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## The Advertisement Call of Centrolene geckoideum

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Centrolene geckoideum is one of the most bizarre, renowned, yet enigmatic elements of the diverse Andean frog fauna. Although some aspects of its reproductive biology have been reported (Lynch et al., 1983; Rueda-Almonacid, 1994), little is known about the unique vocalizations of this species.

While carrying out field work in the Colombian Cordillera Occidental at and around Hacienda San Pedro (Valle del Cauca, Dagua, El Queremal, GPS coordinates 3°29'N, 76°42'W), we had the opportunity to directly observe many calling males; however, the typically low call rate and the fact that many males would not reinitiate vocalization while we were present limited the number of available recordings to three. As this population remains under study, only one of the recorded frogs was collected [viz, Universidad del Valle Colección de Anfibios y Reptiles (UVC) 11836, snout-vent length = 74.0 mm].

Calls were recorded using a Sony WM D6C Professional Walkman and a Sony ECM 909 microphone from a distance of 15 cm to 1 m at 17.0 C. Recordings were digitized and edited using CSRE 4.5 PC-based signal analysis software. Call and note duration was taken from expanded waveforms. Call rate was measured directly from tapes with a stopwatch. Frequencies were obtained through fast Fourier transform (window widths of 512 and 1024 points).

The most striking feature of the advertisement call of Centrolene geckoideum—which Lynch et al. (1983:240) accurately describe as "a loud, high-pitched, trilled whistle"-is the lack of any consistent pattern of amplitude modulation (see Figs. 1, 2 and Table 1). Of the 14 calls analyzed (accounting for 35.75 min of tape), no two signals are temporally alike. We considered the possibility that this variation may be an artifact due to distortion of the signal by water, vegetation, or boulders, but this does not appear to be the case; UVC 11836 was recorded from only 15 cm and was ca. 50 cm above the water and well over 1 m from any structure that could distort the signal, indicating that the variation between the seven calls is real. Also, signal distortion is less likely to affect the relatively long sound waves of these calls. The signal is a weakly to moderately pulsed, short burst of energy. Pulses seem to be emitted randomly, with any one (or none) in a given sequence being dominant or subordinate to the rest. Call duration ranges from 155-373 msec, with no

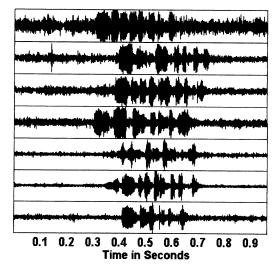
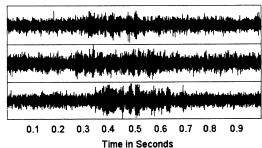


FIG. 1. Oscillograms of advertisement calls of *Centrolene geckoideum* UVC 11836 (74.0 mm SVL, 17.0 C air temperature). The seven calls are shown in chronological order, beginning with uppermost oscillogram. Apparent differences in call definition (i.e., separation from background noise) are an artifact due to decreased recording levels (first call recorded at recording level 7, decreased for each call to a minimum of 2 for the seventh call) and independent analysis of each call.



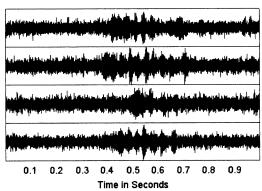


Fig. 2. Oscillograms of advertisement calls of *Centrolene geckoideum* uncollected specimens A (upper) and B (lower), both recorded at 17.0 C air temperature.

TABLE 1. Summary of numerical parameters of *Centrolene geckoideum* advertisement calls (all recorded at 17.0 C). Time from previous call for first call in each series refers to time from beginning of recording. Frequency modulation includes initial, minimum (where applicable, see text) and maximum peaks, and final frequencies in chronological order. <sup>1</sup> Recorded 28 March 1995, 1700 h on tape TG-A 002. On the visit immediately prior, one month earlier, we observed the same male (recognized by scars on the legs and body) calling from the same site, but the call rate was much lower and we were unable to obtain a recording. <sup>2</sup> Recorded calling while sitting above clutch of eggs, 28 May 1995, 2325 h on tape TG-A 005. <sup>3</sup> Recorded 12 July 1995, 2315 h on tape TG-A 005.

Specimen	Time from previous call (min)	Call duration (msec)	No. pulses	Frequency modulation (Hz)
UVC 11836 <sup>1</sup>	≥4.35	300	8	3625–3750–3468
	2.85	345	8	3656-3968-3562
	2.73	338	9	3687-3843-3625
	2.82	373	7	3593-3843-3468
	2.80	281	11	3687-3812-3718
	2.03	354	9	3687-4031-3718
	5.05	242	7	3593-3781-3500
Uncollected A <sup>2</sup>	≥1.28	210	7	3718-3906-3562
	3.09	337	12	3750-4187-3656
	2.35	356	13	3781-3718-3968-3718
Uncollected B <sup>3</sup>	≥0.40	298	6	3687-3656-3750-3656
	1.48	348	10	3687-3656-3781-3625
	2.42	155	3	3625-3718
	2.03	260	7	3781-3656-3718-3625

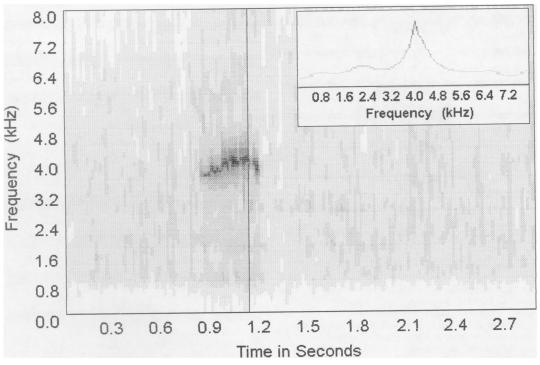


Fig. 3. Typical audiospectrogram of *Centrolene geckoideum* advertisement call. This is the sixth call emitted by UVC 11836 (74.0 mm SVL; 17.0 C air temperature).

discernible pattern of variation or correlation with number of pulses or frequencies. Recorded calls were emitted infrequently (compared with most other anurans in this region) at intervals of 1.48–5.05 min (values in Table 1 for the first call in each series refer to the time from recording initiation, not the actual time from previous call). However, we have witnessed males to typically call much less frequently (i.e., as little as less than once per hour), and only recorded the more acoustically active frogs.

Contrary to the protean nature of pulse amplitude modulation and variable calling rate, spectrographic analysis reveals surprising uniformity in call structure (see Fig. 3 and Table 1). Emphasized frequencies cover a range of 3468-4187 Hz with extensive modulation that is consistent among calls and individuals. Calls begin at a relatively low frequency of 3593-3781 Hz. In some cases (N = 4), a dip appears in the audiospectrograph where frequencies fall initially 31-125 Hz. Invariably, the dominant frequency then rises 62-437 Hz to a maximum of 3718-4187 Hz, after which it falls again, ending at 3468-3718 Hz (the very short third call of uncollected specimen B appears to have been cut short by the frog as it contains only three discernible pulses and lacks the final, low frequency typical of all other calls).

In the anuran acoustic communication system, information may be transmitted through non-random variation of spectral and temporal parameters (Straughan, 1973; Duellman and Trueb, 1986). In the case of *Centrolene geckoideum*, no pattern can be deciphered in the variation of call rate, call duration, or

number or duration of pulses, while spectral structure is highly conservative. Although additional investigation is required to address their origin and significance, we speculate that these unique characteristics may be a response to the singular conditions in which this species calls.

All Centrolene geckoideum have been observed to call from behind waterfalls or within or near spray zones of fast-flowing forest streams (Lynch et al., 1983; Rueda-Almonacid, 1994; pers. obs.), situations characterized by the constant intensity of background noise. We have not measured background noise volume at calling sites, but it is illustrative to consider that human observers must shout or retire to a position several meters from the calling site to be heard over the din of the stream. We are unaware of any other anuran that calls in such continuously loud surroundings. In these conditions, it is conceivable that subtle variations in temporal parameters such as call duration and number of pulses could be lost in the background noise of the stream, and would therefore be an unreliable means of information transmission (see Figs. 1, 2 in which peaks in background noise intensity may equal or surpass those of pulses). All other streamdwelling anurans in this region call from quieter areas, and those that have been analyzed exhibit much more temporally consistent and elaborate calls. On the other hand, fine-tuning of the hearing apparatus to the narrow band of frequencies used by C. geckoideum could potentially overcome many problems associated with background noise. The constancy seen in audiospectrograms supports this scenario.

Still, the predominance of background noise does not explain the extreme variability observed in oscillograms (i.e., it may explain frequency fidelity, but it does not constitute a selective pressure in favor of temporal variation), and it would be more likely for signals to exhibit high redundancy, as typically occurs in similar high-noise environments. For example, Smith (1971) reports a much more simplified and redundant vocal repertoire for the tyrannid bird Serpophaga cinerea, which is "restricted to fast mountain streams," (pp. 261) than for congeners not confined to such areas. We speculate that the surprising protean amplitude modulation may function to reduce signal localizability by predators that use binaural intensity differences to determine signal source. The calling site (see below) of C. geckoideum is usually unprotected (i.e., it is not hidden within vegetation or located on weak branches as in other centrolenids) and is conceivably accessible to a variety of potential predators such as owls and a number of mammals (e.g., the mustelid Eira barbara and the didelphid Didelphis marsupialis which we have seen in these streams), and the extraordinary call-site fidelity demonstrated by males (observed calling at the same site for up to a month) would otherwise seem to make these large frogs easy prey. Of course, a predator avoidance mechanism of this type would also make males more difficult for conspecific females to locate, which suggests that they may use the call as a general indicator of male presence and then resort to non-phonotactic means of localization (e.g., habitat characteristics, odour).

We have heard calls from remarkably far from the source (viz., up to 30 m along the stream or from ca. 5 m through forest). We have observed males to call from smooth, slightly concave, vertical surfaces of boulders in fast-flowing mountain streams, although one male was observed calling from a heavily plantladen fallen log that crossed a stream while chorusing with a male positioned on a clutch of eggs on a boulder. Males on rocks are usually dark gray (as opposed to green) and are often extremely difficult to see. On several occasions we have witnessed males and females at the same site, but no physical contact has been seen despite prolonged observations.

We have observed males sitting on or near up to four clutches of eggs while calling, and have found them by day sitting on clutches or nearby on the rockface or hidden in spaces between rocks. On one occasion, we discovered a firefly larva (Coleoptera: Lampyridae) preying on unguarded eggs. Most of the clutches exhibited the well defined "empty space" depicted in Lynch et al. (1983, their Fig. 1d). Ovoposition has not been observed, but we speculate that ova may be deposited as the female rotates through a circle with the head at the center, a scenario that would explain the origin of the enigmatic space. As pointed out by Lynch et al. (1983), eggs are glued to rock by a brittle jelly unknown in other centrolenids. Clutches have been found within a few cm from the water, a precarious position that would necessitate some method of ensuring that eggs not be washed from the rock, considering that the torrential rains of the Pacific slopes have been observed to cause these streams to rise nearly 1 m in a matter of minutes.

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## Ultraviolet Light-induced Neural Tube Defects in Amphibian Larvae and their Implications for the Evolution of Melanized Pigmentation and Declines in Amphibian Populations

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Reported declines in amphibian populations have been linked to numerous factors, including sensitivity of some populations to increased levels of ambient ultraviolet-B (UV-B) light (Blaustein and Wake, 1990; Wake, 1991). In this connection, attention has been focused most closely on the abilities of eggs to repair damage done to DNA by UV irradiation, and the differential hatching success of embryos exposed to sunlight (Blaustein et al., 1995a, b; Licht and Grant, 1997).

Experimental UV irradiation of amphibian larvae produces a range of developmental defects, including repeated failure of the neural folds to meet entirely to form the neural tube and production of neural folds of unequal size leading to hatchlings with curvature