Reproductive Modes of Atlantic Forest Hylid Frogs: A General Overview and the Description of a New Mode[1]

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ABSTRACT

This paper reports a new reproductive mode in anurans, observed for the green treefrog, *Hyla leucopygia,* a species from the Atlantic Forest of Brazil and a member of the *H. albosignata* group. The reproductive mode of *H. leucopygia* is defined as follows: aquatic eggs and embryos in subterranean constructed nests; subsequent to flooding, feeding tadpoles in ponds or streams. We suggest that the new reproductive mode is widespread among the species in the *H. albosignata* group. The specialized courtship behaviors of *H. leucopygia,* characterized by vocalizations and a stereotyped sequence of mutual touches between male and female, are described. A review of the reproductive modes of hylid frogs is provided, with 11 modes recognized for the Atlantic Forest hylids and 12 modes for hylids around the world.

RESUMO

No presente trabalho descrevemos um novo modo reprodutivo em anuros, observado em *Hyla leucopygia,* espécie de Mata Atlântica, pertencente ao grupo de *H. albosignata.* O modo reprodutivo de *H. leucopygia* é definido como: ovos e embriões aquáticos em ninhos subterrâneos construídos; após a inundação, girinos que se alimentam são observados em riachos e poças. Sugerimos que o novo modo reprodutivo ocorre entre as espécies do grupo de *H. albosignata.* Descrevemos o comportamento de corte especializado, observado para *H. leucopygia,* caracterizado por vocalizações e uma seqüência estereotipada de toques mútuos entre macho e fêmea. É apresentada uma revisão sobre os modos reprodutivos da família Hylidae, sendo reconhecidos 11 modos para os Hylidae da Mata Atlântica e 12 modos para os Hylidae do mundo.

Key words: Anura; Atlantic Forest; Hyla leucopygia; *Hylidae; new reproductive mode; reproductive behavior; subterranean nest.*

MODE OF REPRODUCTION MAY BE DEFINED as a combination of ovipositional and developmental factors, including oviposition site, ovum and clutch characteristics, rate and duration of development, stage and size of hatchling, and type of parental care, if any (Duellman & Trueb 1986). In the class Amphibia, a great diversity of reproductive modes has been described; for anurans, more than 30 modes have been recognized (Lutz 1948, Lamotte & Lescure 1977, Duellman & Trueb 1986, Haddad & Sazima 1992, Weygoldt & Carvalho e Silva 1992, Haddad & Hödl 1997, Haddad & Pombal 1998). The greatest diversity of reproductive modes is found in the Neotropical region (Duellman 1985, Hödl 1990), where anurans have evolved more than 30 modes. Recently, new reproductive modes at familial and ordinal levels have been reported for the Atlantic Forest of Brazil (familial level: Haddad *et al.* 1990; ordinal level: Haddad & Sazima 1992, Weygoldt & Carvalho e Silva 1992, Haddad & Hödl 1997, Haddad & Pombal 1998).

The green species of treefrogs currently considered as belonging to the *Hyla albosignata* group are: *H. albosignata, H. callipygia, H. cavicola, H. fluminea,* and *H. leucopygia.* The species in this group are restricted to the Atlantic Forest of Brazil (Cruz & Peixoto 1984) and their natural histories are nearly unknown; only anecdotal, and sometimes conflicting, information on the vocalizations and reproductive sites has been provided in the litera-

ture. Bokermann (1967) described differences between the vocalizations of two populations of *H. albosignata* from São Paulo state, and stated that the differences could not be considered a consequence of different temperatures or intraspecific variation. Subsequently, Cruz and Peixoto (1984) demonstrated the existence of a species complex; they redescribed *H. albosignata* and described four new species previously considered populations of *H. albosignata.* These authors described the calling site of *H. cavicola,* and Gomes and Peixoto (1997) detailed that of *H. callipygia.* Different reproductive sites have been characterized for *H. leucopygia* by Duellman (1986, 1988), Heyer *et al.* (1990), and Haddad and Sazima (1992).

This paper reports a new reproductive mode in anurans, observed for the green hylid frog *Hyla leucopygia,* a member of the *H. albosignata* group. The specialized courtship behaviors of this species, characterized by vocalizations and a stereotyped sequence of mutual touches between male and female, are described. A review of the reproductive modes in hylid frogs is provided.

MATERIALS AND METHODS

The behaviors of *H. leucopygia* were studied during 67 days and *ca* 190 hours of observations (February 1988–January 1991) at Serra do Japi, Município de Jundiaí (23°11′S, 46°52′W; 800 m elev.), and 47 days and *ca* 180 hours (August 1993–August 1995) at Parque Florestal do Itapetinga, Município de Atibaia (23°5′S, 46°45′W; 900 m elev.), both in the Atlantic Forest of São Paulo state, southeastern Brazil.

The treefrogs were studied near rivulets and temporary ponds. Focal animal and all occurrence samplings were used for behavioral records (Lehner 1979). Descriptions of behaviors were based on individuals observed and photographed in the field. Individuals were marked by toe clipping (Martof 1953) and measured for snout-vent length (SVL) to the nearest 0.1 mm with a caliper ruler. The subterranean nests were cast with plaster and the replicas were measured for details. We recorded the vocalizations with a Nagra E tape recorder using a Sennheiser ME 80 microphone. The sonograms were produced using a Macintosh computer coupled to the MacRecorder Sound System 2.0.5, using 8 bit resolution, 22 kHz sampling frequency, and FFT with 128 points. For the statistical analyses, we used the Student's *t*-test (t) and Spearman's rank correlation test (r_s) with a significance level of 0.05 (Zar 1996).

RESULTS

Hyla leucopygia was acoustically active in all months except April, showing a peak in activity during the rainy season (October–March). Gravid females and effective reproduction, however, were observed only from December to February. Males started to emit advertisement calls during sunset; during the night, males were observed calling on the vegetation, generally on leaves from 0.35 to 7.0 m above the ground ($\bar{x}$ = 2.59 m, SD = 1.88, N = 38), near rivulets and temporary ponds. During the reproductive season, males tended to call from leaves closer to the ground ($\bar{x}$ = 1.42 m, SD = 0.94, range = 0.5–3.8 m, N = 11); when calling and not reproducing, males were observed on higher places in the canopy ($\bar{x}$ = 3.06 m, SD = 1.97, range = 0.35–7.0 m, N = 27). The differences between the two means are statistically significant (t = 2.64, df = 36, P = 0.01). Marked males returned to the same sites on successive nights; one marked male used the same site for *ca* 75 days. Marked males were observed during one reproductive season and were not recaptured in the following season.

VOCALIZATIONS.—We observed males emitting three different vocalization types: advertisement calls, courtship calls, and multi-note calls. The most common was the advertisement call given at a rate of 5 to 48 calls/min ($\bar{x}$ = 24.8, SD = 17.5, N = 5 vocalization series) at an air temperature of 20°C. This vocalization (Fig. 1a, c) was composed of one note with three harmonics having frequencies between 0.65 and 2.9 kHz. The mean duration of the advertisement call was 0.13 sec (SD = 0.008, range = 0.11–0.14 sec, N = 14 vocalizations from four males). The courtship call was structurally identical to the advertisement call, being repeated at a higher rate of *ca* 120 calls/min and emitted at a lower intensity. This vocalization was observed only when the male noted an approaching female (see below). The multi-note call was composed of two to four notes with harmonic structure; the mean duration of the multi-note calls was 0.56 sec (SD = 0.03, range = 0.52–0.59 sec, N = 5 vocalizations from five males); the notes were emitted between 0.75 and 4 kHz (Fig. 1b) and had a mean duration of 0.06 sec (SD = 0.01, range = 0.04–0.08 sec, N = 13). This vocalization was emitted in the following situations: regularly during the night when a male vocalized from the forest canopy and sporadically during the day from the forest canopy, during the night when a male
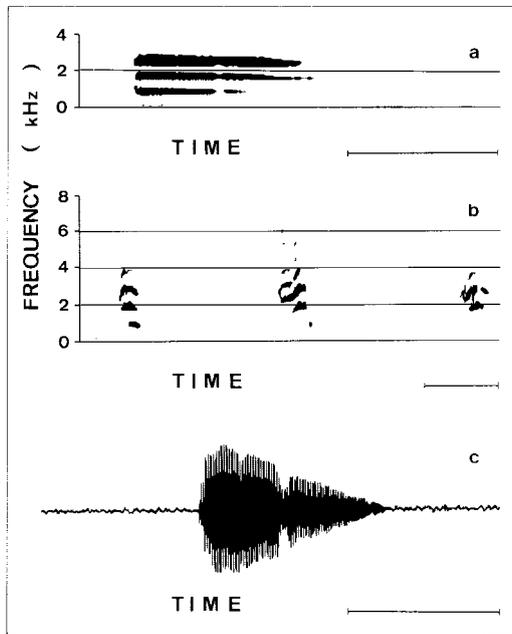
FIGURE 1. Vocalization of *Hyla leucopygia*; (a) sonogram of the advertisement call; (b) sonogram of the multi-note call; (c) oscillogram of the advertisement call. Serra do Japi, Município de Jundiaí, São Paulo; air temperature = 20°C; scales = 0.1 sec.

vocalized near a neighbor that emitted the courtship call, and during the night when a male was excavating a subterranean nest.

COURTSHIP BEHAVIOR.—We observed 12 pair formations for *H. leucopygia*. The steps, up until the pair entered the subterranean nest, were as follows: a male emitted advertisement calls perched on the vegetation (Fig. 2a); an attracted female, walking and jumping on the vegetation, approached the male; when the male noticed the female, it started to emit courtship calls; the female jumped behind the male (Fig. 2b) and touched one of the male's hind limbs with a hand (Fig. 2c) or snout; after being touched, the male stopped the vocalizations and jumped or walked in a descending journey (Fig. 2d), approaching a temporary pond or rivulet; after each jump or some steps, the male interrupted the descending journey and started to emit courtship calls to attract the female; the female again approached and occasionally touched the male before it continued the journey; after being touched by the female, the male sometimes touched the female's head with its gular region (Fig. 2e) or snout; during several interruptions of the journey, there

were mutual touches in which the female touched the male's snout with its hand (Fig. 2f) or foot, and vice versa. When the pair reached the ground, the male guided the female to a previously constructed subterranean nest, using the same behaviors described above; the male entered the nest and emitted advertisement or courtship calls to stimulate the female to follow. In one instance, we observed that after the pair had entered the nest, the male returned and was obstructing the nest entrance from the inside using its snout; after several minutes, the male unblocked the entrance and disappeared inside the nest; immediately after the nest entrance was unblocked, one snake (*Liophis miliaris*, Colubridae) found the nest aperture, entered the nest, and attacked the pair; the female fled and the male was caught by the head and swallowed (Fig. 9 in Sazima & Haddad 1992).

The pair formation and courtship behaviors occurred from 2100 until 2300 h. Courtship (until the pair entered the nest) lasted more than two hours, ending mainly when a pair was disturbed by neighbor males (see below).

MALE–MALE INTERACTIONS AND SELECTION OF MALES BY FEMALES.—Sometimes, when a male guided a female to its subterranean nest, the courtship behavior displayed by the pair attracted another male (*N* = 4). On such occasions, the intruder approached the pair and started to emit advertisement calls at a highly repetitive rate using multi-note calls; the male that was guiding the female stopped the guiding behavior and courtship calls and started to emit advertisement calls also at a highly repetitive rate toward the intruder. Frequently, the interacting males emitted antiphonal advertisement calls for 5 to 15 minutes. These vocal duels were divided into rounds. One complete duel had eight rounds; each round lasted for a variable period ($\bar{x}$ = 81.83 sec, SD = 51.14, range = 22–160 sec, *N* = 8). The duel finished when one male gave up or when the female entered a nest. In one instance, we observed an intruder male that jumped in the direction of a pair and accidentally touched the male engaged in the courtship. They remained motionless for a few seconds and then separated without aggression. We never observed physical aggression between interacting males or between males invading nests of conspecifics.

Intruder males were very disturbing to a pair. Of four pairs that were intercepted by intruders, only one remained after the vocal duels. In this case, when the male entered the nest, the female started to follow the intruder; the original male put
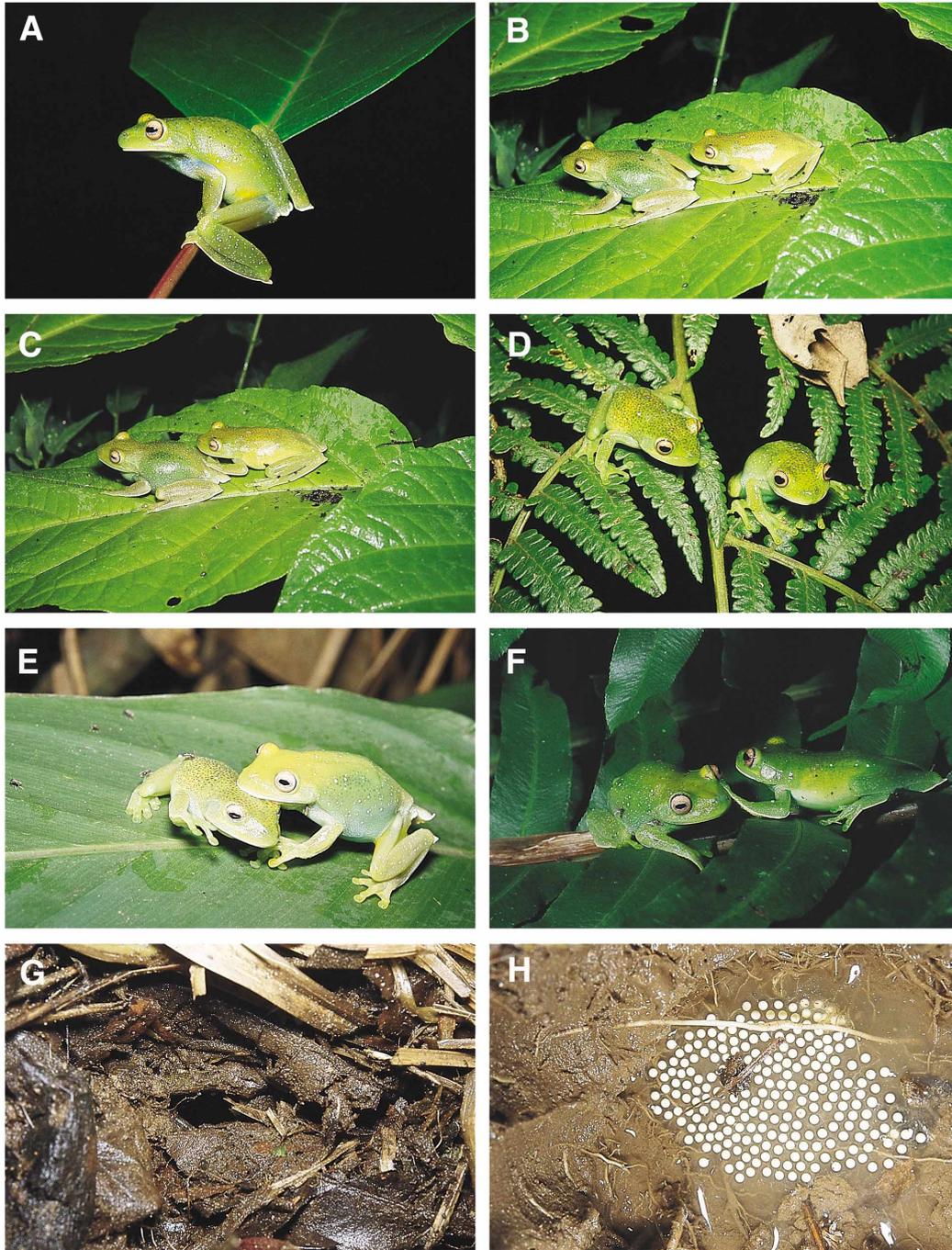
FIGURE 2.   (a) Male of *Hyla leucopygia* calling while perched on the vegetation; (b) calling male of *Hyla leucopygia* attracting a gravid female (female behind the male); (c) female using the hand to touch the male's leg; (d) male stops the vocalizations and jumps or walks in a descending journey, guiding the female (female upper, male lower); (e) male touching the female's head with its gular region; (f) female touching the male's snout with its hand; (g) aperture of a subterranean nest constructed by a male; and (h) unpigmented eggs deposited in a floating layer (inside a subterranean nest; the roof of the nest was removed for the photo).

its head out of the nest and started to emit advertisement calls that attracted the female back to the nest. In two cases, the female abandoned the original male and followed the intruder; in one case, the female fled during the male–male interaction.

In one instance, we observed a female abandoning a male after entering its nest and staying inside for five minutes. Immediately after the female's departure, the male started to emit advertisement calls at a highly repetititive rate inside the nest, but the female did not return. In this case, we did not observe intruder males disturbing the pair and did not find eggs in this nest on the following day.

We observed sexual dimorphism in size; the mean SVL of live females ($\bar{x}$ = 44.9 mm, SD = 1.30, range = 43.4–46.6 mm, N = 6) was larger (t = 3.56, df = 108, P = 0.0005) than the mean SVL of live males ($\bar{x}$ = 42.5 mm, SD = 1.61, range = 39.1–46.2 mm, N = 104). Males observed attracting females were larger ($\bar{x}$ = 43.4 mm, SD = 1.90, range = 39.4–45.7 mm, N = 8) than males that were not observed attracting females ($\bar{x}$ = 42.5 mm, SD = 1.58, range = 39.1–46.2 mm, N = 96), but the difference was not statistically significant (t = 1.64, df = 102, P = 0.1).

Subterranean nests.—At Serra do Japi, subterranean nests were associated with temporary ponds near rivulets. At Atibaia, the nests were constructed next to ponds and rivulets. The subterranean nests were built in muddy soil or banks near the water bodies. The nests had elliptical to nearly circular apertures (Fig. 2g); the largest axis had a mean of 2.3 cm (SD = 1.60, range = 1.0–5.0 cm, N = 6) and the smallest axis had a mean of 1.6 cm (SD = 0.95, range = 0.8–3.0 cm, N = 6). Of six analyzed nests, two had a corridor connecting the aperture to a subterranean chamber; the corridors were 2.0 and 9.0 cm in length. The other four nests did not have corridors; the aperture was connected directly to a subterranean chamber. The chambers were elliptical to nearly circular; the largest axis was, on average, 8.9 cm (SD = 1.43, range = 7.0–10.5 cm, N = 8) and the smallest axis had a mean of 8.0 cm (SD = 1.83, range = 5.5–10.0 cm, N = 8). On the bottom of the chambers, we measured *ca* 4 cm of water that permeated from the natural water body.

The mean distance between a subterranean nest and the nearest water body was 34.4 cm (SD = 14.5, range = 12.0–50.0 cm, N = 12). The mean distance between a subterranean nest and the male vocalization site was 278.8 cm (SD = 166.4, range = 155–510 cm, N = 4). Nests were grouped in suitable patches of muddy soil; the mean distance between the nearest nests, constructed by different males, was 16 cm (SD = 2.2, range = 15–20, N = 5). By opening nests, we observed two males inside that had their heads and snouts smeared with clay; one male was found awake during the night and the other was observed resting during the day. During sunset, a third male was observed starting the vocalization activities inside a nest; after a few minutes it stopped the vocalizations, came out, climbed the vegetation above the nest, and resumed calling activities. These males probably were excavating nests or were using them as shelters.

Clutches and reproductive mode.—Seven dissected females had, on average, 271 mature ovarian eggs (SD = 36.2, range = 220–322). The SVLs of the dissected females were positively correlated with the number of ovarian eggs (r_s = 0.86; P = 0.006). Ovarian eggs were unpigmented and had a mean diameter of 1.79 mm (SD = 0.12, range = 1.5–2.0 mm, N = 70). We observed three clutches in the field, all inside subterranean nests. Two clutches had 219 eggs each; the eggs were deposited in a floating layer, unpigmented (Fig. 2h), and had a mean diameter of 2.04 mm (SD = 0.06, range = 1.95–2.17 mm, N = 30). One nest, in which the roof was destroyed by rain had *ca* 30 embryos that showed active swimming and large vitelinic sacs. Heavy rains caused a rise in the water level of ponds and rivulets and flooded the nests, allowing the tadpoles to escape from the chambers to natural water bodies. Tadpoles were observed during day and night, performing feeding activities in ponds, streams, and lakes. Based on our field observations, we defined the reproductive mode of *H. leucopygia* as follows: aquatic eggs and embryos in constructed subterranean nests; subsequent to flooding, feeding tadpoles in ponds or streams.

DISCUSSION

The sonograms of *H. albosignata* published by Bokermann (1967) clearly are of two distinct species. At that time, the name *H. albosignata* was being used for all species known today in the *H. albosignata* group (Cruz & Peixoto 1984). Both sonograms published by Bokermann (1967) may be saturated; only the three lower harmonics appear in the unsaturated vocalizations of *H. leucopygia* (Fig. 1a; Fig 46 in Heyer *et al.* 1990). The sona-

gram of *H. albosignata* from Serra da Bocaina, São Paulo (Bokermann 1967), corresponds to the vocalizations of *H. callipygia* (Cruz & Peixoto 1984). This vocalization shows lower frequencies and longer duration than the vocalizations of *H. leucopygia* from Serra do Japi, São Paulo (Fig. 1a). The advertisement calls of *H. leucopygia* from Serra do Japi (Fig. 1a) and Atibaia are very similar to that from Paranapiacaba, São Paulo, considered *H. albosignata* by Bokermann (1967), and to that of *H. leucopygia* from Boracéia, São Paulo (Heyer *et al.* 1990). As *H. leucopygia* occurs at Paranapiacaba (Cruz & Peixoto 1984), Figure 6 of Bokermann (1967) is probably a sonogram of this species and not of *H. albosignata* as originally published.

Mutual touches between males and females engaged in courtship and/or the behavior displayed by the male of guiding the female to the oviposition site are typical of anuran species in which the male constructs a concealed nest for the clutch, before the arrival of the female (*e.g., Leptodactylus fuscus,* Martins 1988; *Hylodes phyllodes,* Faria *et al.* 1993; *Hylodes asper,* Haddad & Giaretta 1999; *H. leucopygia,* present study). In these species, the females do not know the location of the nests and must be guided by the males.

Several reproductive strategies are precluded when the oviposition site is a limited resource in a hidden place, as observed for *H. leucopygia.* Satellite males that intercept and join in amplexis with approaching females (Haddad 1991a), active searching for females by males that are not vocalizing (Wells 1979), males that attempt to displace other males already in amplexis to steal the females (Davies & Halliday 1978, Wells 1979), communal oviposition among two or more males and one female or sneaking behavior (Coe 1974, Kaminsky 1997), and males that try to steal exposed structures constructed for egg deposition (Martins *et al.* 1998) are impracticable strategies for *H. leucopygia.* A male of *H. leucopygia* that has a nest can try to intercept a female being attracted by another male; however, in this case the interceptor will try to attract the female by using vocalizations and stereotyped courtship behaviors, which means that the interceptor will not use a typical alternative mating strategy.

Magnusson and Hero (1991) postulated that the pressure of aquatic predators has been the major factor in maintaining, and probably in the evolution of, semiterrestrial development in some Amazonian rain forest frogs. One possible explanation for the evolution of this specialized reproductive mode in *H. leucopygia* may be the selective pressure of predators. When concealed in subterranean nests, adults, eggs, and embryos probably are more protected from strict aquatic predators and from visually oriented terrestrial predators; however, searching predators oriented by olfaction, like the snake *L. miliaris,* can find concealed subterranean nests. Males of *L. fuscus,* a leptodactylid frog that constructs subterranean nests, were observed obstructing the nest aperture from the inside using the snout, when females were inside (Martins 1988; C. F. B. Haddad, pers. obs.). Martins (1988) has indicated that the male of *L. fuscus* that is obstructing the nest aperture does not move even if touched by the observer, and that probably this is a behavior performed to guard the attracted female until it is prone for oviposition. We observed the obstructive behavior in one male of *H. leucopygia* and suggest that, beyond guarding the female, this behavior may be a way to preclude the entry of predators. Another possible pressure leading to oviposition inside protected places is the currents of mountain rivulets (Weygoldt & Carvalho e Silva 1992). The eggs of *H. leucopygia,* which are deposited concealed and far from the currents, are protected from drifting downstream.

A great number of frog species that aggregate for reproduction can be classified as species possessing a lek mating system, because oviposition occurs away from territories defended by males that provide only sperm to the females (Bastos & Haddad 1996). In this mating system, selection of partners generally is performed by females. In these species, the female guides the male, or more frequently, carries the male on its back, choosing an adequate place for egg deposition. In frog species in which the male constructs a nest for egg deposition before the arrival of the female (*e.g., L. fuscus,* Martins 1988; *Hyla faber,* Martins 1993; *Hylodes phyllodes,* Faria *et al.* 1993; *Hylodes asper,* Haddad & Giaretta 1999; *H. leucopygia,* present study), the selection of the partner still remains with the female, but the reproductive place is chosen previously by the male. In these species, the female frequently uses signals emitted by males as initial cues for mate selection; the final selection is performed on the basis of nest characteristics, into which the pair will deposit the clutch (*e.g., H. faber,* Martins 1993; *H. asper,* Haddad & Giaretta 1999). Apparently, as observed for *H. faber* (Martins & Haddad 1988), females of *H. leucopygia* inspect the nests before accepting a male; this is suggested by the observation of a female abandoning a male after staying some minutes in the subterranean nest.

The reproductive mode of *H. leucopygia* in

some aspects resembles those of species in the *Hyla boans* group (Mode I-A3 in Duellman & Trueb 1986) and those of some African frogs in the families Hyperoliidae and Hemisotidae (Mode II-D12 in Duellman & Trueb 1986). In the *H. boans* group, the eggs are pigmented and deposited as a floating layer on the water accumulated in constructed basins (Kluge 1981, Martins & Haddad 1988); however, in *H. leucopygia* the basin is roofed, and the eggs are unpigmented as a result of the concealment. In some hyperoliid and hemisotid frogs, the eggs are terrestrial and deposited in burrows (Duellman & Trueb 1986). Although in *H. leucopygia* the clutch is deposited in a subterranean nest, the eggs are not truly terrestrial since they are deposited as a floating layer on the water accumulated in the nest.

The reproductive mode of *H. leucopygia* described in this study is similar to the summarized description of Haddad and Sazima (1992) for this species. Duellman (1986, 1988), however, indicated that *H. leucopygia* deposits eggs on the vegetation above water and that the species in the *H. albosignata* group have this same reproductive mode. Heyer *et al.* (1990) considered the canopy above the streams as the breeding habitat of *H. leucopygia.* Regarding our data, the reproductive mode of the *H. albosignata* group is different from that indicated by Duellman (1986, 1988), and the breeding habitat published by Heyer *et al.* (1990) must be considered the calling site.

Probably, the reproductive mode observed for *H. leucopygia* here is widespread among the species of the *H. albosignata* group, based on several published and unpublished data. Males of *H. albosignata* may call in subterranean holes (Cochran 1955); we observed one male of this species constructing a subterranean nest and emitting multinote calls. Cardoso observed a male guiding a gravid female on the vegetation, and the pair used mutual touches during the courtship (A. J. Cardoso, pers. comm.). *H. cavicola* vocalizes inside a constructed subterranean nest, the name *cavicola* being an allusion to the excavated nests used as vocalization sites by males of this species (Cruz & Peixoto 1984); *H. callipygia* vocalizes inside rocky crevices (Gomes & Peixoto 1997).

Reproductive modes of the Atlantic Forest hylid frogs.—The family Hylidae, with more than 700 species currently recognized (Frost 1985, Duellman 1993), has evolved several reproductive modes. In a review of reproductive modes in hylid frogs, Duellman (1986) recognized eight modes.

Considering the hylid frogs from the Atlantic Forest, three additional reproductive modes can be recognized. The Phyllomedusinae frogs *Phrynomedusa appendiculata* and *P. marginata* deposit eggs in wet rock crevices; feeding tadpoles develop in mountain rivulets (Lutz & Lutz 1939, Weygoldt 1991). The Hylinae frog *Scinax rizibilis* deposits eggs in a floating foam nest in ponds; feeding tadpoles develop in ponds (Haddad *et al.* 1990). The Hylinae frog *H. leucopygia* deposits aquatic eggs in constructed subterranean nests; subsequent to flooding, feeding tadpoles develop in ponds or streams (Haddad & Sazima 1992; present study). By including these 3 additional modes from the Atlantic Forest, 12 reproductive modes can be recognized for hylid frogs; 11 are known for the Atlantic Forest hylids (only mode number 10 was not observed in this region; Table 1).

The typical forest modes observed for the Atlantic Forest hylids (modes 2, 4, 5, 7, 9, 11, and 12) account for *ca* 65 percent of the total number observed in this region. The other 35 percent (modes 1, 3, 6, and 8) frequently are observed in open and forested areas. Approximately 40 percent of the typical forest modes (modes 2, 7, and 9; Table 1) are associated with high-gradient streams. It generally is accepted that mode 1 (eggs and tadpoles in lentic water) is the most generalized and primitive, the other modes being specializations that can be associated with an adaptive radiation into various environments (Duellman & Trueb 1986).

Some Atlantic Forest hylids may show more than one reproductive mode. In these cases, we can recognize the main and the alternative reproductive modes. At Serra do Japi, *Hyla luctuosa* deposits eggs in ponds; however, after rainfall, the subterranean nests of *H. leucopygia* lose their roofs and become little basins. On these occasions, *H. luctuosa* may deposit eggs in the water accumulated in old nests of *H. leucopygia;* subsequent to flooding, feeding tadpoles of *H. luctuosa* are transferred to ponds (Haddad 1991b). At Ribeirão Branco, São Paulo, *H. faber* deposits eggs as a surface film on the water accumulated in constructed clay nests; however, when the water level rises so that muddy banks are not available for males to construct the clay nests, the eggs are deposited as a surface film in ponds (C. F. B. Haddad, pers. obs.).

For the Amazonian forest, with a much more extensive area than the original distribution of the Atlantic Forest (Collins 1990) and a high diversity of hylid frogs, a lower number of reproductive modes has been observed (Duellman 1986, Hödl

TABLE 1. *Diversity of reproductive modes in hylid frogs (adapted from Duellman 1985, 1986), with examples for hylids from the Atlantic Forest of Brazil. Among hylids, modes 4, 6, and 7 are known only for the Atlantic Forest, but were not included in the last review (Duellman 1986).*

I. Eggs aquatic.
   A. Eggs deposited in water.
      1. Eggs and feeding tadpoles in lentic water (*Aparasphenodon brunoi, Hyla elegans, H. minuta, H. sanborni, Scinax ruber* group, *Osteocephalus langsdorffii, Phrynohyas mesophaea*).
      2. Eggs and feeding tadpoles in lotic water (*Hyla circumdata, H. weygoldti,* some species in the *Scinax catharinae* group).
      3. Eggs and early larval stages in natural or constructed basins; subsequent to flooding, feeding tadpoles in ponds or streams (*Hyla biobeba, H. faber,* and *H. pardalis*).
      4. Eggs and early larval stages in subterranean nests; subsequent to flooding, feeding tadpoles in ponds or streams (*Hyla albosignata* group).
      5. Eggs and feeding tadpoles in water of tree holes or aerial plants (*Phyllodytes, Scinax perpusillus* group).
   B. Eggs in foam nest.
      6. Foam nest floating on pond; feeding tadpoles in ponds (*Scinax rizibilis*).
II. Eggs terrestrial or arboreal (not in water).
   C. Eggs on rocks.
      7. Eggs on rock crevices above water; upon hatching, feeding tadpoles move to streams (*Phrynomedusa appendiculata, P. marginata*).
   D. Eggs arboreal.[a]
      8. Eggs hatch into feeding tadpoles that drop into ponds (*Phyllomedusa, Hyla berthalutzae, H. decipiens*).
      9. Eggs hatch into feeding tadpoles that drop into streams (*Phasmahyla, Hyla ruschii*).
   E. Eggs carried by adult.
      10. Eggs carried in dorsal pouch of female; feeding tadpoles in ponds.[b]
      11. Eggs carried on dorsum or in dorsal pouch of female; non-feeding tadpoles in bromeliads or bamboo (*Flectonotus*).[c]
      12. Eggs carried on dorsum or in dorsal pouch of female; direct development into froglets (*Gastrotheca*).

[a] We consider mode 5 of Duellman (1986) as two distinct modes (8 and 9), using the same criterion as Duellman (1986) for separating modes 1 and 2 (utilization of lentic or lotic water). The species in the Atlantic Forest using mode 9 are associated with high gradient streams, and the adaptive differences between these species and those using lentic water are sufficient to separate both modes.
[b] Not known for the Atlantic Forest species.
[c] Weygoldt (1989) and Weygoldt and Carvalho e Silva (1991) demonstrated that tadpoles of *Flectonotus goeldii* may behave like feeding tadpoles, and immediately after hatching may start to feed on undeveloped eggs or conspecific dying larvae. More information on the other species of *Flectonotus* is necessary for a better comprehension of how widespread this alternative reproductive mode is in this genus.

TABLE 2. *Numbers of species and reproductive modes in the different genera and subfamilies of hylid frogs represented in the Atlantic Forest of Brazil.*

Subfamily[a]	Genus[a]	Number of species[a]	Number of modes
Hemiphractynae	*Flectonotus*	3	1
	Gastrotheca	2	1
Hylinae	*Aparasphenodon*	1	1
	Aplastodiscus	1	1
	Corythomantis	1	1
	Hyla	60	4
	Osteocephalus	1	1
	Phrynohyas	3	1
	Phyllodytes	6	1
	Scinax	47	4
	Sphaenorhynchus	5	1
	Trachycephalus	2	1
Phyllomedusinae	*Hylomantis*	2	1
	Phasmahyla	3	1
	Phrynomedusa	5	1
	Phyllomedusa	7	2

[a] Extracted from Frost (1985) and Duellman (1993), plus species described and resurrected until 1997.

1990). The high diversity of reproductive modes observed for the Atlantic Forest hylids is the result of successfully utilizing the diversified and humid microhabitats in this biome. This region has a highly complex topography that divides the biome into many small microhabitats (Brown & Brown 1992); high humidity, by reducing desiccation risks, enabled the evolution of specialized reproductive modes in which eggs and/or larvae develop out of water.

The trends away from the generalized and primitive mode 1 do not necessarily represent increasing reproductive specialization in phylogenetically advanced groups, but rather, many independently derived reproductive modes in different phyletic lines (Duellman & Trueb 1986). The diversity of reproductive modes in anurans is more a reflection of the environmental characteristics in which frogs live than of the phylogenetic relationships of the families and higher categories (Duellman & Trueb 1986). At lower levels (*e.g.,* family, genus, species group), however, it is possible to recognize some apparent phylogenetic trends (Duellman 1989). The Atlantic Forest has *ca* 150 known species of hylids (extracted from Frost 1985 and Duellman 1993, plus species described and resurrected until 1997); this corresponds to *ca* 20 percent of the hylids in the world. The highest diver-

sification in reproductive modes observed for hylids in this region occurs in the genera *Hyla* and *Scinax*, the largest groups of hylids in the Atlantic Forest (Table 2). We observed a positive correlation ($r_s =$ 0.69, $P = 0.003$) between the number of species and the number of reproductive modes at the genus level for the Atlantic Forest hylids (Table 2). This suggests that the greater the number of species, the greater is the probability of reproductive diversification within phyletic lines; however, the most specialized reproductive modes for the Atlantic Forest hylids have been observed in small genera restricted to the rain forest environments (*e.g., Flectonotus, Gastrotheca*).

Every year, new species of frogs are being described from the Atlantic Forest remnants. As a consequence of this high diversity and lack of studies, the life histories of several anuran species in this region are unknown and new reproductive specialization probably will be discovered in the future.

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