

On the Acoustic Communication System of *Eleutherodactylus fitzingeri* (Anura: Leptodactylidae)

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Frogs of the genus *Eleutherodactylus* are the main component of many neotropical herpetofaunas (Scott 1976). However, very little is known about their natural history, and even less information is available on the form and function of their vocalizations. For most species only short call descriptions are published, and for others it is unknown whether they vocalize at all. Yet, the few members of the genus *Eleutherodactylus* whose vocal behavior has been studied in detail show a great diversity of vocalizations: specialized calls for courtship and mating have been reported (Ovaska and Caldbeck 1997), as well as calls for the defense of retreat sites (Stewart and Rand 1991) and even calls produced by females in response to male calls (Schlaepfer and Figueroa-Sandi 1998).

I studied the vocal behavior of *Eleutherodactylus fitzingeri*, a common inhabitant of the tropical lowland forests of Costa Rica (Savage 2002). Although the distribution of *E. fitzingeri* extends from Nicaragua to central Colombia (Lynch and Myers 1983), to date all available information on the vocalizations of this species comes from frogs recorded in Panama (Fouquette 1960; Ibáñez et al. 1999; Lynch and Myers 1983). I provide data on geographic variation of the advertisement calls within Costa Rica and suggest that a vocalization formerly named the “sporadic call” (Ibáñez et al. 1999) is in fact a highly variable aggressive signal.

Material and Methods.—My main study site was at La Selva Field Station, Heredia Province, in the Caribbean lowlands of Costa Rica. I also recorded some frogs from the Pacific lowlands at Marengo Lodge, Puntarenas Province. I used a Sony WM-D6C tape recorder and a Sony ECM 969 microphone to record the calls of males (at ambient temperature of 25–28°C). I either recorded completely undisturbed calling males or I vocally imitated their advertisement call and recorded their vocal response. Whenever possible, I measured the size of the frogs I had recorded (snout–vent length to the nearest 0.1 mm with calipers and weighted them to the nearest mg with a Pesola scale). I digitized the recordings at a sampling rate of 22kHz and analyzed them using the program CoolEdit96 (Syntrillium Co.) on a portable computer. To test whether call variation between populations was statistically significant I calculated Mann-Whitney’s U-tests.

Results.—I recorded two types of calls: an advertisement call that was produced by solitary calling males, and a distinctly different call which was given during antagonistic interactions between males or in response to vocal call imitations.

The advertisement calls (Fig. 1) recorded from Costa Rican frogs were highly variable, and consecutive calls were given in irregu-

lar intervals of several minutes. There was significant geographic variation in several call parameters. Calls from the Pacific population (N = 6) contained between 7–11 notes and had a mean \pm SD duration of 1228 ± 301 ms (range: 830–1610 ms). Calls in the Caribbean population (N = 16) however contained 12–24 notes and had a mean duration of 2884 ± 597 ms (range: 1700–3900 ms). Both call duration and number of notes per call were significantly different between populations ($P < 0.001$ in both cases). Since the duration of the individual call notes was similar in both sites (mean = 10 ± 2 ms; $P = 0.88$), the difference in call duration results from Caribbean males having more notes per call and having a longer internote interval between consecutive notes (mean = 165 ± 13 ms compared to 138 ± 17 ms; $P < 0.001$). The dominant frequency of the calls of Caribbean frogs was 1931 ± 221 Hz, that of Pacific frogs was 1788 ± 27 Hz. This difference was not statistically significant ($P = 0.27$). Males from the Pacific slope were significantly larger (33 ± 1 mm) and heavier (2.6 ± 0.3 g) than males from the Caribbean site (28 ± 1 mm, 1.7 ± 0.3 g; $P < 0.005$ in both cases).

To loud natural or imitated *E. fitzingeri* advertisement calls males responded with a vocalization that sounded like a series of creaking chirps (Fig. 2). Because I did not make recordings of these vocalizations at Marengo, all data given below refer to Caribbean frogs (N = 16). These response calls were produced within 6.3 ± 3.6 seconds after the offset of the rival/imitated call. On average 5.3 ± 3.0 of these calls were produced sequentially (max: 12 calls), with periods of 3.9 ± 3.8 sec of silence between consecutive calls. The mean duration of a complete sequence of response calls thus lasted 17 ± 10 sec. Individual calls contained between 1–4 notes, each of which could last from 3 to 110 ms. The duration of the individual calls was therefore highly variable (31–375 ms). Their build-up, however, followed a common scheme of increasing duration and complexity (Fig. 2). The first call was generally the shortest and consisted of one prolonged note. The following calls often increased in duration and number of notes, and generally here too an increase of note duration from start to end of the call could be observed. The dominant frequency of these calls was

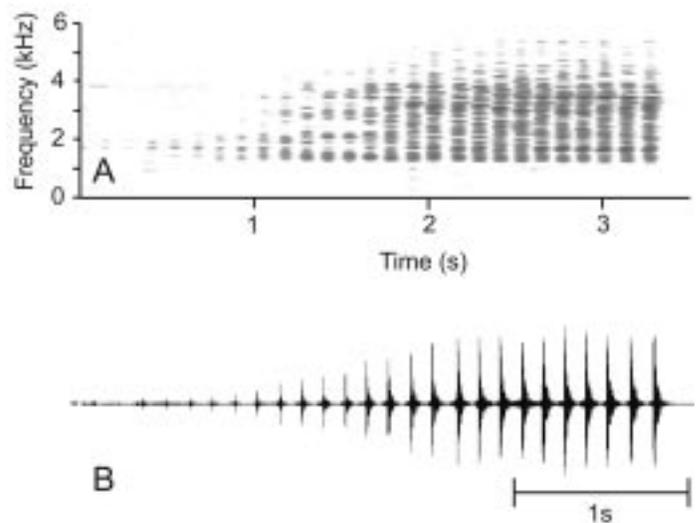


FIG. 1: An advertisement call of *Eleutherodactylus fitzingeri* recorded in Costa Rica. The upper panel (A) shows a sonagram, the lower panel (B) the waveform of the call.

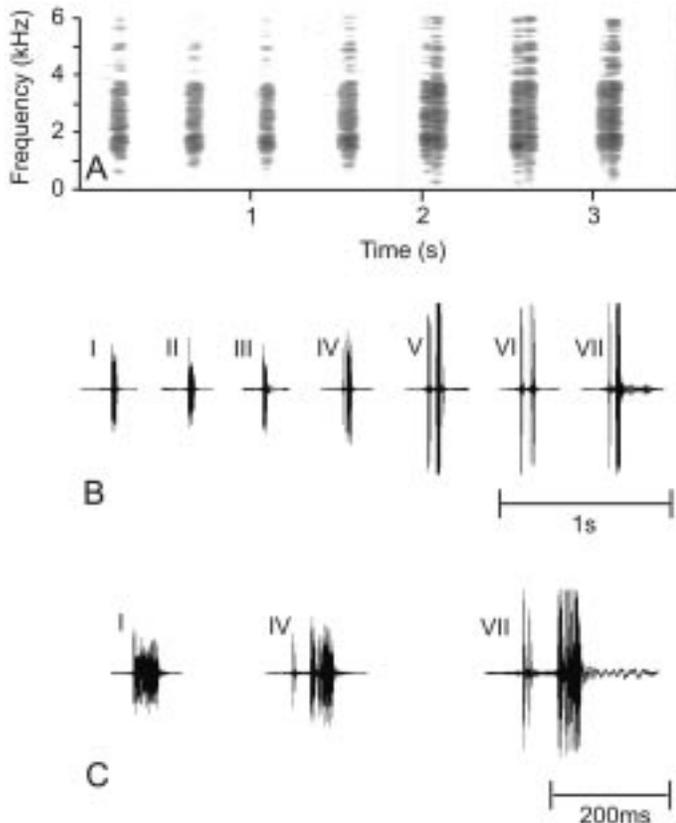


FIG. 2. Aggressive call response of *Eleutherodactylus fitzingeri* consisting of seven consecutive calls. The whole series was 29 sec long, but silent periods between successive calls were deleted in order to show the calls at the same time scale as the advertisement call from Fig. 1. Shown is a sonagram (A) and a waveform (B) of all seven calls. In (C) the waveform of the first, fourth, and last call of the series are shown at expanded time scale. Note how the duration and complexity of the calls increases.

2079 ± 363 Hz. Some males showed positive phonotaxis, turning to face the source of the imitation call before responding, and certain males even moved towards the source of the call, repeatedly emitting this vocalization. Although these calls could be elicited from the majority of males by means of loud call imitations, they were very infrequently heard in nature.

Discussion.—The short advertisement calls are the most frequently heard vocalizations of *E. fitzingeri*, but because of the often large time lapses between consecutive calls, the frogs are very difficult to locate (Fouquette 1960; Lynch and Myers 1983). This may be interpreted as an avoidance mechanism against audio-orientated predators (Tuttle and Ryan 1981), and ties in with the overall life-history pattern of cryptic coloration (Lynch and Myers 1983) and secretive perch choice (Höbel 1999).

Body size might affect spectral call parameters like dominant frequency, and temperature may affect temporal call parameters like note duration, etc. (Gerhardt and Huber 2002). This should ideally be taken into account when comparing populations and describing geographic variation in call parameters. Unfortunately, my data set was not complete enough to run correlation analyses that would have eliminated these confounding factors. However, the most striking distinction between the advertisement calls of the two populations was the difference in the duration of the call,

which was mainly caused by the different number of notes produced per call. Addition of call notes is to my knowledge not affected by temperature. Also, temperature should affect temporal call parameters in similar ways, e.g., lower temperatures should slow down note duration as well as the duration of the inter-note interval. In my analysis however, I found significant differences between populations in one call parameter (inter-note interval), but not the other (note duration).

Although there is geographic variation in the advertisement calls of *E. fitzingeri*, this variation does not follow a clinal pattern. Calls of Panamanian *E. fitzingeri* comprise 2–18 notes per call (Fouquette 1960; Ibáñez et al. 1999; Lynch and Myers 1983), and are thus intermediate to those of the two sites I investigated in Costa Rica. Also, the general structure of the calls is very similar between different Costa Rican and Panamanian populations (Fouquette 1960; Ibáñez et al. 1999; Lynch and Myers 1983). What is the function of this vocalization? As in most frogs, the advertisement call probably serves a dual purpose of mate attraction and territorial function (Wells 1977). Although direct evidence in form of observations of females performing phonotaxis towards a calling male or a speaker broadcasting an advertisement call is still missing, a role in pair formation is nevertheless suggested by the observation that it is the most frequently given vocalization and that it is more often given in the rainy season, e.g., during the period when reproduction takes place (Höbel 1999; Ibáñez et al. 1999). A territorial function, probably regulating inter-male spacing is suggested by males showing phonotaxis while emitting a special aggressive call (see below) when they perceive very loud advertisement calls.

Calls similar to the response calls reported here have been described for Panamanian *E. fitzingeri*. Ibáñez et al. (1999) reported hearing single one-note calls of this type, and termed this vocalization the “sporadic call.” However, they did not comment on its function. Lynch and Myers (1983) elicited a similar vocalization (series of four chirps) by playing back an advertisement call that they had just recorded from the same male, which led them to suggest that this vocalization might constitute a response to conspecific male intruders. The circumstances under which this call type is given, i.e., when hearing a loud advertisement call of a rival male, together with the observation of males moving towards the source of a rival call while giving this vocalization supports the idea that it may be an aggressive call.

As a rule, the structure of a species’ aggressive call differs markedly from the structure of its advertisement call (Schwartz 2001). In *E. fitzingeri* the number of notes in the aggressive call is greatly reduced compared to the advertisement call, but the duration of the aggressive call notes is increased compared to advertisement call notes. This change in call structure is different from the one found in *Eleutherodactylus* species from the West Indies, where the combination and addition of the two basic notes of the advertisement call form calls used in aggressive signaling. *Eleutherodactylus coqui* converts its advertisement call into an aggressive signal by adding advertisement call like notes to the end of it (Stewart and Rand 1991), and the aggressive signal of *E. antillensis* is comprised of a rapid series of notes that resemble the second note of their advertisement call (Ovaska and Caldbeck 1997). Based on these observations there does not seem to be a general pattern in which aggressive calls differ from advertise-

ment calls in *Eleutherodactylus*, but comparative data on aggressive calls in this frog genus is too scarce to draw any conclusions yet.

Eleutherodactylus coqui has highly variable aggressive calls, a graded increase in aggressive call duration is related to retreat site defense (Stewart and Rand 1991). In *E. fitzingeri* the variability in duration and structure of the aggressive call suggests that males may be able to respond in a graded fashion to increasing levels of intrusion/competition as well. However, playback experiments with advertisement calls varying in intensity and thus implying varying distance to rival males are needed to elucidate whether *E. fitzingeri* does in fact have a graded aggressive communication system.

For *E. fitzingeri* from Panama a third vocalization has been described. Ibáñez et al. (1999) mention that females occasionally gave repeated screams when seized, suggesting a distress vocalization. I never heard a distress call while catching frogs in Costa Rica (both males and females), but I also did not make an effort to elicit or record distress calls.

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Seasonal Timing of Follicular Development of the Mud Snake, *Farancia abacura* (Colubridae)

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There is limited information on the seasonality of reproduction of mud snakes, *Farancia abacura*. Observations of reproductive behavior in this species are difficult both in captivity and the wild due to its secretive habits. There are several reports of oviposition and subsequent hatching (Goldstein 1941; Meade 1935b, 1937, 1940a,b, 1945; Reynolds and Solberg 1942), but little is known about seasonally dependent follicle size.

Although complete records of breeding and reproductive habits are limited, Meade (1946) discussed the natural history of *F. abacura*, including reproductive behavior, oviposition, and maternal care. He maintained a live collection of *F. abacura* and produced the first record of breeding habits in *F. abacura* (Meade 1946). Mating and oviposition occurred in July and September, respectively, with the eggs incubating for seven weeks prior to hatching. Hatching of seven clutches occurred between September and October, with incubation periods ranging from seven to nine weeks (Meade 1946). More recently, Robinette and Trauth (1992) investigated both female and male reproductive cycles from mud snakes collected throughout Arkansas. The greatest mean follicle diameter was observed in May and June, synchronal with testicular recrudescence in males.

We examined 129 female *F. abacura* from throughout their range to investigate the seasonal timing of follicular development and discuss the possible relationship between seasonal emergence and the seasonal timing of reproduction.

MATERIALS AND METHODS

Data Collection from Museum Specimens.—Data were collected on oviductal follicle size, snout–vent length (SVL), head width (HW), head length (HL), and total length (TL) of *F. abacura* from adult female museum specimens (Appendix I). Ovarian follicles and oviductal tissue samples were removed through a ventral incision and stored in 70% ethanol for later measurement. Follicles were measured with a Fowler dial caliper and classified based on length according to Betz's (1963) system [Class I = 0.1–5.0 mm; Class II = 5.1–10.0 mm; Class III = 10.1–20.0 mm; and Class IV = 20.1–46.0 mm]. This system allowed for each follicle to be grouped into one of four distinct size classes and is commonly used in studies investigating follicle size and development (e.g., Goldberg 2002; Holycross and Goldberg 2001; Kofron 1979b, 1983; Rosen and Goldberg 2002).

Descriptive Analyses.—We present descriptive data on seasonally dependent follicle length from 76 of 129 females examined. The number of female specimens collected each month was com-