Herpetologists' League

THE EFFECT OF VEGETATION ON THE PROPAGATION OF CALLS IN THE NEOTROPICAL FROG *CENTROLENELLA FLEISCHMANNI*

KENTWOOD D. WELLS AND JOSHUA J. SCHWARTZ

ABSTRACT: Sound pressure levels (SPL) were measured at various positions around male *Centrolenella fleischmanni* calling from the surfaces of broad-leaved plants. The frogs were not directional sound sources, but the configuration of the calling site sometimes resulted in directional beaming of calls. Measurements of SPL made on the side of leaves on which males were perched were much higher than those made on the opposite side. When recorded calls were broadcast through natural vegetation at the chorus site, there was considerable attenuation of sound over distances of less than 3 m. Variations in calling site acoustics may influence male success in attracting females, but there is no evidence that males choose calling sites because of their acoustic properties.

Key words: Amphibia; Anura; Centrolenidae; *Centrolenella*; Acoustic behavior; Call intensity; Call propagation

PROPAGATION of acoustic signals is affected by a wide range of environmental phenomena, including ground attenuation, temperature gradients, humidity, wind speed, and density of vegetation. These may distort signals before they reach a receiver, making it difficult to predict what an animal will hear when it receives a signal broadcast by another animal some distance away (Michelsen, 1978; Richards and Wiley, 1980).

Several investigators have used natural or synthetic sounds to determine the effects of vegetation and height of the signaler on sound propagation (Hunter and Krebs, 1979; Marten and Marler, 1977; Marten et al., 1977; Martin, 1981; Morton, 1975; Richards and Wiley, 1980; Roberts et al., 1979, 1981; Waser and Waser, 1977). Most of these studies have focused on long-distance communication by birds or primates. Except for several studies of the acoustic properties of in-sect calling stations (Bennet-Clark, 1970; Nickerson et al., 1979; Paul and Walker, 1979; Prozesky-Schulze et al., 1975), there is relatively little information on animals that communicate over shorter distances.

Frogs are particularly appropriate for such studies, because they call from a variety of habitats, and many species have pronounced calling site preferences (Crump, 1974; Duellman, 1967, 1970, 1978; Hödl, 1977; Passmore and Carruthers, 1979). Whether males of any species choose calling sites because of their acoustic properties is not known, but physical characteristics of calling sites certainly affect sound propagation. Differences in calling site acoustics could affect male success in maintaining territories or attracting mates (Fellers, 1979), but this has not been demonstrated conclusively. Most previous studies of call intensity have been designed to minimize variation in calling sites (Gerhardt, 1975;

Loftus-Hills and Littlejohn, 1971; Passmore, 1981). However, Bailey and Roberts (1981) investigated the acoustic properties of burrows made by Australian frogs in the genus *Heleioporus*, and Narins and Hurley (1982) studied sound propagation from different types of perches used by the Puerto Rican frog *Eleutherodactylus coqui*.

We investigated the effect of vegetation on call propagation in the neotropical frog *Centrolenella fleischmanni* (Centrolenidae). Males of this small nocturnal species call from broad-leaved plants overhanging streams. Males usually call from the ventral surfaces of horizontal or near horizontal leaves, but sometimes they call from the tops of leaves as well. Females approach males for courtship and deposit eggs at male calling sites (Greer and Wells, 1980).

Greer and Wells (1980) reported that males calling from sites more than 0.6 m above the ground obtained mates at a faster rate than males calling from lower sites. This might be due in part to acoustic properties of the sites. Low sites were surrounded by dense vegetation which could result in considerable call attenuation; high sites were more open. Furthermore, if the leaves reflect sound, then males calling from the undersides of high leaves would broadcast their calls over a wider area than those on the undersides of leaves near the ground. In June and July 1980, we returned to the study site used by Greer and Wells (1980) to test these hypotheses.

METHODS

The study plot was an area approximately 13 × 17 m along Lutz Stream on Barro Colorado Island, Panama (Greer and Wells, 1980). The area was dominated by *Dieffenbachia* plants, mostly 0.5–1.5 m high, growing along a small drainage course. These plants, along with various taller woody shrubs and a large ground bromeliad (*Aechmea magdalenae*), served as the principal calling sites of male *Centrolenella*. Most of the plants

tagged as calling sites in 1978 were still present and still used as calling sites in 1980, and most had been occupied by calling males in the intervening rainy seasons (M. Clark, personal communication). Some plants were taller and had larger leaves in 1980 than in 1978, and the overall density of vegetation along the stream had increased.

We studied the effect of vegetation on intensity and directionality of calls by measuring sound pressure levels (SPL) of vocalizations given by males at natural calling sites. We measured peak SPL in decibels (dB) with a Gen Rad® 1982 Precision Sound Level Meter and a random incidence microphone, calibrated with a Gen Rad® 1562A Sound Level Calibrator. The meter was set for flat weighting. We made measurements at the following positions around 15 frogs: 0° directly in front of the vocal sac, 180° directly behind the frog, and 90° through the plane of the leaf on which the male was calling, on both the frog side (FS) and non-frog side (NFS) of the leaf. Measurements at 0° and 180° were made at both 50 and 100 cm; measurements at 90° were made only at 50 cm.

All SPL measurements were made between 1930 and 2200 at 24–26 C and 100% humidity. After readings for each frog had been completed, we measured the long and short orthogonal axes of the leaves on which the frogs called and the height of the leaves above the ground. Leaves were easily classified into large, broad leaves of *Dieffenbachia* (mean orthogonal axes: 13 × 23 cm) and the small, narrow leaves of other plants (mean orthogonal axes: 6 × 17 cm). Because males in our study area all were nearly the same size (SVL = 21–23 mm, $\bar{x}$ = 21.5, SD = 0.6, n = 14), we did not investigate the effect of male size on call intensity.

To determine the effect of vegetation on call attenuation, we recorded 20 calls of one male on a Uher® 4200 Report Stereo tape recorder and broadcast the calls through the speaker of the tape recorder at an intensity of 101 dB SPL at 50 cm.

TABLE 1.—Peak SPL measurements (dB) for male *Centrolenella fleischmanni* at 0° and 180°. Number of calls measured is given in parentheses. Calling position was either above (A) or below (B) a leaf. Leaf size was either large (L) or small (S). *P* values are for two-tailed Mann-Whitney *U*-tests for differences in medians.

| Frog | Calling position | Leaf size | Distance (cm) | 0° | | 180° | | P |
				Range	Median (n)	Range	Median (n)	
1	A	L	50	100–101	100 (10)	98–100	100 (10)	n.s.
			100	91–96	94 (10)	97–99	98 (10)	<0.001
2	A	L	50	100–103	102 (10)	100–104	102 (10)	n.s.
			100	91–95	92 (10)	95–97	96 (10)	<0.001
3	A	L	50	92–94	93 (11)	101–104	104 (11)	<0.001
4	A	S	50	93–96	94 (11)	93–95	94 (11)	n.s.
5	A	S	50	96–102	100 (12)	93–95	94 (12)	<0.001
6	B	L	50	102–104	103 (15)	97–100	98 (22)	<0.001
			100	96–100	99 (13)	94–96	95 (15)	<0.001
8	B	L	50	101–103	102 (10)	95–98	96 (10)	<0.001
			100	95–98	96 (10)	92–97	94 (10)	<0.001
9	B	L	50	100–104	103 (10)	98–100	100 (11)	<0.001
			100	94–97	96 (10)	88–91	89 (10)	<0.001
11	B	S	50	98–100	99 (10)	95–96	95 (10)	<0.001
			100	95–99	98 (10)	89–93	90 (10)	<0.001

In two tests, calls were broadcast from about 1 m above the ground in areas with no obstructing vegetation. Peak SPL readings were made at 50, 100, 200 and 400 cm. We then performed six tests in which calls were broadcast through stands of *Dieffenbachia* at different heights and angles. In three tests, the speaker rested on the ground and calls were directed through plant stems. In a fourth test, the speaker was 0.5 m above the ground, and calls were directed through stems and leaves. In two additional tests, the speaker was tilted up at a 45° angle to direct calls through leaves. In all tests, SPL readings were made at 50, 100 and 200 cm, and at 300 cm in one test. All experiments were performed during the day at about 27 C and 94% humidity.

RESULTS

SPL Measurements of Natural Calls

Paired measurements of SPL at 0° and 180° were available for nine frogs (Table 1). Males calling on top of leaves did not exhibit a consistent pattern of direction-ality. Two males calling on top of large leaves and one on a small leaf showed no difference in call intensity at 0° and 180° at 50 cm. One male on a large leaf was significantly louder in back, whereas a male on a small leaf was significantly louder in front. Two males were significantly louder in back at 100 cm; both were on large leaves.

The pattern for males calling on the undersides of leaves was more consistent. All were significantly louder in front than in back at both 50 and 100 cm, regardless of leaf size. However, calling from large leaves resulted in higher intensity calls at both 0° and 180° for males calling above or below leaves (Mann-Whitney *U*-tests on pooled data for all males; $P < 0.05$ for all tests). These data suggest that males themselves are not directional sound sources, but calling from below a leaf results in directional beaming of sound in front of the male. The reason for this is not clear, but it probably is related to the angle between the frog's body and the leaf surface. Males calling upside down have their heads and vocal sacs elevated
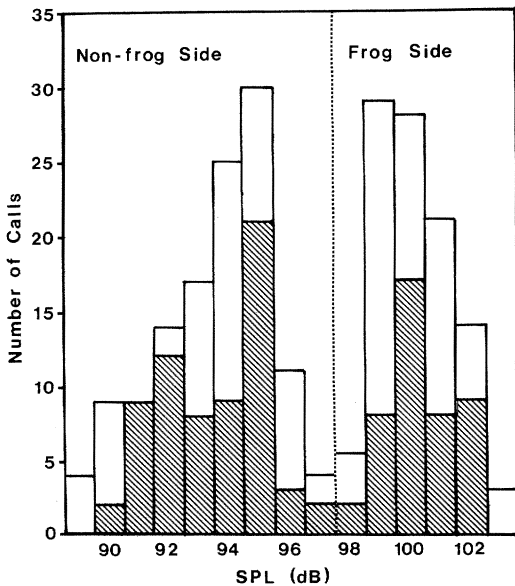
FIG. 1.—Distribution of call intensities measured at 90° on the frog side and non-frog side of leaves at 50 cm. Histograms show pooled data for 10 (FS) and 11 (NFS) individuals (10 or 11 calls per frog). Column height shows the total number of calls at each intensity. Open portions indicate males calling on large leaves; hatched portions indicate males on small leaves. Frequency distributions for frogs on large and small leaves were not significantly different (NFS: $G = 4.15$, 3 df, $P > 0.1$; FS: $G = 5.04$, 2 df, $P > 0.05$).

above the leaf surface, while the back legs are held flat against the leaf. Furthermore, males calling underneath leaves tend to be on a slightly concave surface which would enhance the directionality of their calls, whereas males calling from the tops of leaves often are sitting in the middle of a flat surface.

There was no overlap between SPL measurements made on the frog side and non-frog side of leaves at 90° (Fig. 1). Eight individuals for which paired measurements were available had median SPL values 4–9 dB (median = 6 dB) higher on the frog side, and all differences were statistically significant (Mann-Whitney U-tests, $P < 0.001$ for all tests). The distribution of SPL measurements on the two sides was not significantly different for large and small leaves (FS: $G =$
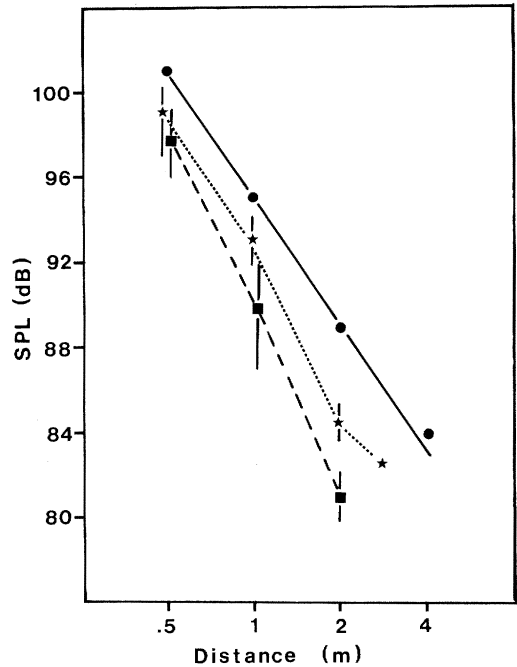

FIG. 2.—Results of sound attenuation experiments using tape recorded calls. Circles show intensities measured with no intervening vegetation (two replicates combined). The solid line shows values expected from the inverse square law (6 dB per doubling of distance). Stars show values for calls broadcast horizontally through plant stems at ground level (three replicates) or 0.5 m (one test). Squares show values for calls broadcast at a 45° angle through leaves (two replicates). Points show pooled median values; vertical lines show ranges of median values for all replicates.

5.04, 2 df, $P > 0.05$; NFS: $G = 4.15$, 3 df, $P > 0.1$) (Fig. 1). There was no correlation between SPL measured at 90° on the frog side and at 0° ($r_s = 0.13$, $n = 7$).

Call Attenuation Experiments

The inverse square law of sound attenuation predicts a 6 dB reduction in SPL per doubling of distance from an omnidirectional sound source (Gerhardt, 1975). When recorded calls were broadcast in areas with no intervening vegetation, the rate of attenuation up to a distance of 4 m was almost exactly that predicted from this law (Fig. 2). These values were used as a baseline for determining the amount

of excess attenuation caused by vegetation. Broadcasting calls through plant stems at ground level or 0.5 m produced excess attenuation ranging from 1.5 dB at 50 cm to almost 4 dB at 2 m (Fig. 2). Broadcasting calls through *Diffenbachia* leaves produced more excess attenuation, ranging from 3.5 dB at 50 cm to 7.5 dB at 2 m (Fig. 2). This means that the source of sound travelling through obstructing vegetation for 2 m would seem to be more than twice as far away as the source of sound travelling through open air. Probably these are conservative estimates, because the tape recorder speaker is a directional sound source which would suffer less excess attenuation than a non-directional source (Richards and Wiley, 1980).

These experiments were designed to determine the general magnitude of excess attenuation caused by plants in this study area. The results cannot be used to predict the precise amount of attenuation of calls originating from a particular calling perch, because this would depend on the number of plants surrounding the calling site, the size of leaves and stems, and the orientation of plant parts to the calling frog and to each other. Furthermore, the results are not applicable to other locations where these frogs call, since the type and density of vegetation varies from site to site. The results do demonstrate that frogs calling in the midst of dense vegetation suffer considerable reduction in the intensity of their calls over relatively short distances.

DISCUSSION

Our work has shown that the substrate on which a frog calls affects the intensity and directionality of his signals. When a frog calls from a large leaf, the reflected sound apparently reinforces the sound waves from the male himself, producing a signal that is louder than those produced by males on small leaves. Although the frogs themselves do not seem to be directional sound sources, the configuration of the calling site may result in some directional beaming of calls. This effect is particularly evident when sound intensity is measured at right angles to the plane of the leaf on which the frog is calling; in every case, sound intensity was much greater on the frog side of the leaf.

Our measurements of SPL 50 cm in front of frogs are equivalent to, or somewhat lower than, measurements reported for North American hylids and African hyperoliids of comparable size (Gerhardt, 1975; Passmore, 1981) and for the similar-sized Panamanian species, *Hyla ebraccata* (Wells and Greer, 1981). However, direct comparisons of call intensities between species are difficult because of differences in calling sites. Many species have been measured at calling sites on the ground or in the water, and these substrates would have acoustic properties quite different from sites used by *C. fleischmanni*.

Gerhardt (1975) and Passmore (1981) reported directional sound fields around several species of North American and South African frogs, but they measured only 2–4 individuals of each species. In many cases, front-to-back intensity differences were less than 3.5 dB, whereas some of our males exhibited differences of 6–8 dB. Narins and Hurley (1982) reported that sound fields around most male *Eleutherodactylus coqui* were non-directional, but some were rendered directional by their choice of calling perches. These authors did not measure sound intensities in the plane perpendicular to the longitudinal axis of the frog. Since many individuals perch vertically on tree trunks or wide leaves, some directional beaming of sound in that plane would be inevitable.

Vegetation may have detrimental effects on signal propagation which we did not investigate. Reverberations can distort the temporal features of calls, although such effects probably are insignificant at short distances. The calls of *C. fleischmanni* are frequency-modulated peeps which lack rapid amplitude modulation (see sonagram in Greer and Wells,

1980). This makes them well-suited for communication in dense foliage (Richards and Wiley, 1980). A potentially more serious problem is that complex arrangements of vegetation probably reflect sound in many directions, making it difficult for females to locate calling males. Females approaching males often spent a considerable amount of time searching through vegetation before locating the callers (Greer and Wells, 1980).

The results of this study support the hypothesis that some males enjoy an advantage in broadcasting their calls because of the acoustic properties of their calling sites (Greer and Wells, 1980). Males calling from the undersides of leaves at low sites would be at a disadvantage because much of the sound energy in their calls is reflected toward the ground and because of excess attenuation due to dense vegetation. Our experimental data predict that calling sites best suited for sound propagation will be those on large leaves at high sites in open areas. Greer and Wells (1980) reported that males at such sites obtained more mates than those at low sites; two males that obtained 35% of the matings but constituted only 15% of the successful males occupied very large leaves at high unobstructed sites.

Our results demonstrate that acoustic properties of a male's calling site can substantially affect the propagation of his calls and perhaps influence his mating success. However, this does not mean that males select calling sites because of these properties. If males cannot evaluate the acoustic properties of different sites, they may choose perches at random, and any effect on mating success may be accidental. Fellers (1979) proposed that male *Hyla versicolor* enhance their ability to attract females by occupying perches well suited for call propagation, but he did not demonstrate that successful males actually spent more time at "superior" sites than unsuccessful males.

Another possibility is that male frogs actively select calling sites, but for reasons not related to call propagation; any acoustic advantages might be incidental. Certain sites might be particularly suitable for egg deposition or survival of hatching tadpoles, although Greer and Wells (1980) could find no evidence of this. Alternatively, some sites might be especially well protected from predators. On Barro Colorado Island, the bat *Trachops cirrhosus* preys on frogs and is readily attracted to *C. fleischmanni* calls (Tuttle and Ryan, 1981). The presence of these bats may explain the tendency of males to call from the undersides of leaves. It also may explain why males call from low sites surrounded by dense vegetation, even if this places them at a disadvantage in attracting females. Unfortunately, observations of bats feeding on *Centrolenella* are not available, so it is impossible to determine whether males at exposed sites suffer increased predation.

We believe that patterns of sound radiation around calling sites of males should be more frequently considered in studies of mate attraction and sexual selection in anurans. Although our data suggest that acoustic properties of calling sites influence male mating success, a rigorous test of the hypothesis would require detailed analysis of call radiation patterns around a large number of males and simultaneous monitoring of their mating success. We hope that our work will encourage others to undertake this type of investigation.

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Biological Sciences Group, The University of Connecticut, Storrs, CT 06268, USA