

Partitioning of vocal activity in a Neotropical highland-frog community

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Abstract

Vocal activity was studied in a Colombian highland-frog community, consisting of five frog species belonging to three families with three different reproductive modes, which reproduced simultaneously in the area. We encountered one diurnal and four nocturnal species. Each species had a distinct call structure, and the 24-hour patterns of calling activity differed significantly between all but two species. Interspecific differences in dominant call frequencies corresponded inversely to differences in male snout-vent length. Only one species called in ponds, whereas all other species used terrestrial sites. Among the terrestrial callers there seemed to be interspecific differences in plant use as calling sites. Our results indicate that despite the low number of species, interspecific vocal partitioning is pronounced, and probably important for reliable vocal communication.

Keywords: Andes, páramo, frog community, vocal partitioning, body size, habitat use, Colombia.

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INTRODUCTION

Partitioning of vocal activity has been described for several frog communities in neotropical lowlands (Hödl, 1977; Duellman & Pyles, 1983) and cloud forest (Heyer et al., 1990), which are species-rich in taxonomic composition and diverse in reproductive modes (Crump, 1974; Toft & Duellman, 1979). This diversity is thought to be possible due to habitat partitioning regarding time, space, and other life-history parameters (Duellman, 1978).

Although neotropical mountains and lowlands contain almost equal total numbers of frog species (Sinsch, 1990), neotropical highland frog communities are typically composed of very few species (Péfaur & Duellman, 1980; Lynch, 1986; Duellman, 1988). Furthermore, in comparison to the lowlands, the species present are usually representatives of only four families (Rivero, 1979). There is a trend towards water-independent reproductive modes and oviposition sites (Lutz, 1947; Tihen, 1965), hence most males call on land, where they may not be aggregated at specific sites like ponds. Therefore, the distances between calling neighbours could be much larger in terrestrial callers than in pond callers. Considering low species richness and terrestrial calling, acoustic interference between heterospecific males could be much reduced.

Lüddecke et al. (1999) described a local highland-frog community which consisted of five species be-

longing to three different families: one species of hylid frogs (*Hyla labialis*), three leptodactylid species (*Eleutherodactylus elegans*, *E. bogotensis*, and *E. nervicus*), and one dendrobatid (*Colostethus subpunctatus*). They observed differences between frog species with regard to calling sites. *Hyla labialis* was the only aquatic caller. Among the terrestrial callers, several plant species were shared to some degree as calling sites.

The general situation in the high mountains, in combination with available information about this particular community, led us to the prediction that in highland-frog communities vocal partitioning is not of prime importance for vocal communication. The purpose of our study was to test this prediction. Apart from frogs, there were no nightly callers in the high mountains, but there were birds of several species calling at daytime. This simplified the situation and largely eliminated the problem of acoustic interference at higher taxonomic levels (frogs versus insects, for instance).

MATERIALS AND METHODS

Study area

The study area was a small highland valley at 3500 m altitude (4°42'N, 73°48'W) in the Chingaza Natural Park in the eastern Andean chain near Bogotá. Annual weather pattern consists of a short dry and sunny

season from December-February, and a long bimodal rainy season with peaks in July and September. Average annual precipitation is 2300 mm. During the rainy months it is usually very cloudy, windy and cold. Daily air temperature fluctuations are generally large (between 3-18°C), and occasional frosts may occur during clear nights in the dry season (Sarmiento, 1986).

The vegetation is of the páramo type (Monasterio & Vuilleumier, 1986), generally low and herbaceous (Van der Hammen & Cleef, 1986), and dominated by grasses, dwarf bamboo, and woolly plants. The terrain in the valley is an alternation of flat areas and slopes, and the valley is bordered by rocky outcrops belonging to the Cretaceous period (Páramo, 1994). There were about 20 permanent ponds scattered along the bottom of the valley, as well as swampy areas where many small puddles formed during the rainy season. Several very small creeks ran along the valley.

Field techniques

From January to June 1998 we visited the study area repeatedly, about once a week, during the breeding seasons of all anuran species. During this time interval, total precipitation was 1026 mm, and ground temperatures fluctuated between -3 and 39°C. During each of three 24-hour periods separated by at least one week, the number of advertisement calls given by a fortuitously chosen focal male of each frog species was counted once per hour. Each sample was obtained in a 5 min session. We also estimated the number of calling conspecific neighbours we could distinguish from our position. These data were used to look for interspecific differences or similarities in the pattern of daily calling activity.

At any time of day, but preferably during hours of high vocal activity, we approached a representative number of focal calling males of each species and tape-recorded at least five consecutive calls of each individual, using different models of SONY tape recorders (WM D6C, TCM-7, TCM S68V). We then captured each of these males, measured their snout-vent length to the nearest mm, and determined substrate or water temperature at the calling site. All males were released afterwards.

We registered the plant species from which each terrestrial focal male was calling. We then sampled their relative abundance in the study area by counting the specimens of each plant species used as call-

ing sites in exclusive circles of 3.8 m², traced around 35 randomly selected points along each of four randomly established transects of 200 m length.

Data analysis

For each 24-h period and species we expressed the calling activity hour by hour as the percentage of the maximum number (equal to 100%) of advertisement calls per 5-min sample period. For each species, we averaged the percentage values per hour for all 24-h periods. These average 24-h calling patterns were compared among species pairs using ten Kolmogorov-Smirnov two-sample tests. Since we intended to test the single null hypothesis that species do not differ in daily calling pattern, we adjusted the significance level to 0.005 using the Bonferroni correction (Scheiner, 1993).

Tape-recorded calls were digitised at 22 kHz and analysed using Canary 1.2 software (Charif et al., 1995) on a Power Macintosh computer. For each focal male, the temporal call characteristics were visualised by oscillograms, and dominant call frequencies were determined by sonograms. We calculated the average dominant call frequency of each focal male from five recorded calls. These means were plotted against snout-vent length (SVL) of males, averaged from three measurements per individual. All average values are given with standard deviation (SD).

Relative plant use as calling site, as obtained from the focal-male sampling, was expressed separately for each frog species. Relative plant abundance was averaged separately for each plant species based on transect-line sampling, and expressed in percentages of the total plant-specimen count. Where not stated otherwise, we used $P = 0.05$ as the significance level.

RESULTS

Call structure

The temporal structure of the advertisement call was species specific (Fig. 1). *Hyla labialis*, *E. nericus*, and *Colostethus subpunctatus* made one-note calls, grouped in series with low numbers of calls in the first two species, and with high numbers in the latter species, whereas the other two *Eleutherodactylus*-species made multi-note calls, separated by long silent intervals. The calls of *E. nericus*, *E. elegans* and *H. labialis* were pulsed, whereas those of *E. bo-*

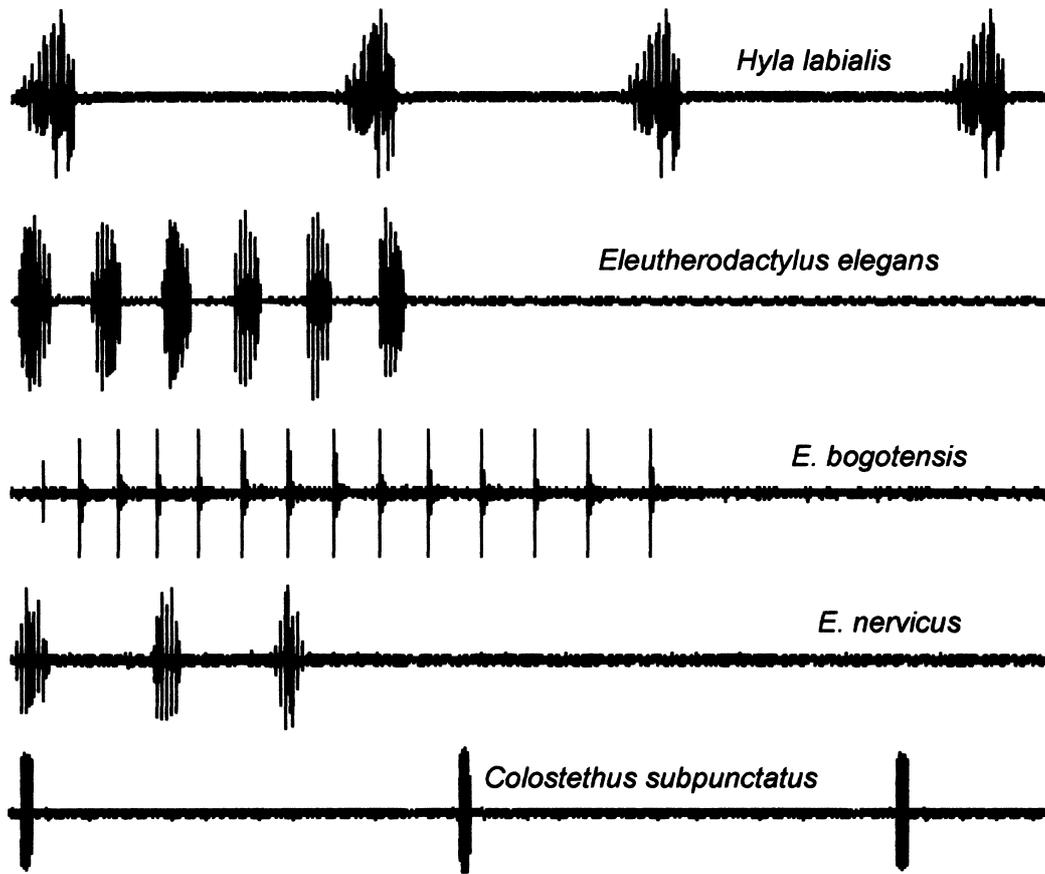


Fig. 1. Oscillograms in a 5-second time-window, showing temporal features of representative advertisement calls of the five species in the frog community. Represented are four calls from a call series of *H. labialis*, three calls from a call series of *C. subpunctatus*, three calls from a call series of *E. nervicus*, a six-note call of *E. elegans*, and a 14-note call of *E. bogotensis*.

Table 1. (a) Five temporal characteristics of call structure of each frog species at Chingaza. (b) Comparison of separated (S) and overlapping (O) call characteristics for species-pairs. Each letter sequence codes, in that order, for call duration, notes per call, note repetition rate, pulses per note, and pulse repetition rate.

a	Call duration (s)	Notes per call	Call rate (min ⁻¹)	Pulses per note	Pulse rate (s ⁻¹)
<i>Hyla labialis</i>	0.14-0.35	1	25.2-52.7	8-21	50.0-66.7
<i>Eleutherodactylus elegans</i>	0.37-2.67	2-7	0.45-12.3	3-7	3.5-71.6
<i>E. bogotensis</i>	1.03-5.58	6-17	0.6-2.2	1	-
<i>E. nervicus</i>	0.01-0.10	1	10.2-109	3-6	37.8-120.1
<i>Colostethus subpunctatus</i>	0.03-0.06	1	10.3-31.0	1	-

b	<i>Hyla labialis</i>	<i>E. elegans</i>	<i>E. bogotensis</i>	<i>E. nervicus</i>	<i>Colostethus subpunctatus</i>
<i>Hyla labialis</i>	-	SSSSO	SSSSS	SOOSO	SOOSS
<i>Eleutherodactylus elegans</i>	-	-	OOOSO	SOOSO	SSOSS
<i>E. bogotensis</i>	-	-	-	SSSSS	SSOOO
<i>E. nervicus</i>	-	-	-	-	OOOSS
<i>Colostethus subpunctatus</i>	-	-	-	-	-

gotensis and *C. subpunctatus* were not. No species at Chingaza had calls similar enough to be confused when heard separately. When calls are compared, any species pair differs in at least one of five temporal characteristics of call structure (Table 1).

Calling activity

The temporal patterns of calling activity over a 24-hour period are presented in Figure 2. Only the dendrobatid *C. subpunctatus* was clearly a diurnal caller; it started after sunrise, reached a peak around mid-day, and stopped during evening twilight, at about 18:30-18:50 h. Males of the other four species were mainly, although not exclusively, calling at night. They started (or increased) calling activity before evening twilight. *Eleutherodactylus nervicus* reached

a first peak of calling activity shortly before dark, the other species reached a peak between about 19:00-21:00 h. Afterwards, calling activity fell off: in two species (*H. labialis* and *E. bogotensis*) to a level which was maintained through the rest of the night, in the other two species (*E. elegans* and *E. nervicus*) giving rise to a second peak between 02:00-06:00 h, which extended well into the morning. Significant correlations were found between the number of calling males and the number of calls produced through the 24-hour cycle (Spearman's correlation coefficients; *H. labialis*: $\rho = 0.47$, $P = 0.008$, $n = 30$; *E. elegans*: $\rho = 0.77$, $P < 0.001$, $n = 35$; *E. bogotensis*: $\rho = 0.56$, $P = 0.005$, $n = 23$; *E. nervicus*: $\rho = 0.84$, $P < 0.001$, $n = 30$), except for *C. subpunctatus* ($\rho = 0.36$, $P = 0.053$, $n = 30$). There were signifi-

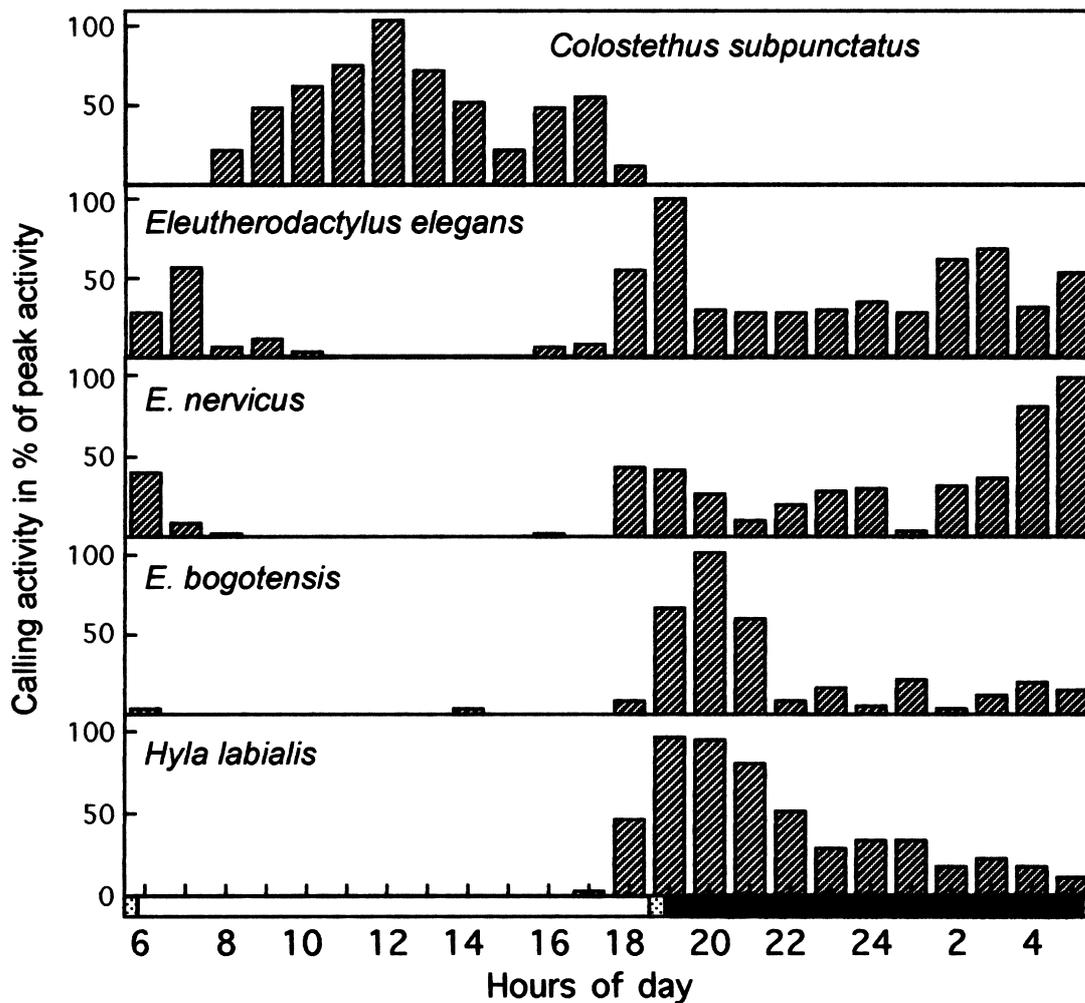


Fig. 2. Comparison of daily calling pattern of the five frog species in the highland community, based on the total number of calls counted during each sampling period. Blanks indicate that no calling activity was detected. Peak calling activity equals 100%. Horizontal bar represents daylight-, twilight-, and night-hours (white, stippled, and black, respectively).

cant differences between the calling patterns of any species pair, except between *E. bogotensis* and *H. labialis* (Kolmogorov-Smirnov 2-sample test, $Z = 0.939$, $P = 0.341$, $n = 145$; in the other nine tests $P < 0.001$).

Male body size

Comparing the body sizes of the captured focal frogs, we found stepwise interspecific differences in male average SVL (Table 2). The steps in average-size differences were of similar magnitude from one species to the next smaller one (mean factor = 1.3). Trans-specifically, the dominant call frequency of the advertisement calls decreased with increasing male SVL (Fig. 3), on average (mean \pm SD) from 4113 ± 219 Hz in *C. subpunctatus*, 2539 ± 226 Hz in *E. nervicus*, 2384 ± 168 Hz in *E. bogotensis*, 1585 ± 105 Hz in *E. elegans*, to 1110 ± 99 Hz in *H. labialis*. The only partial overlap of dominant call frequencies was between *E. bogotensis* and *E. nervicus*. Within each species, dominant call frequencies were not significantly correlated with substrate temperatures at the calling sites (correlation coefficients; *C. subpunctatus*: $r = -0.028$; *E. nervicus*: $r = 0.163$; *E. bogotensis*: $r = 0.070$; *E. elegans*: $r = 0.399$; *H. labialis*: $r = 0.002$; $P > 0.14$ in all cases).

Calling sites

Apart from the aquatic-calling *H. labialis*, the terrestrial-calling frogs were found on six different plant species, three of them small-sized, the other three large-sized (Fig. 4). The moss cushions were mostly horizontal and flat, the grass tufts, dwarf bamboo and shrubs had a predominantly vertical structure, and the leaves of the rosette-structured plants pointed into all directions from vertical to horizontal. *Colostethus subpunctatus* males called in sheltered places, and always at ground level, mainly from the base of spiny rosette plants, or inside grass tufts and moss cushions situated next to areas where small puddles formed in the rainy season. The males of the *Eleutherodactylus*-species usually climbed up the plants and called from elevated sites. *Eleutherodactylus bogotensis* was calling primarily from medium-sized specimens of woolly plants, at about 50 cm above ground level. The other two *Eleutherodactylus*-species were found calling from positions between 10-120 cm above ground level in a variety of plants, showing some similarities, except that *E. elegans* was not found calling from spiny rosettes and grass tufts, and *E. nervicus* was not found on shrubs. We did not find more than one individual calling from the same plant specimen.

Table 2. Interspecific comparison of snout-vent length (SVL) of adult males ($n =$ sample size) in the Andean highland frog community at Chingaza. The scaling factors are the ratio between average body sizes of one species and the next larger one.

Species	n	SVL (mm) mean \pm SD	range	Scaling factor
<i>Hyla labialis</i>	7	53.2 \pm 3.0	57-49	>-----1.3
<i>Eleutherodactylus elegans</i>	16	38.9 \pm 1.1	40-37	>-----1.6
<i>E. bogotensis</i>	17	23.8 \pm 1.4	27-22	>-----1.1
<i>E. nervicus</i>	15	21.4 \pm 2.1	24-18	>-----1.2
<i>Colostethus subpunctatus</i>	15	17.8 \pm 0.9	19-16	

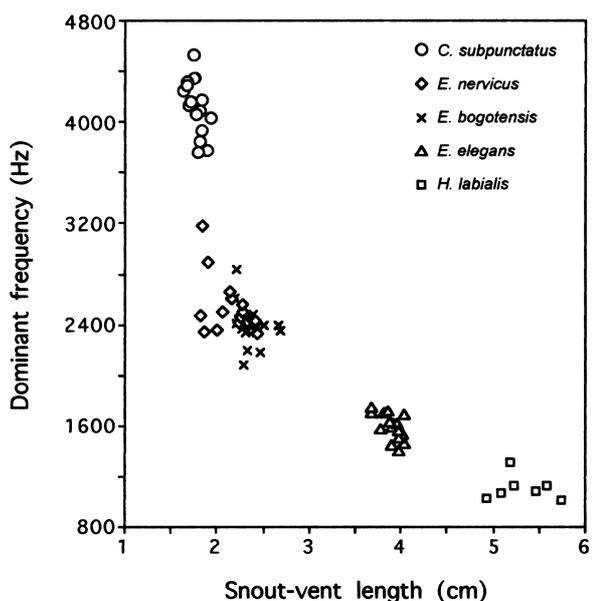


Fig. 3. Plot of body sizes against dominant call frequencies of males of the five frog species in the highland community. Each symbol represents average values of one individual.

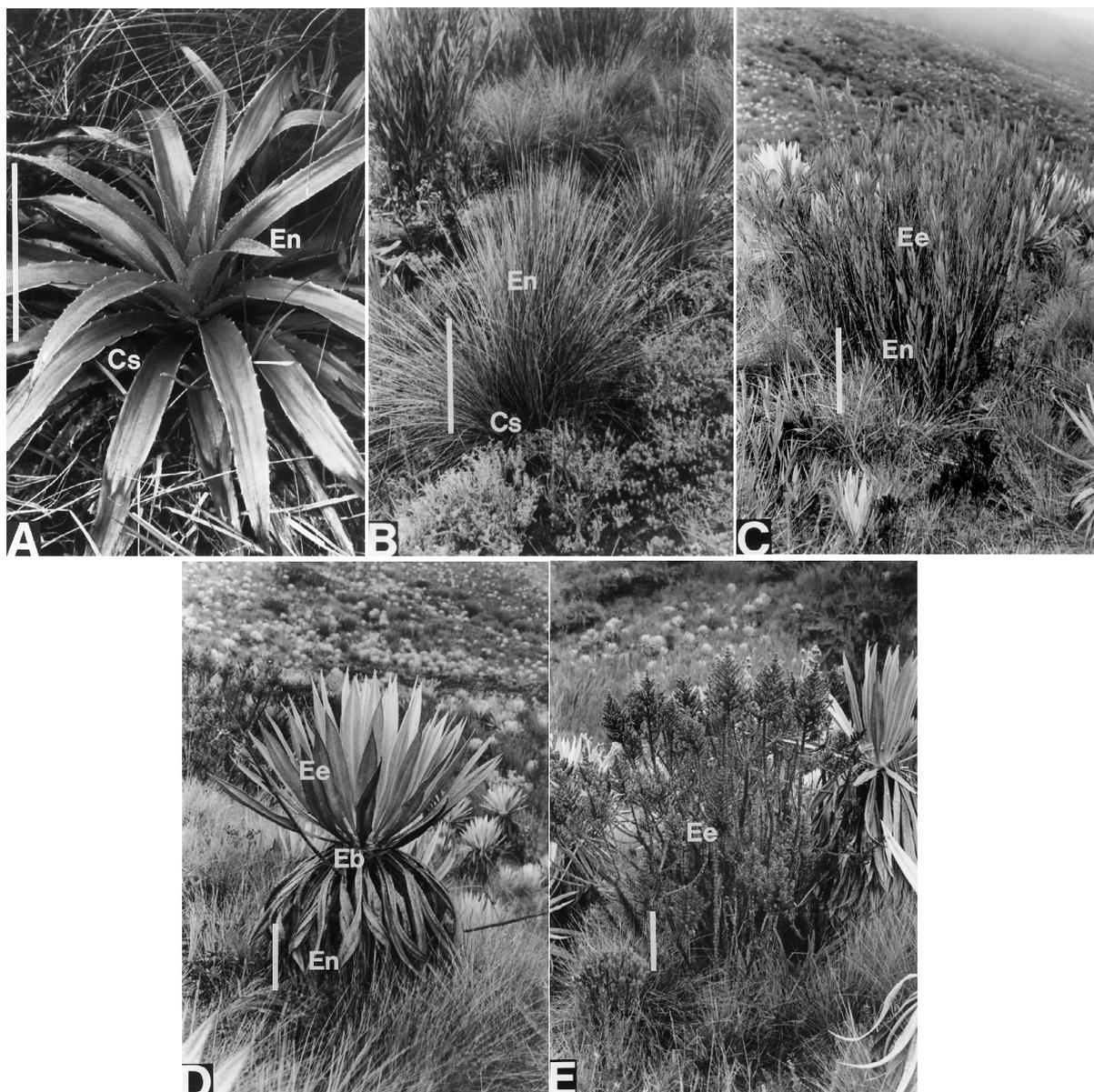


Fig. 4. Specific calling sites of four terrestrial frog species on five plant species, arranged according to the usual size of a plant specimen used as calling site, as follows: A. spiny rosette plant (*Puya* sp.); B. grass tuft (*Calamagrostis* sp.); C. dwarf bamboo (*Chusquea* sp.); D. woolly plant (*Espeletia grandiflora*); E. shrub (*Aragoa* sp.). Moss cushions (*Sphagnum* sp.) are not shown. The positions of letters abbreviating frog names correspond to commonly encountered perches. Cs: *Colostethus subpunctatus*; Eb: *Eleutherodactylus bogotensis*; Ee: *E. elegans*; En: *E. nericus*. Vertical bars represent 20 cm.

The terrestrial-calling frogs apparently used the six plant species differentially (Fig. 5). Although most plant species were shared among frog species as calling sites, some frog species used a certain plant species most frequently, particularly obvious in the case of *E. bogotensis*. The general trend among terrestrial frog species was that the larger the males' body size, the higher the plants they used. Except for *E. nericus*, the terrestrial frog species seemed to use

plants as calling sites in a way different from expected according to relative plant abundance, although we admit that the number of observations per frog species is low.

DISCUSSION

In this study we addressed some aspects of natural forces that can shape the composition of frog com-

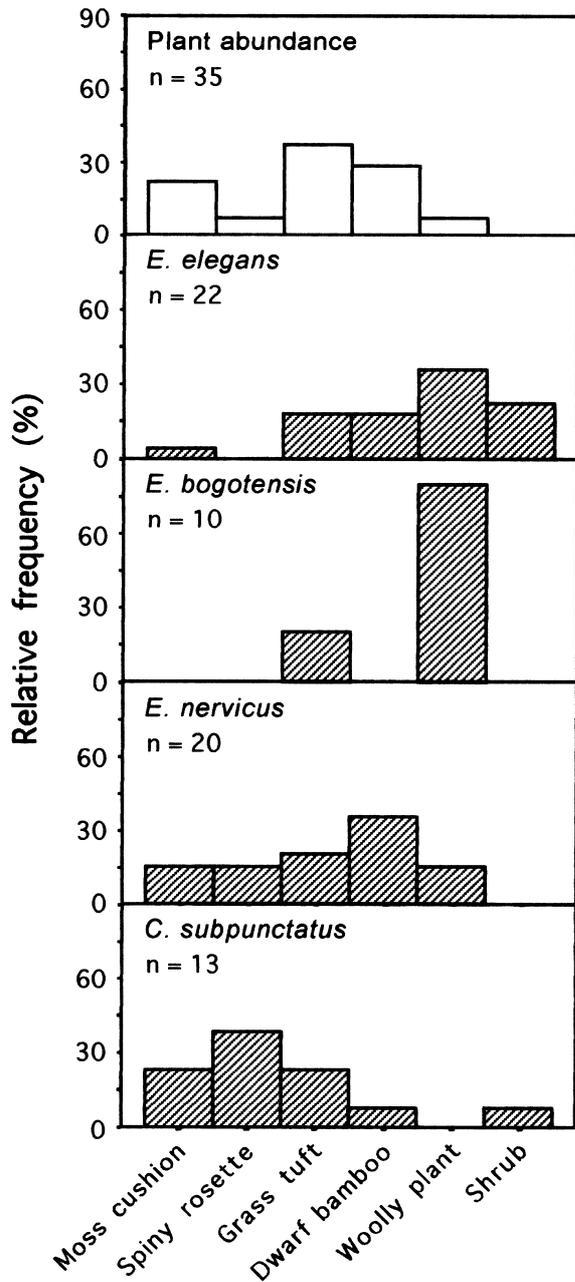


Fig. 5. Comparison between relative plant use as calling sites by four terrestrial frog species in the highland community, and relative abundance of these plant species in the study area. Plant names are arranged from left to right according to the increasing sizes of plant specimens usually used as calling site.

munities (Heatwole, 1982). Regarding the few families represented and the low number of species present, the frog community we studied is similar to others described for several neotropical highland areas (Duellman, 1966; Péfaur & Duellman, 1980; Lynch et al., 1997), a phenomenon probably more

related to biogeographical history rather than to ecological factors (Duellman, 1986). Therefore, the basic situation concerning reproductive modes and habitat use found at Chingaza is likely to be encountered in other highland-frog communities as well.

Call characteristics

Within breeding aggregations, each anuran species tends to have its acoustical niche (Duellman, 1978), where total overlap in all temporal call characteristics is extremely rare even in large communities (Hödl, 1977; Heyer et al., 1990). Females in our highland community should be able to recognise calls of conspecific males on the basis of the temporal characteristics, according to results on auditory sensitivity and call discrimination ability in other female frogs (Gerhardt, 1988). Considering dominant call frequency as an acoustical niche parameter, the differences encountered between the five highland species strongly support that acoustic interference is extremely low. Since dominant call frequency was independent of substrate temperature, it is a highly specific attribute which should enable a female to recognise a conspecific male based on this characteristic alone, which may thus play an important role in intraspecific communication, and perhaps also as a mechanism of premating reproductive isolation (Blair, 1964; Duellman, 1967; Gerhardt, 1988). Results of female-choice experiments strengthen this argument, given that anuran females are able to distinguish between calls of closely related species which differ in dominant call frequency (Gerhardt, 1982), and even between relatively minor differences in dominant call frequency of conspecific males (Gerhardt, 1994; Márquez, 1995).

Within as well as among anuran species, even across families, dominant call frequency is often inversely correlated with male body size (Martin, 1972; Hödl, 1977; Heyer et al., 1990; Lüddecke et al., this study). Therefore, a segregation of dominant call frequencies in any frog community is probably accompanied by interspecific differences in male body size. In species-rich communities, the smallest and the largest frog species may differ in snout-vent length up to ninefold (Pough et al., 1998), and in dominant call frequency up to 20-fold (Heyer et al., 1990). When correlating data from several authors, it becomes apparent that while the interspecific range of body size increases with species number in a frog community, the scaling factor from one species to

the next smaller one decreases. Consequently, in large communities there are more species with similar dominant call frequencies, and then additional factors may play a relatively more important role in avoiding acoustic interference.

Average scaling factors of 1.3 for linear parameters of body size occur in other communities among taxonomically related species at similar trophic levels (Calder, 1984), including leaf litter frogs (Toft, 1981), salamanders (Hairston, 1986), lizard species of the genus *Gallotia* occupying the same island (López-Jurado & Mateo, 1993), and *Anolis* lizards from the Caribbean Islands (Williams, 1983), apparently obeying to a general biological principle for the functioning of animal communities, likely related to competition for some limited resource, e.g., food (Toft, 1985).

Time

Similar to the situation in the highland community, a second peak of calling activity at dawn has also been reported for other *Eleutherodactylus* species (Drewry & Rand, 1983). The four species that called mainly at night had at least partially overlapping peaks of calling activity. Remarkably, the two species (*E. bogotensis* and *H. labialis*) with the most similar 24-hour calling patterns were separated by one being aquatic and the other terrestrial, and their calls differed completely in both spectral and temporal properties. Our data generally confirm the findings of Navas (1996), who described the daily calling pattern of three of the species we studied based on male counts alone. Since we needed a measure to detect potential acoustic interference, we counted the number of calls produced, because this indirectly measures the time occupied by frog sounds. Thereby we arrive at more pronounced peaks of calling activity, in some species probably further enhanced by the social effect on calling activity (Lüddecke et al., 1999), also observed in other anuran species (Pough et al., 1992). When additionally taking into account the call (or note) duration for each species, we would get information about possible sound saturation in a given area. For example, assuming no call overlap, in *H. labialis* sound saturation is approached when 12 neighbours call.

Space

Habitat segregation is characteristic of most anuran communities studied in this regard (Hödl, 1977; Toft,

1985; Seale, 1987). The fact that most of the six plant species used as calling sites were shared by two or more frog species, seems to reflect their quality as shelters and/or perches related to plant structure rather than the selection of plant species according to their taxonomic identity. Shrubs were highest, and *E. elegans*, the only species which climbed them, perched higher than the other species. *Colostethus subpunctatus*, although already temporally separated from the other species, further stayed spatially apart due to its relatively higher occurrence in low-growing spiny rosettes and always at ground level. The two species with the most similar perch use (*E. nervicus* and *E. elegans*), on the other hand, had clearly different dominant call frequencies. Finally, the only two species with partially overlapping dominant call frequencies (*E. nervicus* and *E. bogotensis*), differed in all measured temporal properties of their calls, as well as in plant use as calling sites.

CONCLUSIONS

Our results indicate a very low probability of acoustic interference among the species of the community. It remains unclear what sort of underlying mechanism could have brought about the present situation. Although trophic competition should be considered when trying to explain community structure (Duellman, 1978; Toft, 1985; Caldwell, 1993), Toft & Duellman (1979) proposed that in Amazonian Perú differential utilisation of the breeding habitat and calling sites by some groups of frogs, may be the major way in which species partition the environment, because otherwise there are hardly any limited resources in tropical rainforests, mainly due to their relatively aseasonal climate. The fact that our five frog species realise three different reproductive modes may indicate the importance of breeding-habitat limitation. Strongly seasonal climates, like those of páramos, bring about fluctuations in productivity and thus may limit food availability (Duellman, 1978), and eventually promote stronger competition, as the large scaling factors in our highland community may indicate. A reasonable explanation for the present situation is therefore that competition for limited resources (breeding sites and/or food) led to interspecific differences in body size, which in turn are the basis for the interspecific differences in dominant call frequencies.

We conclude that despite the low number of species in this highland-frog community, there are clear interspecific differences in behaviour related to calling. The factors we studied to estimate acoustic interference seem to have different relative importance: when the voices of the encountered species do not differ in structural or spectral qualities, this is compensated for by either temporal or spatial partitioning, in the extreme demonstrated by the two species which are contributing to resource segregation by calling either at daytime or in ponds. These results support the hypothesis that even in very small frog communities vocal partitioning is important for reliable vocal communication.

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