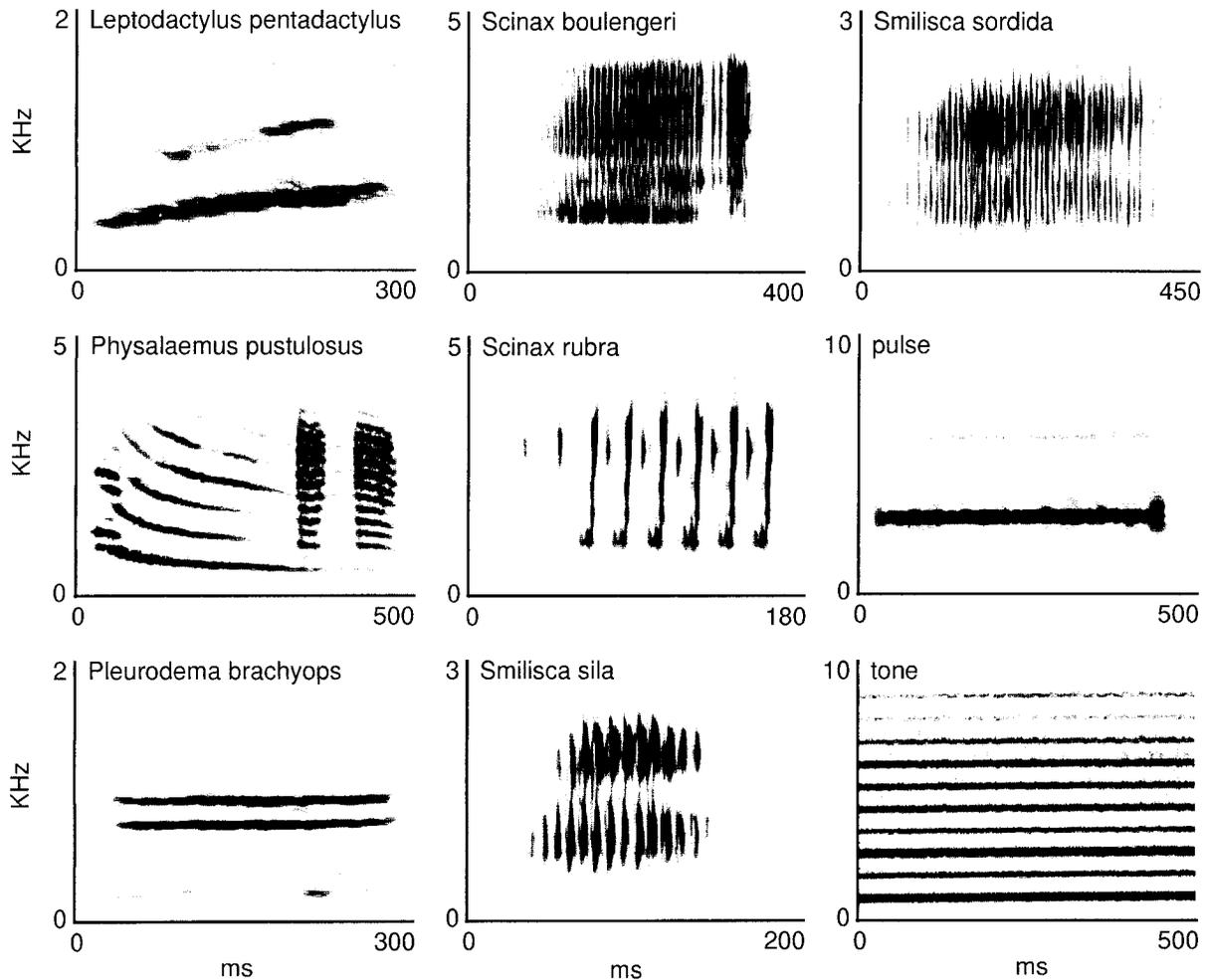


Figure 1
Continued.

environments when calls were transmitted at ground level (Mann-Whitney, $p = .96$; Table 2, Figure 3). At a transmission height of 1.5 m, however, calls transmitted through the tall grass environment exhibited a trend of lower rate of degradation than calls transmitted through the forest environment (Mann-Whitney, $p = .06$; Table 2, Figure 3).

Differences in call degradation among species

In a second set of analyses, we tested the hypothesis that advertisement calls evolved in response to selection generated by habitat acoustics. We first asked whether there were differences in degradation among the different species. We then asked whether there were differences in degradation among calls with different dominant frequencies. Finally, we asked whether these differences were reflected in differences among species that normally call from different heights and environments. The synthetic tone and pulse were not included in any of these analyses. Separate analyses were conducted for each of the four transmission locations; no comparisons were made between transmission heights or environments.

We first evaluated differences among the 22 frog species. Cross-correlation coefficients from all call exemplars from each species were included in this analysis, rather than the species means used in all other comparisons. We found highly significant differences among species at all four transmission

distances in all four locations (Kruskal-Wallis, $p \leq .001$ in all 16 cases). The cross-correlation coefficients of some species ranked consistently higher than the cross-correlation coefficients of other species, especially at the 10 and 20 m transmission distances. *Pleurodema brachyops* (see Figure 1 for representative sonograms) had consistently higher cross-correlation coefficients than most other species in all four transmission locations. The cross-correlation coefficients for both *Physalaemus pustulosus* and *Hyla foliomorta* were higher than those of most other species when calls were transmitted at ground level within both environments. *Leptodactylus pentadactylus* fared better than most other species at both heights within the tall grass environment. *Leptodactylus fragilis* had consistently higher cross-correlation coefficients than many other species for transmission at both heights within the forest environment, as well as within the tall grass environment at a transmission height of 1.5 m.

The cross-correlation coefficients of some species were consistently lower than those of other species at the 10 and 20 m transmission distances. *Colosthesus flotata* and *Hyla microcephala* had lower cross-correlation coefficients than most other species in all four transmission locations. Both *Scinax boulengeri* and *Scinax rubra* had lower cross-correlation coefficients than most other species in the forest environment at a height of 1.5 m and in the tall grass environment at ground level. *Colosthesus inguinalis* had consistently lower cross-correlation

Table 1
Coefficients for sonogram cross-correlations between calls transmitted over each of four distances and a reference distance of 1 m^a

	<i>n</i> ^b	Median	Range	Variance
Forest, 0 m height				
2 m	24	0.968	0.681–0.997	0.006
3 m	24	0.897	0.343–0.990	0.031
10 m	22	0.708	0.153–0.994	0.075
20 m	22	0.378	0.000–0.938	0.099
Forest, 1.5 m height				
2 m	22	0.936	0.769–0.982	0.003
3 m	24	0.934	0.826–0.983	0.002
10 m	19	0.857	0.268–0.968	0.025
20 m	19	0.721	0.001–0.925	0.052
Tall grass, 0 m height				
2 m	23	0.952	0.601–0.996	0.010
3 m	22	0.775	0.433–0.994	0.029
10 m	20	0.726	0.251–0.981	0.067
20 m	17	0.548	0.006–0.955	0.119
Tall grass, 1.5 m height				
2 m	24	0.965	0.877–0.991	0.001
3 m	24	0.950	0.859–0.991	0.001
10 m	21	0.891	0.225–0.991	0.045
20 m	24	0.843	0.235–0.988	0.032

^a Mean cross-correlation coefficients from each of 22 frog species, plus a synthetic tone and a synthetic pulse, were included in these analyses.

^b Sample sizes of <24 represent cases where none of the calls from an individual species could be delineated from the transmission tapes.

coefficients than many other species in the tall grass environment at a transmission height of 1.5 m.

Species with calls of low dominant frequency (<2000 Hz, $n = 11$) were compared to species with calls of high dominant frequency (>2000 Hz, $n = 10$). The classifications for each species are summarized in Table 3. For ground level transmission, there were significant differences between the two groups of species at all four transmission distances within both environments (Mann-Whitney, $p < .05$ for three comparisons, $p < .005$ for the remaining five comparisons). In all cases, calls with low dominant frequencies experienced less degradation than calls with high dominant frequencies (Figure 4B,D). There were, in addition, significant differences between the two groups in the regression slopes of cross-correlation coefficients plotted with respect to distance (Mann-Whitney, $p < .05$ for forest, $p < .005$ for tall grass). In both environments, calls with dominant frequencies >2000 Hz had less negative slopes, and thus exhibited lower rates of degradation, than calls with dominant frequencies >2000 Hz.

For transmission above the ground, there were significant differences in degradation between calls with low and high dominant frequencies for only the longer transmission distances. In forest, calls with low dominant frequencies had higher cross-correlation coefficients than calls with high dominant frequencies only when transmitted over a distance of 20 m (Mann-Whitney, $p < .05$; Figure 4C). In the tall grass environment, calls with low dominant frequencies had significantly higher cross-correlation coefficients than calls with high dominant frequencies at the 10 and 20 m transmission distances (Mann-Whitney, $p < .05$ for the 10 m transmission distance, $p < .001$ for the 20 m transmission distance; Figure 4A). The regression slopes of the cross-correlation coefficients plotted with respect to distance differed between the two

groups in both environments (Mann-Whitney, $p < .05$ for forest, $p < .001$ for tall grass). In both cases, calls of lower dominant frequency exhibited lower rates of call degradation than calls of higher dominant frequency.

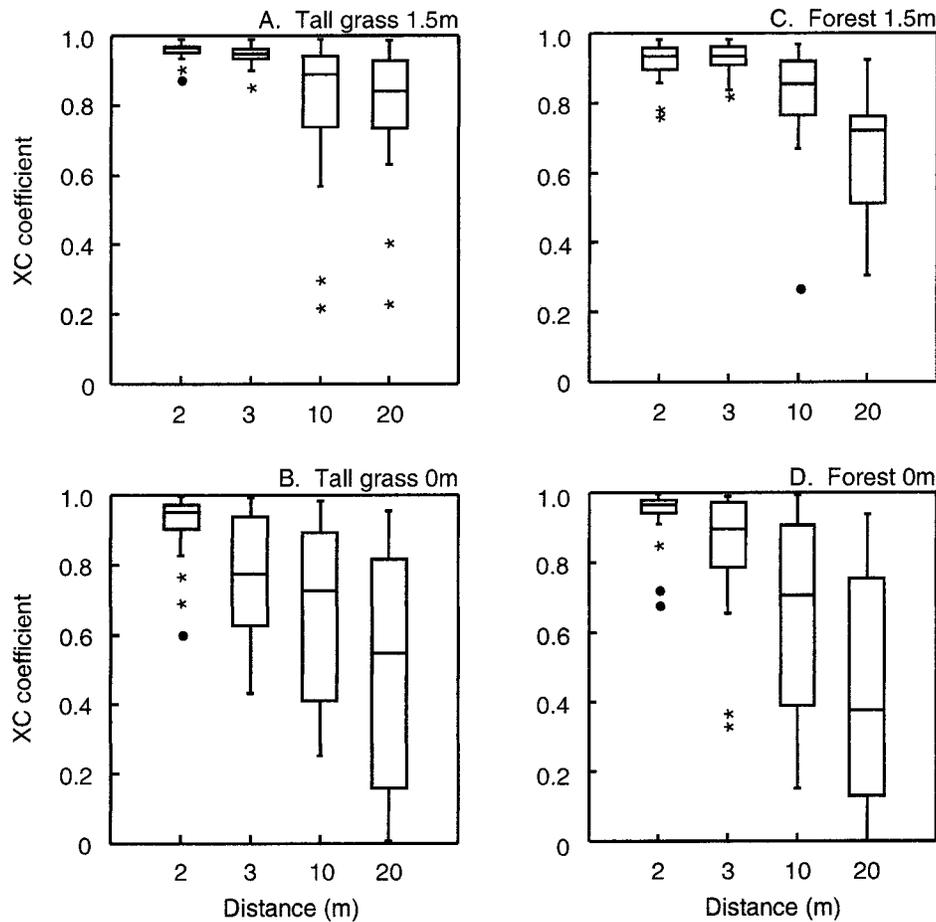
Cross-correlation coefficients tended to decrease with increasing dominant frequency (Figure 5). For transmission at ground level in both environments, cross-correlation coefficients were significantly correlated with dominant frequency at all four transmission distances (Pearson product moment correlation, $r > .6$, $p < .01$ for all four transmission distances in both environments). The slopes of these regressions generally increased with transmission distance (Figure 5B,C). For transmission at a height of 1.5 m in tall grass, cross-correlation coefficients were significantly correlated with dominant frequency for the 3, 10, and 20 m distances (Pearson product moment correlation, $r = .45$, $p < .05$ for the 3 m transmission distance, $r = .83$, $p < .001$ for the 10 m transmission distance, $r = .74$, $p < .001$ for the 20 m transmission distance). Again, the slopes of the regressions generally increased with transmission distance (Figure 5A). For transmission at a height of 1.5 m above the ground through a forested environment, cross-correlation coefficients were in no case correlated with dominant frequency (Pearson product moment correlation, $r < .45$, $p > .1$ for all four distances).

Finally, the 22 frog species were categorized into three natural calling habitats (forest, $n = 9$; open, $n = 6$; stream, $n = 5$) and two calling heights (ground, $n = 12$; above ground, $n = 9$). We compared degradation among groups to test the hypothesis that frog calls have evolved in response to selection for decreased degradation within their home environment. Classifications for each species are summarized in Table 3. As in the above comparisons among species grouped by call dominant frequency, we compared the groups within a single transmission location.

There were no significant differences in degradation among species that normally call from the three different environments; this was true for all four transmission distances within all four transmission locations (Kruskal-Wallis, $p > .2$ for all 16 comparisons; Figure 6). In addition, species that normally call from different environments did not significantly differ in the regression slopes of cross-correlation coefficients plotted with respect to transmission distance (Kruskal-Wallis, $p > .3$ for all four locations). There were also no significant differences between species that normally call from the ground and those that normally call from above the ground at any transmission distance within any transmission location (Mann-Whitney, $p > .1$ for all 16 comparisons; Figure 7). There were no significant differences between these two groups in the slopes of the regression lines drawn through the cross-correlation coefficients over distance (Mann-Whitney, $p > .3$ for all four transmission locations).

DISCUSSION

Our estimates of signal degradation using cross-correlation coefficients revealed that in 22 species of Central American frogs the amount of degradation differed between habitats and between transmission heights. Degradation also differed among species and among calls with different spectral characteristics. These differences were not specific to the species' local calling habitat; thus there is no evidence to support the hypothesis that the calls of these species have evolved in response to selection generated by habitat acoustics. We thus suggest that morphological constraints or selection in other contexts have been more important in determining frog call structure than the need for transmission efficiency.

**Figure 2**

Box plots of cross-correlation (XC) coefficients from the four transmission distances within each of the four transmission locations. The horizontal line in the center of each box represents the median cross-correlation value across species. Boxes are drawn around the midrange (HSPREAD) of values and thus provide an indication of sample variance. The whiskers show the range of values that fall within 1.5 HSPREADs of either edge of the box. Stars denote outside values (farther than 1.5 HSPREADs from the edges of the box). Filled circles denote far outside values (farther than 3 HSPREADs from the edges of the box).

The influence of height and environment on call degradation

We found that both transmission height and environment influenced call degradation and that there was an interaction between the effects of height and environment. Calls transmitted at ground level suffered greater degradation than those transmitted above the ground. This difference was more pronounced in tall grass than in forest. Calls fared equally well in tall grass and forest when transmitted at ground level, but, above the ground, calls experienced slightly lower rates of degradation in the tall grass relative to the forest.

A number of factors, including scattering from dense vegetation, ground attenuation, and temperature and wind gradients, can cause increased attenuation and degradation at ground level (Wiley and Richards, 1978). The effect of caller height on signal transmission has been accordingly demonstrated in a number of transmission studies (see Introduction). The results of the current study are consistent with the results of these previous studies.

Such simple generalizations cannot be made about the differences between open and forested environments. The results of previous experiments have not been consistent with respect to the overall influence of environment on call degradation. In some transmission studies, signals broadcast through forested environments experienced less attenuation or degradation than the same signals transmitted through open environments (Brown and Gomez, 1992; Morton, 1975; Waser and Brown, 1986). Others found the opposite to be true: signals transmitted through open environments experienced less attenuation or degradation than the same signals transmitted through forest (Marten and Marler, 1977; Ryan et

al., 1990; Waser and Brown, 1986). In addition, Marten and Marler (1977) showed that the influence of environment on call attenuation was less than the influence of height. Similarly, Wiley and Richards (1978) suggested that the effects of stationary heterogeneities from objects such as trees in a forest could balance the effects of nonstationary heterogeneities caused by micrometeorological instability in open areas, and that this trade-off could obscure differences in signal transmission between open and forested environments. In light of these previous findings, it is not surprising that we did not find larger differences in degradation between the two environments.

We observed two related interactions between the effects of height and environment on call degradation. Caller height was more influential in the tall grass environment than in the forest environment. In addition, an effect of environment was evident above the ground but not at ground level. In general, calls transmitted through tall grass at a height of 1.5 m experienced less degradation than calls transmitted through any of the other broadcast locations. In our study area, the density of intervening vegetation decreased appreciably with increased height in the tall grass environment but not in the forest environment. This difference between the two environments in the distribution of vegetation is one likely cause of the observed interactions between height and environment. Calls transmitted above the ground in the tall grass environment were freed of much of the influence of intervening vegetation, likely resulting in lower levels of degradation in this location relative to the three locations in which vegetation was more dense.

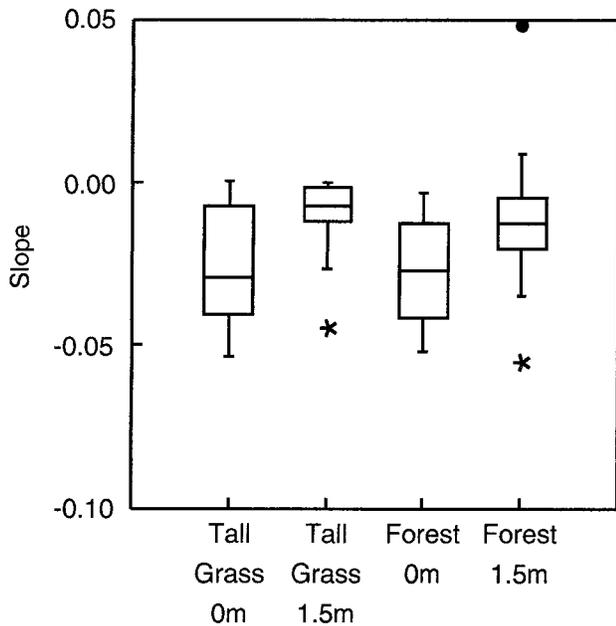


Figure 3

Box plots of the slopes of regression lines drawn through the cross-correlation coefficients of a single species plotted with respect to distance. The four transmission locations are represented separately. The horizontal line in the center of each box represents the median slope across species. Boxes are drawn around the midrange (HSPREAD) of values and thus provide an indication of sample variance. The whiskers show the range of values that fall within 1.5 HSPREADs of either edge of the box. Stars denote outside values (farther than 1.5 HSPREADs from the edges of the box). Filled circles denote far outside values (farther than 3 HSPREADs from the edges of the box).

The influence of dominant frequency on call degradation

Species with high and low frequency calls differed in the amount of degradation they experienced. As in a number of previous transmission studies (see Introduction), we found that call degradation generally increased with increasing call dominant frequency. We also observed an interaction between the influence of call dominant frequency and the effects of transmission height and environment. At ground level, sound degradation increased with dominant frequency at all transmission distances in both environments. Above the ground, on the other hand, sound degradation was higher for calls with high dominant frequencies at only the longer transmission distances. Molecular absorption and scattering disproportionately affect higher frequencies at all heights (Wiley and Richards, 1978), but the effect of scattering should be

greatest near the ground where vegetation is most dense. Our results are consistent with this prediction. We also found that, for above-ground transmission, the difference in the amount of degradation experienced by high and low frequency calls was greater in the tall grass environment than in the forest environment. Above the ground, irregular amplitude fluctuations caused by atmospheric turbulence disproportionately affect higher frequencies (Richards and Wiley, 1980). It may be true that the influence of this environmental factor was stronger in the tall grass environment than in forest.

In our sample, other call characters correlated with dominant frequency may have influenced the results of the cross-correlation analysis. For example, all four of the species with dominant frequencies lower than 1000 Hz also had relatively long calls. However, because previous experimental results point to a strong effect of frequency on signal transmission (Brown and Gomez, 1992; Marten and Marler, 1977; Marten et al., 1977; Morton, 1975; Waser and Brown, 1986; Waser and Waser, 1977), we believe that our results correctly indicate an effect of dominant frequency on call attenuation and degradation.

The effects of environmental selection on call degradation

We found no evidence to support the hypothesis that the advertisement calls of the frogs under study evolved in response to selection to maximize transmission distance within their local calling habitat. This was surprising because it has been repeatedly suggested that the signals used for long-distance communication are selected upon for increased transmission efficiency within the habitat from which a species normally calls (e.g., Endler, 1992; Morton, 1975; Ryan and Brenowitz, 1985; Sorjonen, 1986; Wiley, 1991).

A number of previous studies, conducted mostly on bird song, showed that structural differences in the calls of species from forested and open environments match predictions based on transmission experiments conducted in these environments (Bowman, 1979; Hunter and Krebs, 1979; Gish and Morton, 1981; Morton, 1975; Sorjonen, 1986; Wiley, 1991). It has been concluded that the observed differences in call morphology were the result of evolution in response to environmental selection. Studies of anurans, however, have tended not to support this conclusion. One recent study failed to find predicted differences in call morphology among species that broadcast calls through different environments (Penna and Solis, 1998). In addition, Zimmerman (1983) showed that observed differences in call structure among Amazonian frogs could be more readily explained by differences among species in body size or by phylogenetic relationship than by differences in natural calling environment.

There is evidence that some of the fine-scale call differences between subspecies of cricket frogs, *Acris crepitans crepitans*

Table 2
Rate of change in sonogram cross-correlation coefficients over distance

	<i>n</i>	Median slope ^a	Range	Variance
Forest, 0 m height	23	-0.028	-0.003 to -0.384	0.006
Forest, 1.5 m height	19	-0.014	-0.002 to -0.053	<0.001
Tall grass, 0 m height	20	-0.034	-0.005 to -0.215	0.002
Tall grass, 1.5 m height	19	-0.007	-0.001 to -0.043	<0.001

^a Regression slopes were calculated, for each species plus the synthetic tone and pulse, from the cross-correlation coefficients plotted over the four transmission distances. Only those species for which there was a significant correlation between cross-correlation coefficients and distance were included in these analyses.

Table 3
Classification of species by call morphology and natural calling location

Species	Dominant frequency (Hz)	Natural calling environment	Natural calling height
<i>Agalychnis callidryas</i>	1856	Forest	High
<i>Bufo typhonius</i>	1883	Forest	Low
<i>Centrolenella fleischmanni</i>	5395	Stream	High
<i>Colosthesus flotata</i>	6949	Stream	Low
<i>Colosthesus inguinalis</i>	4516	Stream	Low
<i>Eleutherodactylus diastema</i>	3945	Forest	High
<i>Eleutherodactylus fitzingeri</i>	2124	Forest	Low
<i>Eleutherodactylus taeniatus</i>	2576	Forest	High
<i>Hyla crepitans</i>	2148	Open	Low
<i>Hyla foliomorta</i>	842	Forest	High
<i>Hyla microcephala</i>	6245	Open	High
<i>Hyla rosenbergi</i>	1508	Forest	— ^a
<i>Hyla rufitela</i>	1929	Forest	High
<i>Hyla staufferi</i>	3935	Open	High
<i>Leptodactylus fragilis</i>	1227	Open	Low
<i>Leptodactylus pentadactylus</i>	545	— ^a	Low
<i>Physalaemus pustulosus</i>	546	Open	Low
<i>Pleurodema brachyops</i>	732	Open	Low
<i>Scinax boulengeri</i>	3044	Forest	High
<i>Scinax rubra</i>	— ^a	— ^a	Low
<i>Smilisca sila</i>	1915	Stream	Low
<i>Smilisca sordida</i>	1714	Stream	Low

^a Species with calls that resisted classification by morphology, or that call substantially from different heights or in different environments, were not included in statistical analyses.

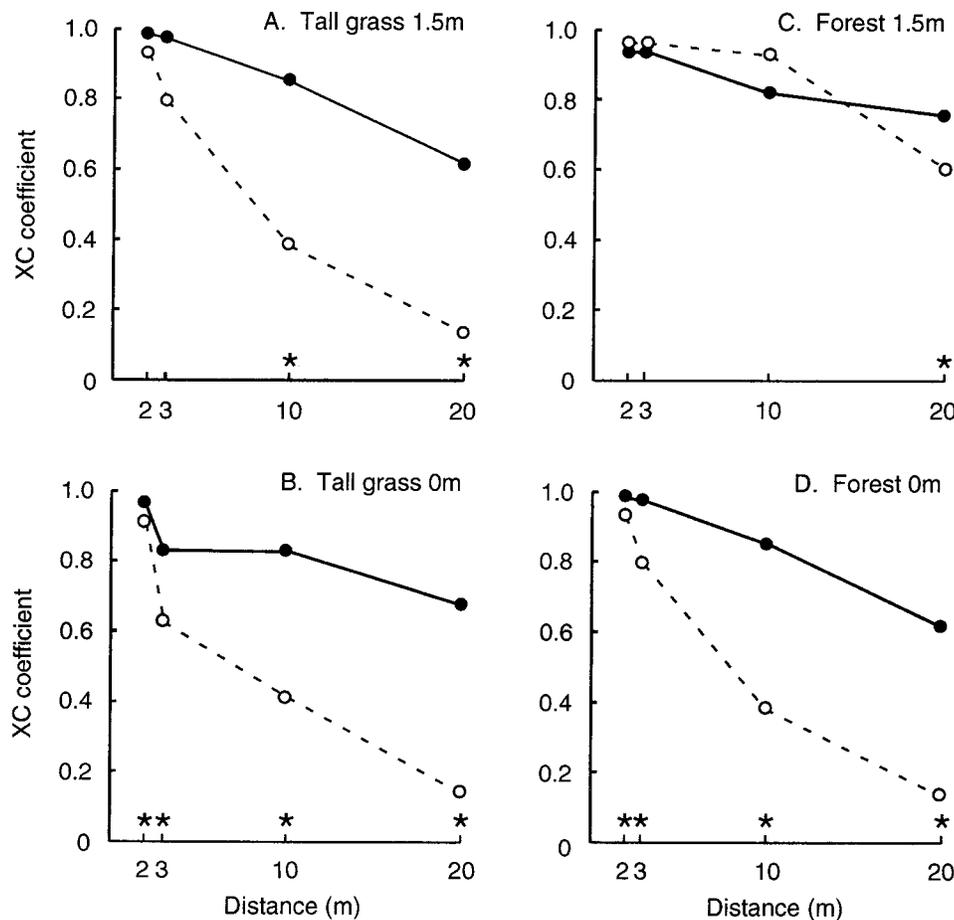


Figure 4
 Median cross-correlation (XC) coefficients for frog calls transmitted over four distances within four transmission locations. Calls were classified by dominant frequency (open circles = calls with a dominant frequency >2000 Hz; filled circles = calls with a dominant frequency <2000 Hz). Sonogram cross-correlations were performed between calls transmitted over 2, 3, 10, or 20 m and a reference call transmitted over a distance of 1 m. Stars near the x-axis denote the distances for which the two groups differed significantly.

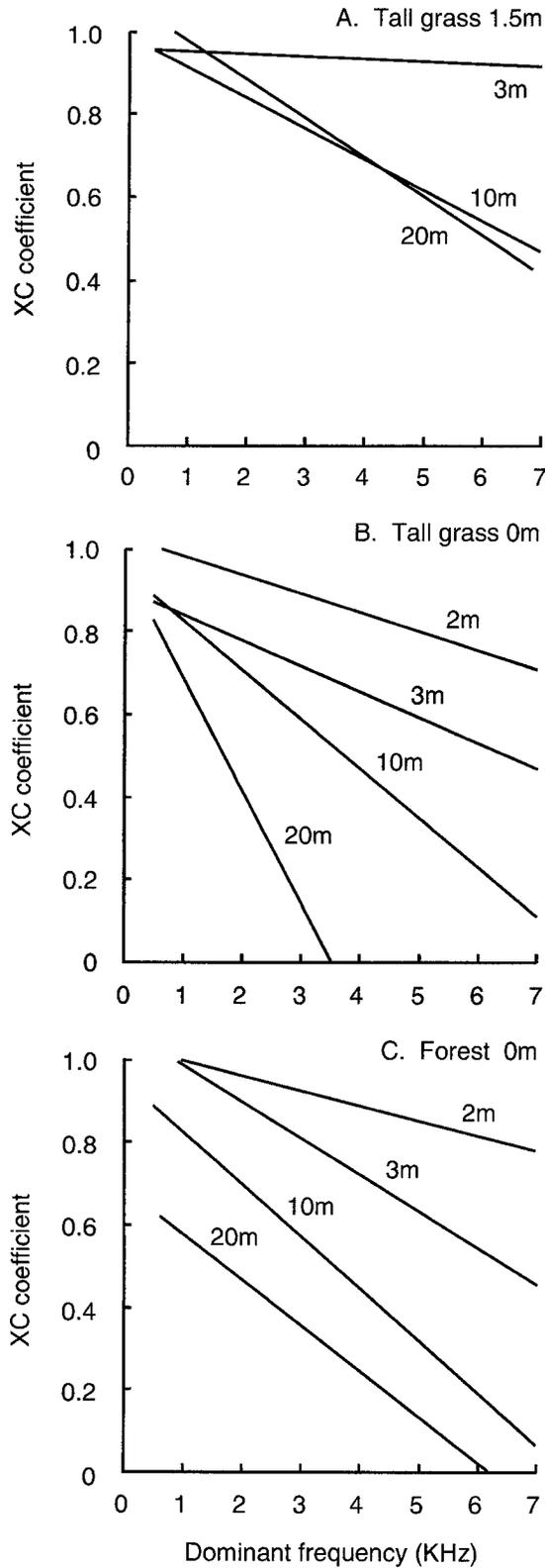


Figure 5
Linear regressions of cross-correlation (XC) coefficients plotted with respect to call dominant frequency. Regression lines are presented for only those locations and distances for which there were significant correlations between cross-correlation coefficients and dominant frequency.

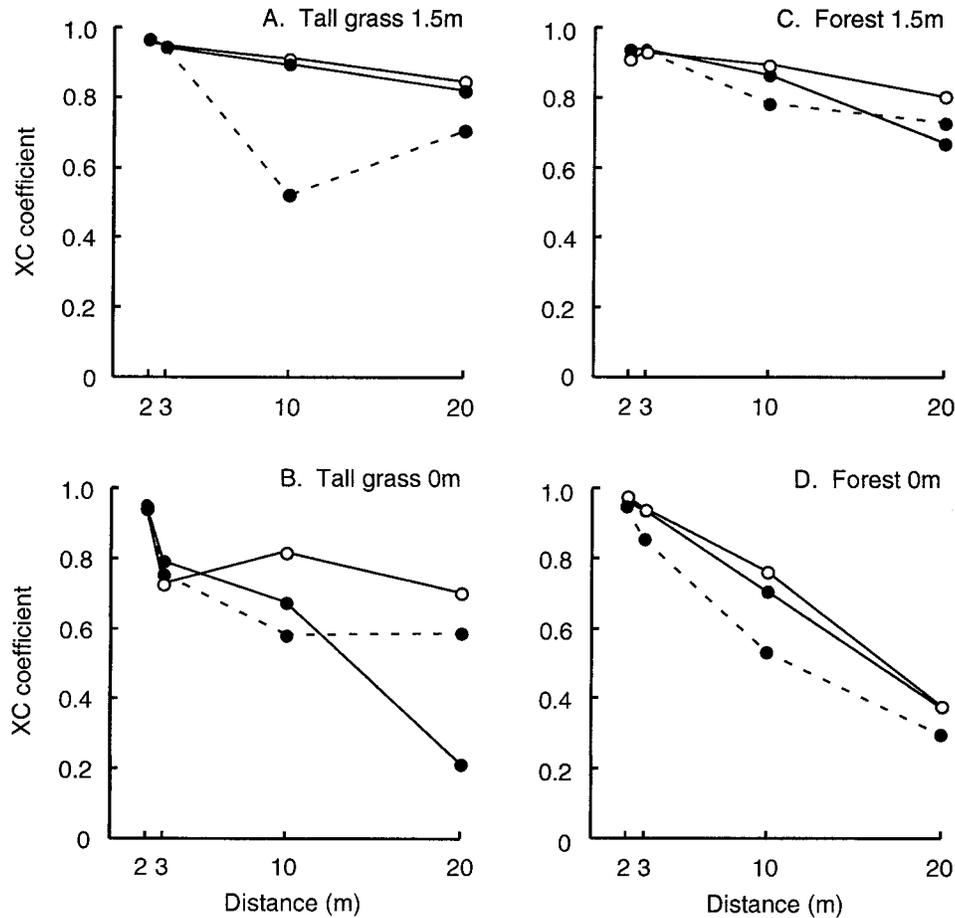
and *A. c. blanchardi*, might derive from an evolutionary response to selection generated by habitat acoustics (Ryan et al., 1990; Wilczynski and Ryan, 1999). *A. c. blanchardi* resides in open habitat that has little effect on call degradation. The forest environment of *A. c. crepitans* has a more severe effect on calls. Both subspecies exhibit little call degradation in the open habitat, with the call of *A. c. crepitans* performing better than that of its sister subspecies; both showed substantial degradation in the forest habitat. There was also an interaction effect; the calls of *A. c. crepitans* experienced a less severe increase in degradation between the open and forest habitats than the calls of *A. c. blanchardi*. Thus the calls of the forest subspecies, *A. c. crepitans*, appears to have evolved in response to selection for transmission efficiency in forest and thus transmit with less degradation in both environments.

We expected similar findings. The results of our transmission studies indicated that the strength of environmental selection is especially high for ground-level callers and that changes in call morphology as a result of this selection could result in increases in transmission efficiency for these species (see previous sections). We thus predicted that the advertisement calls of species that normally call from the ground have evolved in response to selection for more efficient transmission within this location. Furthermore, we expected that the resulting changes in call structure would be reflected in less call degradation, within the ground-level transmission locations, among ground-level callers than among species that normally call from above the ground.

Our failure to find differences in degradation among species partitioned by calling locations can be attributed to a number of different factors, including statistical sampling error, the relatively small active space of the anuran mating signal, morphological constraints on call structure, or selection on signal morphology in other contexts. One possibility is that our failure to find significant differences among the groups of species may have been due to a type II statistical error. Similarly, differences among species might have been obscured by the coarseness of the cross-correlation technique, or by the groups into which we classified species being too broad to detect differences among species that call from more narrowly defined microhabitats (as cautioned by Morton, 1975; Zimmerman, 1983).

A second possibility is that frog advertisement calls simply may not need to travel long distances. The distance over which anuran advertisement calls can be heard varies greatly among species (Loftus-Hills and Littlejohn, 1971; Stebbins and Cohen, 1995; Zimmerman, 1982), and it is possible that the calls of some of the species included in this study have not been selected upon for transmission over the distances we investigated. However, we observed significant differences in degradation among individual species over distances as short as 2 m. Because the calls of most of the anuran species included in this study probably must travel at least this far to reach female receivers (personal observation), we suggest that this alternative is not likely with respect to the current study. Furthermore, in most species of anurans tested there is preference for calls of greater amplitude (reviewed in Ryan and Keddy-Hector, 1992). Decreased degradation might not only increase the active space of the signal but also increase the amplitude and thus the attractiveness of the signal at closer distances.

It is also possible that the morphology of the vocal apparatus constrains call structure (Cocroft and Ryan, 1985) and that phylogenetic constraints on this physical trait can limit call evolution in response to environmental selection (Ryan and Brenowitz, 1985; Zimmerman, 1983). Our results and others (Brown and Gomez, 1992; Marten and Marler, 1977; Marten et al., 1977; Morton, 1975; Waser and Brown, 1986; Waser

**Figure 6**

Median cross-correlation (XC) coefficients for frog calls transmitted over four distances within four transmission locations. Species were classified by their natural calling environment (open circles = species that call through open environments; filled circles = species that call through forested environments; dashed lines = species that call near streams). Sonogram cross-correlations were performed between calls transmitted over 2, 3, 10, or 20 m and a reference call transmitted over a distance of 1 m. In no case were there significant differences among the groups.

and Waser, 1977) demonstrate that dominant frequency is one call characteristic that may be selected upon in the context of habitat acoustics. However, the dominant frequency of a frog's call is partially constrained by its body size. Larger frogs generally call with lower dominant frequencies than smaller frogs (Littlejohn, 1977; Martin, 1967). Frogs can lower dominant frequency independent of body size by direct weighting of the vocal folds. Without a concomitant increase in body size, however, there will be even greater impedance in coupling acoustic energy to the environment. Many frogs use call wavelengths that are several times their body length but exhibit very low energetic efficiencies for calling (Ryan, 1988). Advertisement call dominant frequency may thus be more constrained by the morphology of the caller than by habitat acoustics.

One further possibility is that selection on call structure in the context of species recognition or sexual selection has had a greater influence on call morphology than selection for decreased call degradation. Evolution of call structure in response to environmental selection would necessarily result in some convergence of call structure among the different species occurring in a given habitat. However, some studies have suggested acoustic niche partitioning among species of frogs occurring in a single community (Drewry and Rand, 1983; Duellman and Pyles, 1983; Hödl, 1977). Selection for divergence of signal structure, in order to avoid acoustic interference among species, may have been more influential than selection for decreased degradation in determining the structure of frog calls.

Sexual selection can also influence advertisement call struc-

ture. Female frogs show mating preferences for many characteristics of the frog's advertisement call, and female mate choice with respect to these preferences can exert selection upon male call morphology (e.g., Andersson, 1994; Ryan, 1985). Sexual selection and environmental selection may operate in the same direction (such as toward lower dominant frequencies). If sexual selection opposes environmental selection, however, it may be strong enough to balance or counteract the effects of the latter on call structure.

We suggest that phylogenetic constraints on call morphology, or selection on call structure in other contexts, have been more influential in determining the structure of anuran advertisement calls than selection for increased transmission efficiency. Our experiments included a diverse mix of frog taxa. Further studies investigating the role of environmental selection on call morphology should focus on differences among the calls of closely related species or populations of a single species that have experienced abrupt habitat shifts (e.g., *A. crepitans*, as discussed above). Such studies would allow a more fine-scale analysis of differences in signal structure and call transmission than the current study. In addition, closely related groups should share some morphological and behavioral constraints. The differences in call morphology among these groups could be more effectively used to test hypotheses about the evolution of frog call structure in response to environmental selection.

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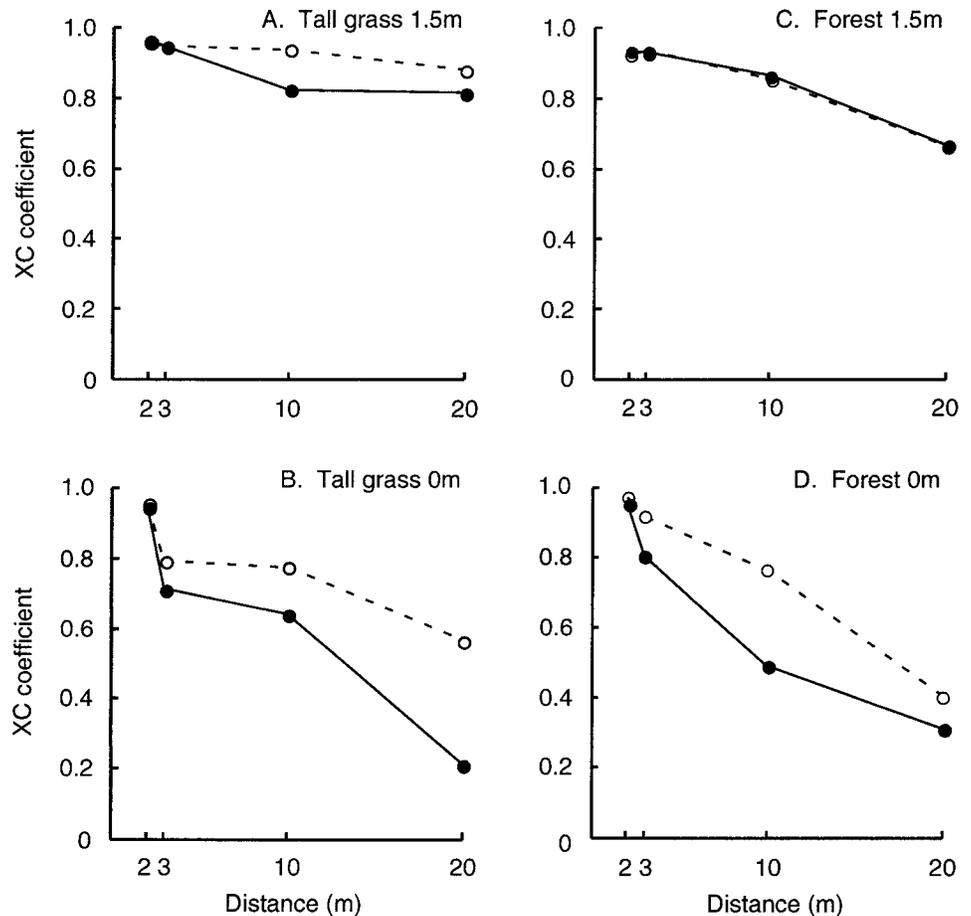


Figure 7
Median cross-correlation (XC) coefficients for frog calls transmitted over four distances within four transmission locations. Calls were classified by natural calling height (open circles = species that call from above the ground; filled circles = species that call from the ground). Sonogram cross-correlations were performed between calls transmitted over 2, 3, 10, or 20 m and a reference call transmitted over a distance of 1 m. In no case were there significant differences between the two groups.

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