

REPRODUCTIVE ECOLOGY OF *HYLA ROSENBERGI* IN COSTA RICA

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ABSTRACT: I studied the calling behavior and reproductive biology of *Hyla rosenbergi* on the margin of a swampy cattle pasture in Southeastern Costa Rica. Males had a complex vocal repertoire with at least five different call types. In contrast with previous studies at other sites, males in this population showed facultative nest building behavior, did not engage in violent fights with each other, and did not guard basins, which might be explained by the abundance of available basin sites. The typical pattern of chorus tenure in *H. rosenbergi* was for males to spend only a few nights calling over about a one-week period. Males occupied 1–10 different nests, and the mean duration of individual nest occupation was 1.5 days. Individual male mating success was highly skewed; only 34% of the males managed to obtain a mate. Mating success was positively correlated with length of residency, chorus tenure, and the number of basins occupied during residency.

Key words: Gladiator frogs; *Hyla rosenbergi*; Reproductive behavior; Male mating success; Chorus tenure; Vocalizations

THE predominant mating system of anurans is for males to gather at aquatic breeding sites and form choruses to attract females (Sullivan et al., 1995). In this situation, males usually provide the females with nothing more than sperm. However, some species have resource defense mating systems, in which males provide females with a resource needed for reproduction. In anurans, this is generally a suitable oviposition site, as in the North American bullfrog (Howard, 1978). Males of some species of hylids and ranids, however, not only defend a territory containing a resource provided to the female, but build the nests used as oviposition sites (Emerson, 1992; Kluge, 1981).

Nest-building gladiator frogs of the *Hyla boans* group of are medium sized to large species with a number of morphological and behavioral specializations. Males have a projecting prepollex and are famed for their aggressive behavior, involving not only vocal interactions but actual fights between males, in which their prepollex spine is used as a weapon to injure or even kill opponents (Kluge, 1981; Lutz, 1960). Members of this group also

share a special mating system in which the males build mud nests on the margins of streams or ponds where eggs are deposited. Egg and early larval development occur in the nest, and subsequent flooding disperses the tadpoles into open water (Kluge, 1981). Studies in a diversity of habitats have revealed facultative nest-building behavior in several species of the nest-building gladiator frogs (Caldwell, 1992; Höbel, 1999), indicating that they can show great behavioral plasticity depending largely on the ecological factors and frog densities in a given habitat. However, clutches are never found in open water, suggesting that providing a basin, male-built or natural, is critical for male reproductive success.

Kluge (1981) studied a Panamanian population of *Hyla rosenbergi*, and he found nest building behavior, lethal fights between males, and male clutch guarding. Subsequently, these behaviors have been considered typical for *H. rosenbergi* and for nest-building gladiator frogs in general. However, a Costarican population of *H. rosenbergi* had facultative nest-building behavior (Höbel, 1999). Here I describe the vocalizations and the social and reproductive behavior of this population, which also differ considerably from previous re-

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ports of the reproductive ecology of *H. rosenbergi*.

MATERIALS AND METHODS

From May–September 1995, I observed a population of *Hyla rosenbergi* in a swampy cattle pasture near the Estación Biológica La Gamba. The station is located 08° 42' N, 83° 13' W at 70 m above sea level in the pacific lowlands of Costa Rica, Puntarenas Province. The study area was about 50 by 40 m, consisting of an unflooded, relatively dry part and an adjacent swampy cattle pasture (Höbel, 1999). Because the pasture was semi-flooded and used by cattle, there were large numbers of water-filled puddles and cattle footprints present, both along the shore and in the swamp proper. The swamp and parts of the shoreline were covered by dense vegetation. Due to the difficulty of entering the swamp without disturbing the frogs, I concentrated my observations mainly along its shoreline. Some data, such as time of residency, chorus tenure, and mating success, might therefore be underestimated. I visited the study area nightly, from 1700–2400 h. Small waterfilled puddles and cattle footprints were very abundant at the site (Höbel, 1999). Thus I did not check all water-filled depressions but rather walked slowly around the area to check for occupied basins by listening for calling males.

I marked every water-filled depression containing a calling male or a clutch of eggs of *Hyla rosenbergi* (hereafter called "basin") with a plastic tape bearing a reference number, and I recorded its location on a map of the study area. There were three basin types easily identified by their characteristic shapes (Höbel, 1999): (1) male-built nests, (2) cattle footprints, filled by water of the swamp or rain, and (3) small puddles. For each basin, I recorded the following data: type of basin, date of appearance, male that occupied it, maximum and minimum diameter of water surface, maximum water depth, estimated percent of covering vegetation, distance to nearest calling male, presence of a clutch, and number of eggs in the clutch. Later I calculated water surface and volume of

each basin (water volume was estimated by calculating the volume of a cylinder).

I marked all encountered specimens of *H. rosenbergi* individually by toe-clipping. For each marked individual, I recorded its sex, date and time of capture, snout–vent length (SVL) to the nearest 1 mm with a plastic caliper, mass to the nearest 0.1 g with a 30-g Pesola scale (all females were weighed before oviposition), and additional observations (e.g., presence of eggs in females, behavior, scars). Because the mass of a frog depends largely on its water uptake and can vary considerably during one day, I estimated male size using SVL.

I recorded the vocalizations of males with a Sony WM-D6C tape recorder and a Sony ECM 969 microphone and later analyzed the recordings with the SonaPC program on a portable computer. Advertisement and courtship calls were recorded from undisturbed males. Recordings of the aggressive calls were elicited with playbacks of advertisement and aggressive calls.

To monitor chorus size, I counted the maximum number of calling males per night on 70 nights. To monitor nightly calling activity of the chorus, I counted the number of calling males every hour from 1800–2400 h on 31 nights, and on 22 nights I counted the call repetition rate (number of calls per minute) of males at different hours of the night ($n = 125$ 1-min counts).

I give means \pm 1 SD. Where the distribution of my data is highly skewed, I also provide the median. Unless otherwise indicated, I used the Mann-Whitney *U*-test for comparison between males and basins.

RESULTS

Males produced five types of vocalizations: an advertisement call of usually two notes, a courtship call of two or three notes, two types of aggressive calls, and a distress call. The temporal and spectral properties of the call types of costarican *H. rosenbergi* are summarized in Table 1.

The advertisement call (Fig. 1a) was the most frequently heard vocalization and was emitted exclusively by males from within basins. It usually consisted of two

TABLE 1.—Temporal and spectral parameters of the calls of *Hyla rosenbergi* from Costa Rica.

	Advertisement call (<i>n</i> = 48)	Courtship call (<i>n</i> = 2)	Type I aggressive call (<i>n</i> = 20)	Type II aggressive call (<i>n</i> = 44)
Number of notes per call	2	2–3	5–10 (\bar{x} = 7.2)	1
Duration of call (ms)	187 ± 13	223 ± 4	331 ± 81	175 ± 80
Duration of notes (ms)	53 ± 3	52 ± 0.1	26 ± 3	175 ± 80
Internote interval (ms)	81 ± 10	119 ± 3	24 ± 6	—
Frequency spectrum (Hz)	241–2467	241–2340	280–2712	314–1675
Dominant frequency (Hz)	474 ± 21	474 ± 5	640 ± 62	527 ± 135

notes and was given at a mean call rate of 47 ± 14 calls per minute.

When a male perceived a female in his vicinity, he changed his call type from advertisement call to courtship call (Fig. 1b). Courtship calls had a significantly longer call duration and internote interval than advertisement calls, but did not differ in the duration of their notes or in their spectral parameters (Table 1). The courtship call was about 5 dB SPL softer than the advertisement call. The call rate of the courtship call was 83 ± 11 , significantly higher than that of the advertisement call ($P = 0.02$).

During antagonistic male–male interactions, males produced two types of aggressive vocalizations: a loud one (type I aggressive call) and a soft one (type II aggressive call)

The type I aggressive call (Fig. 1c) was emitted by males either inside or outside

their basins, from the ground or from higher perch sites. This call type was heard more frequently at dusk and in the early morning, when males walked to their calling sites (basins) or returned to their daytime retreats on scrubs and trees. During the time of high calling activity at night, this call type was emitted by males during acoustic competition with another male. The type I aggressive call was very loud and was emitted as a single call. It consisted of a series of 5–10 short notes.

Type II aggressive calls (Fig. 1d) were emitted only by males inside their basins in response to very loud playbacks (over 85 dB), and the males generally switched to giving type I aggressive calls afterwards or fell silent (as long as the playback continued). This call type ($n = 44$) was of very soft and consisted of only one long note. The spectral composition of this call type varied considerably; in some, calls a dominant frequency was barely detectable, others had 3–7 clear small frequency bands.

Distress calls were heard very rarely. In spite of handling hundreds of frogs, distress calls were only emitted by two males when being separated from the females that they were amplexing. I did not hold or shake animals in order to provoke distress calls for recording.

The first advertisement calls were emitted at dusk at about 1700–1730 h. The number of calling males increased during the night and reached its maximum at about 1900–2000 h, then gradually decreasing again. Calling activity generally ceased at about 2300 h. The mean call repetition rate was highest at the beginning of the night and a high mean call repetition

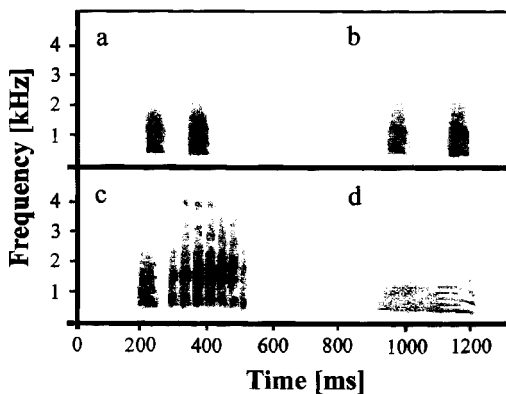


FIG. 1.—Calls of Costarican *Hyla rosenbergi*: (a) advertisement call, (b) courtship call, (c) long range aggressive call (Type I), (d) short range aggressive call (Type II).

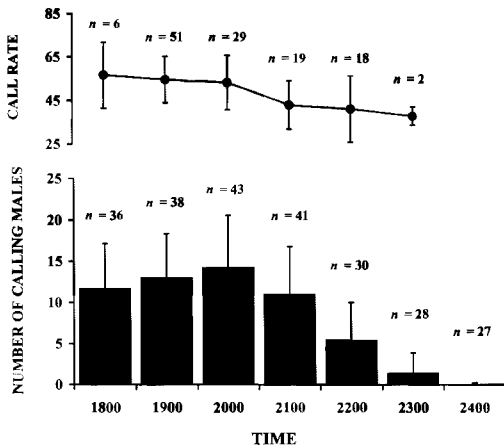


FIG. 2.—Change of number of calling males and call rate (calls/min) of *Hyla rosenbergi* during the night. The highest number of calling males per night, and the highest mean call rate per night coincide with the times that the greatest number of females are searching for mates (before 2000 h).

rate was maintained until about 2000 h (Fig. 2).

Not every male occupying a basin called. Some males remained silent and thus unnoticed in their basins until a calling neighbor was removed for measurement ($n = 2$) or they revealed their presence by giving aggressive calls in response to playback experiments conducted with neighboring males ($n = 2$).

I marked and measured 110 males and 51 females during the 4-mo study period. Most males ($n = 98$) I found calling from within basins, while I found most females ($n = 44$) when already in amplexus with a male. The observed sex ratio was biased 2.2:1.0 towards males, but this might underestimate the number of females due to sampling method bias (using calls to search for males and their basins). During the study period, I only found recently metamorphosed froglets and adult frogs, but no subadult ones. The mean SVL of males at La Gamba was 63.1 ± 3.6 mm (range 55.7–76.0 mm) and their mean mass was 13.1 ± 1.9 g (9.0–20.0 g). The mean SVL of females was 67.2 ± 4.2 mm (57.4–75.5 mm) and their mean mass was 15.5 ± 2.9 g (11.1–21.2 g). Females were significantly larger and heavier than males (in both cases $P < 0.01$).

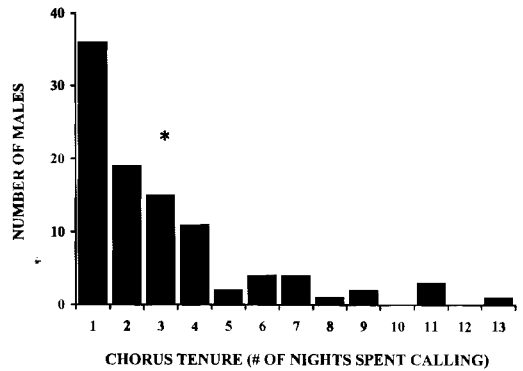


FIG. 3.—Chorus tenure of males of *Hyla rosenbergi*. The mean chorus tenure is indicated by the asterisk (*).

Clutches consisted of a floating monolayer of eggs embedded in transparent gelatinous capsules, which occupied most of the water surface of the basins. Clutches contained 775 ± 142 eggs (513–1231 eggs, $n = 28$).

Recruitment of male and female frogs was continuous. During the 4-mo study period, I marked new frogs at an average rate of 12 (4–21) per week. Females were never observed for more than one night, and most males also stayed only for a short time in the chorus. The mean length of residency (time from first to last observation) was 8.2 ± 12.0 days (median = 3, $n = 98$). Forty-six percent of the males ($n = 45$) stayed only 1–2 days, and only 8% ($n = 8$) stayed >30 days. Residency was significantly correlated with the number of nests occupied by a male ($r_s = 0.84$, $n = 98$, $P < 0.01$). But males spent only a fraction of their residency actually participating in the chorus. Average chorus tenure was only 3 ± 2.6 nights (median = 2, $n = 98$). Most males ($n = 55$) called for 1–2 nights, and the maximum was 13 nights (Fig. 3). Males never spent more than two consecutive nights calling. Residency and chorus tenure were significantly correlated ($r_s = 0.88$, $n = 98$, $P < 0.01$), but the slope of a log-log regression was only 0.51 ($n = 98$, $P < 0.01$), which suggests there may be a high cost of chorus tenure. However, body size was not significantly correlated with chorus tenure ($r_s = -0.15$, $n = 97$, $P = 0.07$).

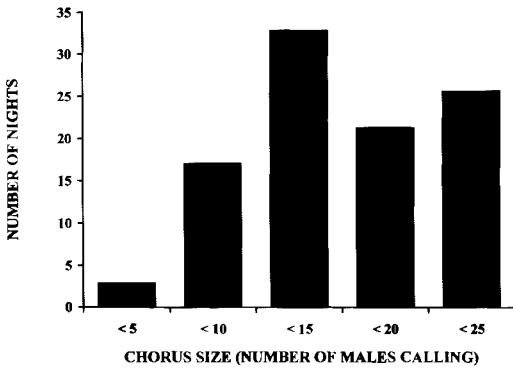


FIG. 4.—Chorus size was often large at the La Gamba study site.

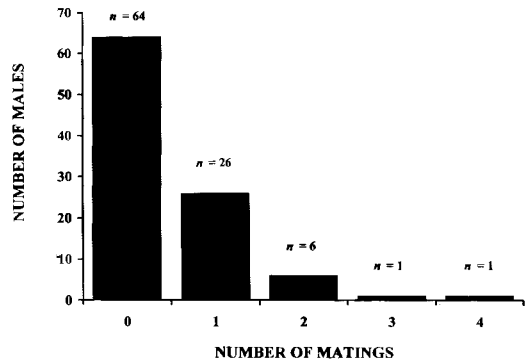


FIG. 5.—Mating success of males of *Hyla rosenbergi* at La Gamba, Costa Rica.

Chorus size varied between 1 and 25 males (15.7 ± 5.6 males; Fig. 4) and was negatively correlated with the amount of precipitation of the same day ($r_s = -0.25$, $n = 67$, $P = 0.02$). Temperature (min/max), however, did not influence chorus size (T_{\min} : $r_s = 0.02$, $n = 67$, $P = 0.43$; T_{\max} : $r_s = 0.16$, $n = 66$, $P = 0.09$). The mean distance to the nearest calling neighbor was 8.4 ± 6.6 m (range 1.5–40 m, median = 6 m, $n = 323$), and there was no difference between basin types (Kruskal-Wallis test: $P = 0.14$). Male size and distance to the nearest calling neighbor were positively correlated ($r_s = 0.137$, $n = 186$, $P = 0.01$).

Males that built or occupied more than one basin over the length of their residency ($n = 49$) tended to do so in a relatively small area of the breeding site. Males occupied only one basin at a time. The mean distance between successive basins of individual males was 6.9 ± 8.9 m (range 0.5–54 m, median = 5 m, $n = 92$ nests from 49 males). In males that occupied more than one basin, the distance between basins was <10 m in 87% of the cases, and <5 m in 64% of the cases. The distance moved between different basins was positively correlated with the time lapsed between basin occupations ($r_s = 0.35$, $n = 92$, $P < 0.01$).

Most of the pairs ($n = 42$) had formed by 1930 h; only twice did pair formation occur later. I observed the approach of two females to calling males in their basins. In one instance, the female turned away after

listening to the courtship call of the male for several minutes, but I am not sure if this was because she rejected the male or his basin, or whether my presence caused her to depart. In the other instance, the female was amplexed only 4 min after the male switched to emitting the courtship call. I did not observe any nest-evaluating behavior of the female, like swimming and diving around in the basin, as described by Kluge (1981), during this time.

Mating success (number of times that amplexus led to oviposition) was highly skewed, and only 34% of the males attracted a mate (Fig. 5). Mean male mating success was 0.46 ± 0.75 .

I could not detect any association between a male's physique, call, or the basin provided and his mating success; there was no correlation of a male's SVL with his mating success ($r_s = 0.12$, $n = 97$, $P = 0.13$), and successful and unsuccessful males did not differ in SVL ($n > 34$, $P = 0.28$). There was also no evidence for size assortative mating, as SVL and mass of males and females in amplexus were not significantly correlated (SVL: $r_s = -0.12$, $n = 43$, $P = 0.22$; mass: $r_s = -0.009$, $n = 46$, $P = 0.48$). There was also no correlation between a male's call parameters (dominant frequency, call duration, note duration, internote intervals) and his mating success (in all cases: $r_s < 0.21$, $n = 47$, $P > 0.08$). I did not compare the call rate between successful and unsuccessful males because call rate can change rapidly and is influenced by a variety of factors

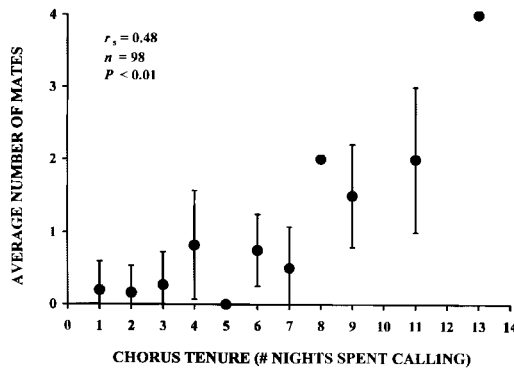


FIG. 6.—Chorus tenure best predicts a male's reproductive success. The number of mates obtained by males of *Hyla rosenbergi* increased with the number of nights a male spent calling in the chorus.

(e.g., time of day, nearest neighbor distance); thus a comparison would only be accurate if I had recorded a male's call shortly before he mated.

No basin type was preferred for oviposition ($\chi^2 = 1.47$, $df = 2$; $P > 0.05$), and basins with and without clutches did not differ in size, vegetation cover, or distance to nearest calling neighbor (in every case $P > 0.05$).

Male mating success was positively correlated with the number of different basins occupied ($r_s = 0.38$, $n = 98$, $P < 0.01$), the length of residency at a single basin ($r_s = 0.25$, $n = 223$, $P \ll 0.01$), the length of overall residency ($r_s = 0.42$, $n = 98$, $P < 0.01$), and chorus tenure ($r_s = 0.48$, $n = 98$, $P < 0.01$) (Fig. 6).

There were no significant correlations between female SVL or mass and the size of the basins females used for oviposition [depth, water surface, and volume of basin: in all cases $r_s < 0.03$, $n = 43$, $P > 0.20$ (SVL) and $r_s < 0.002$, $n = 43$, $P > 0.41$ (mass)]. There was also no correlation between basin size and the number of eggs laid in it (in all cases $r_s < 0.17$, $n = 28$, $P > 0.08$).

I never observed males guarding their basins after amplexus. Of 43 instances, only once did I find a male on a perch near his clutch the night after oviposition, but I observed three males calling from a new basin the night after a mating.

I never observed fighting among males

of *H. rosenbergi*. However, 31% of the males and 25% of the females had some kind of scars or scratches. The proportion of frogs with scars did not differ significantly between the sexes (G -test: $G = 0.45$, $df = 1$, $P > 0.50$).

DISCUSSION

It is difficult to compare population density between Kluge's more linear shoreline site and my costarican two-dimensional swamp site, but chorus size at La Gamba was twice as high as in Kluge's site in a high density year (15.7 compared to 7.8 males calling per night), and nearest neighbor distances were similar (8.4 m compared to 7 m, respectively). Thus the chorus at La Gamba was comparatively large and the density of frogs was high.

Considering this high population density, the rarity of direct fights between males is one of the most remarkable aspect of the reproductive biology of *H. rosenbergi* at La Gamba. Kluge (1981) reported 38% of males exhibiting conspicuous wounds after only a few nights of residency, but only 2% of the males had wounds when first encountered. This suggests that the majority of wounds were inflicted during fights between reproducing males and that an indirect assessment for fights might be made by looking for males with scars. At La Gamba, 31% of males had some kind of scratch or scar, although I would attribute only half of them to fights rather than predation or accidents, because of their location (on upper back and head) and shape (long, thin scratches). However, 25% of females also had scars, and the proportion of frogs with scars did not differ significantly between the sexes, as would be expected if scars originated mainly from fights between breeding males. Finding juveniles with scars would further suggest predation rather than fights as a source of the scars, but I have no data other than from adult frogs. I observed only one predation event of a snake on a male of *H. rosenbergi*, and on another occasion I suspected a frog (*Leptodactylus pentadactylus*) of eating another male. The lack of direct observation of fights, combined with the failure to attribute scars in males to fights as an in-

direct measure of violent aggression between males, indicates that at La Gamba males did not fight. In Kluge's (1981) study, defending or conquering a nest seemed to be the main reason for fights. The abundance of "cheap" basins at La Gamba thus might explain the absence of violent aggression between males.

The lack of clutch guarding by males, the other remarkable difference in social behavior to previous studies, may also be explained by the abundance of basins at La Gamba. In Kluge's (1981) study, intruding males were one of the two principal agents of embryo mortality, and in a high-density year males exhibited more nest guarding than in a low-density year. Such density dependent egg attendance was also observed in *H. faber* (Martins et al., 1998). At La Gamba, the low proportion of reuse of basins and the high availability of basins probably decreased the danger of clutch loss due to foreign male intrusion. Thus, calling in a new basin might be a better strategy than clutch guarding in this population, despite the high density of males.

Males at La Gamba spent much less time on average (8.2 days) in the breeding colony than did Panamanian *H. rosenbergi* (18.3 days: Kluge, 1981) or Brazilian *H. faber* (15.4 days: Martins, 1993), another species of the gladiator frog group. Average chorus tenure was also much shorter (37%, three days of calling out of 8.2 days of residency) than in Kluge's (1981) population (87%; 16 out of 18.3 days). Determinants of chorus tenure in frogs are not clear. Green (1990) suggested that in *Physalaemus pustulosus* predation risk is the main limiting factor, whereas for Murphy (1994) energy limitations were the primary determinant of chorus tenure in *H. gratiola*. Bevier (1997a) proposed a trade off between chorus tenure and calling intensity, so that prolonged breeders compensate for their longer chorus tenure with a more moderate calling activity, while opportunistic breeders are active for only few nights but call vigorously for many hours. The low chorus tenure of Costarican *H. rosenbergi*, a prolonged breeder, is therefore unexpected. I only

have very few repeated measurements of mass of frogs during the season ($n = 3$), but in all cases males lost mass, suggesting an energy cost of chorus attendance.

Only 34% of calling males mated at La Gamba, compared to 57% in Kluge's (1981) study. Mean male mating success in La Gamba was 0.46, compared to 1.2 in Panamanian *H. rosenbergi* (Kluge, 1981) and 1.9 in *H. faber* (Martins, 1993). Martins (1993) attributed the relatively lower mating success of Panamanian *H. rosenbergi* compared to *H. faber* to the fact that males in Panama performed clutch guarding, and thus did not call for 1–2 nights after mating, whereas *H. faber* had no such break in their calling activity. However, males of *H. rosenbergi* at La Gamba did not perform clutch guarding, but still had a very low average mating success. Male mating success has been found to be associated with days of residency and chorus tenure in a variety of anuran families (Halliday and Tejedo, 1995), as well as in *H. faber* (Martins, 1993), Panamanian (Kluge, 1981) and Costarican *H. rosenbergi* (this study). Because males can only attract females when advertising, the low mating success at La Gamba is probably an effect of the low residency and chorus tenure at the study site.

Females of Panamanian *H. rosenbergi* (Kluge, 1981) and Brazilian *H. faber* (Martins and Haddad, 1988) seemed to inspect the nests of males prior to amplexus. So far, however, no study has yielded conclusive evidence that females discriminate among males on the basis of the quality of their nests (Kluge, 1981; Martins and Haddad, 1988; this study). Additionally, the occurrence of facultative nest construction behavior in several species (Caldwell, 1992; Höbel, 1999) suggests that basin parameters may sometimes not be important for females, in which case males may simply have to provide a basin for oviposition.

The vocal repertoire of *H. rosenbergi* includes a variety of aggressive calls (Kluge, 1981; this study), which has also been reported for *H. faber* (Martins and Haddad, 1988; Martins et al., 1998). While Kluge (1981) identified a total of six aggressive calls, in Costarican *H. rosenbergi*, only one

loud and one soft aggressive vocalization were recorded. The loud (type I) aggressive call in Costa Rica resembled structurally Kluge's "territorial call", and it was given in the same context and from the same calling sites. However, the soft aggressive calls were issued in Kluge's study (1981) mainly during or after fights between males, while the soft (type II) aggressive calls recorded in present study, although structurally similar to the "mew" and "growl" encounter calls described by Kluge (1981), were given exclusively from single males inside their nests. Because these calls were mainly issued as a response to very loud playbacks of advertisement or (type I) aggressive calls, the context in which these soft calls are given seemed to be that of a male being in conflict of escalation (aggressive call) or retreat (stop giving advertisement calls). Because I never observed fights between males at La Gamba, I have no data on the vocalizations produced during fights, which might explain why only one soft aggressive call was identified as compared to five in Panama (Kluge, 1981).

The courtship call was the call type that differed most between my study and the data given by Kluge (1981) for a Panamanian population. In Costa Rica, the courtship call was only a little softer than the advertisement call, but much faster, while Kluge described the courtship call as much softer and slightly slower. Moreover, although the call varied a lot, the number of notes of the courtship call in Kluge's study was frequently two notes; that is the males lowered the number of notes when switching from advertisement to courtship call, while in my study the number of notes remained equal to the advertisement call (two notes) or increased to three notes per call. Females of most species tested so far prefer higher call rates (see review in Sullivan et al., 1995). Considering the high energetic cost of calling (Prestwich et al., 1989), increasing the call rate when the female is already close might be a strategy to help a male conserve his energy stores.

A similar reasoning might also explain the observed overlap of highest calling activity in males with the time the greatest

number of females searched for mates. After 2000 h, most of the females who would mate during a given night would already have chosen a mate; thus calling at a lower call rate or even stop calling completely after that time might help males to use their energy stores efficiently and may contribute to their overall success in attracting mates. Brevier (1997) also found that peak periods of calling activity coincided with the arrival of females in several other neotropical frogs.

Finally, Kluge (1979) noted a gradual decrease in size along the range of *H. rosenbergi* from Ecuador towards Costa Rica, and the frogs at La Gamba, at the western margin of his range, had the smallest size ever published for the species. Clutch size was also about three times smaller than in Panama (Kluge, 1981). Considering the absence or low level of physical combat, the decrease in body size in males could reflect less intense intrasexual selection in Costa Rica. However, as body size decreases proportionally in males (23.6% smaller than in Panama) and females (21.4% smaller than in Panama), some yet unknown ecological effects seem more likely to account for the geographic difference in body size.

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