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Female Reciprocal Calling in a Costa Rican Leaf-Litter Frog, *Eleutherodactylus podiciferus*

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Most male frogs vocalize to attract mates (Wells, 1977). Female frogs generally remain silent during courtship, although in a few cases females have been found to reciprocate vocally to male courtship advertisement. Female reciprocal calling (Littlejohn, 1977) is different from female territorial, aggressive, or release calling (e.g., Stewart and Rand, 1991; Given, 1993, and references therein). To date, female reciprocal calling has been reported in 13 species of anurans from Central America (Dixon, 1957), Europe (e.g., Frazer, 1983; Marquez and Verrell, 1991; Lizana et al., 1994), North America (Given, 1987), South-East Asia (Emerson, 1992), India (Roy et al., 1995), and Africa (Tobias et al., 1998). In this paper, we describe the previously unknown female call of a small Costa Rican leaf-litter frog, *Eleutherodactylus podiciferus* (Leptodactylidae).

MATERIALS AND METHODS

Observations took place in February and April 1997, in small forest fragments (1–2 ha) on Fila Cruces, 5 km south of San Vito, Coto Brus, Costa Rica (82°59′W, 8°48′N). *Eleutherodactylus podiciferus*, as presently understood, is a small frog that is locally abundant in the leaf litter. Males measure up to 28 mm SVL and females up to 35 mm (Savage and Villa, 1986), although in Fila Cruces males and females tend to be on average 7–8 mm shorter (pers. obs.; J. Savage, pers. comm.). We observed three sequences of calling between males and females that ultimately led to amplexus. The males and females from the first and third observed sequence were collected and deposited as voucher specimens at the University of Costa Rica (ref. 13238–13239) and in the Vertebrate Collection of Cornell University (ref. 12631–12632), respectively. We recorded male and female calls in the field using a hand-held tape recorder with a built-in microphone (General Electric, Model 3-5363A) and deposited the recordings at Cornell's Library of Natural Sounds at the Laboratory of Ornithology. We used Canary software to produce sound spectrographs. Spectrographs were analyzed using a filter band width of 1398.8 Hz, a grid resolution of 0.36 msec, an overlap of 87%, and a Hamming window.

RESULTS

Calling behavior.—All male *E. podiciferus* appear to have the ability to either "trill" or "squeek" (examples of which are shown in Fig. 1). Most males appear to squeek primarily, and the trill is given occasionally. The significance and use of these two different calls is unknown.

Three sequences involving female calling were observed. The first sequence took place at 1945 h on 13 February, after a light afternoon rainfall. A trilling male was caught and placed into a small transparent plastic bag, and it continued to call every 10–20 sec. A short squeek from an approaching female followed each of the male's trills. The calling female eventually reached the plastic bag. She was caught and placed inside the bag with the male. They quickly entered axillary amplexus. No eggs were laid during the following two days, at which point the pair was preserved.

The second sequence (25 Feb., 2100 h, also after a period of rain) was similar to the first, with the notable exception that the female was caught first, and placed in a transparent plastic bag, from which she continued to call. We observed a male approach her, from about 100 cm away, alternately trilling and making short jumps (5–10 cm) in the female's direction. When the male was within a few centimeters of the bag containing the female, the male switched to a squeek that resembles the female squeek, although somewhat softer (for examples of female and male squeeks, see Fig. 2). After the male was placed in the bag, the pair entered amplexus.

In the third sequence (18 April 1900 h, after an afternoon of rain following a month of dry weather), amplexus had already occurred when the pair was found. The pair became separated as they were placed in a plastic bag, from which they continued to call (both emitting squeeks). This sequence was recorded (Fig. 2). Using indirect light, MAS was able to observe the female extend her throat as she called. Three eggs were laid in the bag by the following morning.

The strength of a male's attraction to female calling is illustrated in the following sequence. On April 22, RFS, imitating the squeek of a female with a soft whistle, apparently deceived a male *E. podiciferus*. The male, squeeking in al-

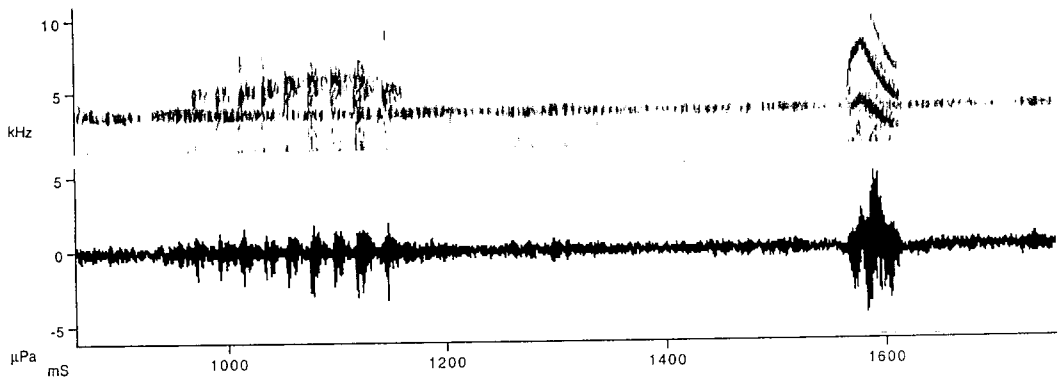

Fig. 1. Audiospectographs (top) and oscillograms (bottom) of two types of male calls in *Eleutherodactylus podiciferus*: the "trill" (left, SVL = 15.5 mm) and the "squeek" (right, SVL = 15.9 mm). Both calls were recorded on 10 April 1997 (18 C, 1343 m). Calls were placed next to one another synthetically. The time scale illustrates call duration only and does not reflect the true interval between calls.

ternation with RFS's whistles, emerged from beneath the leaf litter, jumped onto RFS's boot, up his leg, and on to his stomach (RFS was sitting down), presumably in search of the elusive female.

Calling characteristics.—The male trill is characterized by 8–9 pulsations, with a mean frequency of 5.5 kHz, and no harmonics (Fig. 1). Female squeeks resemble male squeeks superficially (Fig. 2), but the female call has a higher average dominant frequency (3100 vs 2700 Hz), more harmonics (5 vs 3), and a longer duration (57.7 vs 43.7 msec) than a typical male call (n = 3 for female calls, n = 2 for male calls). The female call was also noticeably louder than the male call (± 5µPa vs ± 2.5µPa).

Discussion

Eleutherodactylus podiciferus males are able to produce at least two different calls (Fig. 1), although the function of these two calls is not clear. In general, both trills and squeeks are frequently heard, although the latter are more common. In one sequence, we observed a male switch from trills to squeeks as he approached a female. Interestingly, Dixon (1957) observed the reverse calling pattern in a congeneric frog, *E. angustidigitorum*, where the male switched from a simple "peep" to a repeated trill as he approached a reciprocating female.

In some species, females will occasionally initiate courtship calling if they are heavily gravid and about to lose their eggs (Bush, 1997). We

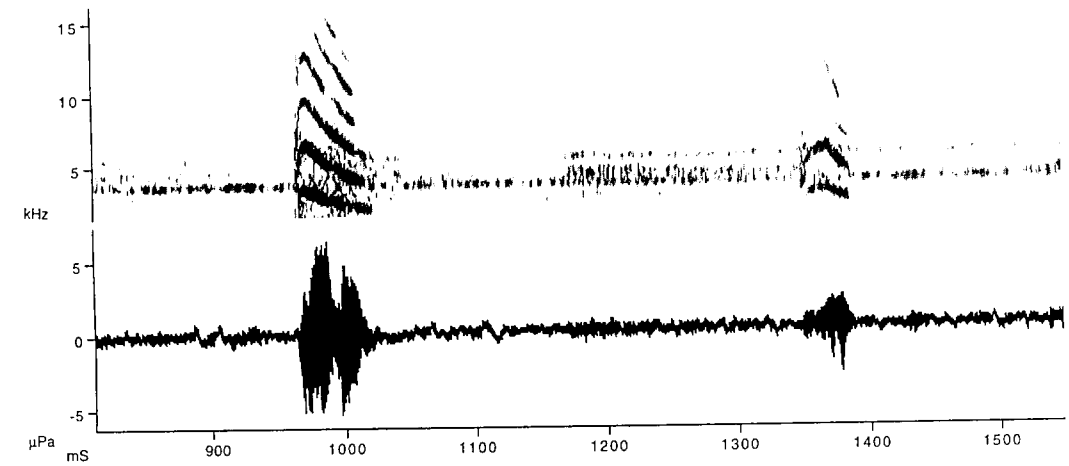

Fig. 2. Audiospectograms (top) and oscillograms (bottom) of female (left, SVL = 24.1) and male (right, SVL = 17.0) "squeeks" in *Eleutherodactylus podiciferus*. Both calls were recorded on 18 April 1997 (18 C, 1322 m). Calls were placed next to one another synthetically. The time scale illustrates call duration only and does not reflect the true time interval between calls.

TABLE 1. COMPILATION OF KNOWN ANURAN SPECIES WITH FEMALE RECIPROCAL CALLING,[a] With Duration of Breeding Season, Mean Dominant Frequency of Female and Male Calls, Presence of Male Parental Care, and Type of Breeding Location. Symbols: A = aquatic, T = terrestrial, N/A = information not available, Y = present.

Species	Reference	Family	Duration of breeding season	Dominant frequency (Hz)		Male care?	Breeding location
				female	male		
Alytes cisternasii	Marquez and Verrell (1991)	Discoglossidae	3–4 months	1182	1443	Y	T
Alytes muletensis	Bush (1997)	Discoglossidae	N/A	1700	1800	Y	T
Alytes obstetricans	Heinzmann (1970)	Discoglossidae	5 months	1380	1340	Y	T
Eleutherodactylus podiciferus	present study	Leptodactylidae	min. 5 months	3100	2700	N/A	T
Eleutherodactylus[b] *angustidigitorum*	Dixon (1957)	Leptodactylidae	N/A	N/A	N/A	N/A	T
Pelobates cultripes	Lizana et al. (1994)	Pelobatidae	35–41 days	582	544	N/A	A
Pelobates fuscus insubricus	Andreone and Piazza (1990)	Pelobatidae	28 days	4000[c]	8000[c]	N/A	A
Xenopus laevis	Tobias et al. (1998)	Pipidae	6 months	1200	N/A	N/A	A
Rana blythi	Emerson (1992)	Ranidae	12 months	N/A	N/A	Y[d]	A
Rana cyanophlyctis	Roy et al. (1995)	Ranidae	4 months	740	1650	N/A	A
Rana erythraea	Roy et al. (1995)	Ranidae	4 months	1050	2460	N/A	T
Rana limnocharis	Roy et al. (1995)	Ranidae	4 months	1530	2140	N/A	A
Rana ridibunda	Frazer (1983)	Ranidae	N/A	N/A	N/A	N/A	A
Rana virgatipes	Given (1993)	Ranidae	3 months	740	500–850[e]	N/A	A

[a] Andreone and Piazza (1990) include *Physalaemus pustulosus* as an example of female reciprocal calling, based on Brattstrom (1962). However, there is no clear reference in Brattstrom (1962) to female calling in *P. pustulosus*, and to date there is no other evidence of female reciprocal calling in this species (M. J. Ryan, pers. comm.)

[b] Previously known as *Tomodactylus angustidigitorum*

[c] Duetting calls

[d] Nest building

[e] Aggressive call (Given, 1993)

could not determine which sex initiated courtship calling in *E. podiciferus*, although males call more frequently, and also in the absence of female calling. We suspect that males produce a general courtship advertisement or territorial call (e.g., after a period of rain) to which receptive females respond, thereby initiating a series of interacting calls and behavioral sequences that may culminate in amplexus.

Species for which female reciprocal calling has been documented appear to share certain general characteristics (Table 1). They all have prolonged breeding seasons, with the exception of *Pelobates* species. Mating is reported to occur in "diffuse" (nonaggregated) populations in the discoglossids, leptodactylids, and certain ranids (e.g., *Rana blythi, R. ridibunda*). The male calls from these species, particularly male aggressive calls, are often structurally relatively simple (peeps or squeeks). Given (1993) has suggested that female calling may have evolved in species where females could have easily replicated the structurally simple male aggressive call, thereby eliciting an aggressive response and bringing the male into her vicinity: a first step leading to amplexus. The female call may therefore function to indicate her receptivity and to help her isolate a desirable mate (Marquez and Verrell, 1991). The breeding and calling behavior of *E. podiciferus* (long breeding period, terrestrial mating, simple calls) corroborate the general pattern observed in many other species where female reciprocal calling occurs.

The evolution of female reciprocal calling also may have been favored in species with extensive male parental care. Male midwife toads (genus *Alytes*) carry strings of eggs around their hind legs for about a month before depositing them in water (Heinzmann, 1970; Marquez and Verrell, 1991; Bush, 1997). Male parental care may lead to a female-biased operational sex ratio, which could favor calling females. There is presently no evidence of parental care in *E. podiciferus*, although there are many known examples of both female and male parental care within the genus (Townsend, 1996; for review of parental care, see also Crump, 1995). Future work may reveal the potential link between the role of male parental care and female calling.

The 14 known cases of female reciprocal calling come from five different families and geographically distinct locations (Table 1), suggesting that female reciprocal calling may have evolved several times independently. We therefore suspect that female reciprocal calling may be much more prevalent than what has been documented to date. Furthermore, female calls often fall outside of the most acutely audible range for humans (2000–5000 Hz; Roy et al., 1995). We urge investigators to not assume, as is sometimes done, that a calling frog is necessarily a male one.

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