

Facultative Nest Construction in the Gladiator Frog *Hyla rosenbergi* (Anura: Hylidae)

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The egg-laying basins and basin dynamics of the gladiator frog *Hyla rosenbergi* were studied in southeastern Costa Rica from May to August 1995. The majority of basins with calling males inside were water-filled puddles or cattle footprints; only 29% of the basins were male-constructed nests. Basin occupation time was generally short, lasting on average 1.5 days. Up to two different males used a single basin consecutively, but the proportion of reused basins was very low (15%), which is explained by the high number of available basins at the study sites.

DEPOSITION of eggs as a film on the water surface of shallow basins excavated by males is known in relatively few species of frogs but probably arose independently in distinct lineages within the Anura (Duellman and Trueb, 1986). Egg and early larval development occur in the basin, and subsequent flooding results in the tadpoles dispersing into open water. Within tree frogs (Hylidae), at least six species in the *Hyla boans* group are known to build nests for egg deposition: *H. boans* (Duellman, 1970), *H. crepitans* (Caldwell, 1992), *H. faber* (Lutz, 1960a), *H. pardalis* (Lutz, 1960b), *H. rosenbergi* (Breder, 1946), and *H. waurini* (Martins and Moreira, 1991). Detailed descriptions of the nests have been published for only a Panamanian population of *H. rosenbergi* (Kluge, 1981), for *H. boans* (Caldwell, 1992), and for *H. faber* (Martins and Haddad, 1988; Martins, 1993). In *H. faber* and *H. rosenbergi*, nest construction was obligatory, but in *H. boans* and *H. crepitans*, it was facultative, depending largely on the substrate of the frogs' breeding habitat (Caldwell, 1992).

Hyla rosenbergi ranges from eastern Costa Rica to northern Ecuador but has a discontinuous distribution with gaps in western Panama and Colombia (Kluge, 1979). *Hyla rosenbergi* from Panama are typical nest builders (Kluge, 1981): males constructed sand or clay nests at the margin of streams or ponds, where advertisement calling, oviposition, and early larval development take place. Because *H. rosenbergi* males advertise only from within nests and egg deposition occur exclusively in the nests, occupying a nest is crucial for male reproductive success. Here, I describe the basins and the basin dynamics of a Costa Rican population of *H. rosenbergi* and report for the first time facultative nest building in this species.

MATERIALS AND METHODS

Observations were made from May to September 1995 in a swampy cattle pasture adjacent

to the Estación Biológica La Gamba. The station is located at 08°42'N, 83°13'W and 70 m above sea level in the Pacific lowlands of Costa Rica, Puntarenas Province. The study area was about 40 × 50 m, and consisted of an unflooded but relatively wet area belonging to the Biological Station and an adjacent swamp (Fig. 1). The swamp was bordered on two sides by the slopes of a low hill, and on the other two sides, it merged with a cattle pasture. Secondary forest was present on the hilltops and behind the Biological Station, about 10–15 m away from the swamp. A leaking pipe created a wet area on a hillside and probably supplied the water for the swamp, at least outside the peak of the rainy season. Because cattle entered the swamp, there were many cattle footprints filled with water as well as puddles. Parts of the swamp and most of the area near the Biological Station were covered by dense vegetation, mainly tall grasses.

Because of the difficulty of entering the swamp without disturbing the frogs, observations were concentrated mainly on the hillside shoreline. The study area was visited almost every night, from 1700 to 2400 h. Previously marked basins were checked, and newly occupied basins were located by listening for calling males. Observations were made using a headlamp.

Many puddles and flooded cattle footprints were used as calling and oviposition sites by *H. rosenbergi* (henceforth called basins). There were also male-constructed basins (henceforth called nests). All basins and nests found were marked with plastic tape bearing a reference number and recorded on a map of the study area. Nests and cattle footprint and puddle basins could be easily distinguished by their characteristic shapes (Fig. 2) and because nests contained grass pressed onto the bottom. Data recorded for each basin and nest were as follows: date of appearance, male that occupied it, maximum and minimum diameter of water surface,

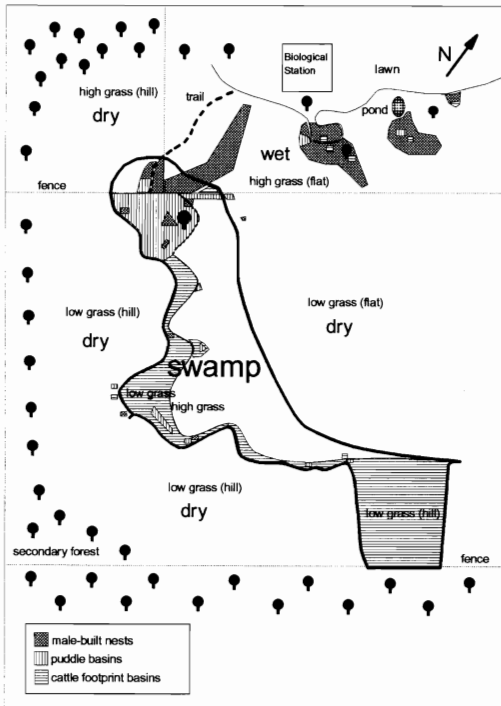


Fig. 1. Study site at La Gamba, Costa Rica. The bold continuous line denotes the margin of the swamp. Male *Hyla rosenbergi* called from all parts of the swamp and from the wet zone near the Biological Station, but because of difficulties of entering the tall grass part of the swamp without disturbing calling males, male-occupied basins were studied mainly in the low grass area.

maximum water depth, estimated percent of covering vegetation, distance to nearest calling male, and presence of a clutch. Water surface area and volume were calculated later (water volume was estimated by calculating the volume of a cylinder).

All encountered male *H. rosenbergi* were marked individually by toe clipping, a standard technique for marking anurans by removing toes in unique combinations (Donnelly et al., 1993). Thumbs were never removed, because males might need them to clasp females or for fighting. For each marked male, the date and time of capture was recorded, and its snout-vent length (SVL) to the nearest 0.1 mm was measured with a plastic caliper.

Because the weight of a frog depends largely on its water uptake and can vary considerably during one day, male size was estimated using SVL. Averages are given ± 1 SD. Unless otherwise indicated, data were analyzed using the Kruskal-Wallis nonparametric analysis of variance.

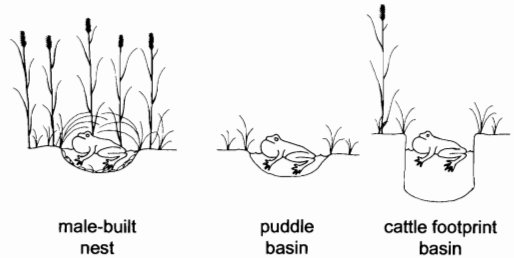


Fig. 2. Basin types of *Hyla rosenbergi* at La Gamba, Costa Rica.

RESULTS

A total of 110 males of *H. rosenbergi* were measured. Most ($n = 98$) were found calling within basins or nests, the rest were found sleeping during the day or sitting on vegetation at night. Their mean SVL was 63.1 ± 3.6 mm ($n = 110$).

Basins and nests were found on the margins of the swamp and on wet ground up to 30 m away from the margin of the swamp. Basins and nests lacked the typical wall ("rampart") of other *Hyla* nests described so far (Lutz, 1960b; Duellman, 1973; Kluge, 1981). Because of this and the dense vegetation, basins and nests were difficult to find and to distinguish from unoccupied puddles or cattle footprints until the resident male began calling.

Males were never observed building a nest, but, deducing from their shape, males built nests by pushing vegetation down and away to create a shallow water-filled depression. Males were also never seen renovating or changing the shape of cattle footprints or puddles they occupied. Ramparts were never observed, in spite of the availability of soft mud, especially in water-filled cattle footprints. Females in amplexus sometimes swam around within the basins and nests and muddied the water but did not noticeably change the shape or remove material from them.

Of 198 male-occupied basins, 33 (17%) were puddles, 106 (54%) were cattle footprints, and 56 (29%) were nests. The category of the remaining three depressions occupied by males was unclear. Basins originating from cattle footprints were significantly deeper than the other two types. Puddle basins had significantly greater water surface, and nests had significantly more vegetation cover (Table 1). Water volume did not differ between basin types, however (Table 1). The SVL of males occupying the three different basin types did not differ significantly ($P = 0.39$), and male SVL was not significantly correlated with the water surface, water volume, or vegetation cover of the basins they occupied

TABLE 1. MEASUREMENTS OF BASINS AND NESTS USED FOR CALLING AND OVIPOSITION BY *Hyla rosenbergi* AT LA GAMBA. See text for details.

	Male-constructed nests (n = 56)	Puddle basins (n = 33)	Cattle-footprint basins (n = 106)	Kruskal-Wallis test
Water surface area (cm ²)	218 ± 115	257 ± 153	188 ± 91	<i>P</i> = 0.04
Depth (cm)	6.3 ± 1.7	7.1 ± 2.7	9.0 ± 4.0	<i>P</i> < 0.001
Water volume (cm ³)	1452 ± 1127	1954 ± 1631	1776 ± 1321	<i>P</i> = 0.30 NS
Vegetation cover (%)	84 ± 26	49 ± 28	35 ± 33	<i>P</i> < 0.001

(for all basin types: $r_s < 0.10$, $n = 172$, $P > 0.09$). However, male SVL was negatively correlated to the depth of the basin (for all basin types: $r_s < 0.15$, $n = 177$, $P = 0.023$). Males that constructed nests might have exercised more influence over nest parameters than males simply occupying a natural depression, but there also were no significant correlations when only male-built nests were considered (in all cases: $r_s < 0.23$, $n = 43$, $P > 0.07$).

Some males occupied more than one nest or basin during their stay in the breeding colony. The degree of vegetation cover of the first and second nest or basin of individual males was significantly correlated ($r_s = 0.4$, $n = 48$, $P = 0.002$), but there were no significant correlations among size parameters (water surface, depth, and volume: $r_s < 1.7$, $n = 49$, $P > 0.11$).

Most basins and nests were occupied by only one male (168 of 198, 85%). Thirty (15%) were used consecutively by more than one male, and only five of these 30 basins were used 3–4 times but never by more than two different males. Re-occupation was either by the original occupant ($n = 8$) or by a different male ($n = 11$). Nests were not reoccupied more often by individual males than other basins ($G^2 = 1.02$, $df = 1$, $P > 0.30$). Reoccupation of a basin or nest occurred 9.7 ± 10.2 days (1–36 days, $n = 36$) after the previous occupation. The time between occupations did not differ significantly between basin types ($P = 0.40$).

Basins and nests were generally occupied for short periods of time. Basin occupation by a male lasted on average 1.5 ± 0.9 days (1–6 days,

$n = 227$) and did not differ significantly between basin types ($P = 0.82$). Seventy-two percent of the basins were occupied for just one night, 24% were occupied for 2–3 consecutive nights, and only 4% were occupied for 4–6 nights. Basins occupied for only one night ($n = 163$) did not differ significantly from basins occupied for ≥ 3 days ($n = 28$) in any of the measured parameters (nest type, water surface, depth, water volume, vegetation cover: in all cases $P > 0.11$).

Of the 198 male-occupied basins and nests, 142 (72%) received no clutches and 56 (28%) received one clutch. For comparison with other studies the average was calculated: 0.28 clutches per basin or nest. There was no significant difference between basin types in whether they received a clutch or not ($\chi^2 = 1.47$, $df = 2$; $P > 0.05$). Basins and nests with and without clutches did not differ in size, vegetation cover, or distance to nearest calling neighbor (in every case $P > 0.05$).

DISCUSSION

Costa Rican *H. rosenbergi* seem to be always smaller than those from other parts of their range, and the frogs at La Gamba were even smaller than other *H. rosenbergi* populations studied so far (Table 2). Although nest size in *H. rosenbergi* is quite variable, nests found in Costa Rica show the same trend to smaller size as do the frogs (Table 2). The smaller size of Costa Rican frogs does not seem to account for the smaller size of their nests, because neither in

TABLE 2. COMPARATIVE DATA ON SIZE OF FROGS AND MALE-CONSTRUCTED NESTS OF *Hyla rosenbergi*. Costa Rican specimens are smaller than Panamanian ones and also have smaller nests.

	Costa Rica		Panama	
	(present study)	(Kluge, 1981)	(Breder, 1946)	(Kluge, 1981)
Male SVL (mm)	63.1 ± 3.6	70.3	79.2	82.4
Mean diameter of nest (mm)	190.0 ± 58.0	121.3	269.9	—
Water surface area of nest (cm ²)	218.0 ± 115.0	—	—	282.9
Depth of nest (mm)	63 ± 17	—	—	—

the present nor in previous studies of *H. rosenbergi* (Kluge, 1981) and *H. faber* (Martins, 1993) was any correlation between male size and nest size found. Males apparently lack individual nest size preferences (no correlation between size measurements of basins and nests used subsequently by individual males). The observation that all *H. rosenbergi* nests found in Costa Rica (Kluge, 1981; this study) were built on hard earth and in dense vegetation, whereas Panamanian *H. rosenbergi* nests were found in soft mud (Breder, 1946; Kluge, 1981), corroborates the suggestion of Kluge (1981) that this difference in nest size associated with geographic location was because of differences in the substrate and not male size.

The correlation with vegetation cover of basins and nests used subsequently by individual males might be less a real preference of the males but rather an artifact of those males returning to the same small area of the swamp to call on different nights (unpubl.). Thus, males returning to an area with low vegetation would have used basins with lower vegetation cover than males returning to an area with taller grasses.

Nest construction is a time- and energy-consuming activity, taking about half a night in Panamanian *H. rosenbergi* (Kluge, 1981). Because males of *H. rosenbergi* can attract females only with a basin or nest from which to call, decreased nest construction time should enhance a male's chance of reproduction. Thus, using existing depressions on the ground to initiate nest construction or occupying previously built nests, puddles, or cattle footprints should allow males to begin calling earlier and maximize their chances of attracting a mate. Indeed, Panamanian *H. rosenbergi* (Breder, 1946; Kluge, 1981) and *H. faber* (Martins, 1993) preferred initiating nests in preexisting depressions. However, the occupation of suitable depressions without major renovation, as observed in the present study, has never been described for *H. rosenbergi*. In Panama, Breder (1946) dug holes resembling the nests in the area, but they were not used by male *H. rosenbergi*.

Similarly, the reoccupation of basins or nests should also result in time and energy savings for males and be selectively advantageous for nest-building frogs. Reuse of nests occurred in *H. faber*, in which 1-4 ($\bar{x} = 1.3$) males occupied each nest (Martins, 1993). In Panamanian *H. rosenbergi*, 64% of nests were used by more than one male (Kluge, 1981). The low proportion of basins used by more than one male (15%) in the present study may result from the abun-

dance of water-filled depressions available in the study area.

Basins and nests were generally occupied for a short time (1.5 days), and more than 70% of the basins were occupied for just one night by one male. Kluge (1981) reported similar results for his Panamanian population, but the mean duration of nest occupation was higher ($\bar{x} = 4.1$ days). One might expect that a nest built by a male should be a relatively valuable resource to him. However, males in the present study did not occupy self-constructed nests longer than other basins.

In the present study, most male-occupied basins and nests did not get a clutch of eggs. The average number of clutches per basin was 0.28, low compared to an average of 0.97 reported by Kluge (1981) for Panamanian *H. rosenbergi* or of 1.7 reported by Martins (1993) for *H. faber*. This difference may relate to the availability of natural depressions and the low rate of reuse of basins by males at La Gamba.

The nature of facultative nest construction reported here differed from reports of facultative nest construction in other gladiator frogs. In *H. boans* and *H. crepitans*, frogs used natural water-filled depressions and even protected sites on the edges of a stream as basins when the substrate was unsuitable for nest construction but did construct nests whenever the substrate of the breeding site allowed for it (see Caldwell, 1992). The population of *H. rosenbergi* observed in the present study, however, used suitable water-filled depressions whenever available, although the substrate would have allowed for nest construction and only constructed nests when no easier alternatives were available.

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