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Predation upon eggs of the terrestrial foam-nesting frog *Leptodactylus fuscus* (Leptodactylidae) by larvae of the ground beetle *Loxandrus oophagus* (Carabidae: Loxandrini)

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Many aquatic and terrestrial invertebrates (Lacey, 1979; Villa et al., 1982; Duellman and Trueb, 1994; Wells, 2007) and vertebrates (Duellman and Trueb, 1994; Rödel et al., 2002; Roberts, 1994; Lingnau and Di-Bernardo, 2006) have been reported to prey on anuran eggs. Ephydrid and phorid fly maggots are well-known predators of eggs of foam-making frogs, infesting exposed foam nests of leptodactylids (Menin and Giaretta, 2003; Villa et al., 1982), leiuperids (Bokermann, 1957), rhacophorids (Yorke, 1983), hyperoliids (Vonesh, 2000) and myobatrachids (Davis and Disney, 2003).

Species of the *L. fuscus* group share the behavior of building foam nests within previously excavated underground chambers, putatively protecting their eggs from fly maggots predation (Menin and Giaretta, 2003; Carvalho and Giaretta, pers. comm.). However, after the discovery of the ground beetle *Loxandrus oophagus* Costa, Vanin and Carvalho (2011) with morphologically specialized larvae, being predators of anuran eggs inside underground chambers, it is possible to recognize a way back pattern of predation pressure against Neotropical terrestrial foam-making anurans (*Leptodactylus fuscus* species group). As this interaction was only described recently, many aspects of the predator-prey relationship are still unknown. This work aims to quantify the impact of predation by larvae of the ground beetle *Loxandrus oophagus* on egg clutches of the terrestrial foam-nesting frog *Leptodactylus fuscus* and analyze the influence of breeding site and month on predation frequency. Our hypothesis is that predation rate might vary (i) spatially, as the breeding sites are different with respect to vegetation, water, human-generating processes, and (ii) temporally, according to Menin and Giaretta (2003), which reported that predation rate on exposed foam nests by dipteran larvae increases along the breeding season. Additional data on *L. oophagus* natural history are described in Costa, Vanin and Carvalho (2011).

Field works were conducted from 2008 to 2010 in Uberlândia (18°55′23″S, 48°17′19″W; 865 m a.s.l.), Minas Gerais, Brazil. The regional climate is classified as Aw, according to the revised Köppen-Geiger climate classification (Peel et al., 2007), characterized by two well-defined seasons, a rainy/hot summer (September to March) and a dry/mild winter (April to August) with occasional frosts. The mean annual precipitation is around 1,580 mm (1,015–2,220 mm; Silva and Assunção, 2004). The original vegetation was the Cerrado Biome (Oliveira and Marquis, 2002).

Preliminary field observations revealed that males of *L. fuscus* often built underground chambers underneath burlap sacks and females were receptive to this behavior by promptly choosing those places as nesting sites. Considering this, we distributed 220 folded (four layers) burlap sacks made of vegetal fiber (approximately 65 x 40 cm^2) in areas in which calling males where previously recorded. Sacks were settled onto previously cleared and softened soil on ten breeding sites of the *L. fuscus*, located around temporary and permanent ponds (human altered areas) of natural grasslands or pasture bordered by Cerrado stricto sensu (Appolinario and Schiavini, 2002) and palm grove marshes (regionally called Veredas).

We searched for foam nests underneath sacks by raising each one twice a week from October to December 2008 and from September to December 2009. Whenever we found foam nests, we handled them with a teaspoon delicately to seek for *L. oophagus* (adults or larvae). Neither was the frogs' eggs nor carabids removed from

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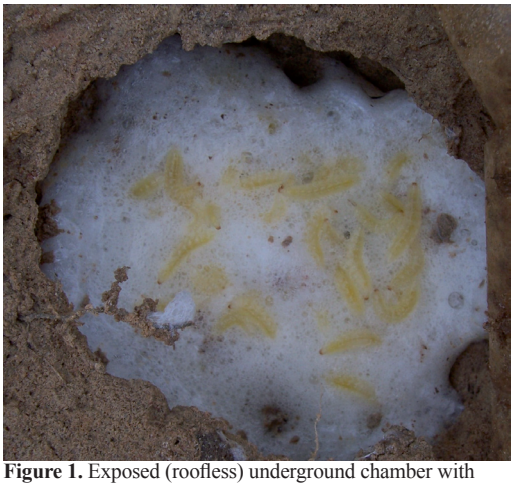

Figure 1. Exposed (roofless) underground chamber with a foam nest of *Leptodactylus fuscus* infested by *Loxandrus oophagus* larvae.

foam nests. When we found foam nests, we poured about 50 ml of water into them, and covered them with an extra small piece of transparent plastic (about 5x5 cm²) to compensate for the desiccation caused by the removal of the chamber roof and manipulation. The influence of site and month on nest fate (preyed or not) was tested using a two-factor log-linear model (Gotelli and Ellison, 2004) with R (version 2.13) (R Development Core Team, 2011).

We found foam nests and predators in all sampling months (Table 1). We recorded 60 foam nests (7 out of 8 monitored sites) in 2008, 15 (25.0%) of them were infested by *L. oophagus* larvae. We recorded 79 foam nests (6 out of 7 monitored sites) in 2009, seven (8.9%) of them were infested by *L. oophagus* larvae (Table 2). The relative frequency of foam nests infested by site in each year varied from zero (three sites in 2008 and two sites in 2009) to 57% (4 of 7 foam nests infested at one site in 2008; Table 2). All the infested egg clutches were completely consumed (Figure 1). *Loxandrus oophagus* larvae (between 7 and 23 by egg clutch; N = 20 foam nests) consumed the eggs, but the foamy aspect of the clutch was kept almost intact. Breeding site and month did not influence the presence of *L. oophagus* larvae in foam nests in both 2008 (Likelihood ratio = 18.06; D.F. = 20; P = 0.58) and 2009 (Likelihood ratio = 14.22; D.F. = 23; P = 0.92; Tables 1–2).

Carabid, tenebrionid, and staphylinid beetles are known to prey upon eggs/embryos of terrestrial/arboreal (non-aquatic) breeding frogs (Villa, 1977, 1984; Villa and Townsend, 1983; Duellman and Trueb, 1994; Neckel-Oliveira and Wachlevski, 2004), yet predation upon terrestrial foam nests by beetles has not hitherto been reported until the beginning of the last year (Costa, Vanin and Carvalho, 2011). Martins (1988) reported on hydrophilid beetle larvae in *L. fuscus* foam nests, but he noticed that the eggs were in putrefaction. In contrast, our study was conducted considering only viable foam nests as samples.

Although Downie et al. (1995) demonstrated that one species of phorid fly is able to infest even underground foam nests of *L. fuscus*, it seems that females are supposed to lay their eggs whereas the foam nests are somehow exposed during foam beating, when the chamber roof is still uncovered. So, the ground beetle *Loxandrus oophagus* is the first effective egg predator of Neotropical foam-making anurans with nests in subterranean chambers.

Fly maggots infested foam nests of all six species of foam-making frogs with exposed spawns in our study area (see Menin and Giaretta, 2003). A previous study found that egg infestation increased throughout the reproductive season, when the number of maggots in exposed nests reached 326, and maggots represented an important source of mortality (mean 74%) for both eggs and embryos of *P. cuvieri* in the middle of the reproductive season (Menin and Giaretta, 2003). In contrast, mortality by *L. oophagus* larvae on egg clutches of *L. fuscus* apparently does not have such a strong sole influence on their populations, since the percentage of preyed egg clutches among sites, months, or even years can be very low (about 15% of 139 monitored clutches). Besides, infestation by carabid larvae did not show any temporal pattern and they prey only upon eggs. The lower frequency of preyed egg clutches by the ground beetle may be related to the difficulty of predators to find subterranean egg clutches.

Predation has long been thought as a strong selective force that influences and shapes the behavior, morphology, and life history of prey species (Caldwell, 1986; Laurila et al., 1998; Hoverman, 2010). In this context, it has been hypothesized that high predation upon eggs and larvae in aquatic environments is a major selective pressure that might have been led to the evolution towards non-aquatic reproductive modes in frogs, such as terrestrial breeding (Magnusson and Hero, 1991). Our data indicated that anurans that spawn in excavated chambers cannot avoid egg predation by insects, yet the mortality due to predation (proportion of infested foam nests) may be proportionally very lower in comparison with exposed spawns (see Menin and Giaretta, 2003).

Table 1. Number of foam nests per month, number of infested foam nests, and monthly proportions of infested foam nests of *Leptodactylus fuscus* in 2008-2009.

Month/Year	Number of sampled foam nests	Number of infested foam nests	Frequency of predation
October/2008	27	4	14.8%
November/2008	22	10	45.5%
December/2008	11	1	9.1%
September/2009	10	1	10.0%
October/2009	26	3	11.5%
November/2009	24	2	8.3%
December/2009	19	1	5.3%
TOTAL	139	22	---------

Table 2. Number of foam nests of *Leptodactylus fuscus* in 2008-2009 according to the occurrence of predation.

	Predation in 2008		Predation in 2009	
Site	No	Yes	No	Yes
1	21	6	26	2
2	3	4	4	1
3	2	0	-	-
4	2	0	-	-
5	-	-	-	-
6	6	0	15	3
7	3	1	-	-
8	8	4	22	1
9	-	-	2	0
10	-	-	3	0
TOTAL	45	15	72	7

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