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Whipped cream cravings in the rainforest: predation of foam nests of *Physalaemus ephippifer* (Anura: Leptodactylidae) by *Platemys platycephala* (Testudines: Chelidae) in central Guyana

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Non-aquatic oviposition has long been recognized as a major trend in amphibian evolution (LUTZ 1947, DUELLMAN & TRUEB 1986, WELLS 2007) and the selective pressures that drive the evolution of non-aquatic reproduction, particularly in anurans, have long been a subject of speculation (e.g., GOMEZ-MESTRE et al. 2012, MÜLLER et al. 2013). The most widely accepted explanation for this recurring trend is predator avoidance during the most vulnerable life-history phases (i.e., egg and early larval development) in aquatic environments. However, this theory ignores the fact that terrestrial eggs and subsequent early ontogenetic stages are preyed upon by a wide range of both vertebrate and invertebrate predators, often at rates similar to those reported for aquatic breeders (e.g., MENIN & GIARETTA 2003). Several alternative driving factors for terrestrial anuran reproduction have therefore been discussed, including reduced larval competition, reduction of the risk of unpredictable drying-up of aquatic sites, limited oxygen availability in tropical ponds, avoidance of strong currents in lotic environments (reviewed in WELLS 2007), and a range of habitat factors that are considered promoting terrestrial reproduction (MAGNUSSON & HERO 1991, MÜLLER et al. 2013). Given the observed diversity of amphibian reproductive modes that, particularly in the tropics, co-occur in the same general habitat, it seems challenging if not unlikely to find a universal explanation for the evolution of non-aquatic reproduction in amphibians. Different species or lineages simply seem to have developed different strategies to cope with similar selective pressures.

The use of foam nests as incubation environments for anuran eggs and larvae is probably one of the most fascinating examples of an adaptation to the various selective pressures associated with terrestrial reproduction. It is also a striking example of convergent evolution of life history strategies, as it appears to have evolved independently in several major anuran lineages. At least seven anuran families (Hylidae, Hyperoliidae, Leptodactylidae, Limnodynastidae, Microhylidae, Myobatrachidae, and Rhacophoridae) with representatives on all continents that support amphibians are currently known to make use of foam nests. Members of the mainly Neotropical family Leptodactylidae generally deposit their eggs in foam nests, but construction and deposition as well as the extent to which larval development is confined to these nests differ among genera and even between species within the same genus (HÖDL 1986, PRADO et al. 2002, HADDAD & PRADO 2005). Leptodactylid foam nests are thought to protect eggs and developing embryos from predation and desiccation (HEYER 1969, DOWNIE 1988). The materials used for foam nest construction must therefore be environmentally resilient and comparatively resistant to physical and chemical damage (e.g., imposed through invertebrate and vertebrate predators as well as bacteria and fungi), yet compatible with naked eggs and sperm. These are properties that seem to be mutually exclusive, but a recent study on the components of foam nests of the Túngara frog (*Engystomops pustulosus*) showed how this seemingly paradox situation is resolved through a combination of several proteins that predominate in foam nests (FLEMING et al. 2009). The noc-

turnal Neotropical frog *Physalaemus ephippifer*, closely related to the Túngara frog, which was previously placed in the same genus, exhibits a reproductive strategy that can be characterised as r-selected reproduction (high number of small eggs, fast larval development) that likely evolved in response to the unpredictable and high-risk environments in which the species occurs. At our study sites in central Guyana (Mabura Hill Forest Reserve, MHFR, 05°09'19.30" N, 58°41'58.96" W; and Iwokrama Forest, 04°40'17.5" N, 58°41'06.6" W), where all observations presented in this paper were made, the species is either most abundant in disturbed habitats (Iwokrama Forest) or exclusively occurs at heavily disturbed sites (Mabura). Here it reproduces in puddles and ditches mainly along logging roads and skid trails. Nest densities can be very high. At Iwokrama, up to 50 foam nests per search hour were recorded in a single night in the main rainy season (July 2004), along a single stretch of approximately 2 km of access road connecting the field station with the main road that crosses the forest. Throughout a short observational period from May to July 2004, 32 nests were recorded at a single site, a small, shallow puddle (app. 50 cm diameter, maximum depth 20 cm) located at an access road close to the field station in the Mabura Hill Forest Reserve. In Guyana, *P. ephippifer* can be regarded as a prolonged breeder that reproduces throughout the year, even during the dry season, but with reproductive and calling activity peaks at the onset and throughout the core rainy season (May to July in average years).

Foam nests are produced at night, at the edges of small to medium temporary bodies of water (see above). The construction behaviour of *P. ephippifer* from Belém, state of Pará (Brazil), has previously been described in detail by HÖDL (1990). Our own observations largely correspond to these descriptions (Fig. 1). However, while several nests (up to three) could be observed at the same time in a single locality, communal nests as reported by HÖDL (1990) were not observed in either of the two study sites. The major-



Figure 1. Amplexant pair of *Physalaemus ephippifer* constructing a foam nest, observed on 02 May 2003 between 01:00 and 01:30 h, Mabura Hill Forest Reserve, Guyana. Photo: RE.

ity of nests (75%, $N = 32$) were located at the edge of the water surface of the respective aquatic sites and usually attached to, or covered by, plant structures, such as large *Cecropia* sp. leaves (88% of all recorded cases, $N = 32$). The foam nests of *P. ephippifer* exhibit the typical hemispherical shape as reported for other members of the genus. The mean nest diameter observed at Mabura Hill was 6.33 cm ($sd = 2.6$, $N = 28$) and nests contained an average of 500 tadpoles ($sd = 172$, $N = 20$). Embryogenesis was found to be rather rapid, and tadpoles were usually ready to leave the nest after two days at GOSNER stage 21. However, tadpoles could still be retrieved from nests on consecutive days after the first “hatching” was observed. Environmental persistence time of nests depended largely on prevailing weather conditions and occurrence of predation. After two to four days, the majority of nests would show signs of partial damage, i.e., collapsed foam hemisphere or missing segments, and had completely dissolved or vanished after four to six days. These observations largely correspond to previous observations of developmental times and environmental persistence of foam nests in *Engystomops pustulosus* with the exception that here, persistence times were reported to extend to 10 days in tropical conditions (DOWNIE 1993, FLEMING et al. 2009).

While a comparatively small percentage of nests were found to have been partially or completely damaged, none of the recovered nests showed clear signs of desiccation. Further evidence for the assumed protective function of foam nests that prevent eggs and larvae from desiccation and lethal overheating (GORZULA 1977) was obtained from thermal buffering experiments, in which internal temperatures of ten *P. ephippifer* nests and ambient air temperatures were monitored at continuous intervals (mean temperatures in °C integrated for three time-increments: [1] 02:00–10:00 h, [2] 10:00–18:00 h, [3] 18:00–02:00 h) over the course of three days (from shortly after the production of foam nests to first hatching of tadpoles). Temperatures were recorded using thermobutton data loggers (i-Button-TMEX, Version 3.12 ± 0.1 °C). Pairs of data loggers were placed in the centre of each nest and on a wooden pedestal at approximately the same height outside nests, respectively. All tested nests ($N = 10$) showed significant differences between the internal nest temperature and ambient air temperature, with internal nest temperatures being generally lower than the ambient air temperatures (mean 0.5 °C, $sd = 0.1$, $N = 90$, $p < 0.01$). The majority of observed deviations (55%) were recorded for time-increment two (time of the day with the highest ambient temperatures and most intense solar exposure), while the remainder (45%) were distributed across time-increments one and three (periods with lower ambient temperatures). Temperature increases of as little as 0.5°C have previously been shown to result in increased mortality in tadpoles of the leptodactylid frog *Leptodactylus petersii* (ERNST et al. 2007). In terrestrial eggs that are exposed to higher temperatures, metabolic rates and development of embryos are limited by rates of gas diffusion (SEYMOUR & LOVERIDGE 1994). The buffering capacity provided by *P. ephippifer* foam nests may therefore

represent an effective protection during periods with increased temperatures. However, this assumption still needs to be tested systematically.

Apart from these abiotic environmental factors that can affect larval development and mortality in terrestrial breeders, biotic factors such as predation are important regulatory elements, affecting both larval development, for example through predator-induced hatching (e.g., WARKENTIN 1995, 2011), and population viability through increased mortality (e.g., MENIN & GIARETTA 2003). In our study area at the Mabura Hill Forest Reserve, predation and parasitism of foam nests were found to be important factors influencing mortality in at least four different leptodactylid species that were monitored systematically (KONRAD 2005 unpubl. data, ERNST et al. 2007). The majority of observed instances of predation were associated with invertebrate predators. Predation impacts ranged from single egg removal (i.e., observation of *Angiopolybia* sp. wasps pulling several eggs from a foam nest of *Leptodactylus rhodomystax*) to total predation (i.e., total consumption of nests of *L. rhodomystax* and *L. knudseni* by freshwater crabs of the family Pseudothelphusidae). Parasitism by flies of the families Ephydriidae (*Beckeriella willistoni*) and Phoridae (unidentified species) was observed in two *Leptodactylus* species (*L. knudseni*, mean number of fly larvae per nest = 550, sd = 483, min. = 30, max. = 1196, N = 4; *L. petersii*, 92 pupae per nest, N = 1) and found to have varying effects on larval mortality (low in *L. knudseni*, mean = 14 tadpoles per nest, sd = 1.6, N = 4, and high in *L. petersii*, 812 tadpoles per nest, N = 1). High mortality rates caused by parasitic flies have previously been reported for *L. knudseni* in the Manaus region of Brazil (GASCON 1991). In this study, only 5% of all investigated nests were found to be parasitised, but mortality was 100% whenever parasitic fly larvae were present. Interestingly, nests of the co-occurring species *L. rhodomystax* and *P. ephippifer* were found to be not parasitised by flies despite the fact that in several cases, infested *L. knudseni* nests were located in direct proximity to nests of *P. ephippifer*. Whether the short environmental persistence time of *P. ephippifer* nests that may not allow full larval development of the parasitic flies is responsible for the observed absence of parasitism in this species is yet to be tested. However, observations of parasitism of nests of the closely related *P. cuvieri* by the Ephydriidae *Beckeriella niger* (MENIN & GIARETTA 2003) contradict this assumption. These authors even go as far as proposing an obligate relation between the dipteran parasite and its host species. *Physalaemus* specimens from Guyana have recently been referred to as *P. cuvieri* (COLE et al. 2013), which was originally described from the Brazilian Cerrado. This classification still requires confirmation. However, if specimens from Guyana indeed turn out to be conspecific with the specimens observed by MENIN & GIARETTA (2003) in the Cerrado of the Brazilian state of Minas Gerais, our observations would show that the nature of this fly-frog interaction might vary between populations. Another interesting detail in this context is an observation reported by KOK & ERNST (2007): Nests of the two species (*P. ephippifer*

and *L. rhodomystax*) that were found to be unaffected by parasitic flies are used as alternative larval deposition sites by the syntopically occurring Aromobatid frog *Allobates spumaponens*. This behaviour is the only known case of interspecific brood-parasitism in which the male is the acting parasite (KOK & ERNST 2007). The nature of this interspecific interaction has not been fully resolved, and so far there is no clear indication that *Allobates* larvae actually feed on eggs or larvae of their hosts.

In contrast to related studies (e.g., RÖDEL et al. 2002), vertebrate predators that prey on terrestrial developmental stages (eggs, larvae, or entire foam nests) seem to play only a minor role in affecting the reproductive success of foam nest-constructing frogs at our study sites. Here, the impact of invertebrate predators appears to be much more severe. However, there is one remarkable exception, reported for the first time in this study: Although detailed studies are lacking (SOUZA 2004), the monotypic chelid turtle *Platemys platycephala* is assumed to be a strictly carnivorous predator with a preference for tadpoles and anuran eggs (reviewed in BÖHM 2013). Apart from a single observation in captive-reared specimens (THIEME & THIEME 1996), previous studies exclusively reported on predation in aquatic environments where surface spawn films of several microhylids (*Chiasmocleis* sp.) or bufonid spawn (*Rhinella* sp.) were consumed. *Platemys platycephala* has traditionally been referred to as a highly aquatic species, but this view was corrected by BÖHM (2013) who found the species to be much more terrestrial than previously assumed. This makes the species unique among the generally aquatic family Chelidae and it corresponds to our observations from central Guyana where the species was frequently found in closed forest habitats at a considerable distance from the nearest larger aquatic sites. Particularly during heavy rainfall events, *P. platycephala* appears to move over land for larger distances and regularly invades small- to medium-sized ponds and large puddles where it is regularly observed feeding on tadpoles of the genera *Leptodactylus* and *Phyllomedusa*, as well as on small fish (Rivulidae). The latter are most likely ingested as carrion rather than actively hunted. Although active feeding could not be observed, the occurrence of *P. platycephala* in water bodies used as breeding sites by *Phyllomedusa* sp. has also been recorded from central French Guiana (observation by SB).

On 02 May 2003 at around 9:30 a.m., we observed an adult *Platemys platycephala* specimen feeding on a *Physalaemus ephippifer* nest that had been produced the previous night between 01:00 and 01:30 h (Figs 1 & 2). The locality corresponds to the oviposition site at MHFR, described earlier (shallow puddle on access road) and is situated several hundred metres from the nearest larger aquatic habitat (Maiko Creek, a medium-sized black-water stream) from which it is separated by a steep lateritic ascend. The entire foam nest was consumed within approximately 15 minutes, leaving nothing behind but a few foamy fragments (Fig. 2). To our knowledge, this is the first report of *P. platycephala* predation on the terrestrial foam nest of a leptodactylid frog, and in fact the first record of turtle



Figure 2. Predation on the foam nest depicted in Fig. 1 by an adult *Platemys platycephala* the following morning. A) close-up showing *Physalaemus ephippifer* larvae (indicated by white arrow) and foam attached to the head of *P. platycephala* during feeding; B) Total view, approximately ten minutes after beginning of observation.

predation on foam nests in general. Moreover, it is the first report of a South American chelid actively feeding in a terrestrial habitat. This is peculiar insofar, as previous studies on the buccopharyngeal mucosa of turtles showed that aquatic species, such as the closely related *Acanthochelys pallidipectoris* have smaller and less movable tongues than more terrestrial turtles and tortoises (BEISSER et al. 1995),

impeding their feeding outside their aquatic environments (WINOKUR 1988). Like other chelid turtles, *P. platycephala* are typical suction feeders. This feeding mode basically necessitates water to properly ingest food. Terrestrial feeding in *P. platycephala* is therefore likely to be bio-mechanically complex and restricted to less mobile or stationary prey items, such as foam nests.

So far, we do not know whether this observation represents standard behaviour and whether foam nests are typical items in the diet of *P. platycephala*. Therefore we cannot quantify the potential impact of this kind of predation on leptodactylid frog populations. Given the observed terrestrial mobility of *P. platycephala*, particularly during the rainy season, and the reproductive phenology of a vast number of foam nest-constructing frogs, it is at least likely that predation of foam nests by *P. platycephala* is the norm rather than an exception. Whether more terrestrial species, such as the syntopic tortoise *Chelonoidis denticulata*, exploit the same resource is as yet unknown. It is also unclear whether different foam nest-predators and/or -parasites (freshwater crabs, parasitic flies, “parasitic” frogs, and chelonians) are actually engaged in competitive interactions for a potentially limited resource. To answer these open questions, more intense dietary and movement pattern studies, covering different seasons and focusing on populations from various localities across the distributional range of *P. platycephala*, as well as quantitative assessments of the impacts on the populations of potential prey species are required.

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