The Rise and Fall of a Population of *Hyla boans*: Reproduction in a Neotropical Gladiator Frog

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ABSTRACT.—A population of *Hyla boans* was studied in central Amazonian rainforest during 15 years. The species differs from other intensively-studied gladiator frogs, *Hyla rosenbergi* and *Hyla faber*, in that males reach larger sizes than females, most reproduction is in the dry season, males call mainly from trees and rarely from nest basins, and most nest basins have aquatic connections to streams. Many adults (15% of females, 21% of males) were captured over more than one breeding season, and some were captured over five breeding seasons. Sizes of juveniles, and growth of one individual, indicate that males require at least two years between hatching and entering the breeding population. Daily calling was bimodal, with peaks after dusk and before dawn. Rainfall reduced calling activity during the peak of the breeding season. The population at the site declined to zero density after nine years of study and the site still had not been recolonized six years later. The exponential rate of decline of the population (−0.58) was more than three times the exponential rate of increase (0.15) at the beginning of the study.

RESUMO.—Reprodução de uma população de *Hyla boans* foi estudado em floresta tropical úmida na Amazônia central durante 15 anos. A espécie difere de outras espécies do grupo que tem sido estudados intensivamente, *Hyla rosenbergi* e *H. faber*, em que a maior parte da reprodução ocorre na época seca, machos atingem tamanhos maiores que fêmeas, chamam principalmente de árvores e raramente de bacias de nidificação, e a maioria das bacias de nidificação tem conecções aquáticas com os riachos. Muitos adultos (15% de fêmeas e 21% de machos) foram capturados sobre mais que uma estação reprodutiva, e alguns foram capturados sobre cinco estações reprodutivas. Os tamanhos de jovens, e crescimento de um indivíduo, indicam que machos requerem pelo menos dois anos depois da eclosão para entrar na população reprodutiva. Vocalização diária foi bimodal, com picos depois do crepúsculo e antes do amanhecer. Chuva reduziu atividade de vocalização durante o pico da época de reprodução. A população local foi extinta depois de 9 anos e o sítio de estudo ainda não foi recolonizado depois de seis anos. A taxa exponêncial de declínio na população (−0.58) foi mais que três vezes a taxa exponêncial de aumento (0.15) no começo do estudo.

Neotropical gladiator frogs are distinctive elements of the neotropical fauna because of their large size, male-male combat, pronounced vocalization, and conspicuous nest-building behavior (Crump, 1974; Lamotte and Lescure, 1977; Duellman, 1978; Kluge, 1981; Martins, 1993a). Although members of the group are often mentioned in faunal lists, detailed studies

have been carried out on only two species: *Hyla rosenbergi* (Kluge, 1981) and *Hyla faber* (Martins and Haddad, 1988; Martins, 1993a, b; Martins et al., 1993). Both species primarily breed in the wet season and occupy relatively open, and often disturbed, habitats including ponds (*H. faber*, Martins, 1993a) and intermittent streams (*H. rosenbergi*, Kluge, 1981).

Hyla boans has a broad distribution (Crump, 1974; Duellman, 1978) which overlaps that of other gladiator frogs. The species is often found in relatively undisturbed rainforest, but in some areas it occurs syntopically with open-area species such as *Hyla wavrini* (Azevedo-Ramos, 1995). Unlike *Hyla faber* and *H. rosenbergi*, *H. boans* breeds along permanent streams in the dry season (Duellman, 1978; this study). Here we report the results of a 15 year study of *Hyla boans* in a relatively undisturbed rainforest reserve in central Amazonia. The principal aim of the study was to compare the biology of the population with those of previously-studied populations of gladiator frogs. However, the population declined to zero density nine years after the study began, so the pattern of population fluctuations may be of interest to researchers studying amphibian declines (e.g., Blaustein et al., 1994).

MATERIALS AND METHODS

The study was undertaken in Reserva Florestal Adolpho Ducke (Reserva Ducke), a 100 km² rainforest reserve 25 km northeast of Manaus, Amazonas, Brazil (Lat. 3°08′S Long. 60°01′W). The vegetation consists of "terra firme" rainforest, a well-drained forest not subject to seasonal inundation (Guillaumet, 1987). The climate is dominated by distinct wet and dry seasons, with most rain falling between December and May; the mean annual rainfall for Reserva Ducke between 1965 and 1980 was 2362 mm (Marques Filho et al., 1981).

The study site was at the junction of the stream Igarapé Acará and one of its tributaries (see Fig. 3 in Magnusson and Lima, 1991). All data reported here were collected within 100 m of the junction of the streams. Regular surveys of the streams were carried out in a 16 km² area around the junction (Magnusson and Hero, 1991; Magnusson and Lima, 1991). However, *Hyla boans* was rarely found further than 100 m from the study site.

The area is characterized by deep sedimentary soils and the banks of most streams are sandy. However, rock outcrops form waterfalls less than one meter high around the confluence of the streams. Rock platforms up to one meter wide with shallow pools occur around the waterfalls. The water is naturally acidic (pH < 4.5)

and tinted reddish brown by organic acids, especially during the rainy season.

Temporary flooding and fluctuations in stream depth of over a meter as a result of heavy rainfall are common during the wet season. However, spates are short lived and the stream usually returns close to base flow within 24 h. The site is in relatively pristine forest and the closest agricultural/urban development is 2 km downstream. The headwaters of the streams are in undisturbed rainforest.

The study was conducted from January 1982 to October 1996. The number of individuals calling within 100 m of the stream junction at 1900 h was recorded at approximately weekly intervals until 1994 when surveys were made more irregularly. The number of surveys in each year are presented in Fig. 6. Most data on morphology and behavior were recorded before the population crashed in 1989.

Attempts were made to capture all individuals at the study site, principally in the drier months, between August and December, from 1982 to 1987. Frogs were detected visually and acoustically by wading along the stream sections. Not all individuals could be captured as some were inaccessibly high in trees and others escaped by jumping into the stream. Capture efforts were usually at weekly intervals and often coincided with the counts of individuals calling. However, effort was not standardized, so we effectively sampled less than 20% of the nights during the 5 yr period.

Frogs were weighed with "Salter" spring scales read to the nearest 0.5 or 1.0 g, measured with vernier calipers read to the nearest 0.01 mm, and marked by toe clipping. The lengths of frogs were measured from the tip of the snout to the posterior end of the urostyle (SUL) as it was easier to standardize a bone to bone measurement. However, SUL is very similar to snout–vent length. Sex was determined from the presence of the prepollical spine in males and color (light yellow with a vertebral stripe in females, dusky brown in males).

Only the last joint with the toe pad was removed during marking and few individuals regenerated toe pads. Individuals that regenerated toes had been marked at the beginning of the study period and the toe clipping had severed a bone. When we removed the toe pad by separating the last joint, regeneration was not detected and the process appeared to cause minimal distress to the frogs as judged by the lack of flinching, struggling, or vocalization which typically occurred when a frog was inadvertently injured. No recaptured frogs showed signs of infection. Removal of up to three toes with a maximum of one toe per foot did not appear to affect the agility of the frogs

which quickly climbed back into the trees and generally resumed calling within an hour. The intensive marking study was terminated in 1986, two years before the decline in the population.

For each frog captured, we recorded its horizontal and vertical distances from water with a measuring tape graduated in cm, and whether it was vocalizing. We also recorded the presence of scratches and scars, which are presumably caused by the prepollical spines during agonistic encounters (Kluge, 1981), and other injuries.

We evaluated the effects of ambient conditions on the number of frogs calling during the height of the breeding season by analysis of covariance. We only used data for the months of August and September between 1982 and 1988 for this analysis. Other months and years had more than 20% of days with no frogs calling and inclusion of those data would have confounded behavioral and population processes. Explanatory variables were minimum temperature on the day of the survey, rainfall on the day of survey, rainfall during the four days preceeding the survey, moon intensity and an index of moon angle. Rainfall during the previous four days was used as this was the maximum period that did not overlap with subsequent surveys. Minimum temperature was not correlated with rainfall ($r \leq 0.13$, $P > 0.05$). Maximum and mean temperatures were not included as they were correlated with rainfall ($r \geq 0.45$, $P < 0.001$). Moon intensity (illumination of the moon on each survey night as a proportion of maximum illumination at full moon) was obtained from the program ALMANAC written by Ross Alford. The time after moonrise or time to moonset, whichever was less, was used as an index of moon angle. Year was entered as a categorical variable as the maximum number of calling males varied among years. Deviations from cell (yearly) means (Wilkinson, 1990) were used to illustrate the relationship between the significant continuous variables and the number of calling males.

To determine the daily calling phenology, we recorded the number of individual males vocalizing, and the number of individuals present at the site but not calling, at half-hour intervals between 1800 and 0600 h on five separate nights (24 October 1987, 10 August 1988, 23 August 1988, 8 September 1988, and 20 September 1988). Calling data are presented as the proportion of the maximum number recorded for a census on each night (7, 18, 13, 9 and 9, frogs respectively).

The characteristics of all nests with eggs within the study area were recorded on four nights (18 October, 8 November, and 28 November 1986). Additionally, characteristics of some nests

were recorded on 16 nights between November 1983 and November 1988. Substrate was recorded as sand, rock, and/or roots. Aquatic connections through which fish or macroinvertebrates could obtain access to nests were recorded and the maximum dimensions of the basin measured with a tape graduated in millimeter. Basins excavated in sand or leaf litter with distinct rims were recorded as constructed. Basins with hard substrates and sides made of roots and/or rocks which the frogs could not have modified were recorded as natural.

The total number of hatched eggs and dead eggs were counted in four clutches collected from separate basins in 1983. Eggs represented only by capsules were presumed to have hatched. Eggs containing yolk with a bluish color (with or without fungal mycelia) were recorded as undeveloped because development of such eggs to hatching was never observed. Searches of the basins in which these clutches were laid revealed no large tadpoles or invertebrates which could have removed the yolk from capsules so we believe that the number of capsules probably represents the number of tadpoles that hatched successfully. The newly hatched tadpoles lodged among roots and rock crevices and we could not count them accurately. The number of undeveloped eggs were recorded in another five nests. In those nests, the capsules had been disturbed and broken up and we could not confidently count them.

RESULTS

Sexual Size Dimorphism.—Males (Mass: mean = 91.7 g, S = 12.9, min. = 63.0, max. = 130.0, N = 86; SUL: mean = 11.6 cm, S = 0.55, min. = 10.1, max. = 12.8, N = 86) were significantly longer ($t_{118} = 7.6$, $P < 0.001$) and heavier ($t_{118} = 5.8$, $P < 0.001$) than females (Mass: mean = 76.5 g, S = 13.2, min. = 46.0, max. = 103.0, N = 34; SUL: mean = 10.7 cm, S = 0.66, min. = 9.1, max. = 12.3, N = 34). Males fought frequently and often one or both frogs fell from the tree. Most males (72%) carried scars (mean per individual = 5.6, S = 7.95, min. = 0, max. = 40, N = 134) attributable to scratches by prepollical spines. However, no cases of mortality or ruptured tympanic membranes could be attributed to the use of spines during fights. Some females (26%) also had scars (mean per individual = 2.8, S = 7.0, min. = 0, max. = 21, N = 34). There was no significant difference between the length of males (N = 12, mean SUL = 115.9 mm) recorded in amplexus with females and the length of males (N = 74, mean SUL = 115.7 mm) not recorded in amplexus ($t_{84} = 0.16$, $P = 0.87$).

Nest Characteristics.—Most nests (10 of 16) in the complete surveys were in natural pools with no evidence of modification by frogs. Construct-

ed nests were in sand, leaf litter, and/or fine roots, and most (four of six) were modifications of pre-existing pools formed by root mats. Eight of ten natural nests and four of six constructed nests were connected to the stream by channels 2–10 cm deep through which fish and macroinvertebrates could enter. Of 27 nests for which data were recorded, 74% had connections to the stream. Basins frequently contained fish (*Pyrrhulina* sp., *Aequidens* cf. *tetramerus*) and shrimp (*Macrobrachium inpa, M. nattereri*). No other amphibians laid eggs in the basins nor were any tadpoles of other species found in the basins, though *Centrolenella oyampiensis* deposited eggs on overhanging vegetation and *Osteocephalus buckleyi* laid eggs in the stream nearby. Nest sizes varied widely (Depth: mean = 8.5 cm, S = 4.4, min. = 3.0, max. = 20.0, N = 13; Length: mean = 44.0 cm, S = 31.8, min. = 18.0, max. = 100.0, N = 14; Width: mean = 36.1 cm, S = 31.5, min. = 12.0, max. = 100.0, N = 14).

Males defended the area around calling sites (hence the observed wrestling bouts) and the presence of two clutches in the same basin was rare. Of 48 nests checked, only three had two clutches of eggs, and only one clutch was laid in a basin which already had tadpoles. The four clutches counted between January and September 1983 had 1374, 2709, 2525, and 3516 egg capsules. Of those, 228 (17%), 699 (26%), 1064 (42%), and 3510 (99%), respectively, contained dead tadpoles or undeveloped yolk. Undeveloped or dead eggs were recorded for another five nests for which we could not confidently count the number of capsules. The mean number of undeveloped or dead eggs was less than in the four completely counted clutches but all nests contained dead or undeveloped eggs (971, 447, 364, 190, 23).

Tadpoles remained in the basins for at least a week after egg laying. Some large tadpoles sometimes remained after two weeks, but tadpoles had always dispersed into the stream within three weeks of egg deposition (either through the connection or in periodic inundation following rainfall).

Adult Behavior.—Males called at a mean height of 229 cm (S = 187, min. = 0, max. = 750, N = 220) and a mean horizontal distance from water of 71 cm (S = 93, min. = 0, max. = 500, N = 215). Most were less than 50 cm from the bank or over water (Fig. 1a), and frequently jumped into the water when pursued. Few males called from the ground or in the nest basin (Fig. 1b). On two occasions that females were observed before and during amplexus, the females approached from the forest at a height of about 1 m and climbed up the tree to a position less than 1 m from the male. The male then ceased calling and the female followed him down to
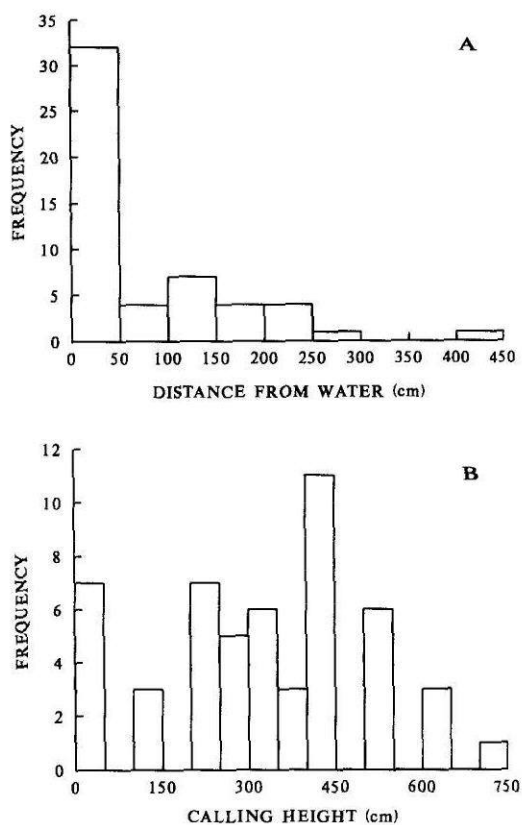

FIG. 1. (A) Horizontal distances of calling males from stream. (B) Vertical distances of calling males from stream.

the nest basin. Contact between the pairs was made only after entering the basin.

On one occasion, a non-calling male sitting near the base of a tree with a calling male attempted to intercept an incoming female. The calling male descended from the tree and engaged him in combat, suggesting that males may be able to determine the sex of conspecifics at distance without auditory cues.

Seasonal and Diel Patterns of Reproductive Activity.—Calling was strongly seasonal (Fig. 2). Some males were calling at 1900 h on most nights surveyed in August (89.5% of nights), September (80%), October (64%), and July (58%). Calling was registered on a small proportion of nights (0–16%) in the months between February and May. Seasonal variation in calling may occur due to individual behavior or may result from seasonal recruitment of adolescents from previous breeding seasons.

Only three juveniles (SUL < 8 cm) were captured and only one was recaptured. Two juveniles of unknown sex were 6.4 cm SUL and 7.7 cm SUL when captured in August 1982 and
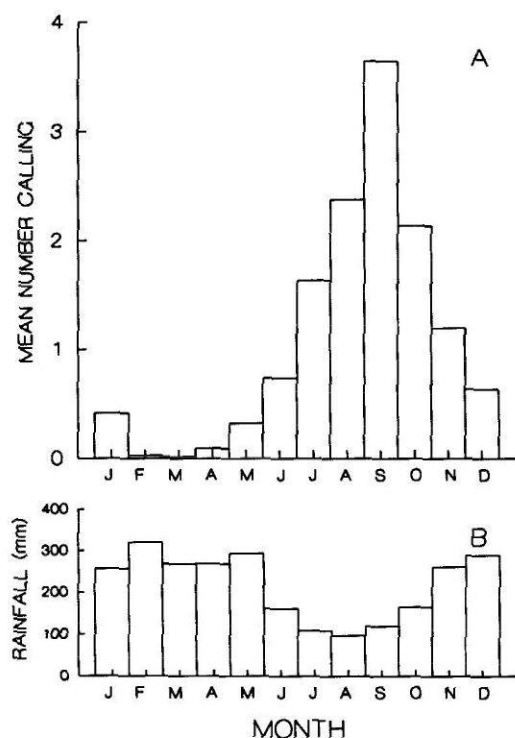
FIG. 2. Numbers of *Hyla boans* recorded calling at 1900 h in different calendar months, between 1982 and 1988.
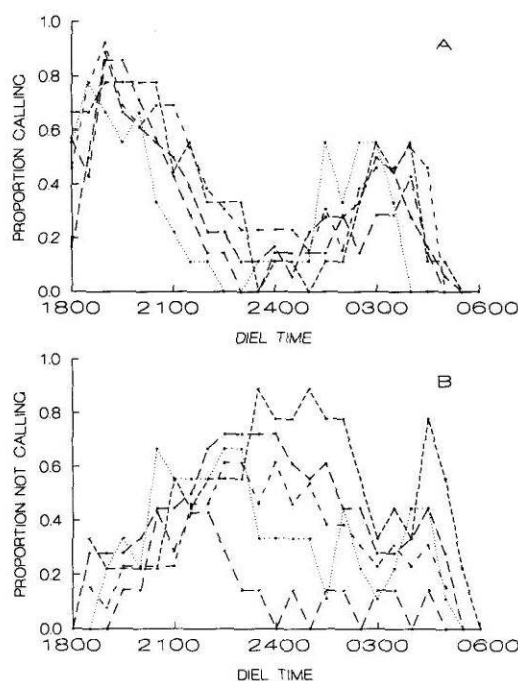

FIG. 3. (A) Diel pattern of calling during the night on 5 nights. Lines connect points for the same night. (B) Diel presence of male frogs that were not calling during the night for the same 5 nights illustrated in part A. Data are presented as the proportion of the maximum number of males recorded, calling or not calling, on any census during a given night.

February 1986, respectively. One juvenile, subsequently determined to be a male, had a SUL of 6.7 cm when captured in August 1982. Presumably, these three juveniles had hatched in breeding seasons immediately previous to when they were captured and were >1 yr old. The male was recaptured 1.74 yr later (May 1984) at an SUL of 11.9 cm. The limited data indicate that individuals would require a minimum of two years following hatching before entering the reproductive population.

The diel pattern of calling was similar during the five days in which calling was registered throughout the night (Fig. 3a). Calling peaked at about 1900 h, dropped to close to zero at 2400 h, and increased to a secondary peak at about 0400 h. The number of non-calling frogs in the area generally showed an inverse pattern (Fig. 3b), indicating that males generally remained quiescent during the middle hours of the night and did not leave the area. Rainfall was recorded on only one night, between 0300 and 0330 h on 20 September 1988. Calling ceased before 0400 h on that night, rather than at or after 0500 h as on the other nights.

Within the peak months of calling (August and September), the number of calling males per night was significantly negatively related to rainfall during the four days before the day of survey (ANCOVA: $F_{1,31} = 5.9$, $P = 0.021$) and year of survey ($F_{6,31} = 3.0$, $P = 0.019$), but not minimum temperature ($F_{1,31} = 0.28$, $P = 0.60$), rainfall on the day ($F_{1,31} = 0.43$, $P = 0.52$), moon intensity ($F_{1,31} = 0.33$, $P = 0.57$) or moon angle ($F_{1,31} = 1.96$, $P = 0.17$). To illustrate the effect of rainfall, independent of yearly variation in population density, we plotted the deviations from cell (year) means against rainfall (Fig. 4). There was a reduction of about 0.8 animals calling (C) for each 10 mm of rainfall accumulated (R - mm) during the previous 4 days (C = 1.0–0.084 R, $r^2 = 0.23$, $N = 44$, $P = 0.021$).

Longevity, Injuries and Diseases.—The recapture results indicate that adult survival can span 2–5 breeding seasons. Of the 34 females captured in this study, five were recaptured in more than one year (Fig. 5a). The weekly gap in surveys and the short period that females remained at the breeding site implies that this greatly underestimates the probability of females surviving from one season to the next. Eighteen of 86 males (21%) were recaptured over more than one breeding season (Fig. 5b).
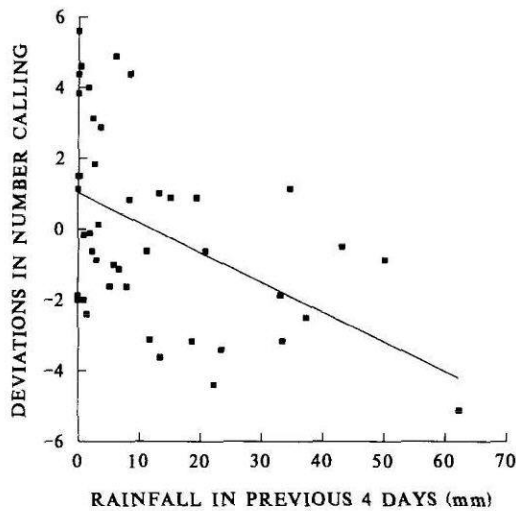
FIG. 4. Relative number of frogs calling (deviations from yearly means for those months) in relation to rainfall during the previous four days, for the months of August and September between 1982 and 1988.

Males remained at the breeding site much longer than females, but even so, it is likely that we missed many potential recaptures because of irregular intervals between surveys, and because many frogs were inaccessibly high, or escaped capture by leaping into the stream.

We registered few indications of major injuries or diseases. One female became entangled in roots after laying in September 1982 and had a broken leg. The same female was recaptured in June 1984 with a deformed ileum, but she was otherwise healthy. One male, captured as a juvenile in August 1982, was recaptured in May 1984 with its back legs paralyzed and the urostyle apparently broken. We necropsied this frog and discovered a large spongy growth around the base of the spine and the urostyle. Unfortunately, the animal was lost before we could carry out histology on the growth. No major injuries or deformities were recorded after 1984.

The maximum number of calling males generally increased from 1982 to 1989, but the population declined precipitously from 1989 to 1992 (Fig. 6). Despite continued surveys since 1992, no more than two frogs have been recorded calling at any survey and we lack evidence of females, eggs or tadpoles. The exponential rate of increase (r_{oba}) was calculated by regressing $\log_e$ of the maximum number registered calling (N) each year (circles on Fig. 6) on time (T) in years. The exponential rate of increase ($r_{oba} = 0.15$, SE $= 0.03$) was much lower in the period 1982–1988 ($\log_e N = -295 + 0.15$ T, $N = 7$, $r^2 = 0.80$, $P = 0.006$) than the rate of decrease ($r_{oba} = -0.58$, SE
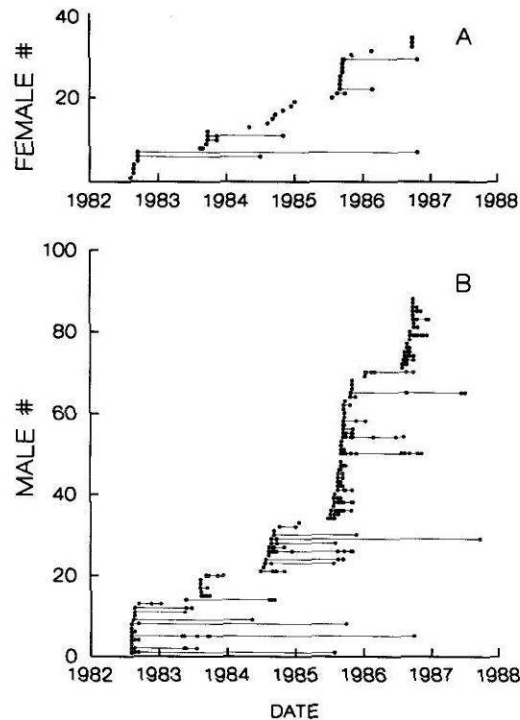

FIG. 5. Captures and recaptures of individual female (A) and male (B) frogs throughout the study. Lines join data for the same individual.
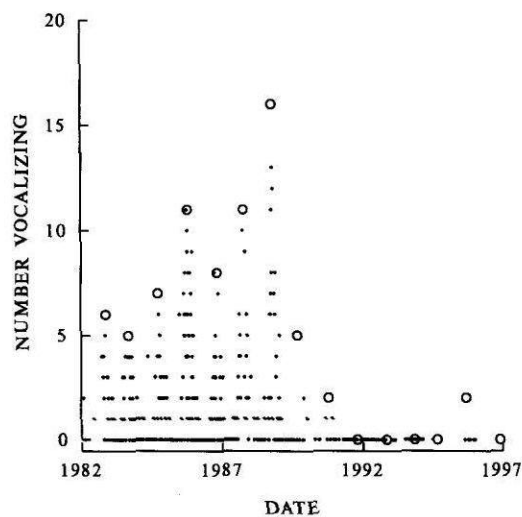

FIG. 6. Number of frogs calling in the study area on each of 629 nights between January 1982 and September 1997. Circles indicate the maximum number recorded in that year.

= 0.11) in the period 1988–1993 ($\log_e N = 1146 - 0.58$ T, $N = 6$, $r^2 = 0.87$, $P = 0.007$).

DISCUSSION

Sexual Size Dimorphism.—Adult male *Hyla boans* at Reserva Ducke are significantly larger than females. This agrees with predictions based on the presence of combat in males (Shine, 1979), but contrasts with data on the neotropical gladiator frogs, *H. rosenbergi* (Kluge, 1981) and *H. faber* (Martins, 1993b), which do not show sexual dimorphism in size. The sizes of *H. boans* at Reserva Ducke were similar to those at Santa Cecilia Ecuador (Crump, 1974), which are smaller than those in Panama (Duellman, 1978). Males fought with their prepollical spines, and most males bore scratches and scars attributable to spines of rivals. One or both combatants often fell from the trees, but we found no injuries attributable to falls. Kluge (1981) reported that male *H. rosenbergi* often inflicted severe injuries which ultimately led to the loser's death through increased risk of predation, or in some cases, at the hands of rivals through prepollical spine-inflicted injuries. Despite the presumed advantage of large size in male-male combat, no significant difference existed between the mean sizes of males encountered in amplexus and those vocalizing, but not found in amplexus. Some of the males not seen in amplexus undoubtedly mated when we were not there, but the large sample size indicates that if a difference in size exists between successful and unsuccessful males, it is small.

Large size and fighting ability may be of advantage to protect nests with eggs from intruding males. *Hyla rosenbergi* defends the nests, without calling, for 1–2 d (Kluge, 1981). *Hyla boans* resumed calling soon after egg laying, but usually from a position above or close to the nest where it could defend the area from intruding males. Males usually inspected or constructed nest cavities nearby after mating, suggesting that males may avoid leading females to nests which already have eggs or tadpoles. However, our observations are scant, and female choice may be involved in avoiding egglaying in occupied nests. It would be disadvantageous for both males and females to have another pair lay in the same nest; the second pair could destroy or remove eggs and tadpoles while remodelling the nest. Nevertheless, some advantage to the male may exist if a female laid in a nest occupied by his offspring as the larger tadpoles from the first clutch might consume the eggs in the second clutch. Egg cannibalism by *H. boans* has been demonstrated under experimental conditions (Magnusson and Hero, 1991).

Nest Characteristics.—Nest dimensions varied, mainly because the frogs often used natural embayments caused by roots and depressions in the rock platforms around the stream. The most obvious difference between the nests of this population and those of other populations of *H. boans* (Lamotte and Lescure, 1977), *H. rosenbergi* (Kluge, 1981) and *H. faber* (Martins and Haddad, 1988), was that most nests, natural and constructed, had aquatic connections to the stream. Fish and shrimp had free access to most nests, but fish and shrimp generally do not eat eggs of aquatic frogs in this area (Magnusson and Hero, 1991). Generalist scavenging insects and tadpoles known to eat frog eggs (Magnusson and Hero, 1991) do not occur in the shallows of the stream, and may be limited by fish predators (Hero et al., 1998). *Osteocephalus buckleyi* also lays its eggs in the stream (Hero, 1990), but its tiny egg rafts are always found in natural embayments that would be too small for the large clutches of *H. boans*. Nests could potentially serve to separate newly laid eggs and recently hatched tadpoles from larger tadpoles of *H. boans* which readily eat them under experimental conditions (Magnusson and Hero, 1991). However, this seems unlikely as tadpoles in the stream usually had access to the nests and were never observed in them.

Alternatively, the nests of *H. boans* in our study area may function to prevent the eggs from being swept away in the current and small fluxes in stream level associated with brief rains in the dry season. *Hyla rosenbergi* and *H. faber* reproduce during rainy seasons, and tadpoles are washed, or swim into the stream during rises in the water levels following rain (Kluge, 1981; Martins, 1993b). In contrast, *H. boans* reproduces in the dry season when spates caused by heavy rainfall are rare (this study; Crump, 1974; Lamotte and Lescure, 1977; Duellman, 1995). Individuals of this species may use natural cavities with connections, and often leave connections to streams in constructed nests, because the infrequent rainfall may not be synchronized with the period in which the tadpoles are ready to leave the nest.

The nest of *Hyla boans* at our study site spanned all levels of complexity, from the use of natural depressions, to simple nests formed by pushing away leaf litter, and basins constructed in sand with high retaining walls. Duellman (1978) also reported *H. boans* using natural depressions. Martins (1993a) suggested that *H. wavrini* constructs simpler nests than *H. boans*, but we have seen well-formed nests of *H. wavrini* on the sandy beaches of the Tapajós River that are very similar to the most elaborate nests of *H. boans*. All nest-building gladiator frogs may exhibit variation in the form of the nests, depending on the substrate available.

The range of clutch sizes reported here (1374–

3516) was similar to that reported by Crump (1974) for Santa Cecilia, in Ecuador (1300–4800). Data for 1983 indicate that often several hundred to several thousand eggs in each clutch do not develop for reasons other than predation. However, these data were collected during a period of population growth, so such mortality apparently was not limiting the population.

Adult Behavior.—Most males called from elevated perches and they were rarely seen in nest basins except at dusk when they descended to inspect or construct basins, and when accompanied by a female. Males were not heard calling when females were perched nearby, or while leading females to nests, and presumably communication between the sexes was visual. *Hyla rosenbergi* calls from the ground or from nest basins, and Kluge (1981) reported a distinct "courtship call" and complex behavioral contact between the sexes that initiated amplexus. Males in the population of *H. faber* studied by Martins (1993b) called from the ground, but this may have been due to lack of trees, as the author considered that the species occurred in forests before wide-scale clearing for pasture. Females of *H. faber* usually made contact with the male in the nest basin (Martins, 1993b), but the male sometimes left the basin to guide the female (Martins and Haddad, 1988). *Hyla boans* calling from trees could jump into the stream or to adjacent trees to escape predators and we have no evidence of the heavy predation on calling males reported for *H. faber* (Martins et al., 1993).

Hyla boans calls during the dry season (Crump, 1974; Lamotte and Lescure, 1977; Duellman, 1995; this study). We lack estimates of when the tadpoles metamorphose but we found tadpoles scattered on sandy stream bottoms throughout the dry season. *Hyla rosenbergi* metamorphoses in about 40 d (Kluge, 1981), but *H. faber* requires more than eight months (Martins, 1993a). Metamorphosis before the start of the rainy season would be maladaptive for *H. boans* due to the risk of desiccation to small frogs. As some adults live from one season to the next, we assume that the extreme peak of calling activity at the height of the dry season is a behavioral response, and not simply the result of the lag between metamorphosis and sexual maturity.

Distinct peaks in calling activity were recorded after dusk and before dawn, and calling activity was reduced around midnight even though many adult male frogs remained around the stream. Kluge (1981) reported that *H. rosenbergi* ceased calling by 2200 h. We do not know whether the reduction in activity resulted from circadian rhythms (e.g., Robertson, 1976), exhaustion due to calling (e.g., Wells et al., 1995), lack of light for general activity (e.g., Jaeger,

1981), or lack of light for predator avoidance (e.g., Ryan et al., 1982; Nunes, 1988). However, frogs showed the same pattern on bright moonlit nights, so we consider the lack of light hypotheses less probable than those associated with physiological processes.

Rainfall reduced calling during the breeding season. Although the frogs stopped calling when it rained heavily, the general level of calling was not related to rainfall on that day. Rather, it seemed to be a cumulative effect over the previous several days, which could indicate an increased chance of stream level rising and hence fresh clutches could suffer from desiccation when the creek level returned to base flow levels. Kluge (1981) reported that *H. rosenbergi* reduced calling after heavy rainfall, even though it bred in the wet season. *Hyla boans* also reduced calling activity in heavy rains, suggesting avoidance of rising stream levels. Although lunar rhythms (Robertson, 1976), and effects of ambient light on activity (Jaeger, 1981) have been shown for frogs, neither moon intensity nor moon angle significantly affected the number of frogs calling at 1900 h. Temperature affects calling in many species of frogs (e.g., Weathers and Snyder, 1977; Pough et al., 1992) but no significant effect of minimum temperature on activity in *Hyla boans* was detected.

Longevity and Population Decline.—Many adults (15% of females, 21% of males) were captured over more than one breeding season, and some individuals, both male and female, were captured over five breeding seasons. Based on limited data on sizes and growth of juveniles, those individuals were probably > 7 yr old. Kluge (1981) reported that few (0% of males and 4% of females) *H. rosenbergi* were recaptured between seasons and he presumed that this resulted from high mortality. Martins (1993b) assumed that the short time (mean of 15.5 nights) spent by male *H. faber* in the chorus indicated high mortality. Our data indicate that individuals often remained several weeks in the chorus and then disappeared, only to be captured again in subsequent seasons, so time in the chorus is probably a poor indication of survival. However, Martins et al. (1993) had other evidence that mortality of male *Hyla faber* may have been as high as 60% during the period in the chorus. None of the studies could estimate mortality reliably, as emigration was probably confounded with estimates of survival. However, the available evidence suggests different population processes exist at each site. Long-term survival of *H. boans* in the period 1982–1988 was much greater than that of the large ground frog, *Leptodactylus pentadactylus*, at the same site, which rarely survived to breed in two seasons (Galatti, 1992).

The population rose steadily in the period 1982–1988, before falling to local extinction in 1991. We do not know how many frogs were at the study site before 1982, but local forestry workers, who had camped at the site for long periods in the dry season in the mid 1970s, did not remember hearing the frogs. They may not have been present, as the loud, raucous call of *Hyla boans* is distinctive, and often irritating to non-herpetologists. We recorded little evidence of disease or serious injuries during the study, and none during the decline. Although we have not recorded females or reproduction at the site since 1990, one or two males have been heard calling in the area in subsequent years. However, they never remained for more than three days. The site has not been modified and appears to us to be essentially identical to its state in 1981 when we commenced intensive studies in the area. We lack evidence of introduced organisms that may have brought novel diseases (Laurance et al., 1996). A caiman (*Paleosuchus trigonatus*) whose home range encompassed the site disappeared in 1986, and he was replaced by a neighbor (Magnusson and Lima, 1991). The new caiman had the habit of sitting in the stream exactly under calling *Hyla boans* and it is not inconceivable that this individual could have extirpated the population by capturing pairs when they descended to lay eggs.

Independent of what caused the decline, the question arises as to why the species has not recolonized the area. Males reach the site but do not remain, possibly because of the lack of females, or possibly because too few males exist to form a lek. As with seabirds (Forbes and Kaiser, 1994), there may be an "information barrier," caused by lack of conspecifics, that inhibits colonization of new sites.

Other populations of *H. boans* occur around and at the edge of the reserve a few kilometers from the study site (M. Martins and M. Gordo, pers. comm.), and in parks in the region (R. Souza, pers. comm.), so the species has not been extirpated regionally. Although population density was high relative to other areas where we have seen *Hyla boans*, this may not have been conducive to the maintenance of the population. In the case of epidemic disease (May, 1983), or the possibility of development of specialized behavior by a predator, rarity may be a refuge, and dense populations may be sinks rather than sources.

Long-term monitoring of populations is rare (Blaustein et al., 1994; Dickson, 1995), and the asynchrony of local population fluctuations (Mclaran et al., 1995) may make patterns difficult to recognize. Amphibians often show high turnover at breeding sites between years, and surveys of many localities are necessary to interpret regional dynamics (Hecnar and M. Closkey, 1996). Our data indicate that such fluctuations may occur in apparently undisturbed lowland tropical forest, and that changes may occur on a decadal scale.

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