Terrestrial and communal nesting in *Eupemphix nattereri* (Anura, Leiuperidae): interactions with predators and pond structure

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(Accepted 11 November 2006)

Abstract

We report on the behaviour of *Eupemphix nattereri* in Brazil. Reproduction started with the beginning of the rains and, in peak season, could extend into the diurnal period. Pairs built either isolated or communal foam nests close to, but isolated from, water. The density of nests on steep ground was greater than on flatter terrain. After 40 h, nests collapsed and formed a mucus string allowing early tadpoles to enter the water. Infestation of nests by flies was delayed in relation to the beginning of the reproductive season. Tadpoles of two *Leptodactylus* species preyed upon eggs or tadpoles leaving the foam of *E. nattereri*; adults were preyed on by water bugs, raccoons and two bird species. Amplectant pairs took refuge under communal nests when approached. Terrestrial nesting appears to be a response to loss of eggs/early tadpoles to aquatic predators. Communal nesting is facultative behaviour and appears to result unintentionally from (1) the massive aggregation of adults, (2) the selection of steep/bare ground to anchor nests, and (3) disturbed couples restarting egg-laying beside previously built nests.

Keywords: Anura, foam nesting frogs, South America, Brazil, predation, tadpoles, *Leptodactylus fuscus*, *Leptodactylus labyrinthicus*, *Eupemphix nattereri*

Introduction

Among South American foam-nesting frogs (Leiuperidae and Leptodactylidae), the nest is primarily related to predation avoidance (Downie 1988, 1990, 1993; Menin and Giaretta 2003), but facilitation of physiological processes, such as respiration, excretion (Downie and Smith 2003; Kokubum and Giaretta 2005) and water regulation, appear to be important in those species whose tadpoles spend a long time in the nest (Kokubum and Giaretta 2005). Most Leiuperidae frogs build floating foam nests in temporary or/and permanent water bodies (Bokermann 1967; Cei 1980; Ryan 1985; Heyer et al. 1990; Giaretta and Menin 2004) and particular nesting sites include water filled footprints (Ryan...
1985), axils of terrestrial bromeliads (Cruz and Peixoto 1985; Haddad and Pombal 1998) and tree holes near the ground (Pombal and Madureira 1997). Communal nesting is a facultative behaviour in some *Physalaemus, Engystomops* (Ryan 1985; Hödl 1990; Barreto and Andrade 1995; Giaretta and Menin 2004) and *Pleurodema* species (Hödl 1992; Cardoso and Arzabe 1993), and it is believed that communality can reduce egg/embryo mortality by offering protection against desiccation (Ryan 1985). Hödl (1990) and Giaretta and Menin (2004) commented that the physical structure of a water body, such as the distribution of resting supports for egg-laying females, may play a role in the occurrence and distribution of communal foam nests within a water body.

Adult frogs are particularly susceptible to predation when aggregated around water bodies for reproduction (Ryan 1985; Ryan et al. 1981; Duellman and Trueb 1986; Toledo 2003) and aquatic predators may also inflict severe loss of eggs/tadpoles (Alford 1999; Silva et al. 2005). *Engystomops pustulosus* (Cope, 1864) has been a model organism for study of the tradeoffs between calling and the risk of predation (Ryan 1985; Ryan et al. 1981) but, for most other Leiuperidae species, little is known about their interactions with predators. *Eupemphix (=Physalaemus) nattereri* Steindachner 1863 is known to call from pond margins (Rossa-Feres and Jim 2001) and adults appear to be toxic to vertebrate predators (Sazima and Caramaschi 1986; Rodrigues and Oliveira Filho 2004), often displaying large inguinal eye-like glands when disturbed (Sazima and Caramaschi 1986; Mattos et al. 2003). In southeastern Brazil, maggots of the ephydrid fly *Beckeriella niger* (Williston, 1897) infest foam nests and consume eggs/embryos of all Leiuperidae and Leptodactylidae frogs with exposed foam nests, including *E. nattereri* (Menin and Giaretta 2003). Predatory frogs also feed on adults of *E. nattereri* (França et al. 2004).

In this study, we report on the reproductive behaviour of *E. nattereri*, including a strategy to remove foam nests from direct contact with the water, and present data on mortality of eggs/embryos, tadpoles and adults. The factors influencing communal nest formation in the species, such as the physical structure of the pond, are also discussed.

**Study area**

The present study was conducted in natural and artificial water bodies in Cerrado (savannah-like environments) in the municipalities of Uberlândia (around 18°55’S 48°17’W, ~750 m altitude) (State of Minas Gerais) and Caldas Novas (around 17°46’S 48°39’W, 700 m altitude) (State of Goiás), Brazil. The regional climate has two well-defined seasons, wet/warm from September to March and dry/mild from April to August. The monthly mean temperature in both sites ranges from 19 to 30°C; the annual rainfall is about 1550 mm; in the drier months the precipitation can be zero (Giaretta and Kokubum 2004). Rains can fall erratically at the beginning of the rainy season and recently filled ponds may dry out from one day to the next. The vegetation around the studied water bodies was low (<50 cm) grass (pastures) with sparse shrubs and recently burnt areas along stream-side marshes (*Mauritia flexuosa* L.f. palm groves, regionally called Veredas).

**Methods**

Field observations were carried out weekly from September to November 2001 and from September to December 2004; data collected sporadically between December 1998 and January 2005 were also considered. When following up the fate of egg clutches, field trips
were made daily for 4/5 days. The determination of the reproductive season was based on the calling activities of males. Museum preserved adult males (external vocal sac and nuptial thumb asperities present) and females (egg bearing) were measured and analyzed for differences in size using ANOVA (Zar 1999). We learned to differentiate the foam nests of *E. nattereri* from the syntopic *Physalaemus cf. fuscomaculatus* (Steindachner, 1864) by following pairs of both species while egg-laying. Egg number was determined by counting all eggs in 5% formalin-preserved egg clutches; eggs were measured using a micrometer coupled to a stereomicroscope. To test if the couples preferred steeper banks for nest anchoring, we counted nests built on each of two categories of ground steepness (estimated using a 180° protractor) as those above and below 30° and measured the length (availability) (50-m measuring tape) of the banks in each of them. We correlated the extension reached by the tadpoles in the mucous string of individual collapsing foam nests with ground steepness using the Pearson correlation coefficient (Zar 1999); only clutches that died from drought were used in this analysis. We tested if *E. nattereri* and *P. cf. fuscomaculatus* were able to build foam nests without a resting support for the female by enclosing individual amplexant pairs in buckets containing a 10-cm deep water column. The tested pairs were captured in the early morning, prior to egg-laying, and monitored for 24 h.

Frog predation events were recorded. Bird attacks on frogs were observed from within a car, ~15 m away, using binoculars. Avian nomenclature follows Sick (1997). The tadpoles of *Leptodactylus fuscus* (Schneider, 1799) and *L. labyrinthicus* (Spix, 1824) found consuming eggs and/or early tadpoles were identified by raising them to metamorphosis; some were analyzed for gut contents to confirm consumption. We examined foam nests for the presence of adults of the predatory fly *Beckeriella niger*. After nights of intense reproductive activity, we looked for buried frogs at pond margins (10–100 cm from water) during the day by turning up the superficial (<10 cm) soil. Tadpole staging followed Gosner (1960). The new anuran nomenclature followed Frost (2006). Voucher specimens are in the frog collection of the Museu de Biodiversidade do Cerrado (AAG-UFU 2460) at the Universidade Federal de Uberlândia.

**Results**

Male *E. nattereri* averaged 39.5 mm in SVL (SD=1.8 mm; n=24) and females 44.4 mm (SD=2.1 mm; n=14), the difference being statistically significant (ANOVA $F_{1, 36}=56.8$, $P<0.001$). Three egg clutches, collected between October and November 2003, averaged 2516 eggs (SD=213); the yolk averaged 1.6 mm (SD=0.06 mm, n=30 eggs from three egg clutches) in diameter. Reproduction started with the first heavy rains of the August–October period, and the calling activities of males extended until mid March. Dense (e.g. hundreds of individuals in a 15×20-m pond) reproductive aggregations were common during the first heavy rains in October–December. Ordinarily, reproduction took place in temporary ponds (n=20 sites) in open areas. On two exceptional occasions, foam nests (n=3) were observed anchored at the margins of a permanent stream (100 cm wide, 50 cm deep) after recent (<2 days) fires cleared grass. Reproduction usually took place after sundown; exceptionally, between October and December, calling and spawning extended to the diurnal (07:00–14:00 h) period (n=6 events). Diurnal activities followed nights of heavy rains that filled previously dry ponds. Intense vocal activities may last for 2 days after heavy rains. Within a pond, males changed their position constantly while calling, which was done while floating or sitting at water level at the pond margin. Pairs (n=65) left the
Males looked actively for females, swimming around most of the time, even amplexing already mated conspecific (n=2) and heterospecific females (Physalaemus cf. fuscomaculatus, n=2); the interception of heterospecific pairs apparently resulted in the death of the female by drowning (n=2).

The pairs built either isolated (Figure 1) or communal foam nests (Figure 2, above and middle) anchored to the ground (Figure 1) in such a way that when the water level lowered, they became isolated from it. To anchor a foam nest, the couple in amplexus actively made a base for it (Figure 1) by scraping away earth with their enlarged metatarsal tubercles. When in communal nests, individual nests were tightly compacted and the number of individual components was hard to determine; maximum estimated around 20 nests. Foam nests were built on ground sloping between 5 and 90° (n=128); around ponds with large extensions of steep (>30°) banks, communal nesting was rare (n=3 sites). Considering only water bodies with banks of variable inclination, the density of nests anchored to steep (>30°) ground was about seven times greater (0.62 nest/m; n=89 foam nests, n=7 ponds) than on flatter terrain (0.09 nest/m; n=16 foam nests, n=7 ponds) (Table I).

After about 40 h, the foam nests collapsed (n=25) and those on steep ground formed a string of wet mucus that made it possible for the tadpoles to enter the water (Figure 1, below). Among egg clutches that died from drought, the extension of the mucous strings varied from 11 to 27 cm (mean=17.7; SD=5.1; n=16) and was positively correlated with the ground steepness (r=0.78; P<0.002; n=13). When the water level of a pond receded excessively (>30 cm), the tadpoles died because the collapsing mucous string could not reach the water (n=15 nests). When ponds were bordered by grass, the frogs tended to concentrate foam nests at grass-free areas (bare soil) if available or built them spread out (not communally) amidst dense vegetation (n=2 sites, n=12 foam nests).

Amplectant pairs of E. nattereri (n=5) did not release eggs or make foam in the buckets (no resting support) within the 24 h of observation; those of P. cf. fuscomaculatus (n=3) built foam nests during the early morning following collection, but their nests appeared more flattened than those found in natural conditions.

The tadpoles fed, grew and completed their larval phase (about 40 days) in the water. Pond drying (n=15 events) was a severe source of mortality of eggs/early tadpoles near the beginning (September–November) of the reproductive season, with about a thousand nests lost during the study period. Foam nests did not substantially delay mortality after the nest had collapsed; maximal observed survivorship in communal nests was 2/3 days after pond drying, depending on the occurrence of cloudy wet days.

Infestation of foam nests by predatory maggots of the fly B. niger was delayed in relation to the beginning of the reproductive season and started as late as November (2003); these flies were ubiquitous in nests from December onwards. Tadpoles of Leptodactylus fuscus (Leptodactylidae) (15.0 mm TL; Gosner stage 25) preyed upon tadpoles of E. nattereri (6.4 mm TL; Gosner stage 23) that were leaving collapsing nests through the mucous string; these predatory tadpoles entered the water when the pond was formed, about 40 h before. Examination of the gut contents of 20 L. fuscus tadpoles, collected when aggregated under a collapsing E. nattereri nest, revealed that four of them had ingested one or two E. nattereri tadpoles. In October (2003), we found tadpoles (40–55 mm TL; n=3) of Leptodactylus labyrinthicus (Leptodactylidae) feeding on eggs of a freshly built E. nattereri foam nest that was partially in contact with water.

An adult male E. nattereri (SVL 41.7 mm; AAG-UFU 2460) was found being preyed on by a giant water bug Lethocerus sp. (Heteroptera, Belostomatidae) (~70 mm TL; voucher
Figure 1. Above: foam nest anchoring in *Eupemphix nattereri*. Note that the foam nest (~40 h old) is on a platform excavated in the soil and far from the water level (thin arrow). There are also platforms (thick arrow) to the left that are unoccupied. Bar ~9 cm. Below: a nearly 40-h-old collapsing foam nest. Note the wet mucous string through which the early tadpoles moved towards the water. Scale bar ~6 cm.
Figure 2. Several aspects of the predation of *Euphemix nattereri* by the whistling heron (*Syrigna sibilatrix*). Above: a couple of herons, each one with an adult *E. nattereri* in the beak. Middle: a male heron with an amplexant pair of *E. nattereri* in his beak (the male frog did not release the female and both escaped predation). Below: a female heron washing an adult *E. nattereri* prior to consumption; note the foam released by the frog while being washed. Note also in the above and middle pictures, the communal foam nests at the pond’s margin. More illustrations on several aspects of the natural history of the species are at the Amphibiaweb (http://elib.cs.berkeley.edu).
AAG-UFU 2461) at 01:30 h. We observed \(n=2\) times crab-eating raccoons \((Procyon cancrivorus\) (G. Cuvier, 1798), Mammalia, Carnivora) preying upon adult frogs that were aggregated for reproduction. Five times we found empty skins \((n=20)\) and carcasses \((n=8)\) of adult E. nattereri in association with raccoon tracks. Besides skins, raccoons did not ingest female reproductive systems (ovaries and oviducts filled with eggs) \((n=18)\) body remains). During diurnal \((07:00–10:00 h)\) calling and spawning activities, four bird species were observed preying on or seizing adults. Whistling herons, Syrigna sibilatrix (Temminck, 1824) (Ciconiiformes, Ardeidae), were observed preying upon adults \((n=6)\) (Figure 2). Before ingesting a frog, herons washed \((n=2)\) it or not \((n=1)\) by shaking it back and forth in water for 2–7 min (Figure 2, below). The herons also consumed \((n=2)\) frog remains left by raccoons. Two guira cuckoos, Guira guira (Gmelin, 1788) (Cuculiformes, Cuculidae), were observed preying upon adult frogs. One bird let the frog free after 2 min shaking it with its beak; the other swallowed the frog, but regurgitated it seconds later; it was captured again and swallowed definitely. Two other bird species tried unsuccessfully to feed on adult E. nattereri. One great kiskadee, Pitangus sulfuratus (Linnaeus, 1766) (Passeriformes, Tyraniidae) \((225\ mm\ TL)\), caught frogs \((n=3)\) while they were floating on the water. In all cases the frog fled immediately after the bird landed close to the pond. After handling a frog, this bird seemed distressed and cleaned its beak by wiping it on earth. One individual of the striated heron, Butorides striata (Linnaeus, 1758) (Ciconiiformes, Ardeidae), was unsuccessful in capturing frogs because calling males \((n=3)\) or amplexing couples \((n=5)\) took refuge under a communal foam nest when the bird approached. Diving \((n=15)\) and hiding within the communal foam nest \((n=15)\) were also typical behaviours performed by the couples when approached by a human observer. When calling, floating or when in the beak of a bird, the frogs kept all the four limbs well stretched (Figure 2), making the eye-like lumbar glands quite visible. In the studied region, fire ants \((Solenopsis\ sp.)\) were ubiquitous around ponds. Although they swarmed around newly built foam nests, they could not remove eggs or embryos from it while it remained wet \((n=15)\) events).

Digging the soil around the pond during the day allowed us to find 12 individuals (males and females) of E. nattereri that were buried between 5 and 50 mm below the surface.
Discussion

Construction of a terrestrial foam nest anchored on an excavated platform is a previously unknown reproductive behaviour for a Neotropical frog and it appears to represent a strategy for removal of the eggs/embryos from direct contact with water to avoid aquatic egg predators, such as *L. labyrinthicus* tadpoles. At our study site, *L. labyrinthicus* tadpoles are known to enter floating foam nests and consume conspecific eggs, and eggs of Leiuperidae species, such as *P. cuvieri* (Silva et al. 2005) and *P. cf. fuscomaculatus* (Giaretta and Menin 2004). *Leptodactylus fuscus* tadpoles preyed upon early tadpoles of *E. nattereri* (present study) and they are also known to swarm under foam nests of *Engystomops pustulosus* (Downie 1988). Anchoring the foam nest on steep terrain facilitates its isolation from the receding water and makes it easier for the tadpoles to reach the water with the aid of gravity after the nest breaks down. The dependence of *E. nattereri* on foam nest breakdown to deliver the tadpoles to the water closely resembles the reproductive strategy observed in some Rhacophoridae frogs (*Chiromantis* spp.) (Coe 1974; Seymour and Loveridge 1994). Some Leiuperidae species can construct foam nests while floating without a solid base for the female to rest on (Sexton and Ortleb 1966; Hödl 1990; this study); our data suggest that female *E. nattereri* are so dependent on a resting platform to build the foam nest that they cannot even start to release eggs without such a supporting point.

As in other Leiuperidae frogs (Hödl 1990, 1992; Ryan 1985, Giaretta and Menin 2004), communal nesting was facultative in *E. nattereri* and related to dense reproductive aggregations. The known communal foam nests of Leiuperidae frogs are simple aggregates of nests built side by side in a single layer (Hödl 1992; Giaretta and Menin 2004); those of *E. nattereri* were very compact, in such a way that individual nests could hardly be recognized. As couples of *E. nattereri* preferentially built their foam nests on bare steep banks, the physical structure of the water body seems to play an important role in nest aggregation, but other factors may be promoting this behaviour as well. A positive effect on the extension attained by the mucous string is expected in communal nests, but this appeared to be modest in *E. nattereri*. In *Pleurodema diplolister* (Peters, 1870), another foam nesting Leiuperidae frog, the females do not produce mucus constantly while spawning and if the foam platform is experimentally removed in the middle of the process all the subsequently released eggs sink, even with the male beating them (Hödl 1992). Couples of *E. nattereri* readily left nest construction site if disturbed. When they returned to restart egg-laying, they might use any previously constructed nest, a behaviour that would also favour communal nesting formation. Behaviour, such as hiding from approaching predators under already built communal foam nests and burrowing into earth at the pond margins, appear to allow *E. nattereri* to extend their reproductive activities (calling and spawning) into the daytime by reducing the risks of death by predation.

The congregation of individuals for reproduction may primarily represent a lack of suitable sites for reproduction, but, as in other frogs, it may result in a dilution of the predatory pressure (Ryan et al. 1981). Burrowing behaviour has also been described in *Pleurodema diplolister* (Carvalho and Bailey 1948; Hödl 1992) and, in both species, earth scraping is facilitated by the presence of enlarged horny inner metatarsal tubercles, which in *E. nattereri* also assist in anchoring the foam nest.

In the studied region, from mid-rainy season on, the predatory maggots of *B. niger* may inflict severe loss of offspring of *Physalaemus cuvieri* (Menin and Giaretta 2003) and probably also of *E. nattereri*. Starting reproduction with the onset of rains may allow *E. nattereri* to avoid nest infestation by these flies, but also represents a greater risk of offspring loss due to pond drying.
Disturbances to the water surface, such as those produced by frogs while calling or swimming, could trigger predatory behaviour by water bugs (Hinshaw and Sullivan 1990; Toledo 2003). After amplexus begins, females of *E. nattereri* may leave the water while waiting for ovulation. This behaviour may minimize the chances of being preyed upon by the water bugs; a similar behaviour has been observed in several *Physalaemus* species (Hödl 1990; Ryan 1985; Giaretta and Menin 2004). In our region, the predatory water bug is also known to prey upon *Physalaemus* cf. *fuscomaculatus* and *Scinax* sp. (Anura, Hylidae) (Giaretta and Menin 2004).

The toxins present in the skin of a frog can prevent predation (Duellman and Trueb 1986). In *E. nattereri*, skin substances, such as physalaemins, are to be expected (Erspamer et al. 1964; Duellman and Trueb 1986). Behaviour, such as washing (herons), skinning (raccoons) and regurgitation (guira cuckoos) (see also Sazima and Caramaschi 1986; Rodrigues and Oliveira Filho 2004), are indicative of the presence of toxic cutaneous secretions in *E. nattereri*. Vertebrates known to consume adult *E. nattereri* include frogs (França et al. 2004), possibly snakes (Martins and Duarte 2003) and foxes (Bezerra 1998).

Eggs of *Engystomops pustulosus* were consumed when freed of the foam and offered to *Leptodactylus fuscus* tadpoles (Downie 1988, 1990), but, as far as we know, there is no report of consumption of eggs in foam nests of any Leiuperidae species by terrestrial vertebrates. The behaviour of the crab-eating raccoon in refusing to feed on oviducal eggs may also be indicative of the presence of toxic or distasteful substances in the foam or eggs. In the present study, the display of the eye-like lumbar glands by individuals of *E. nattereri* was not effective in inhibiting visually orientated predators such as birds.

In conclusion, the terrestrial foam nest of *E. nattereri* appears to have evolved as an adaptation to avoid loss of eggs and early tadpoles to aquatic predators. In this species, the communal foam nesting is facultative and appears to result unintentionally from (1) the massive aggregation of adults for reproduction, (2) the selection of steep and bare ground to anchor the nests, and (3) disturbed couples restarting egg-laying beside previously built nests. A possible function for the communal nest in the species is that it can act as a shelter under which egg-laying couples can take refuge when threatened by visually orientated predators.

**Acknowledgements**

Financial support by CNPq and FAPEMIG. Grants by CNPq (AAG) and CAPES (KGF). A. S. Rand, J. R. Downie and G. Machado critically reviewed an early version of the manuscript. M. Menin, M. N. de C. Kokubum and R. C. Costa helped in the field work.

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