Reproductive Modes in Frogs and Their Unexpected Diversity in the Atlantic Forest of Brazil

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Amphibians, and especially the anurans (frogs and toads), exhibit a greater diversity of reproductive modes than other tetrapod vertebrates. Twenty-nine reproductive modes have been recognized for the anurans; we propose 10 more, elevating by more than 34% the number of reproductive modes known for anurans worldwide. These newly recognized reproductive modes for the frogs elevate by almost 48% the number of anuran reproductive modes known for the Neotropics. The highly complex topography of the Atlantic forest, breaking up the biome into many small microhabitats, and the high humidity, which reduces desiccation risks, have enabled the evolution of reproductive specializations such as eggs or tadpoles that develop out of water. Nearly 90% of the Atlantic forest has been cleared, and because several anurans are endemic to this region or have specialized reproductive modes dependent on the forest, this partly explains the generalized population declines and large numbers of species that have disappeared in the last few decades.

Keywords: reproductive modes, anurans, Amphibia, Atlantic forest, conservation

The concept of reproductive mode in amphibians was defined by Salthe and Duellman (1973) as a combination of traits that includes oviposition site, ovum and clutch characteristics, rate and duration of development, stage and size of hatchling, and type of parental care, if any. The approximately 5770 living species of amphibians are grouped into three orders—Gymnophiona (caecilians), Caudata (salamanders), and Anura (frogs and toads). The latter is the largest, including more than 5065 species currently recognized (AmphibiaWeb 2005). The most typical and generalized reproductive cycle in anurans is characterized by aquatic eggs that develop into exotrophic aquatic tadpoles that, in turn, metamorphose into four-legged terrestrial or semiterrestrial frogs, so part of the developmental energy is obtained from vitellogenic yolk and part by feeding in water. However, amphibians—and especially the anurans, for which 29 reproductive modes have been recognized—exhibit greater reproductive diversity than any other group of tetrapod vertebrates (Duellman and Trueb 1986). The greatest diversity of reproductive modes is found in the Neotropics, where anurans have evolved 21 modes, 8 of which are known only for this region (Duellman and Trueb 1986, Hödl 1990). New and complex reproductive behaviors have recently been described for frogs (Caldwell 1997), and since the latest published overviews of reproductive modes in frogs (Duellman 1986, 1988, 1989, Duellman and Trueb 1986, Hödl 1990), new reproductive modes at the genus, family, and order level have

been discovered for Neotropical frogs (genus, De La Riva 1995; family, Juncá et al. 1994; order, Prado et al. 2002), especially for those from the Atlantic forest of Brazil (family, Haddad et al. 1990; order, Weygoldt and Carvalho e Silva 1992, Haddad and Hödl 1997, Haddad and Pombal 1998, Haddad and Sawaya 2000).

Here we present a review of the reproductive modes in anurans, adding 10 more modes, including 7 recently described for the threatened coastal Atlantic forest in Brazil and 3 resulting from rearrangements of previously known modes. We did not include information on the rate and duration of development or the stage and size of hatchlings, since these traits have not been used in practice in the most recent research. Moreover, we used a criterion of discrete variation of traits when considering a new mode. Small and continuous variations were not considered to characterize a new mode. We also discuss selective pressures leading to reproductive specialization and the decline of the Atlantic forest frogs.

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Reproductive modes of the Atlantic forest frogs

Beyond the 29 reproductive modes previously accepted for anurans (Duellman and Trueb 1986), 7 additional modes can be recognized in the Atlantic forest (box 1, figure 1). These modes include an ample array of adaptations (mode numbers refer to box 1):

- Eggs deposited in constructed subaquatic chambers, a mode previously known only for fishes (mode 3; leptodactylid frogs in the genera *Crossodactylus* and *Hylodes;* Weygoldt and Carvalho e Silva 1992, Haddad and Giaretta 1999).

- Eggs deposited in water accumulated in subterranean constructed nests, an uncommon mode for a typically arboreal group (mode 5, known for *Aplastodiscus perviridis, Hyla albofrenata,* and *Hyla albosignata* complexes of hylids; Haddad et al. 2005).

- Eggs deposited in floating bubble nests, a mode previously known only for anabantoid fishes (mode 10,

known for the microhylid frog *Chiasmocleis leucosticta;* Haddad and Hödl 1997).

- Foam nest floating on water accumulated in constructed basins, an intermediate step between the more aquatic and the more terrestrial foam nests associated with floor (mode 13, known for the leptodactylid frogs *Leptodactylus labyrinthicus* and *Leptodactylus podicipinus;* Prado et al. 2002, Rodrigues Silva et al. 2005).

- Foam nest floating on water accumulated on the axils of terrestrial bromeliads, an intermediate step between the more aquatic and the more arboreal modes associated with foam nests (mode 14, known for some leptodactylid species in the *Physalaemus signifer* group; figure 2a; Haddad and Pombal 1998).

- Terrestrial eggs and semiterrestrial tadpoles that develop on a film of water running on rock face or in the water–land interface, frequently with paternal guarding of egg clutches and with extreme adaptations in tadpoles that include suctorial structures and reduced fins (mode 19, known for several species in the leptodactylid genera *Cycloramphus* and *Thoropa;* figure 2b, 2c, 2d; Lutz 1948, Wassersug and Heyer 1983).

- Foam nest on the humid forest floor, a mode that represents the last step toward terrestrial modes in the genus *Physalaemus* (mode 28, known for several leptodactylid species in the *Physalaemus signifer* group; Haddad and Pombal 1998).

By including these seven additional modes, and after some rearrangements in the outline of reproductive modes as proposed by Duellman and Trueb (1986), 39 reproductive modes can now be recognized for anurans around the world (box 1). These additional modes and rearrangements elevate by almost 48% the number known for the Neotropics, and by more than 34% the number known for the world.

Besides these seven reproductive modes at the order level, new reproductive modes at the family and subfamily level have been described for Atlantic forest frogs. In the nearly cosmopolitan family Hylidae, with more than 870 species, only the Atlantic forest tree frog *Scinax rizibilis* is known to deposit eggs in an aquatic floating foam nest (Haddad et al. 1990), and only the leaf-frog genus *Phrynomedusa* is known to deposit eggs in wet rock crevices near mountain rivulets, where hatchling tadpoles move to the rivulets (mode 18; Lutz and Lutz 1939). In the Neotropical subfamily Leptodactylinae (Leptodactylidae), with more than 140 species, only the Atlantic forest frog *Paratelmatobius poecilogaster* is known to deposit eggs on rocks above water,
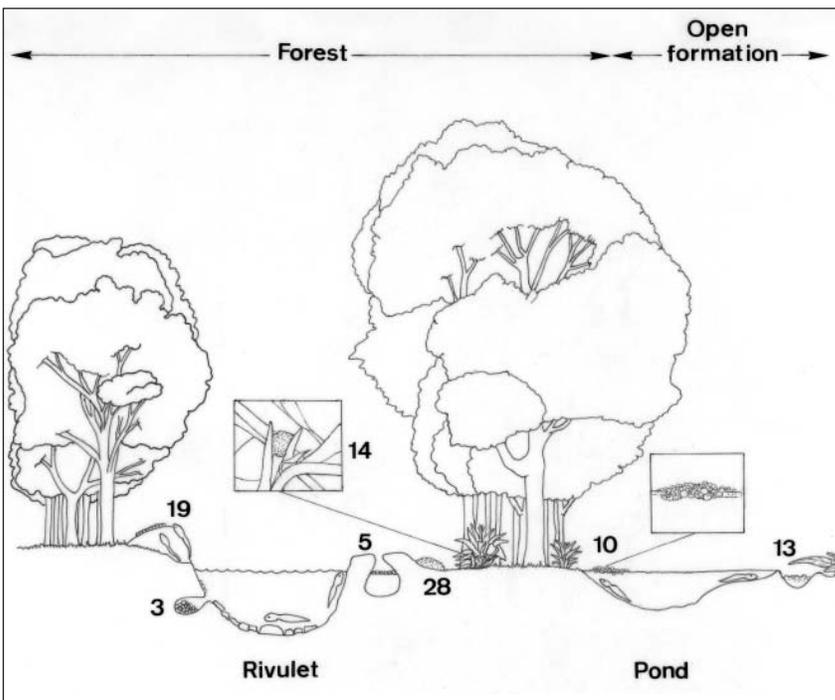

Figure 1. Schematic representation of the seven additional reproductive modes described for the Atlantic forest (modes 3, 5, 10, 13, 14, 19, and 28 in box 1): eggs and early larval stages in constructed subaquatic chambers, with exotrophic tadpoles in streams (mode 3); eggs and early larval stages in subterranean constructed nests, with exotrophic tadpoles in ponds or streams after flooding (mode 5); bubble nest floating on a pond, with exotrophic tadpoles in ponds (mode 10); foam nest floating on water accumulated in constructed basins, with exotrophic tadpoles in ponds (mode 13); foam nest floating on water accumulated on the axils of terrestrial bromeliads, with exotrophic tadpoles in ponds (mode 14); eggs on humid rocks, in rock crevices, or on tree roots above water, with exotrophic semiterrestrial tadpoles living on rock and rock crevices in a water film or in the water–land interface (mode 19); foam nest on the humid forest floor, with exotrophic tadpoles in ponds after flooding (mode 28).

Box 1. Diversity of reproductive modes in anurans.

Thirty-nine reproductive modes have been recorded for anurans (updated from Duellman and Trueb 1986). Reproductive modes observed in the Atlantic forest of Brazil are accompanied by examples of species, species groups, and genera for which the reproductive mode has been observed. The seven additional reproductive modes described for this biome are marked with an asterisk (*).

Aquatic eggs

Eggs deposited in water

Mode 1: Eggs and exotrophic tadpoles in lentic water (*Bufo crucifer, Hyla minuta, Phrynohyas mesophaea, Scinax fuscovarius, Macrogenioglottus alipioi, Paratelmatobius cardosoi*).

Mode 2: Eggs and exotrophic tadpoles in lotic water (*Hyla alvarengai, Hyla nanuzae, Hyla sazimai, Hyla weygoldti, Scinax canastrensis, Scinax machadoi*).

* Mode 3: Eggs and early larval stages in constructed subaquatic chambers; exotrophic tadpoles in streams (*Crossodactylus, Hylodes;* Weygoldt and Carvalho e Silva 1992, Haddad and Giaretta 1999).

Mode 4: Eggs and early larval stages in natural or constructed basins; subsequent to flooding, exotrophic tadpoles in ponds or streams (*Hyla circumdata, Hyla faber, Hyla lundii, Hyla pardalis*).

* Mode 5: Eggs and early larval stages in subterranean constructed nests; subsequent to flooding, exotrophic tadpoles in ponds or streams (*Aplastodiscus perviridis, Hyla albofrenata,* and *Hyla albosignata* complexes; Haddad et al. 2005).

Mode 6: Eggs and exotrophic tadpoles in water in tree holes or aerial plants (*Phyllodytes, Scinax perpusillus* group, *Scinax alcatraz, Crossodactylodes*).

Mode 7: Eggs and endotrophic tadpoles in water-filled depressions.

Mode 8: Eggs and endotrophic tadpoles in water in tree holes or aerial plants (*Dendrophryniscus, Frostius pernambucensis*).

Mode 9: Eggs deposited in a stream and swallowed by female; eggs and tadpoles complete development in stomach.

Eggs in bubble nest

* Mode 10: Bubble nest floating on pond; exotrophic tadpoles in ponds (*Chiasmocleis leucosticta;* Haddad and Hödl 1997).

Eggs in foam nest (aquatic)

Mode 11: Foam nest floating on pond; exotrophic tadpoles in ponds (*Scinax rizibilis,* genus *Physalaemus, Leptodactylus ocellatus* group).

Mode 12: Foam nest floating on pond; exotrophic tadpoles in streams.

* Mode 13: Foam nest floating on water accumulated in constructed basins; exotrophic tadpoles in ponds (*Leptodactylus labyrinthicus* and *Leptodactylus podicipinus;* Prado et al. 2002, Rodrigues Silva et al. 2005).[a]

* Mode 14: Foam nest floating on water accumulated on the axils of terrestrial bromeliads; exotrophic tadpoles in ponds (*Physalaemus spiniger*; Haddad and Pombal 1998).

Eggs embedded in dorsum of aquatic female

Mode 15: Eggs hatch into exotrophic tadpoles (*Pipa carvalhoi*).

Mode 16: Eggs hatch into froglets.

Terrestrial or arboreal eggs (not in water)

Eggs on ground, on rocks, or in burrows

Mode 17: Eggs and early tadpoles in excavated nests; subsequent to flooding, exotrophic tadpoles in ponds or streams.

Mode 18: Eggs on ground or rock above water; upon hatching, exotrophic tadpoles move to water (*Phrynomedusa appendiculata, Phrynomedusa marginata, Paratelmatobius poecilogaster*).

* Mode 19: Eggs on humid rocks, in rock crevices, or on tree roots above water; exotrophic semiterrestrial tadpoles living on rocks and rock crevices in a water film or in the water–land interface (several species in the genera *Cycloramphus* and *Thoropa;* Lutz 1947, Wassersug and Heyer 1983).[b]

Mode 20: Eggs hatching into exotrophic tadpoles that are carried to water by adult (*Colostethus*).

Mode 21: Eggs hatching into endotrophic tadpoles that complete their development in the nest (*Zachaenus parvulus*).

Mode 22: Eggs hatching into endotrophic tadpoles that complete their development on the dorsum or in the pouches of adults (*Cycloramphus stejnegeri*).

Mode 23. Direct development of terrestrial eggs (*Brachycephalus, Eleutherodactylus, Myersiella microps*).

Box 1. (*continued*)

Arboreal eggs

Mode 24: Eggs hatching into exotrophic tadpoles that drop in lentic water (e.g., *Hyla berthalutzae, Hyla decipiens, Phyllomedusa*).[c]

Mode 25: Eggs hatching into exotrophic tadpoles that drop in lotic water (e.g., *Hyalinobatrachium, Hyla ruschii, Phasmahyla*).[c]

Mode 26: Eggs hatching into exotrophic tadpoles that develop in water-filled cavities in trees.

Mode 27: Eggs hatching into froglets (*Eleutherodactylus nasutus, Eleutherodactylus venancioi*).

Eggs in foam nest (terrestrial or arboreal)

* Mode 28: Foam nest on the humid forest floor; subsequent to flooding, exotrophic tadpoles in ponds (species in the *Physalaemus signifer* group; Haddad and Pombal 1998).

Mode 29: Foam nest with eggs and early larval stages in basins; subsequent to flooding, exotrophic tadpoles in ponds or streams.[d]

Mode 30: Foam nest with eggs and early larval stages in subterranean constructed nests; subsequent to flooding, exotrophic tadpoles in ponds (*Adenomera bokermanni, Leptodactylus fuscus, Leptodactylus mystacinus, Leptodactylus notoaktites*).[d]

Mode 31: Foam nest with eggs and early larval stages in subterranean constructed nests; subsequent to flooding, exotrophic tadpoles in streams (*Leptodactylus cunicularius*).[d]

Mode 32: Foam nest in subterranean constructed chambers; endotrophic tadpoles complete development in nest (some species in the genus *Adenomera*).

Mode 33: Arboreal foam nest; hatchling tadpoles drop into ponds or streams.

Eggs carried by adult

Mode 34: Eggs carried on legs of male; exotrophic tadpoles in ponds.

Mode 35: Eggs carried in dorsal pouch of female; exotrophic tadpoles in ponds.

Mode 36: Eggs carried on dorsum or in dorsal pouch of female; endotrophic tadpoles in bromeliads or bamboo (*Flectonotus*).

Mode 37: Eggs carried on dorsum or in dorsal pouch of female; direct development into froglets (*Gastrotheca*).

Eggs retained in oviducts

Mode 38. Ovoviviparity; nutrition provided by yolk.

Mode 39. Viviparity; nutrition provided by oviductal secretions.

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a. This mode is known for species with ample distribution and is not necessarily restricted to the Atlantic forest.

b. Similar modes are also recorded in the ranid frogs *Amolops* spp. from China, *Nannophrys ceylonensis* from Sri Lanka, and *Indirana beddomii* from India, and in the petropedetid frog *Petropedetes palmipes* from Cameroon and Equatorial Guinea in Africa (Wassersug and Heyer 1983).

c. We consider mode 18 of Duellman and Trueb (1986; arboreal eggs that hatch into exotrophic tadpoles that drop into ponds or streams) as two distinct modes (24 and 25), because species in the Atlantic forest using mode 25 are generally associated with high-gradient streams, and the adaptive differences between these species and those using lentic water (mode 24) are sufficient to separate both modes. Moreover, species that reproduce using lentic water generally do not use lotic water, and vice versa. This same criterion has been used by some authors (Duellman and Trueb 1986, Hödl 1990) to separate mode 1 (eggs and tadpoles in lentic water) from mode 2 (eggs and tadpoles in lotic water).

d. We consider mode 21 of Duellman and Trueb (1986; foam nest in burrow) as three modes (29, 30, 31), because some species deposit the foam nest in an open basin in the floor (mode 29), whereas others deposit the foam nest in a roofed basin constructed in the floor, with exotrophic tadpoles in ponds (mode 30) or with exotrophic tadpoles in streams (mode 31).

from which hatchling tadpoles move to the water (mode 18; Pombal and Haddad 1999).

Some Atlantic forest anurans may show both a primary and an alternative reproductive mode. The tree frog *Hyla prasina* frequently deposits eggs in ponds and lakes (mode 1). However, on nights when large choruses are formed and all the calling sites are occupied on the banks of the pond, some males call from the margins of rivulets, and the eggs are deposited in flowing water (mode 2). This species glues the eggs around submersed vegetation, which prevents them from drifting away. The nest-building gladiator frog of the Atlantic forest, *Hyla faber,* deposits eggs as a surface film on water accumulated in constructed clay nests (mode 4; Martins 1993); however, when the water level rises so that muddy banks are not available for males to construct their nests, the eggs are deposited as a surface film in ponds (mode 1). Another plasticity in the reproductive mode of *H. faber* is the density-dependent paternal guarding of nests with eggs; in low densities of

males, nests with eggs are not guarded by males; however, when the density of males is high, nests containing eggs are protected by males (Martins et al. 1998). An extreme situation is observed for the leptodactylid frog *Physalaemus spiniger,* which has three different reproductive modes (Haddad and Pombal 1998): (1) foam nest and exotrophic tadpoles in ponds (mode 11), (2) foam nest in water accumulated in the axils of terrestrial bromeliads and exotrophic tadpoles in ponds (mode 14), and (3) foam nest in humid places on the forest floor near ponds and exotrophic tadpoles in ponds (mode 28). The larvae of species in the egg-brooding hemiphractine genus *Flectonotus* have sufficient yolk for complete development, and the genus has been described as having endotrophic tadpoles (i.e., all of the developmental energy is obtained from vitellogenic yolk) that develop in bromeliads or bamboo chambers in holes made by rodents or insects (mode 36; Duellman 1986, 1988). The larvae of the Atlantic forest species *Flectonotus goeldii* can metamorphose successfully without food; however, tadpoles may alternatively feed on undeveloped eggs or conspecific dying larvae (Weygoldt 1989, Weygoldt and Carvalho e Silva 1991). More information on other species of *Flectonotus* is necessary for a better comprehension of how widespread this alternative form of nourishment is in tadpoles of this genus. Although Salthe and Mecham (1974) stated that there are no reports of reproduction in anuran tadpoles, the hyline tree frog *Sphaenorhynchus bromelicola,* known from the transition between the Atlantic forest and xeric vegetation in northeastern Brazil, is exceptional in being facultatively paedomorphic. Adult males and metamorphosing tadpoles vocalize near permanent ponds, and both male and female larvae may have functional gonads (Bokermann 1974). Paedomorphosis may be a common phenomenon in this genus, since it was also observed in *Sphaenorhynchus palustris,* from the Atlantic forest in the state of Espírito Santo (figure 2e). In vitro fertilization indicates that the metamorphosing individuals of *S. palustris* are actually reproductively mature (Ivan Sazima, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil, personal communication, 30 June 2004).

The typical forest modes observed for the Atlantic forest anurans (modes 2, 3, 5, 6, 8, 10, 14, 18–23, 25, 27, 28, 36, and 37) account for two-thirds of the total number of modes observed in this region. The remaining third (modes 1, 4, 11, 13, 15, 24, and 30–32) may be observed in open and/or forested areas. Approximately 30% of the typical forest modes (modes 2, 3, 5, 19, and 25) are associated with high-gradient streams. Excluding modes strictly associated with ponds and streams (modes 1–5, 10, 11, 13, and 15), the reproductive specialization observed for the Atlantic forest anurans can be divided into two major groups: modes associated with vegetation (modes 6, 8, 14, 24, 25, 27, 36, and 37) and modes associated with the floor (modes 4, 5, 13, 18–23, 28, and 30–32).

It is generally accepted that mode 1 (eggs and tadpoles in lentic water) is the most generalized and ancestral among amphibians, and that other modes represent grades of special-

ization associated with adaptive radiation into various environments (Duellman and Trueb 1986). The trends away from this generalized and ancestral mode do not necessarily represent increasing reproductive specialization in phylogenetically advanced groups, but rather may represent many independently derived reproductive modes in different phyletic lines (Duellman and Trueb 1986). However, at lower levels (e.g., family, genus, species group), some apparent phylogenetic trends can be recognized (Duellman 1989). In the Atlantic forest, the families Hylidae and Leptodactylidae show the greatest number of reproductive modes. For hylids, there are four modes associated with vegetation (modes 6, 24, 25, and 36) and three modes associated with the floor (modes 4, 5, and 18); for leptodactylids, there are three modes associated with vegetation (modes 6, 14, and 27) and 10 with the floor (modes 13, 18, 19, 21–23, 28, and 30–32). The differences observed in the proportions of reproductive modes associated with vegetation and floor between these two families reflect general patterns of adaptations toward habitat occupation. Leptodactylids are frequently associated with the floor, generally lacking arboreal adaptations (with the notable exception of a great number of species in the genus *Eleutherodactylus*). In some species in the subfamily Leptodactylinae, different stages of a continuum from aquatic to terrestrial reproductive modes associated with the floor are known for species that reproduce using foam nests (modes 11, 13, and 28–32; Heyer 1969, Prado et al. 2002); this same tendency can be observed for other leptodactylids that do not produce foam nests. The hylids generally have well-developed adhesive discs, opposable first fingers and toes, or both; these are adaptations for an arboreal life, and the main trend in hylids' reproductive modes is from water to vegetation (modes 1, 2, 4, 5, 6, 24, 25, 36, and 37).

In Santa Cecilia, Ecuador, and the Philippines, the two frog families with the greatest diversity of species exhibit the greatest diversity of reproductive modes (Crump 1974, Brown and Alcala 1983). The same situation is observed in the Atlantic forest, where the greatest diversification in reproductive modes occurs in the large families Hylidae and Leptodactylidae. Considering all frog families in the Atlantic forest (table 1), the number of reproductive modes is significantly and positively correlated with the number of genera (Spearman rank correlation test, $r_s = 0.97$, $P < 0.001$, $N = 8$) and species ($r_s = 0.91$, $P < 0.001$, $N = 8$), indicating that reproductive diversification may be correlated with the origins of morphological, behavioral, or physiological novelties. The more specialized reproductive modes in Atlantic forest frogs are generally observed in genera that have few species (an exception is the large genus *Eleutherodactylus*), restricted to forest environments (e.g., *Brachycephalus, Dendrophryniscus, Frostius, Flectonotus, Gastrotheca, Crossodactylodes, Zachaenus,* and *Myersiella*). At the specific level, the small-bodied species that are restricted to forest environments have more specialized reproductive modes (e.g., *Brachycephalus ephippium, Frostius pernambucensis, Flectonotus goeldii, Chiasmocleis leucosticta,* and *Myersiella microps*).

Figure 2. Examples of reproductive modes observed for the Atlantic forest frogs. (a) Foam nest of the leptodactylid frog Physalaemus spiniger *(mode 14). This species has three alternative reproductive modes, one of them being the deposition of foam nest on water accumulated on the axils of terrestrial bromeliads (Haddad and Pombal 1998). Photograph: Célio F. B. Haddad. (b) Terrestrial eggs of the leptodactylid frog* Cycloramphus dubius *(mode 19). These eggs were deposited on a humid tree root above a swift stream. Photograph courtesy of Marcio Martins. (c) Semiterrestrial tadpole of* Cycloramphus boraceiensis *(mode 19). The larvae of this species live on rocks in the water–land interface, sometimes invading terrestrial environments such as this humid rock. Photograph: Célio F. B. Haddad. (d) Eggs, tadpoles, and subadult of* Thoropa miliaris *on a humid rock near the seashore of the Atlantic Ocean. The entire life cycle of this species occurs on humid rocks (mode 19). Adult males were recorded preying on hatching tadpoles (Ivan Sazima, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil, personal communication, 30 June 2004). Photograph: Célio F. B. Haddad. (e) Metamorphosing female of* Sphaenorhynchus palustris. *This species has a generalized reproductive mode (mode 1, eggs and exotrophic tadpoles in ponds and lakes); adults and metamorphosing individuals can reproduce, indicating facultative paedomorphosis. Note the reabsorbing larval tail and ripe eggs that can be seen through the translucent abdominal wall. Photograph courtesy of Ivan Sazima. (f) Male of the nest-building gladiator frog,* Hyla faber, *on the wall of a clay nest guarding a floating clutch of eggs (mode 4). In places where high densities of males are observed, the paternal guard is necessary because conspecific males try to steal the constructed nest. When a stealing male invades a nest with eggs, it disturbs the water surface, sinking the eggs to the bottom, where the embryos die by oxygen starvation (Martins et al. 1998). Photograph: Célio F. B. Haddad.*

Selective pressures and reproductive diversification

Few vertebrates are as dependent on environmental moisture as amphibians, whose life histories are strongly influenced by the distribution and abundance of water, usually in the form of rain (McDiarmid 1994). Although aquatic habitats are continuously available in humid forested regions, most frogs with specialized reproductive modes, with eggs and tadpoles that develop out of water, occur in this formation (Magnusson and Hero 1991). One possible explanation for the evolution of specialized reproductive modes is the selective pressure of predators on aquatic eggs and larvae (e.g., Lutz 1948, Crump 1974, Downie 1990, Prado et al. 2002). Magnusson and Hero (1991) have postulated this pressure as the major factor in the maintenance, and probably in the evolution, of several different semiterrestrial reproductive modes of Amazonian rainforest frogs. These authors attempted to demonstrate that aquatic predators have exerted, and are exerting, a significant selective pressure on the evolution of terrestrial oviposition in anurans. However, a table and figure that are central to their arguments and conclusions (table 2 and figure 1 in Magnusson and Hero 1991) clearly show that they used an outlier data point. When we ran the linear regression excluding the outlier data point, the adjusted r^2 dropped from 0.374 to 0.056, and the results changed from significant ($P = 0.027$) to nonsignificant ($P = 0.251$). Thus, Magnusson and Hero's results hang on a single data point, and are not robust enough to demonstrate that predators exerted a significant selective pressure leading to terrestrial oviposition in frogs.

Although the selective pressure of predators is not demonstrated, it may be a good explanation for the evolution of some specialized reproductive modes observed in Atlantic forest anurans. The tree frogs *Aplastodiscus perviridis, Hyla leucopygia,* and *Hyla* sp. (aff. *ehrhardti*), for example, construct subterranean nests where eggs and embryos develop (mode 5). These concealed nests protect sheltered males, adults in reproductive activity, eggs, and embryos from strict aquatic predators and from visually oriented terrestrial predators (Haddad and Sawaya 2000, Haddad et al. 2005, Hartmann et al. 2004). Furthermore, the subterranean nests may prevent desiccation of eggs and embryos (Hartmann et al. 2004), and we cannot discard the possibility that desiccation was an important selective pressure in these cases. At least two different selective pressures may have been involved in the evo-

Table 1. Numbers of genera, species, and reproductive modes in the different anuran families from the Atlantic forest of Brazil.

Family	Number of genera	Number of species	Number of reproductive modes
Brachycephalidae	1	8	1
Bufonidae	5	23	4
Centrolenidae	1	3	1
Dendrobatidae	1	4	1
Hylidae	17	176	11
Leptodactylidae	23	173	17
Microhylidae	7	17	3
Pipidae	1	1	1
Total	56	405	

Note: Numbers of species are based on Frost (2004) and AmphibiaWeb (2005).

lution of the reproductive mode of the nest-building gladiator frog, *H. faber* (mode 4). The behavior of depositing clutches in constructed clay nests isolates eggs and embryos from some aquatic predators (Martins 1993); on the other hand, the facultative parental egg attendance performed by males (figure 2f) apparently evolved as a consequence of intrasexual competition for suitable places for clay nest construction (Martins et al. 1998).

Drying of ponds has been proposed as an important selective pressure leading to the evolution of reproductive modes that are more terrestrial (Magnusson and Hero 1991). The three alternative modes of deposition of the foam nest in the environment that are observed in the Atlantic forest species *Physalaemus spiniger* (modes 11, 14, and 28) are apparently related to rainfall unpredictability, leading to pond desiccation (Haddad and Pombal 1998). As long as the eggs or larvae are within the foam nest, most are protected from desiccation (Heyer 1969). When the rains fill the pond, the larvae are released from the foam nest.

However, a number of other functions have been attributed to the foam nest constructed by anurans: (a) a protective refuge for eggs and embryos against predators (Downie 1990), (b) a device that enables an adequate oxygen supply for the eggs (Seymour and Loveridge 1994), (c) a device that provides adequate temperatures for developing eggs and embryos (Dobkin and Gettinger 1985), (d) a growth inhibitor for eggs and embryos (Pisano and Del Rio 1968), and (e) a

Table 2. Number and percentage of reproductive modes in the Atlantic forest, the Amazonian forest, the Neotropics, and the world.

Area	Number of reproductive modes (percentage)	Reproductive modes[a]
Atlantic forest	27 (69.2)	Modes 1–6, 8, 10, 11, 13–15, 18–25, 27, 28, 30–32, 36, 37
Amazonian forest	22 (56.4)	Modes 1, 2, 4, 6, 8, 11, 13, 15, 16, 18, 20, 21, 23–27, 30, 32, 35–37
Neotropics	31 (79.5)	Modes 1–8, 10, 11, 13–16, 18–28, 30–32, 35–37
World	39 (100)	Modes 1–39

a. Reproductive modes are described in box 1.

food source for hatchlings (Tanaka and Nishihara 1987). Considering these diverse functions of the foam nest, as well as the different ways in which it is constructed (Tyler and Davies 1979, Downie 1990, Haddad and Hödl 1997), the different places where it is deposited (Glaw and Vences 1994, Haddad and Pombal 1998, Prado et al. 2002), and its independent origins in the six anuran families for which it is known to occur (Haddad et al. 1990, Glaw and Vences 1994), it is highly likely that different selective pressures were involved in the evolution of the foam nest.

The reproductive specialization of the Atlantic forest frogs may be due in part to the rough topography of a significant part of this biome. The high number of terrestrial reproductive modes observed for anurans in humid mountainous regions was interpreted as resulting from the inadequacy of swift streams as reproductive sites, insofar as sperm, eggs, and larvae might be swept away by the current (Goin and Goin 1962). This suggestion that water currents in montane conditions were the selective pressure leading to reproductive modes that are more terrestrial (Goin and Goin 1962, Weygoldt and Carvalho e Silva 1992) was refuted by some authors, who argued that the evolution of terrestrial breeding is better explained by the selective pressure of predators on the amphibian eggs, embryos, and larvae (Poynton 1964, Magnusson and Hero 1991). Some reproductive modes observed for Philippine frogs are clearly influenced by the currents of swift streams (Alcala 1962). The same situation is observed for some Atlantic forest frogs that have adaptations to prevent their eggs and tadpoles from drifting downstream. A simple adaptation is observed in the tree frogs *Hyla weygoldti,* which reproduces in mountain streams, and *H. prasina*, which sometimes may reproduce in this habitat. The eggs of these species are glued on submersed vegetation and rocks, which prevents them from being carried away by currents (Weygoldt and Carvalho e Silva 1992). The same adaptation is observed in several species of the genus *Hyla*. An entirely aquatic and specialized reproductive mode in current water is observed in the hylodine frog genus *Crossodactylus.* These rheophilic frogs construct subaquatic chambers to protect the eggs from currents; furthermore, the chambers are concealed to protect the eggs against conspecific tadpoles that are egg predators (Weygoldt and Carvalho e Silva 1992). Frogs of the hylid genus *Phasmahyla* deposit eggs in an envelope of folded leaves over swift streams; hatchling tadpoles drop into the currents and drift downstream to deeper and quieter pools along the montane stream, where frequently they form schools near the water surface (Haddad and Sazima 1992). The centrolenid frogs of the genus *Hyalinobatrachium* deposit eggs on leaves above swift streams; hatchling tadpoles drop into the currents and are fossorial, living buried in the sandy or gravelly bottom of streams as a way to escape the rigors of currents (Duellman and Trueb 1986). As a consequence of their burrowing behavior, these tadpoles are nearly unpigmented, and have elongated bodies, narrow tails and fins to facilitate excavation, and reduced eyes that are covered with skin (Lutz 1947). Eyes and pigmentation develop during metamor-

phosis, when the animal abandons its secretive life and assumes an arboreal life.

The reproductive diversification of the Atlantic forest frogs (box 1) appears to have been favored by the rough topography of the environment, but this does not mean that the topography was the only source of selective pressures leading to the ample array of specialization. The highly complex topography of a significant part of the Atlantic forest, which breaks the biome up into many small microhabitats (Brown and Brown 1992), and the high humidity of the forest, which reduces desiccation risks, have enabled the evolution of specialized reproductive modes that are more independent from the aquatic environments. The reproductive diversification of Atlantic forest frogs was made possible by adequate environmental conditions (the large number of humid microhabitats), by the action of diversified selective pressures (e.g., swift streams, rainfall unpredictability, predators, and intraspecific competition), by the occupation of the available microhabitats, and by the prolonged evolution of different phylogenetic groups in this biome. In addition to these diverse selective pressures and circumstances, the fact that the anurans evolved in the water–land interface allowed them to use a large number of microhabitats in the continuum from aquatic to terrestrial environments.

Topographic heterogeneity, reproductive specialization, and the decline of the Atlantic forest frogs

Of the 39 reproductive modes recognized for anurans around the world (including the 10 modes proposed here), 31 are recorded for Neotropical species, and 27 of those are for Atlantic forest species. For the Amazonian forest, with an area five times greater than that of the Atlantic forest and with an elevated diversity of frogs, 22 reproductive modes have been observed (table 2; Duellman 1986, 1988, Duellman and Trueb 1986, Hödl 1990, Zimmerman and Simberloff 1996). Among the frog communities analyzed in table 3, the three from the upper Amazon basin (Panguana, Parque Nacional da Serra do Divisor, and Santa Cecilia) have greater numbers of species depositing terrestrial or arboreal eggs when compared with those from the Atlantic forest. Apparently this is a consequence of the high number of centrolenids, hylids, dendrobatids, and eleutherodactylines in western Amazonia that deposit eggs out of water (Hödl 1990). However, the Atlantic forest frog communities have a proportionally higher number of reproductive modes when compared with the frog communities from the Amazonian forest (table 3). The most diversified frog community known for the Atlantic forest (Boracéia, São Paulo state, Brazil) has proportionally more reproductive modes (ratio of modes to species = 0.24) than Parque Nacional da Serra do Divisor, Brazil, the most diversified frog community known for the Amazonian forest (ratio of modes to species = 0.10). The frog communities from Rio de Janeiro, Santa Tereza (the Atlantic forests of the states of Rio de Janeiro and Espírito Santo, respectively), and Manaus (Amazon forest) have the highest known number of reproductive modes (17), while the frog community from Ribeirão

Table 3. Number of species, number of reproductive modes, ratio between numbers of modes and species, and number of species depositing eggs out of water (modes 17–39 in box 1) for nine well-studied Neotropical localities in the Atlantic and Amazonian forests.

Location	Number of species	Number of modes	Ratio of modes to species	Number of species depositing eggs out of water (percentage)	Reference
Atlantic forest					
Boracéia (São Paulo, Brazil)	68	16	0.24	25 (37)	Heyer et al. 1990
Ribeirão Branco (São Paulo, Brazil)	46	15	0.33	11 (24)	–
Ubatuba (São Paulo, Brazil)	50	16	0.32	18 (36)	–
Rio de Janeiro (Rio de Janeiro, Brazil)	63	17	0.27	26 (41)	–
Santa Tereza (Espírito Santo, Brazil)	58	17	0.29	22 (38)	–
Amazonian forest					
Manaus (Amazonas, Brazil)	66	17	0.26	22 (33)	Hödl 1990
Parque Nacional da Serra do Divisor (Acre, Brazil)	124	12	0.10	51 (41)	Souza 2002[a]
Santa Cecilia (Ecuador)	88	16	0.18	45 (51)	Duellman 1978, Hödl 1990
Panguana (Peru)	66	14	0.21	34 (52)	Hödl 1990

Note: If no reference is given, data are from the authors' research.
a. Also based on the authors' research (C. F. B. H., working with Moisés B. Souza).

Branco (the Atlantic forest of São Paulo state) has the highest proportion of reproductive modes (ratio of modes to species = 0.33; table 3).

The diversity of reproductive modes is more a reflection of the environmental characteristics in which the anurans live than of the phylogenetic relationships of the families and higher categories (Duellman and Trueb 1986). The high diversity of reproductive modes observed for the Atlantic forest frogs is the result of a successful utilization of the diversified and humid microhabitats present in this biome. The repetition of such microhabitats across the landscape of the Brazilian Atlantic formation has been suggested as an explanation for the persistence of rare species and the low number of extinctions after the destruction of more than 90% of this biome (Brown and Brown 1992). However, quantification for endemic Atlantic forest birds indicates that the deforestation is leading to extinction at levels predicted by species–area analysis (Brooks and Balmford 1996).

Considering the general process of destruction of the tropical moist forests, the decimation of the Brazilian Atlantic forest is one of the most alarming and desperate conservation problems in the world (Morellato and Haddad 2000). When European colonization started in 1500, the original area covered by this forest was approximately 1,300,000 square kilometers (km^2), stretching from the state of Rio Grande do Norte at the easternmost tip of South America to Rio Grande do Sul, the southernmost Brazilian state (Collins 1990). The Atlantic forest was cleared mainly for timber, firewood, charcoal, agriculture, cattle ranching, and the construction of cities. Today, 120 million Brazilians live in more than three thousand cities in cleared lands of the Atlantic forest (Morellato and Haddad 2000). This occupation, with no planning, caused a reduction of the forest to approximately 98,800 km^2, or 7.6% of its original extent, and the remaining fragmented forest is still under severe anthropogenic pressure (Morellato and Haddad

2000). Even considering that this destruction is leading only to minimal extinction of entire species, it must result in the elimination of many populations and consequently in the erosion of genetic diversity (Brown and Brown 1992).

The deforested areas became drier and more seasonal, reducing the number of species or eliminating those that depend on humid forest microhabitats. Frogs that depend on the forest humidity for reproduction in the Atlantic forest (modes 5, 6, 8, 14, 18–23, 25, 27, 28, 32, 36, and 37) disappear suddenly after deforestation. The population declines observed for several anurans from the Atlantic forest (e.g., Heyer et al. 1990, Haddad 1998) and the disappearance of some species (e.g., *Colostethus olfersioides, Colostethus carioca, Holoaden bradei, Paratelmatobius lutzii, Thoropa petropolitana*) may be a consequence of environmental alteration produced by humans. At the same time that human actions are reducing or eliminating a great number of frog species that depend on the forest environments, the artificially open environments produced by humans are being invaded by a few generalist species (Haddad 1998). A common situation after deforestation is the invasion of the cleared areas by a few frog species from the Cerrado region (savanna) that are more resistant to desiccation and have more generalized reproductive modes (modes 1 and 2) or modes adapted to insolation (e.g., modes 11, 13, and 30–32). Examples are *Hyla sanborni, Leptodactylus fuscus,* and *Physalaemus cuvieri* that are being favored by the deforestation and are expanding their areas of occurrence in cleared lands of the Atlantic forest. Some forest species (e.g., *H. faber, Phyllomedusa burmeisteri,* and *Physalaemus crombiei*) apparently are resistant to deforestation, adapting to disturbed environments after forest removal. The result of deforestation in the Atlantic forest frog communities is a generalized impoverishment in terms of species richness, in which a low number of species adapted

to open conditions substitute for a large number of specialized species adapted to the forest.

Aproximately 405 species of anurans are known from the Atlantic forest (Frost 2004, AmphibiaWeb 2005), corresponding to approximately 8% of the anurans in the world. This frog fauna is characterized by a high level of endemism (Duellman 1999). Of the anuran species occurring in this biome, 81% (327) are endemic, 34% (137) are endemic to just one locality, and 40% (161) have specialized reproductive modes dependent on the forest environments. More than endemic species, entire groups are restricted to this formation (e.g., family Brachycephalidae; genera *Dendrophryniscus, Frostius, Hylomantis, Phrynomedusa, Crossodactylodes, Cycloramphus, Euparkerella, Megaelosia,* and *Paratelmatobius*) (Duellman 1999, Frost 2004). On the basis of the almost total destruction of this biome and the high number of endemic species specialized for the forest environment, it is reasonable to suppose that many of them have become extinct before being discovered and that many others will soon vanish. New genera and species of frogs are still being found and described in Atlantic forest remnants (e.g., Izecksohn 1996, Heyer 1999, Cruz et al. 2003), including forms of highly unusual morphology (Peixoto et al. 2003); some of these species are already threatened by extinction (Giaretta and Aguiar 1998). As a consequence of this high diversity and lack of studies, the life histories of several anuran species in this region are practically unknown. Entire genera (e.g., *Megaelosia*) have not been adequately studied, and new reproductive modes will certainly be discovered in the future, which will facilitate our understanding of the evolution, ecology, and behavior associated with reproduction in anurans.

Acknowledgments

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