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Morphological Variation, Diet, and Vocalization of *Eleutherodactylus eugeniae* (Anura: Leptodactylidae) with Notes on its Reproduction and Ecology

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Eleutherodactylus eugeniae was described by Lynch and Duellman (1997) from a small area of cloud forest, at elevations of 1700–2010 m in Provincia Pichincha in northwestern Ecuador. These authors examined very few specimens from the type locality. We collected 29 new individuals (7 juveniles, 9 females, 13 males), 7 from the type locality, and the rest from two new localities (see Appendix I). Herein, we describe aspects of the diet, vocalization, morphological variation, ecology, and reproductive biology of this species.

Materials and Methods

Ecological, reproductive, and morphological data were gathered on *Eleutherodactylus eugeniae* from three localities of cloud forests in northwestern Ecuador between 1994 and 2001. This region has an annual precipitation of 2600 mm, with a rainy season from December to May, and moderate rains from July to November; mean annual temperature is 15.6°C (Cañadaz-Cruz 1983). The localities and specimens examined are listed in Appendix I.

We recorded 12 individuals and collected four of them (Appendix I). Calls were recorded from 14–28 February and 10–24 September 1998, and from 27 February–11 March and 13–17 August 1999 in Bosque Integral Otonga reserve (BIO) with a Sony WM D6C Professional Walkman tape recorder and an Optimus Unidirectional Condenser Microphone. Calls were digitized at a sampling rate of 22 kHz at 8-bit precision with the built-in A/D converter on Power Macintosh 7100/80 AV computer and the software Canary 1.1 (Charif et al. 1993). Waveforms and spectra were analyzed with Canary 1.1. Acoustic terminology follows that de-

FIG. 1. *Eleutherodactylus eugeniae*, QCAZ 16041, adult female, SVL 38.4 mm.

FIG. 2. *Eleutherodactylus eugeniae*, QCAZ 16040, subadult female, SVL 30.3 mm.

scribed in Heyer et al. (1990).

Morphological measurements were taken with digital calipers to the nearest 0.1 mm, and follow the methodology described in Gray and Cannatella (1985) and Lynch and Duellman (1980). Additionally, we measured: internarial distance—distance between nostrils; snout to eye distance—distance from tip of snout to anterior margin of eye; and radio-ulna length—length of flexed forearm from elbow to proximal border of palmar tubercle.

We examined the intestine and stomach contents of 10 females and 10 males (Appendix I). Prey items were identified to the lowest possible taxonomic level. Adults and larvae were analyzed separately because of their differences in body form. The volume of each complete prey item was estimated using the formula for a prolate spheroid (i.e., Volume = $4/3\pi$ [greatest length of prey/2] [greatest width of prey/2]^2; Dunham 1983). The trophic niche breadth, was estimated using the reciprocal of Simpson's (1949) diversity measure

$$(\text{i.e., } B = 1/\sum_{i=1}^{n} p_i^2).$$

Frog habitat and microhabitat were recorded. Sexual maturity was recognized by the presence of eggs or convoluted oviducts in females and by the presence of vocal slits and enlarged testes in males. Abbreviations as follows: SVL = snout-vent length; IOD = interorbital distance; BIO = Bosque Integral Otonga reserve; REG = Reserva Florística Ecológica Río Guajalito; QZ = Quebrada Zapadores; QCAZ = Museo de Zoología, Pontificia Universidad Católica del Ecuador.

RESULTS

Variation in measurements and proportions are presented in Tables 1 and 2. In addition to the coloration pattern described in Lynch and Duellman (1997) (Fig. 1), a cream-yellow interorbital bar occurs in five individuals (QCAZ 11691, 13119, 13120, 16039, 16040; Fig. 2). Contrary to Lynch and Duellman (1997), we found that the tympanic annulus, described as indistinct externally in males (N = 1), is evident in all the males we sampled (N = 13).

Fifty-nine prey items, corresponding to 18 prey categories, were found (Table 3). The diet of *Eleutherodactylus eugeniae* consisted mainly of insects (86%), followed by spiders (10.2%), and Acari (3.4%). Most of the insects consumed were adult Coleoptera (32%), followed by Araneae (10%), and Hemiptera (8%) (Table 3). Within the identified Coleoptera, the family Chrysomelidae is the most important prey category (Table 3). Volumetrically, the most important items are Coleoptera (adult 26%, larvae 20%) and adult Orthoptera (19%) (Table 3).

In females, the most common prey category is adult Coleoptera (49%), followed by Araneae (14%), and Hemiptera (11%) (Fig. 3); the volume ingested by females consists of adult Coleoptera (32%), Orthoptera (20%), and Dermaptera (14%) (Fig. 3).

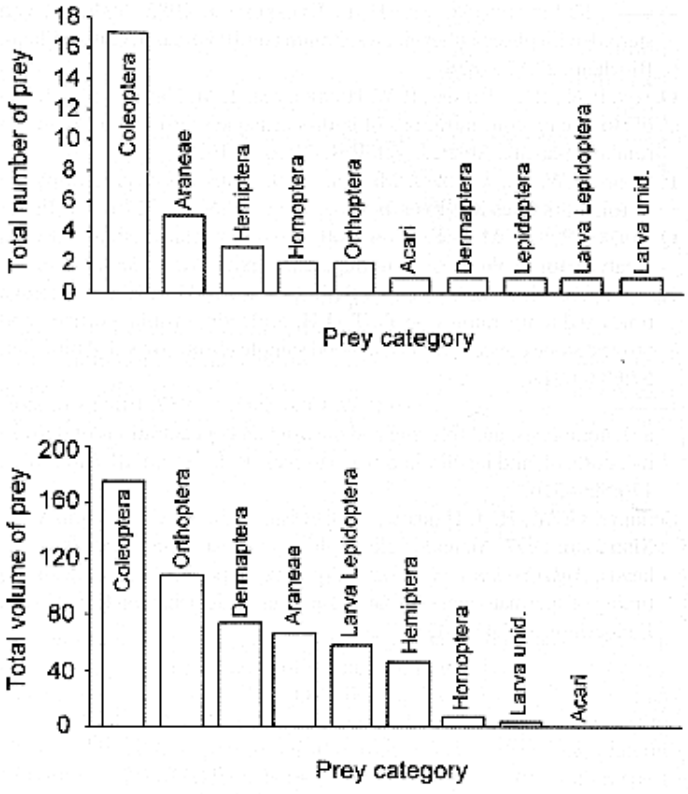

FIG. 3. Numeric (top) and volumetric (bottom) importance of prey categories in females of *Eleutherodactylus eugeniae*.

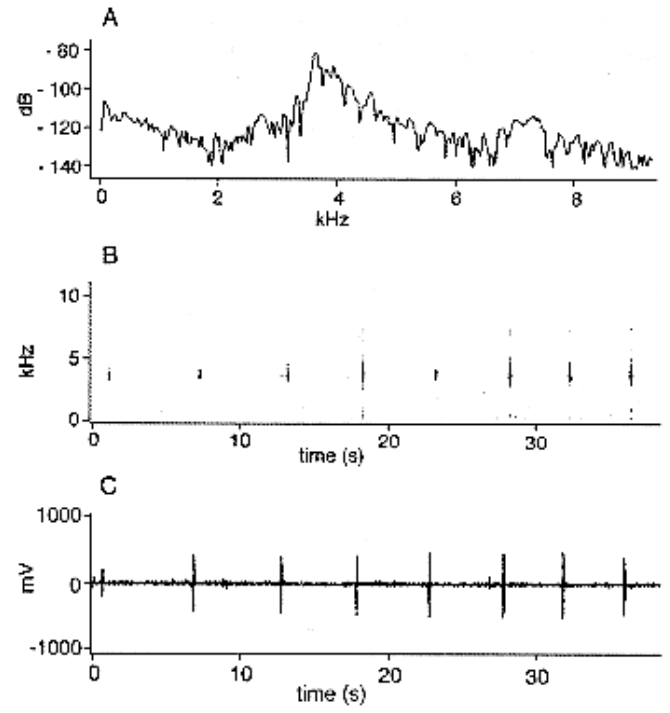

FIG. 4. Call group of *Eleutherodactylus eugeniae*, QCAZ 13199, SVL 27.1 mm. (A) Spectrum, (B) Spectrogram, and (C) Waveform.

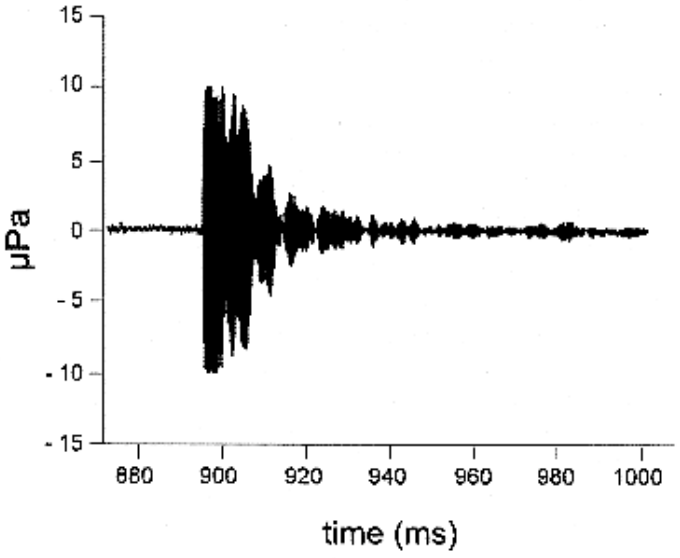

FIG. 5. Expanded waveform of a single call of *Eleutherodactylus eugeniae*, QCAZ 13199, SVL 27.1 mm.

In males, we found only nine prey items (3 Coleoptera, 2 Orthoptera, 1 Acari, 1 Araneae, 1 Hemiptera, 1 Formicidae); this low number prevent us from generalizing about the composition of their diet. On average, we found fewer prey items in males (1.3 prey items per individual) than in females (3.7 items per individual).

We found 66 to 149 ovarian eggs in different developmental stages in six of the eight females examined. They are covered by a membrane pigmented with minute dark brown spots, and have a diameter of 0.1–3.9 mm. Variations in number and size of eggs for

TABLE 1. Measurements of 21 adults of *Eleutherodactylus eugeniae* (range followed by mean ± standard deviation; in mm).

	SVL	Tibia length	Foot length	Head length	Head width	IOD	Upper eyelid width	Internarinal distance	Eye to nostril distance	Snout to eye distance	Eye diameter	Tympanum diameter	Radio-ulna length	Hand length	Finger I length
Females	30.6–38.6	15.5–19.3	13.8–18.0	11.1–13.9	11.3–14.3	3.4–4.5	2.7–3.4	2.3–3.0	2.2–4.6	5.2–6.5	3.3–4.3	1.3–2.0	7.2–8.5	9.7–12.4	5.5–7.4
(N = 8)	35.5 ± 2.7	17.8 ± 1.3	16.1 ± 1.4	12.9 ± 0.9	13.3 ± 1.0	4.1 ± 0.3	3.1 ± 0.3	2.7 ± 0.2	4.2 ± 0.5	6.0 ± 0.5	3.8 ± 0.3	1.8 ± 0.3	8.1 ± 0.4	11.3 ± 0.9	6.6 ± 0.7
Males	22.5–28.9	11.3–14.2	9.5–12.8	8.5–10.9	8.7–10.9	2.6–3.5	2.1–2.9	1.7–2.3	2.6–3.3	4.0–5.1	2.8–3.7	0.9–1.5	5.0–6.5	6.9–9.0	3.7–5.1
(N = 13)	26.1 ± 1.9	13.4 ± 0.7	11.6 ± 0.8	9.8 ± 0.7	9.9 ± 0.6	3.1 ± 0.2	2.6 ± 0.3	2.0 ± 0.2	2.9 ± 0.2	4.5 ± 0.3	3.2 ± 0.3	1.2 ± 0.2	6.1 ± 0.4	8.0 ± 0.5	4.5 ± 0.4

TABLE 2. Morphological proportions (in percentages) in adults of *Eleutherodactylus eugeniae* (range followed by mean ± standard deviation).

	Tibia length/ SVL	Foot length/ SVL	Foot length/ tibia length	Head width/ SVL	Head length/ SVL	Head width/ head length	Eye to nostril distance/ eye diameter	Upper eyelid width/ IOD	Tympanum diameter/ eye diameter	Radio-ulna length/ SVL	Hand length/ radio-ulna length	Thumb length/ hand length
Females	43.2–48.7	43.4–54.3	82.9–109.7	36.5–38.8	35.2–35.7	101.5–104.6	97.0–124.3	62.2–82.9	39.4–54.1	21.4–25.5	124.4–149.4	55.3–61.8
(N = 8)	45.5 ± 2.0	50.4 ± 3.5	90.7 ± 8.6	37.4 ± 0.7	36.2 ± 0.8	103.1 ± 1.3	109.9 ± 8.9	76.4 ± 6.2	46.4 ± 5.0	22.8 ± 1.6	139.7 ± 7.7	58.5 ± 2.2
Males	41.2–48.1	47.4–59.1	81.2–92.8	35.8–40.9	36.2–40.9	98.1–105.2	75.7–103.4	65.6–93.5	29.7–45.5	20.9–26.7	123.3–152.5	51.3–59.0
(N = 13)	44.4 ± 2.1	51.6 ± 2.9	86.2 ± 3.4	38.1 ± 1.4	37.6 ± 1.4	101.5 ± 2.2	90.2 ± 8.0	83.9 ± 8.3	38.6 ± 5.2	23.4 ± 1.5	132.4 ± 7.4	55.9 ± 2.1

the six females, associated with SVL, locality, and collection date of specimens are summarized in Table 4.

We heard males calling during all of our fieldwork (February and September, 1998; March and August, 1999; June and July, 2001). In *Eleutherodactylus eugeniae*, calls are organized into groups, which are emitted approximately every 15–30 min. Call groups (Fig. 4) are no frequency modulated; they have a duration of 4.7–63.7 s (mean = 32.507 ± 15.547, N = 12), and contain 3–16 calls (mean = 7.694 ± 3.344, N = 12). Each call is formed by one note. Notes have a length of 0.008–0.403 s (mean = 0.131 ± 0.061, N = 12); internote length is 0.473–23.361 s (mean = 5.264 ± 2.578, N = 12); notes are pulsed, with pulses decreasing in amplitude through note (Fig. 5); notes with no noticeable frequency modulation. Fundamental frequency (when evident) is distributed between 99 and 190 Hz (mean = 160 ± 31.224, N = 4) and dominant frequency is between 3370 and 3776 Hz (mean = 3514 ± 117.745, N = 12). The frequency of the first harmonic lies between 6669 and 7415 Hz (mean = 6926 ± 298.771, N = 8) and that of the second harmonic (when evident) between 10257 and 10594 Hz (mean = 10479 ± 119.169, N = 3).

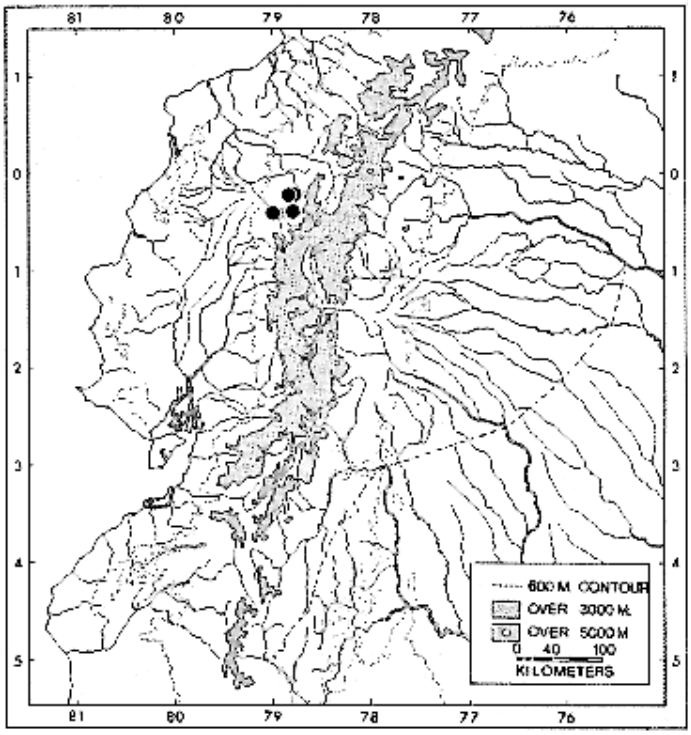

FIG. 6. Distribution of *Eleutherodactylus eugeniae* in Ecuador (circles).

Eleutherodactylus eugeniae was mainly found in disturbed (45.8%, N = 24) and undisturbed primary forests (41.7%, N = 24), but few individuals were found in secondary (8.3%, N = 24) and gallery forests (4.2%, N = 24). Individuals were collected at night, on vegetation between 40 and 340 cm (mean = 180 ± 79.3, N = 26) above ground, but several calls originated near the forest canopy (at least 8 m high). In BIO, we found one individual in a bromelia 50 cm above ground on three consecutive mornings. We also recovered one individual of *Eleutherodactylus eugeniae* (QCAZ 13424) from the bill of a Striped Wood-haunther, *Hylocistes subulatus* (Aves: Furnariidae), which had been trapped in a mist net placed near its nest.

The known altitudinal distribution and range is here expanded. The species has a known altitudinal distribution of 1700–2200 m and has been recorded from four localities in western Ecuador—viz., QZ, REG, and 6.3 km E Tandapi (ca. 00° 24' S, 78° 47' W) in Provincia Pichincha (Lynch and Duellman 1997); and BIO in Provincia Cotopaxi (Fig. 6).

DISCUSSION

The description of *Eleutherodactylus eugeniae* (Lynch and

TABLE 3. Diet and niche breadth of *Eleutherodactylus eugeniae* based on 20 individuals. No = Total number of prey items found in all individuals examined; No % = Percentage of prey item number in relation to total number of items found in the species; Vol = Total volume of prey category in all individuals examined; Vol % = Percentage of prey item volume in relation to total volume of items found in the species; * = Number of prey items used to calculate volume, this value is used because not all prey were found complete; Frequency = Number of individuals containing prey item.

Prey category	No	No (%)	Vol (mm^3)	Vol (%)	*	Frequency
Acari	2	3.39	0.450	0.06	2	2
Araneae	6	10.17	67.105	8.81	6	6
Coleoptera	11	18.64	108.594	14.25	11	4
Brentidae	1	1.70	19.055	2.50	1	1
Chrysomelidae	7	11.86	71.863	9.43	7	4
Staphylinidae	1	1.70	1.431	0.19	1	1
Dermaptera	1	1.70	74.810	9.82	1	1
Formicidae	1	1.70	0.190	0.03	1	1
Hemiptera	4	6.78	47.019	6.17	4	4
Lygaeidae	1	1.70	3.337	0.44	1	1
Homoptera	2	3.39	7.405	0.97	2	2
Hymenoptera (Formicidae)	1	1.70	0	0	0	1
Larva unidentified	**1**	**1.70**	**3.953**	**0.52**	**1**	**1**
Larva Coleoptera	1	1.70	150.773	19.79	1	1
Larva Lepidoptera	1	1.70	57.955	7.61	1	1
Lepidoptera	1	1.70	0	0	0	1
Orthoptera	4	6.78	141.873	18.62	4	4
Plant material	13	22.03	6.216	0.82	13	8
TOTAL	**59**	**100**	**762.029**	**100**	**57**	—
Niche breadth	—	8.191	—	7.643	—	—

Duellman 1997) is adequate, but it does not address the range of morphological variation (Table 1; Fig. 2). This information is especially relevant to males, which originally were described on the basis of a single individual.

Eleutherodactylus eugeniae is a nocturnal, sit-and-wait forager; once a prey item is sighted, individuals of *E. eugeniae* have been observed to pursue it for a short distance (< 30 cm) before capture (D. F. Cisneros-Heredia and A. León-Heredia, pers. comm.). Our results (Table 3) agree with the hypothesis that the sit-and-wait foraging strategy might favor capture of relatively large, highly mobile prey (e.g., Coleoptera, Orthoptera, solitary spiders), rather than small prey species with predictable patterns of movement and clumped distributions (e.g. ants, termites, social spiders; Eckhardt 1979; Huey and Pianka 1981; Krebs 1978). Moreover, because *E. eugeniae* principally inhabits the upper strata of the forest, its diet might depend mostly on those arthropods that either fly or climb to the forest canopy; this is supported by the high frequency of Coleoptera, Araneae, and Hemiptera in their stomachs (Table 3). The presence of plant material in the stomachs of eight specimens is considered to be accidental and related to the ingestion of animal prey (Lajmanovich 1995; Zug and Zug 1979).

TABLE 4. Number and size of ovarian eggs in six adult females of *Eleutherodactylus eugeniae* associated with SVL, locality and collection date of specimens. REG = Reserva Florística Ecológica Río Guajalito; BIO = Bosque Integral Otonga reserve; QZ = Quebrada Zapadores; Max = Maximum; Min = Minimum.

	Collection Year					
	1994		1999		2001	
Collection month	April	March	August	August	August	April
QCAZ no.	6559	13117	13424	13425	13426	16041
Locality	REG	BIO	BIO	BIO	BIO	QZ
SVL	36.8	36.7	35.7	33.6	38.6	38.4
Egg no. ≥ 2 mm	18	1	0	0	25	1
Egg no. < 2, ≥ 1 mm	8	9	15	18	25	12
Egg no. < 1 mm	68	67	51	131	74	77
Total egg no.	94	77	66	149	124	90
Max egg size (mm)	3.1	2.6	1.9	1.8	2.5	2
Min egg size (mm)	0.1	0.1	0.2	0.1	0.2	0.1

Appendix I

Specimens examined of *Eleutherodactylus eugeniae*. J = Juvenile; JF = Juvenile female; AF = Adult female; JM = Juvenile male; AM = Adult male; SAF = Subadult female; REG = Reserva Florística Ecológica Río Guajalito (00°14' S, 78°48' W, 1800–2200 m, near Chiriboga, Provincia Pichincha); BIO = Bosque Integral Otonga reserve (00°25' S, 79°00' W, 1800–2200 m, near San Francisco de Las Pampas, Provincia Cotopaxi); QZ = Quebrada Zapadores, type locality of *E. eugeniae* (00°14' S, 78°45' W, 1700–2010 m, 5 km ESE Chiriboga, Provincia Pichincha).

Museum No. QCAZ	Sex	Diet	Morphology	Reproduction	Call	Locality	Collection Date
6551	J	—	—	—	—	REG	October 1994
6559	AF	x	x	x	—	REG	April 1994
11691	J	—	—	—	—	BIO	February 1998
11692	AF	x	x	—	—	BIO	February 1998
11693	AM	x	x	—	—	BIO	February 1998
11694	AM	x	x	—	—	BIO	February 1998
11695	AM	—	x	—	—	BIO	February 1998
12228	AM	—	x	—	—	BIO	June 1998
12304	JF	x	—	—	—	BIO	September 1998
12305	AM	x	x	—	x	BIO	September 1998
12306	AM	x	x	—	x	BIO	September 1998
12307	AM	x	x	—	x	BIO	September 1998
12308	AM	x	x	—	—	BIO	September 1998
13117	AF	x	x	x	—	BIO	March 1999
13118	AM	—	x	—	—	BIO	March 1999
13119	AM	x	x	—	x	BIO	March 1999
13120	AM	x	x	—	—	BIO	March 1999
13424	AF	x	x	x	—	BIO	August 1999
13425	AF	x	x	x	—	BIO	August 1999
13426	AF	x	x	x	—	BIO	August 1999
16036	AF	—	x	—	—	QZ	April 2000
16037	JF	—	—	—	—	QZ	April 2000
16038	JM	—	—	—	—	QZ	April 2000
16039	J	—	—	—	—	QZ	April 2001
16040	SAF	x	—	—	—	QZ	April 2001
16041	AF	x	x	x	—	QZ	April 2001
16042	JF	x	—	—	—	QZ	April 2001
16935	AM	x	x	—	—	BIO	February 2000
16936	AM	x	x	—	—	BIO	February 2000

Males eat fewer prey items than females; this might be a consequence of differences in size (SVL = 30.6–38.6 mm in females; 22.5–28.9 in males), and/or behavior. Several studies have shown a positive relation between the number and size of prey items with the SVL in anurans (Menéndez 2001; Parmelee 1999). Additionally, reproductive effort in calling males might restrict the time spent in feeding activities (Jenssen 1972; Lamb 1984; Woolbright and Stewart 1987). This might be exacerbated in *Eleutherodactylus eugeniae*, in which males seem to call throughout the year. The results of our diet study might be biased toward hard-bodied prey. Specimens collected were not preserved immediately and, surely, many soft-bodied prey were digested (Caldwell 1996; Parmelee 1999). Another variable that probably influenced our results is the spatial and temporal fluctuations of arthropod populations.

Females with eggs larger than 2 mm in April and August (Table 4), and males calling in February, March, June, July, August, and September (Appendix I), suggest that *Eleutherodactylus eugeniae* breeds throughout the year. This mode of reproduction could be sustained by the high humidity of the region and by the reproductive strategy of *Eleutherodactylus:* terrestrial eggs with direct development (Duellman and Trueb 1994; Lynch and Duellman 1997).

The calls of *Eleutherodactylus* are poorly known. The only other call description available for the 61 species of *Eleutherodactylus* that inhabit western Ecuador is of *E. achatinus* in Provincia del Carchi, Ecuador (Lynch and Myers 1983). This lack of information prevents us from comparing the vocalization of *E. eugeniae*

with sympatric or related species.

Our records document the distribution of the species within the Montane Cloud Forest formation as described by Valencia et al. (1999). We collected specimens as high as 340 cm above ground, but most calling individuals were in sub-canopy and canopy. These data suggest, as mentioned by Lynch and Duellman (1997), that *Eleutherodactylus eugeniae* primarily inhabits the upper strata of the forest. Field observations suggest that this species might have site fidelity to diurnal retreats; *E. eugeniae* might depend on trees with epiphytic vegetation (e.g., bromeliads) for diurnal retreats as part of its habitat requirements. The species tolerates habitat disturbance (45.8% of individuals in disturbed primary forest). Individuals have been heard calling in forest patches < 3 m^2 and in solitary trees with bromeliads (D. F. Cisneros-Heredia and A. León-Heredia, pers. comm.), however, it seems to be susceptible to drastic habitat modification (only 8.3% where found in secondary forest, and none in grasslands).

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