Notes on the natural history and habitat use of *Eleutherodactylus fitzingeri* (Anura: Leptodactylidae)

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Abstract. *Eleutherodactylus fitzingeri* were studied during the dry and rainy seasons at an Atlantic lowland rainforest in Costa Rica. The frogs had one of three dorsal colour patterns (mottled, striped, uniform) and one of two ventral colour patterns (white, yellow). Males had significantly more often a yellow venter than females. Juveniles with a white belly were significantly smaller than juveniles with a yellow belly. Males perched higher than females and juveniles. Perch height in males did not vary with the time of day, weather conditions or behaviour. Calling males used more sheltered perches than silent males, and males calling by day used more sheltered perches than males calling by night. Reproductive activity increased greatly at the onset of the rainy season. Males showed little site attachment.

Introduction

The new world genus of rain frogs *Eleutherodactylus* is the richest of all vertebrate genera, comprising more than 500 species (Duellman, 1993). In many places it is the main component of the herpetofauna (Scott, 1976; Miyamoto, 1982). As either predators on arthropods (Lieberman, 1986), or prey for many invertebrates (Szelistowski, 1985) and vertebrates (Tuttle and Ryan, 1981; Tuttle et al., 1981; Lynch and Myers, 1983), this diverse group of frogs is clearly important in the ecology of a forest (Donnelly, 1994). However, little is known about the natural history of these frogs (Donnelly, 1994).

Eleutherodactylus fitzingeri O. Schmidt is a medium sized species, occurring from Nicaragua to Colombia, mainly in lowlands (Lynch and Myers, 1983). It shows a broad ecological tolerance, inhabiting a variety of wet forests and being found in forest edge situations as well as primary forests (Lynch and Myers, 1983). Miyamoto (1982) studied vertical habitat use of *Eleutherodactylus* frogs, and classified *E. fitzingeri* as "ground active by day and arboreal by night". The present paper gives further data on the natural history of *E. fitzingeri* in Costa Rica, concerning especially habitat use and colour patterns.

Materials and methods

Observations were made at the La Selva OTS field station, in the Atlantic lowlands of Heredia Province, Costa Rica, from March to June 1994. The heavy rainfalls of the rainy season started at the beginning of May. March and April are referred to as the dry season, and May and June are referred to as the rainy season. Observations were conducted for 1 to 3 consecutive days once every fortnight, totalling 22 days of observation. Observations were focused on four areas: a clearing near the Lab; a forest triangle made by the intersection of the trail to the River Station and the Sendero Surá trail; the forest along the Sendero Experimental trail; and the forest along the first 600 m of the Sendero Tres Rios trail (for details of La Selva trails see McDade and Hartshorn, 1994). Each night I walked slowly along the trails with a headlamp, checking the vegetation and listening to calling males. To locate males I first approached them by following their advertisement calls, and then elicited encounter calls by imitating advertisement calls. By day I did the same, but mainly after rainfall, when calling activity indicated that frogs were active.

For every frog found the following data were recorded: sex, date and time of capture, snout-vent length (SVL) to the nearest mm with plastic callipers, weight to the nearest 0.1 g with a 30.0 g-pesola scale, presence of eggs in females, behaviour, and colour pattern. The following perch features were also noted: height, vegetation cover and substrate. The vegetation cover of the perch was classified in four categories (perch seen from above): 1) frog not covered by vegetation, 2) 1/3 of frog covered by vegetation, 3) 2/3 of frog covered and 4) frog completely covered by vegetation.

The data on site fidelity were collected on the forest triangle (above). The triangle had an area of about 1300 m^2 and consisted of old secondary forest. Every 1 to 3 weeks this area was searched for *E. fitzingeri* and all encountered animals were captured for identification. On first capture, the frogs were toe-clipped for individual recognition. Upon recapture, the frog's location and data on habitat use as described above were noted.

Averages are given $\pm$ one standard deviation (s). Unless otherwise indicated, two-tailed Mann-Whitney U-tests were used.

Results

Morphometry and colour patterns

Eleutherodactylus fitzingeri showed a strong sexual dimorphism in size (fig. 1). Females were significantly larger and heavier (SVL $= 43.9 \pm 4.7$ mm, weight $= 7.26 \pm 2.23$ g) than either males (28.5 ± 1.5 mm, 1.78 ± 0.35 g) or juveniles (14.3 ± 3.6 mm, 0.3 ± 0.2 g, Kruskal-Wallis test: $P \ll 0.0001$ in both comparisons, all groups different with Tukey's test) (fig. 1).

The frogs had one of three dorsal colour patterns: 1) mottled: dark spots on light brown, often with a large interorbital W-shaped marking; 2) striped: broad middorsal

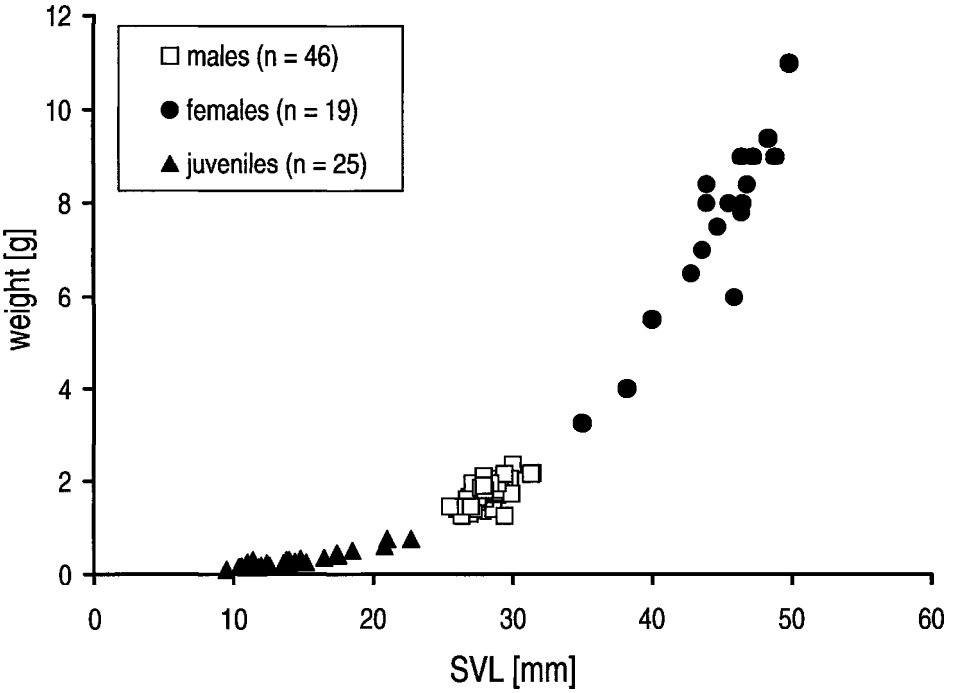

Figure 1. Size groups of *Eleutherodactylus fitzingeri* at La Selva.

Table 1. Dorsal colour patterns of *Eleutherodactylus fitzingeri* at La Selva.

pattern	males	females	juveniles
mottled	41 (89%)	18 (95%)	17 (68%)
dorsal stripe	4 (9%)	–	6 (24%)
uniform	1 (2%)	1 (5%)	2 (8%)

stripe of a light brown colour contrasting with rest of dorsum; 3) uniform: uniform brown coloration. Mottled was the most common pattern overall, and the occurrence of the different dorsal colour patterns did not differ significantly between sexes ($G^2 = 0.84$, df $= 2$, $P > 0.50$) nor between adults and juveniles ($G^2 = 5.87$, df $= 2$, $P > 0.05$) (table 1).

Individuals had varying intensities of white and yellow coloration on their venters, independent of the hour of the day or illumination. A yellow ventral coloration was significantly more frequent on males (44 of 46) than on females (12 of 19, $G^2 = 10.82$, df $= 1$, $P < 0.002$). Juveniles with a white belly were significantly smaller (12.3 ± 1.7 mm, $n = 17$) than juveniles with a yellow belly (18.7 ± 2.6 mm, $n = 8$, $P = 0.00009$).

Table 2. Distribution of males, females and juveniles of *Eleutherodactylus fitzingeri* in the four areas sampled.

sampling area	males	females	juveniles
forest triangle	25	2	3
clearing	8	1	0
Sendero Experimental	7	1	0
Sendero Tres Rios	6	15	21

Demography

In all, 46 males, 19 females and 21 juveniles were found, but the sex ratio varied between areas. In three of the four areas sampled repeatedly (forest triangle, clearing, Sendero Experimental), males always outnumbered females and juveniles, but on the Sendero Tres Rios, females and juveniles outnumbered males (table 2) ($G^2 = 41.9$, df $= 6$, $P < 0.001$). The first three sites had little leaf litter, while the fourth site had many places where the leaf litter was deep, and there most females and juveniles were found.

Due to the translucent skin in the groin of the females, it was easy to see if they had mature eggs inside. During the dry season only one of five females had visible eggs, but the proportion was seven of twelve females in the rainy season ($G^2 = 12.5$, df $= 1$, $P < 0.001$).

During the dry season no juveniles were found among 22 frogs, but during the rainy season 25 juveniles were found among 72 frogs ($G^2 = 11.1$, df $= 1$, $P < 0.001$).

Site attachment

Thirty frogs (25 males, 2 females, 3 juveniles) were marked at the forest triangle. Eight males (32%) were recaptured, seven only once and one five times (on every sampling date over a period of 83 days). The distances between capture and recapture sites varied between 0.5 and 35 m (6.9 ± 9.8 m), and the time between capture and recapture varied between 3 and 74 days (17.6 ± 19.0 d). The time lapsed between capture and recapture was not significantly correlated with the distance between the respective sites ($r_s = 0.18$, $n = 12$, $P = 0.29$).

Habitat use

The height of the perch site varied between 0 and 1.6 m. Males perched significantly higher (0.36 ± 0.4 m) than either females (0.13 ± 0.18 m) or juveniles (0.17 ± 0.08 m, Kruskal-Wallis test: $P = 0.006$, female perch height did not differ from juvenile perch height with Tukey's test). Males were most often found on leaves or branches, while females were seen more frequently on leaf litter, stones, soil, and grass ($G^2 = 17.64$, df $= 1$, $P \ll 0.001$) (fig. 2). Juveniles were only seen perching on green leaves.

There were no significant differences in perch height between calling and silent males, between males calling by day or night, nor between males calling on dry or rainy nights

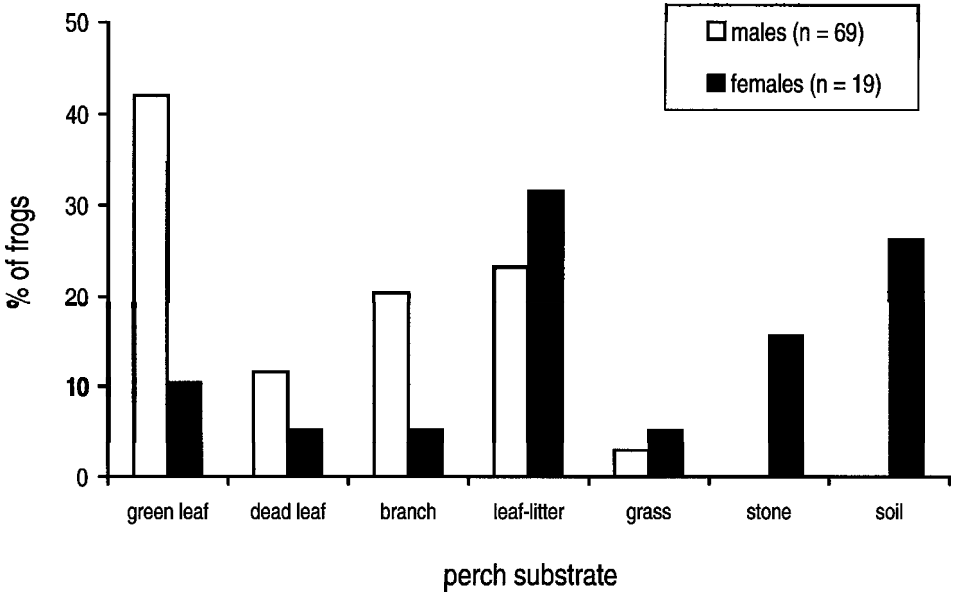

Figure 2. Perch substrates of *Eleutherodactylus fitzingeri*.

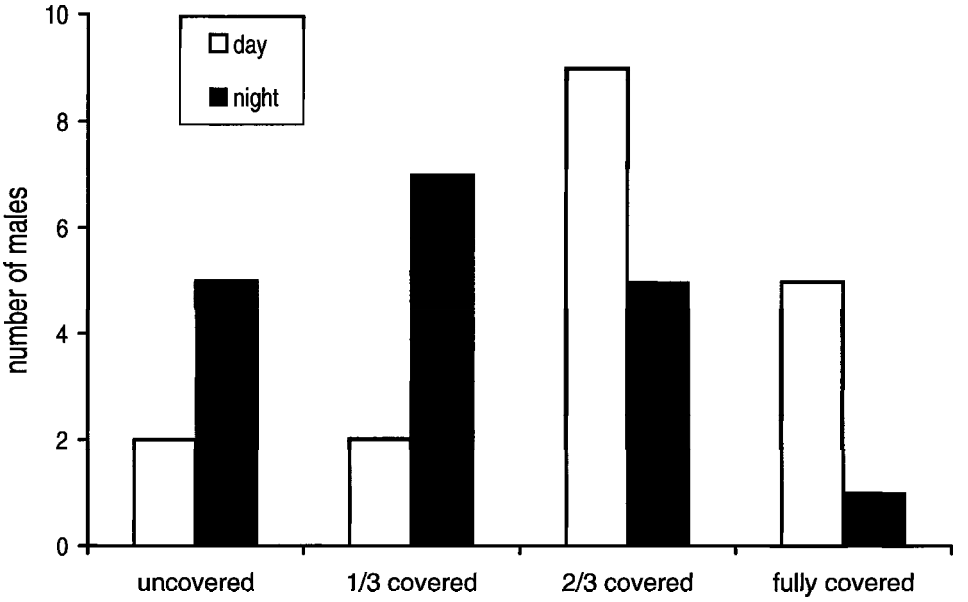

Figure 3. Cover of perch sites used by calling males during the day and during the night.

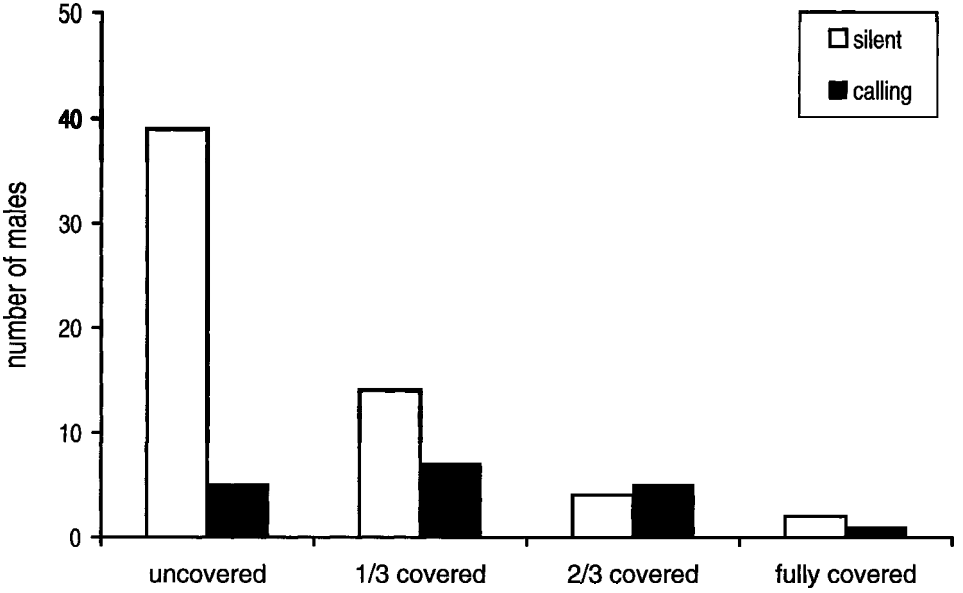

Figure 4. Cover of perch sites used by silent and calling males during the night.

(in all cases $P > 0.07$). When the perch height of males found in the clearing or the forest was compared, there were no significant differences using either calling males or the total of the encountered males ($P > 0.82$ in both cases).

The vegetation cover of the perch of males was associated with their behaviour and with the time of day. Calling males used better covered perches during the day than at night (comparison between vegetation cover categories: $G^2 = 8.34$, df $= 3$, $P < 0.05$) (fig. 3). At night silent males used less covered perches than calling males ($G^2 = 9.69$, df $= 3$, $P < 0.05$) (fig. 4). Juveniles and females were mostly found at night on uncovered or only slightly covered perches, but this probably does not reflect a preference for these perches, but the difficulty of encountering these small and well camouflaged animals on other perches. Males were mainly encountered by calls, so data on their perches are probably less biased.

Discussion

Eleutherodactylus fitzingeri showed a strong sexual dimorphism, with females being much larger and heavier than males, as is common in the genus (Lynch and Myers, 1983).

A middorsal pale line is a common disruptive colour pattern in many species of *Eleutherodactylus* (Duellman and Trueb, 1986). However, for polymorphic species in which quantitative data are available, mottled or uniform patterns are more common

than the striped pattern (present study; Lynch and Myers, 1983 on *E. crassidigitus*, *E. raniformis*, *E. longirostris* and *E. fitzingeri* from Colombia and Panama; Savage and Emerson, 1970 on *E. bransfordii*). As in *E. bransfordii* (Savage and Emerson, 1970) there was no correlation between sex and the dorsal colour pattern of *E. fitzingeri* in the present study.

As suggested by Lynch and Myers (1983), the ventral coloration of *E. fitzingeri* varied sexually, with males tending to have yellowish bellies and females white ones.

The observed variation in sex ratio and abundance of juveniles between the sites in the present study may be explained by the reproductive ecology of *E. fitzingeri*. Lynch and Myers (1983) reported that *E. fitzingeri* uses the leaf litter for oviposition and suggested that females may perform clutch guarding. This may indeed be the case, as *E. fitzingeri* females have been found below the leaf litter guarding their egg clutches (F. Bolaños, pers. comm). Thus, the high abundance of females and juveniles at the Sendero Tres Rios site might be due to the great abundance of possible oviposition sites in the form of deep leaf litter.

The increase in the proportion of females with eggs at the beginning of the rainy season indicates that reproductive activity increases with heavy rainfalls. The increase in the proportion of juveniles after the onset of the rainy season may be due to increased clutch frequency or higher clutch survival during this time, as the danger of desiccation, the main agent of clutch mortality in *E. coqui* (Townsend et al., 1984), decreases.

Compared to the well-studied *E. coqui*, *E. fitzingeri* showed only weak site attachment. Only one-third of the marked *E. fitzingeri* males were recaptured, and the distances moved between recaptures were on average 7 m, while *E. coqui* consistently remained within 5 m of the original capture site (Stewart and Rand, 1991). Male *E. fitzingeri* have intraspecific response vocalisations (Lynch and Myers, 1983; Höbel, in prep.), so they may be territorial to some degree. However, judging from the weak site attachment seen in the present study, they do not seem to occupy territories for long periods. Maybe the aggressive calls function in maintaining inter-male spacing during calling nights.

Miyamoto (1982) found *E. fitzingeri* on the ground during the day, and on bushes at night (mostly calling males). He suggested this might be explained by the danger of desiccation during the day and the selection of appropriate calling sites at night. If this were the case, elevated calling sites should become available after rainfall with the increase of moisture above the ground. Indeed, in the present study males that called after rainfall during the day perched at similar heights than males that called at night.

Narins and Hurley (1982) found that some shelter provided by surrounding vegetation is also a characteristic common to the perches of calling *E. coqui* males. The use of perches with more vegetation cover by calling males may be a strategy to avoid predators, especially acoustically oriented predators such as the frog-eating-bat *Trachops cirrhosus* and opossums that are attracted to the advertisement calls of frogs (Tuttle and Ryan, 1981; Tuttle et al., 1981).

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