ARTHROPOD PREDATORS OF LEPTODACTYLID FROG FOAM NESTS

Jaime Villa, Roy W. McDiarmid and José M. Gallardo

Department of Biology, University of Missouri, Kansas City, Missouri 64110 U.S.A.
Sección Herpetología, Museo Argentino de Ciencias Naturales, Avenida Angel Gallardo 470, Buenos Aires, Argentina.

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ABSTRACT

Several species of arthropods prey upon or utilize foam nests made by leptodactylid frogs. A spider (Lycosa pampeana) enters burrows made by Leptodactylus latinasus in Argentina and eats most of the eggs. Two genera of dytiscid beetles have representatives that lay eggs on the foam mass of Physalaemus pustulosus in Guatemala; beetle larvae hatch and swim in temporary ponds, where they feed on free-swimming tadpoles. Flies of the ephydrid Gastrops willistoni oviposit on Leptodactylus pentadactylus egg masses in Costa Rica and Brazil; maggots eat the developing embryos and may destroy the entire mass. Literature records of similar associations are reviewed.

One of the most specialized aspects of amphibian reproduction is the construction of foam nests by some frogs. Foam nests are built on vegetation or on the ground above water by many frogs of the families Leptodactylidae and Rhacophoridae (Noble, 1931; Porter, 1972). The foam is made by the male or female beating jelly with its limbs while in amplexus (Villa, 1972; Heyer and Rand, 1977). Once the eggs are fertilized, the egg mass is kicked vigorously by either or both parents into a froth resembling whipped meringue.

This breeding pattern, independently evolved in New and Old World frogs, is advantageous to some species because: (1) eggs and embryos are protected against desiccation when the outer foam dries forming a water-resistant surface; (2) eggs may be laid on dry land or in pits or holes in the ground, in areas that are likely to be flooded later; thus, embryonic development is well advanced when water becomes available; (3) eggs and embryos are not available to aquatic predators, such as fishes, leeches, planariae and larval arthropods, during the precarious immobile stages. Be-
cause of the foamy consistency of the nests, they are not swallowed readily by snakes, and field observations made by Villa indicate that mammals such as dogs, cats and raccoons, pay little attention to the nests. Insects including ants, wasps and some beetles, are potential predators of the eggs but, when placed on the foam, they often become hopelessly stuck and die after hours of struggle.

Therefore, it is interesting to note that several unrelated arthropods are adapted to exploit this potential food source thus taking advantage of this “Amphibian Egg Microhabitat” (Villa, 1978, 1980). Observations on these predators made independently by the authors over a number of years, together with literature records, are summarized herein.

**Spiders**

*Leptodactylus prognathus* Boulenger (= *L. latinasus* Jiménez de la Espada; see Heyer, 1978) is a small leptodactylid frog found in Southern Brazil, Argentina and Uruguay (Gallardo, 1964). Males build nearly spherical burrows in the mud that measure 4-5 cm in diameter and communicate to the outside by a tunnel up to 8 cm in length. Females are attracted to the tunnel by calling males. Amplexus occurs in the caves; a foamy nest containing about 370 eggs (each 2 mm in diameter) is produced. When the area becomes flooded, foam nests leave the caves and float to the surface. Upon hatching, tadpoles leave the foam nests and take on an aquatic existence (Gallardo, 1958).

Recent observations made near Buenos Aires (Argentina) by Gallardo indicate that the spider *Lycosa pampeana* Holmberg (Lycosidae) may enter the caves and eat the developing embryos sometimes causing the destruction of the entire clutch; approximately 40 percent of the nests recently observed had been attacked.

No other cases of spider predation on eggs of South American leptodactylids have been reported, nor is it known if *L. latinasus* nests are similarly attacked in other parts of its range. *L. latinasus* tadpoles are subject to heavy predation by the turtle *Hydromedusa tectifera*, the snake *Leimadophis poecilogyrus* and several insects, including bollworms, dytiscids (larvae and adults) and dragonfly nymphs (Gallardo, 1958).

**Dytiscids**

Adults and larvae of beetles of the family Dytiscidae are known to prey on tadpoles but are opportunistic and eat many other aquatic organisms as well. Two species in the subfamily Colymbetinae, *Rhantus* sp. (callidus Fab.) and species “near Ilybius” (Williams 1936:6), show some specialization for feeding upon leptodactylid tadpoles. In an interesting account unearthed from the entomological literature, Williams (1936) reported collecting frothy masses of a unidentified “frog or tree toad” in Escuintla, Guatemala.
From the description of the masses, and the geographic locality, the nest almost assuredly was that of the leptodactylid frog *Physalaemus pustulosus*, an identification with which Dr. L.C. Stuart (in litt. 1977) concurs. Four of the masses gathered on different occasions produced not only tadpoles but also “a number of larvae of a dytiscid beetle”; one of the masses was “dissected out and several dytiscid beetle eggs were found in the froth” (Williams 1936:6–7). Like the tadpoles, after hatching the beetle larvae find their way through and into the water.

“These larvae were about 5 mm long, exclusive of appendages, at the start... protected by dark chitinous plates, and were likewise graceful swimmers, though in no wise equaling the tadpoles in speed. For the most part they hung jaws agape, at the surface, breathing at the tail end of the body. But they quickly attacked the tadpoles, catching them suddenly in their sickle-like jaws, soon quieting their violent struggles, and sucking out the juices. They strove to gain the surface with their heavy prey so as to feed at leisure and to take in the air at the same time... As the larva grows, it sheds its skin, so that eventually it is a least a half inch long” (Williams 1936:6–7).

These dytiscids, like many other aquatic insects, feed on tadpoles as well as on other animals and may resort to cannibalism (as Williams also observed) when food supplies run short; thus, they are not prey specific. However, unlike most other predators, their eggs are laid on the egg masses of their future prey, an adaptation that assures that the larvae will have an abundant food supply for their development. This is especially critical in small temporary ponds and roadside ditches where *P. pustulosus* often breeds.

Williams’ report is especially interesting because it illustrates the initial stages in the evolution of an intraspecific association that many lead to the exploitation of a restricted food source, such as “frogflies” appear to have achieved by developing exclusively on centrolenid egg clutches (Villa, 1977, 1978, 1980).

**Ephydrid Flies**

Ephydrid flies were the first “frogflies” recorded in the literature*. Bokermann (1957) reported that the larvae of *Gastrops niger* Williston attack and consume the embryos of at least one amphibian species, the leptodactylid *Physalaemus cuvieri*. It is not clear if the relationship is obligatory for *G. niger* or it is able to develop in other media. A literature survey revealed surprisingly little natural history information for the entire genus *Gastrops*.

* After this paper was accepted for publication Villa came across and earlier publication describing a new frogfly. *Rhysops berthae* Costa-Lima (1946) (Diptera: Syrphidae; Melanostomini) is a fly whose larvae feed on eggs of *Centrolenella eurygnatha* Lutz in Rio de Janeiro, Brasil.
Shortly after Bokermann’s report, Wirth’s (1958) revision of Gastrops was published. Six species were recognized, but no natural history notes for any species, except Gastrops willistoni, were given. Brazilian specimens of G. willistoni were collected in the spawn of a species of Euphempix (= Physalaemus) by the late Bertha Lutz as noted by Wirth (1958:249; “parasita despostura de baterchio do genero Euphempix”). No other data were recorded, and Dr. Lutz died before she could be contacted for further information.

Recently Lawrence A. Lacey (in litt. 1978) found large numbers of G. willistoni adults ovipositing on L. pentadactylus egg masses near Manaus, Brazil (Fig. 1A). He noted that maggots (Fig. 1B) actually eat the frog eggs, and “in some of the nests one can find developing tadpoles right alongside of the hundred of fly larvae”, which is a clear indication that flies are ovipositing in healthy (as opposed to decomposing) foam nests. However, Lacey believes the maggots are not subsisting solely on frog eggs; the number of maggots found in each nest seems large enough to kill all of them. He is presently studying the interaction (Lacey, 1980).

In July, 1973, McDiarmid obtained a L. pentadactylus foam nest from a previously used depression near Rincón de Osa (Puntarenas Province), Costa Rica. The large foam nest (23 x 35 cm wide, 3-5 cm deep) was brought to the laboratory for observation; a frog egg was collected from the nest on that day. Four days later one small tadpole was found in the foam. Several maggots and a few pupae also were noticed, (Fig. 2). Six days after collecting the nest a thorough search of the foam revealed no L. pentadactylus larvae but many fly larvae in, and pupae on, the foam. Although it is not certain if the Leptodactylus were consumed by the maggots, considering Bokermann’s and Lacey’s reports, and the fact that the larvae of still another species of Gastrops also feed on frog embryos (Villa, 1980), this seems likely. It is not known if the larvae of G. willistoni always pupate on the surface of the foam as they did under laboratory conditions, of if they seek emergent vegetation, or float as Bokermann (1958) observed in the case of G. niger. Considering the paucity of natural history data for any species of Gastrops, the life history of G. willistoni certainly seems worthy of further study.

No estimates were made of the percentage of L. pentadactylus foam nests attacked. This species is the largest of Central American leptodactylids (Villa 1969, 1972), and has a large egg complement. One clutch reported by Muedeking and Heyer (1976) contained 952 eggs averaging 2.9 mm in diameter, and thus could provide an abundant food supply for fly larvae.

Flies emerging from the pupae collected from L. pentadactylus foam nests were identified as G. willistoni Cresson by Drs. GS. Byers and J. Scheiring. It is not certain if they are conspecific with Bokermann’s (1958) specimens identified as G. niger. Cresson (1914) reported that G. willistoni is “allied to G. niger”, and both occur in Brazil (Wirth 1958). Unfortunately the whereabouts of Bokermann’s specimens are unknown (Bokermann in litt., 1976).
W. Ronald Heyer (in litt., 1977) observed numerous maggots, probably fly larvae, in some of the foam nests of *Leptodactylus bufonius* Boulenger examined in Argentina (Embarcación: Salta). Apparently the maggots were eating the embryos, but this was not confirmed. Like *L. latinasus*, *L. bufonius* builds foam nests in hollow cavities dug in the mud near temporary ponds, and may seal the entrance with mud (Cei, 1949).

**Wasps**

Wasps have been occasionally reported to feed on frog eggs (McDiarmid, 1975, 1978), but little information has been given on the incidence and nature of the association. McDiarmid (1978) observed an unidentified wasp removing eggs, one by one until all were gone, from *Centrolenella colymbiphyllum* in Rincón de Osa (Puntarenas Province), Costa Rica. Similar observations were made on *Agalychnis callidryas* egg masses in Matagalpa, Nicaragua (Villa, 1978). In both cases the taxonomic identity of the wasp was unknown.

The only case of wasp predation on leptodactylid foam nests was studied by Lacey (1980) near Manaus, Brazil. The vespid *Angiopolybia pallens* (Lepeltier) was frequently seen removing eggs and foam from *Leptodactylus pentadactylus* nests (Fig. 3a). Attempts were also made to remove tadpoles (Fig. 3b) but they were unsuccessful because of the large size of the tadpole relative to the wasps.

**Discussion**

It is widely believed that in some amphibians the development of arboreal or terrestrial breeding habits freed their larvae from predation. However, while depositing their egg clutches outside water makes them unavailable to aquatic predators, they become exposed to a wide variety of terrestrial ones, and these may be more devastating and widespread than hitherto recognized.

Little attention has been paid to organisms associated with amphibian eggs, although several interesting relationships with organisms ranging from fungi and algae to insect larvae, have been found or are suspected to exist (Villa, 1977, 1978, 1979a-b, 1980). Rather than occurring as isolated instances, these interspecific associations probably are more common than hitherto expected, particularly in tropical habitats. In the cases cited herein, spiders, wasps, and insect larvae have been found associated with amphibian eggs. While details of the associations are not well known, the impact on the reproductive success and population dynamics of these frogs may be considerable. Undoubtedly other associations involving amphibian eggs exist. The discovery of new egg-associates, and the clarification of the nature of the associations already known, or suspected to exist, should prove to be an extremely interesting field of study.
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Resumen

 varias especies de artrópodos se alimentan de los huevos de ranas leptodactilidas depositadas en nidos espumosos. Una araña, Lycosa pampeana (Familia Lycosidae) entra a las madrigueras excavadas por la rana Leptodactylus latinasus cerca de Buenos Aires, Argentina, y se come la mayoría de los huevos de la rana. Dos especies diferentes de coleópteros acuáticos (Familia Dytiscidae) depositan sus huevos en las masas espumosas de Physalaemus pustulosus en Escuintla, Guatemala. Las larvas del coleóptero atraviesan la espuma y caen al agua, donde comen renacuajos. Moscas (Gastrops willistoni) de la familia Ephydridae depositan sus huevos en las espumas de Leptodactylus pentadactylus en Rincón de Osa, Costa Rica y Manaus, Brasil. Las larvas de las moscas se alimentan de los embriones de la rana, con frecuencia destruyendo todo el nido. Se revisan y comentan previos registros de asociaciones semejantes.

Literature Cited


Williams, F.X. 1936. Two water beetles that lay their eggs in the frothy egg masses of a frog or tree toad. Pan-Pacific Entomol., 12:6-7.

Fig. 1. Adults of the ephyrid fly *Gastrops willistoni* on a *Leptodactylus pentadactylus* foam nest near Manaus, Brazil. (A): larvae (maggots) of *G. willistoni* among the *L. pentadactylus* eggs (white spheres). Photos: Lawrence A. Lacey.
Fig. 2. Puparium (A) and opercle (B) of a Brasilian G. willistoni. Pupae, found on the surface of foam nests of floating nearby, are easier to identify than are larvae or adults. Opercula often become detached from the puparia after flies emerge and are extremely useful in recognizing the infesting species. The opening on the puparium is an exit hole of a parasitoid hymenopteran. Line = 1 mm.
Fig. 3. The vespid wasp Angiopolybia pallens in a Leptodactylus pentadactylus foam nest near Manaus, Brazil. (A): wasps foraging in a foam nest. Eggs are removed and taken away. (B): wasp attempting to remove a developing frog embryo from its foam nest. Larvae were too heavy for wasps to carry away. Photos by Barbara Gibbs, courtesy of Lawrence A. Lacey.