

Distinct Architectures of Subterranean Nests in the Genus *Leptodactylus* of the *fuscus* Group (Anura, Leptodactylidae)

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Though dietary analysis has suggested *C. montium* to occasionally forage near the ground (Hofer et al. 2003) and it is known that females must descend for egg laying, our observations of this forest species to readily and routinely utilize such barren expanses is somewhat surprising. Total territory estimates for this species must be executed with caution because of the tendency for some animals to remain stationary for extended periods of time and then spontaneously relocate to distances relatively far. Models based upon movements of lizards and mathematical formulas used to interpret the number of sightings required to determine home range of lizards (Christian and Waldschmidt 1984; Rose 1982; Stone and Baird 2002) might not fit for this species.

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Nest construction requires time and energy investment and different defensive strategies are known for the protection of these structures. In social insects like termites, some species invest a great amount of energy constructing nests that are resistant to the attack of vertebrate predators, while other species show low investment in building activities, but nest fortification and nest defense is accomplished by toxic soldier secretions (Coles and Howse 1983). Among vertebrates with nests built solely or mainly by one sex, several features of the construction may reveal or amplify characteristics of the builder to potential mates (see Barber et al. 2001).

Frogs of the *Leptodactylus fuscus* group comprise about 25 species (Frost 2004) that build subterranean chambers used for the deposition of eggs enclosed in foam (Heyer 1969). However, the architecture of the subterranean nests has been described for only a few species (e.g., Crump 1995; Giaretta and Kokubum 2004; Martins 1988; Sazima 1975; Sazima and Bokermann 1978). The evolution of such specialized nest structures in anurans is generally related to avoidance of aquatic predators on eggs and embryos, prevention of desiccation of eggs and larvae, and protection of adults from visually-oriented predators (e.g., Haddad and Sawaya 2000; Heyer 1969; Prado et al. 2002). We describe the subterranean nests of three *Leptodactylus* species in the *fuscus* group: *L. fuscus*, for which nests are well-known from several South American regions; and *L. notoaktites* and *L. mystaceus*, for which we describe nests for the first time.

Methods.—Nests of *L. fuscus* were recorded in the southern Pantanal, municipality of Corumbá (19°34'S, 57°00'W), State of Mato Grosso do Sul, southwestern Brazil, in November 1997 and November 2000. Nests of *L. notoaktites* were recorded in the State of São Paulo, southeastern Brazil, in the municipalities of Barra do Turvo (24°56'S, 48°25'W) and between Iporanga and Apiaí (24°33'S, 48°40'W) in September 2003, and Ribeirão Branco (24°21'S, 48°44'W) in January 2004. Nests of *L. mystaceus* were recorded in the municipalities of Areia (06°58'S, 35°41'W), State of Paraíba, northeastern Brazil, in April 1993, and Rio Claro (22°16'S, 47°42'W), State of São Paulo, southeastern Brazil, in October 2001.

Results.—Nests of *L. fuscus* in the Pantanal (N = 2) were observed being constructed by males on muddy soil at the edge of temporary ponds. They had an access tunnel 5–30 cm long and 2.5 cm wide ending in an oval chamber (4.5 cm high, 5.4 cm wide). On 05 November 2000, males started to call at late afternoon (1900 h) from the muddy edge of a puddle. The first nest was built by a male between 2000 and 2055 h, in the same way described by Martins (1988). Then, this male started to emit advertisement calls at a distance of about 1.0 m from the nest access opening. The second nest was built by another male between 2100 and 2130 h; subsequently it started to call at a position 1.5 m from the nest. The distance between these nests was about 0.5 m and the whole process lasted 30 and 55 min, respectively. On 14 November 1997 we found a nest access near a calling male. Digging along the access tunnel we found an empty chamber (5.0 cm high, 5.5 cm wide). We dug a little more and found a second chamber (5.1 cm high, 5.3 cm wide) containing foam with tadpoles. After further digging we found two additional chambers, with similar sizes, also with foam and tadpoles. We could not find any access to these three chambers with tadpoles and they seemed completely closed.

Nests of *L. notoaktites* (N = 3) had two chambers. The first one was smaller (6.5 cm long, 3.0 cm wide, 1.8 high) than the second one (7.5 cm long, 7.5 cm wide, 5.5 cm high) and both were interconnected; although no tunnel was present, these chambers were adjacent to each other with a constriction between them. The males apparently were emitting advertisement calls from the first, smaller chamber. These nests had only one opening that measured 1.9 cm

wide.

For *L. mystaceus*, we recorded two nests. One was found in northeastern Brazil and exhibited a complex structure (Fig. 1). It had one access opening and three chambers connected by tunnels. In this subterranean system, the first two chambers were empty and a foam containing eggs was in the last chamber (Fig. 1). This subterranean nest was built during the first rains on muddy and wet soil in a temporary pond in an upland forest when the pond was still dry. The second nest was observed in southeastern Brazil. It consisted of one access opening and an oval chamber without a tunnel.

Discussion.—Similar to the *L. fuscus* nests we report in the Pantanal, Martins (1988) observed subterranean nests of this species in the State of Roraima, northern Brazil. These nests consistently are comprised of a single access and a tunnel connecting the opening with a subterranean chamber. The tunnel is large enough to allow the entrance of only one individual, whereas the size of the chamber permits the occurrence of amplex and oviposition. Sazima (1975) and Gonsales (2004) described the same nest structure for *L. fuscus* (referred as *L. sibilatrix* by Sazima 1975) from different populations in the State of São Paulo, southeastern Brazil. Due to the highly territorial nature of these frogs, the most likely explanation for the “four-chambered” nest we describe is that the four chambers were dug out by the same male, and sealed after egg-laying.

Although not observed in the Pantanal, females of *L. fuscus* were recorded sealing the nest opening after oviposition in the State of

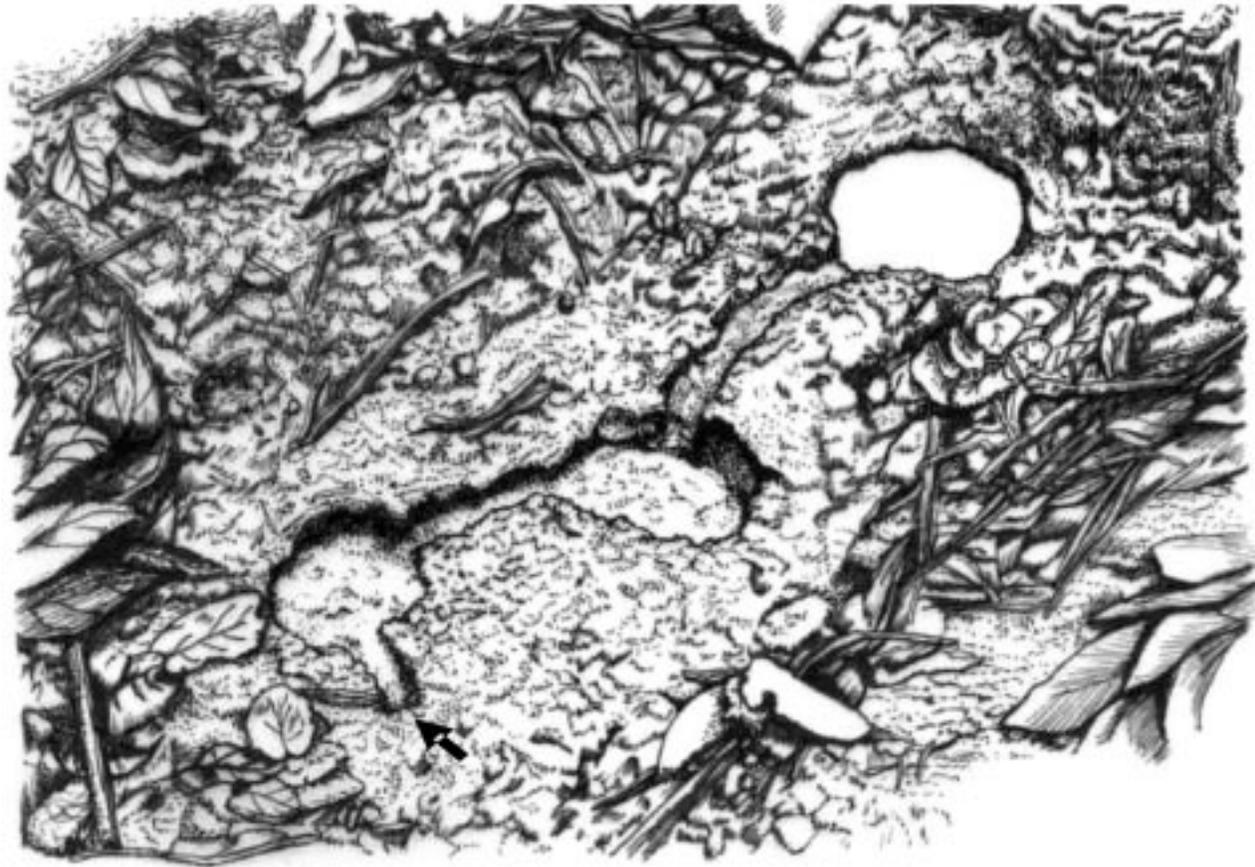


FIG 1. A cross-sectional view of an excavated subterranean nest of *Leptodactylus mystaceus*, showing one access tunnel (arrow) and three chambers connected by tunnels. Note that only the last chamber (right) is filled with a foam nest.

São Paulo (Gonsales 2004). For *L. bufonius* in Argentina, females also were recorded sealing the nest opening after oviposition (Crump 1995, Reading and Jofré 2003). Sealing of the nest tunnel after oviposition was recorded for a few nests of *L. camaquara*, which digs its nest under rock slabs, as well as for *L. cunicularius*, which builds a globular nest and seals the roof access after oviposition takes place (Sazima and Bokermann 1978, I. Sazima pers. comm.). However, the sex responsible for the sealing in these two species was not documented.

Nest building by *Leptodactylus* of the *L. fuscus* group may occur in different soil types, such as sand (Arzabe and Almeida 1997) or mud (Reading and Jofré 2003). We found nest digging took 30 to 55 min. Martins (1988) also recorded one nest being dug over 40 min by a *L. fuscus* male on muddy soil. The time spent in building activities varies from 10 min in *L. troglodytes* on sand (Arzabe and Almeida 1997) to 90 min in *L. bufonius* on mud (Reading and Jofré 2003). It appears that construction of nests on mud takes longer. We suggest that total time needed to nest digging is related with soil type and nest architecture.

The nest architecture varies considerably among the species of the *L. fuscus* group. The presence of at least one additional chamber, as described here for *L. notoaktites* and one nest of *L. mystaceus*, also has been recorded for other *Leptodactylus* species, such as *L. albilabris*, *L. latinasus*, and also may occur in *L. fuscus* nests (see Solano 1987). The nest of *L. mystacinus* is an elliptical chamber with a short tunnel and access opening partly or totally sealed (Sazima 1975). The nests of five *Leptodactylus* of the *fuscus* group from open areas in southeastern and central Brazil were described by Sazima and Bokermann (1978). *Leptodactylus furnarius* builds a half oval nest with no tunnel and seals it at the top after egg-laying; *L. jolyi* builds a sinuous corridor connecting the chamber and does not seal the access; *L. cunicularius*, *L. camaquara*, and *L. tapiti* dig their nests under rock slabs, the two latter species with the chamber connected to a short tunnel with the opening facing streams at sites subject to periodical floods (Sazima and Bokermann 1978, I. Sazima pers. comm.). The nest of *L. cunicularius* has a long tunnel compared to the other four above-mentioned species, and is dug in slopes far from temporary streamlets, to which the tadpoles are carried by water draining the slopes (Sazima and Bokermann 1978, I. Sazima pers. comm.). The nest of *L. troglodytes* that lives in open areas has two access openings (Arzabe and Almeida 1997). The nest of *L. bufonius* is described as cone-shaped and extends up to 5.5 cm above the ground, with an opening in the upper part of the cone (Crump 1995).

Subterranean nests and their variable nest architectures may serve several purposes, including an antipredation function. Several invertebrates and vertebrates prey on frogs, mainly during their reproductive activity (e.g., Haddad and Bastos 1997, Prado 2003, Toledo 2003). Hawks and snakes have been reported preying on adults of *Leptodactylus* species of the *fuscus* group at reproductive sites (Arzabe and Almeida 1997, Giaretta and Kokubum 2004). Giaretta and Kokubum (2004) recorded a colubrid snake inside a nest chamber of *L. furnarius*; it was a juvenile *Liophis meridionalis* which contained 17 tadpoles in its stomach. Gonsales (2004) observed eggs and tadpoles of *L. fuscus* and *L. mystacinus* being eaten by ants of the genus *Camponotus* that were inside the chambers. The hylid *Hyla leucopygia* also builds subterranean cham-

bers, and Haddad and Sawaya (2000) observed a colubrid snake, *Liophis miliaris*, preying on a pair of adults inside the chamber. Haddad and Sawaya (2000) commented upon the evolution of this specialized reproductive mode in hylids, and suggested that adults, eggs, and embryos are probably more protected from strictly aquatic predators and from visually oriented terrestrial predators in these subterranean nests. However, predators oriented by olfaction, such as snakes, can find concealed subterranean nests (Haddad and Sawaya 2000). Additionally, several invertebrates, such as ants (Gonsales 2004), spiders (Villa et al. 1982), and fly larvae (Downie et al. 1995) also seem to be important predators within concealed subterranean nests of *Leptodactylus* species. The presence of two access openings, as recorded for one nest of *L. troglodytes* (Arzabe and Almeida 1997), may allow the frog to escape from a predator entering the subterranean chamber. The presence of two or more chambers in the nests of *L. notoaktites* and *L. mystaceus* may be built to accommodate additional clutches, as reported for *L. fuscus* in this study, but additionally may have evolved into a more complex structure, increasing the frog's chances of fleeing from predators.

Calling from within the nest, as recorded herein for *L. notoaktites*, as well as for *L. fuscus* (Martins 1988), and *L. bufonius* (Reading and Jofré 2003), may protect males from predators during calling activity, when they are exposed to predation. It is also important to note that the construction of the subterranean chambers may initiate both after or before female approach, depending on the species (Sazima 1975, Martins 1988). Sazima (1975) suggested that when nest initiation occurs after female approach, the distance kept among males is apparently smaller compared to species that build the nests before the approach of the female. This suggests that when nests are built before female approach, as observed here for *L. fuscus* and *L. notoaktites*, nests may have other functions than only protecting the foams, such as shelter sites, reinforcing territorial behavior in these species.

Another selective pressure molding nest architecture in *Leptodactylus* may be related to habitat type. Open or forested areas may exert different selective pressures during breeding. These may include the exposure of frogs to visually-oriented predators, as recorded for rodents by Jackson (2000). Also, thermal differences and different soil types may be other factors related to nest architectures of species in the *L. fuscus* group.

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Sexual Maturity of Farm-Released *Caiman latirostris* (Crocodylia: Alligatoridae) in the Wild

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One strategy to enhance small populations of crocodylians is to release captive-reared individuals into the wild. However, information is scarce on the success of relocated and translocated animals (Dodd and Siegel 1991). There are concerns about released animals and their ability to hunt for food and adapt to their environment (Blake and Loveridge 1975) that might result in low survivorship following release. Low survivorship would result in very poor recruitment of captive-reared animals as compared to wild crocodylians.

Despite these concerns, successful recruitment of captive-reared females into wild breeding populations has been demonstrated for *Crocodylus palustris* (Choudhury 1981), *C. porosus* (Kar 1996), *C. intermedius* (J. Thorbjarnarson, pers. comm.), and *Alligator mississippiensis* (Elsey et al. 2000a, 2000b). In most of these programs animals are released at 1.0–1.5 m total length (TL), after 2–4 years of captive rearing.

Sexual maturity is an important variable in population dynamics and is a useful datum for conservation programs, such as Proyecto Yacaré (MAGIC/MUPCN), that are attempting to facilitate the recovery of crocodylian populations. Since 1990, Proyecto Yacaré (*Caiman* Project), has been working to enhance the wild population of *Caiman latirostris* in Santa Fe Province, Argentina. We collect eggs from wild nests soon after laying (December–January) and artificially incubate the eggs. Hatching occurs during February and March. Hatchlings are marked by removing selected caudal scutes (indicating hatching year and nest of origin). Hatchlings are raised in concrete pools until November; therefore animals are kept in captivity for a maximum of nine months, and reach an average size of 45 cm TL prior to release. They are then reintroduced in the same place where the eggs were collected. While in captivity, animals are fed chicken *ad libitum*, supplemented with vitamins and minerals, three times a week (for details see Larriera 1993).