LEPTODACTYLUS SILVANIMBUS (AMPHIBIA: ANURA: LEPTODACTYLIDAE): NATURAL HISTORY NOTES, ADVERTISEMENT CALL, AND RELATIONSHIPS

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In July 1995, we visited two of the three previously known localities for *Leptodactylus silvanimbus* in Departamento de Ocotepeque, Honduras. We found a new breeding site for the species, recorded its advertisement call, and collected and observed its adults and larvae. The purpose of this paper is to present the results of these new findings and to comment on the relationships of *L. silvanimbus*.

NATURAL HISTORY NOTES

The two localities we visited, El Chagüitón and Belén Gualcho, were originally covered by cloud forest. El Chagüitón has been largely converted to pasture; Belén Gualcho is a regionally important city lacking intact forest in the environs (see Wilson et al. 1986, for further information).

The El Chagüitón site had been productive in previous years. We worked the site both by day and night, in periods preceded by, during, and following rain. No Leptodactylus silvanimbus were observed or heard, although Bufo coccifer, Hypopachus barberi, and Rana berlandieri were calling. These same species were collected from the same marshy portion of the pasture in previous years when the Leptodactylus also were present. We learned from local residents that the road bed was rebuilt after JRM and LDW had last visited the site in 1987; this resulted in the lowering of

the water level in the marshy pasture. Additionally, during the rebuilding process, the marshy area was almost completely drained.

We searched the road on the outskirts east of Belén Gualcho for the second historical breeding site. The area had undergone considerable change since JRM and LDW first worked the area in 1980. The only pond system we located that had the greatest likelihood of being the previously sampled Leptodactylus silvanimbus site is now a bare field where the stream had been dammed and shallow artificial pools created. There was very little vegetation around the pools, and the area was mostly exposed earth. A large chorus of Bufo marinus was heard and seen and their larvae were abundant in the pools. The fact that B. marinus were not collected previously by JRM and LDW at Belén Gualcho, suggests that the site had been modified significantly, thereby providing new habitat for B. marinus and likely destroying the conditions necessary for L. silvanimbus reproduction.

The site at which we found Leptodactylus silvanimbus was in the town of Belén Gualcho at an artificial, temporary pond that was surrounded and overgrown with a tangle of herbaceous and woody growth. The pond was approximately $3 \times 8 \times 0.5$ m. On the night of 19 July 1995, we heard advertisement calls of L. silvanimbus, which was the only species calling from that particular pond (Hypopachus barberi and Ptychohyla salvador-

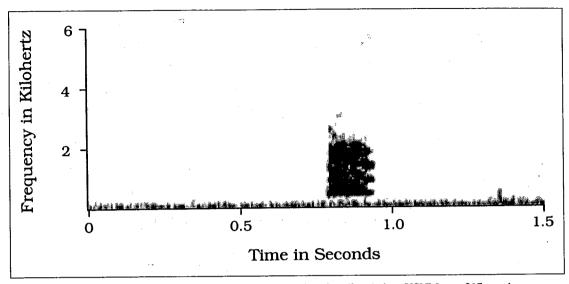


Figure 1. Audiospectrogram of advertisement call of Leptodactylus silvanimbus, USNM tape 317, cut 1.

ensis were calling from within hearing distance). Owing to the thick vegetation surrounding the pond, we were unable to collect frogs. The following morning, males were calling nearly as vigorously as they had been the previous night. We recorded the single call type we heard. We collected one male under thick vegetation at the pond's edge from where we had recorded the call. Also, several juveniles were collected from a grassy, inundated region adjacent to the pond. That night (without the recorder), most males gave a few initial "chirp" calls before starting the normal advertisement call. Three or four males were calling, but were hidden within cavities or under vegetation or debris and eluded capture. One adult male and one adult female, however, were collected from exposed sites along the pond's edge. These limited observations together with those of Wilson et al. (1986), suggest that vegetation surrounding moderately deep water is required for successful reproduction.

At night, the larvae of Leptodactylus silvanimbus seemed to be concentrated in a single aggregation, but they were not organized to the level of schools, as occur with L. ocellatus (Vaz Ferreira and Gehrau 1974). We did not see evidence of larval aggregation during the day when we sampled specimens (Gosner stages 26 to 36) with dipnets. The larvae were most abundant in the deepest part of the pond. There

was no evidence of maternal attendance of the larvae, as has been described for *L. ocellatus* (Vaz Ferreira and Gehrau 1975) or *L. validus* a member of the *melanonotus* species group (Downie 1996).

ADVERTISEMENT CALL

The call (USNM tape 317, cut 1) was recorded on 20 July 1995, at Belén Gualcho, by RdS at 1005 h, with an estimated air temperature of 21 C. The calling individual was not captured. A Marantz model PMD-430 stereo cassette tape recorder and a KE66 Sennheiser microphone were used to record calls. The calls were analyzed using the software package "Canary" (Charif et al. 1993) on a Macintosh IIci computer. Call rate was determined for a 3 min recording period. Other call characteristics are based on analyses of 10 calls, all from the same individual.

The call consists of a single, relatively long, partially pulsed note (Fig. 1). The average call rate is 22 per min, ranging from 17-27 calls/min. The faster calling rates occurred when a second individual was calling. Average call duration is 152 ms (milliseconds). There are about 160 partial pulses per second per call. When the entire call is analyzed, the loudest broadcast frequency is equal to the fundamental frequency, 510 Hz (Fig. 2A). However, there is a complex relation-

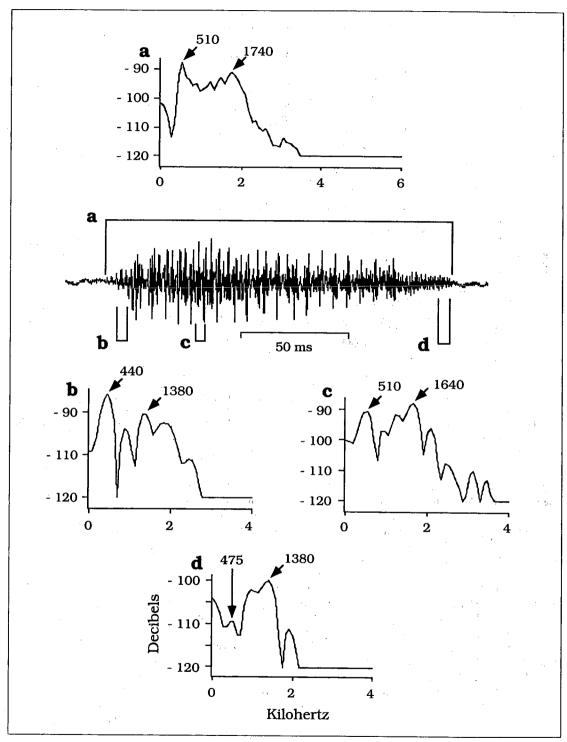


Figure 2. Wave form and spectral analyses of advertisement call of *Leptodactylus silvanimbus* (same call as in Fig. 1). Peak frequency values indicated by arrows for entire call (a) or portions of call (b, c, d).

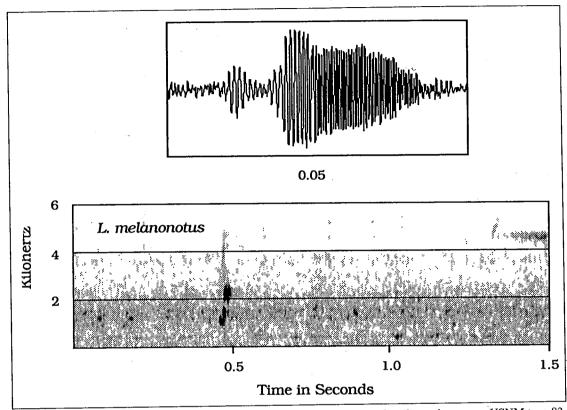


Figure 3. Wave form and audiospectrogram of advertisement call of Leptodactylus melanonotus, USNM tape 83, cut 1 (Costa Rica)

ship between the broadcast and fundamental frequencies within the duration of the call. At the onset of the call, the fundamental is also the broadcast frequency and ranges from 420-510 Hz (Fig. 2B). Just after call initiation, the overall fundamental frequency ranges from 510-620 Hz. The broadcast frequency is either the fundamental frequency or the first harmonic (1310-1400 Hz; both situations about equally common). At the peak intensity of the call (about 1/3 the call duration), the fundamental frequency ranges from 510-540 Hz and the broadcast frequency is always the third harmonic (1640-1820 Hz; Fig. 2C). At the end of the call, the fundamental frequency ranges from 440-530 Hz and the broadcast frequency is either the third or fourth harmonic (1380-1920 Hz; Fig. 2D). In terms of the fundamental frequency, the call is typically initiated at 440 Hz, quickly rises to 510 Hz, then slowly falls to 440 Hz by the end of the call. The human ear neither perceives the slight drop in frequency during the call, nor responds quickly enough to process the rapid rise in frequency at the beginning of the call.

RELATIONSHIPS

When first described (McCranie et al. 1980), Leptodactylus silvanimbus could not be allied on the basis of data derived from adults and juveniles with any of the four species groups of Leptodactylus then recognized. Subsequently, based on the larval morphology, L. silvanimbus was allied with the L. melanonotus species group (McCranie et al. 1986).

Two features precluded inclusion of L. silvanimbus in the Leptodactylus melanonotus group at the time L. silvanimbus was described. (1) Adult L. silvanimbus lacked lateral toe fringes, whereas all members of the L. melanonotus

species group possess them as adults. (2) Male forelimbs are hypertrophied in L. silvanimbus. but not in males of the L. melanonotus group. Examination of specimens of L. silvanimbus collected after 1980, together with our specimens and the type material, indicates that most females have weakly developed lateral toe fringes, while males have either ridges or weakly developed fringes (especially on toe III), rather than extensive fringes. The holotype (USNM 212046) is the most extreme in this continuum, in that the toes are barely ridged. Male forearm hypertrophy was documented in other members of the L. melanonotus species group (Heyer 1994). Thus, the adult morphology of L. silvanimbus can be accomodated within the L. melanonotus group with a modest broadening of the group definition to include toe fringe reduction.

The frequent initiation of calling sequences with a distinctive sounding "chirp" call in Leptodactylus silvanimbus allies the call of this species with those of the L. melanonotus group. The calls of the members of the L. melanonotus group are rather complicated. They are usually very short calls, having an initial low frequency pulse followed by a higher frequency pulse or pulses. However, some L. melanonotus group members have short calls with extremely fast rise times, and others have calls with both rising and falling frequencies (Heyer 1994). However, the advertisement call of L. silvanimbus can be distinguished from those of all other known Leptodactylus because it is relatively long in duration and has a slightly falling broadcast frequency throughout most of the call,

Other than Leptodactylus silvanimbus, there is only one other member of the L. melanonotus group in Middle America, L. melanonotus itself (assuming that L. silvanimbus is in fact a member of the L. melanonotus group). From a zoogeographic point of view, it is critical to know whether L. silvanimbus and L. melanonotus are sister species (i.e., share the most recent ancestor) that differentiated within Middle America, or whether they represent independent derivations from the South American L. melanonotus stock that entered Middle America twice. Thus, it is of interest to know if the call of L. silvanimbus could be derived from the call of L. melanonotus (or vice versa). However, comparison of the calls (see Figs. 1 and 3), shows no obvious and simple way to derive one call from the other, suggesting

that the differences in calls are due to both morphological and behavioral differences. Given the distinctive adult morphologies and calls of the two species, we suggest that *L. silvanimbus* represents an early dispersal event from South America to Middle America by a member of the *L. melanonotus* group and *L. melanonotus* represents a later dispersal event from South America to Middle America by a member of the *L. melanonotus* group. We intend to test this hypothesis by means of appropriate molecular analyses.

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