

Cannibalism by large tadpoles of *Rhinophrynus dorsalis* (Anura: Rhinophrynidae)

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Adult burrowing toads (or “sapo borracho”), *Rhinophrynus dorsalis* Duméril and Bibron, 1841, live underground in tropical dry forests of Central America. They forage on ants and termites and emerge to the surface only a few days of the year at the first heavy rains of the wet season to breed (Stuart, 1961; Trueb and Cannatella, 1982; Trueb and Gans, 1983; Sandoval et al., 2015). Their tadpoles develop in dense conglomerations in ephemeral puddles and pools for a brief period each year, typically in May and June (Stuart, 1961). Orton (1943) first described the tadpole based on museum specimens, with additional morphological reports about this species by Tyler (1974), Altig and Kelly (1974), Trueb and Cannatella (1982), Trueb and Gans (1983), Satel and Wassersug (1981), Lannoo (1987), and Swart and de Sá (1999). However, information about the natural history and behaviour of tadpoles is scarce (Altig et al., 2007).

While describing the natural history of the tadpoles of various Central American anurans, Starrett (1960) noted evidence of cannibalism in *R. dorsalis* tadpoles from Tehuantepec, Mexico, finding small tadpoles (20 mm) in digestive tracts of various larger tadpoles (40–50 mm). She also described differences in the digestive tracts and overall morphology of these two size classes. However, after examining the intestinal tracts of 12 tadpoles from Tikal, Guatemala ranging from 17 to 25 mm, and finding only algae, diatoms, gastrotrichs, oligochaetes, and crustaceans, Stuart (1961) referred to his samples

of *R. dorsalis* tadpoles as “strictly filter-feeders”. Then, Altig and Kelly (1974), Satel and Wassersug (1981), and Altig et al. (2007) also described *R. dorsalis* tadpoles as midwater filter-feeders specializing on phytoplankton, possessing guts lined with large caecum-like areas. Additionally, Altig et al. (1975) referred to them as filter-feeders after finding that 12 young *R. dorsalis* tadpoles (Stage 25–26; Gosner, 1960) lacked pepsin and had low levels of amylases and lipases in their gut, which are digestive proteins that would presumably be necessary to digest cannibalised tadpole prey. Although researchers have further described aspects of the reproductive behaviour and larval interactions of *R. dorsalis* (Foster and McDiarmid, 1982; Sandoval et al., 2015), the question of cannibalism among *R. dorsalis* tadpoles has been largely overlooked in the literature since the initial report by Starrett (1960). Interestingly, Foster and McDiarmid (1982) noted that *R. dorsalis* tadpoles reared in isolation grew more slowly than those reared in groups, and exhibited an avoidance reaction when subsequently presented with conspecifics.

Methods

In June 2014, we captured approximately 100 *R. dorsalis* tadpoles in a net from a seasonal wetland in Palo Verde National Park (10.3428°N, 85.3375°W) in northwestern Costa Rica. While rearing the tadpoles in the laboratory, we observed five events in which larger tadpoles (Stage 26; Gosner, 1960) fed on conspecifics at earlier stages. At first, we interpreted this behaviour as scavenging. However, after observing more closely during two subsequent events, we noticed that the predated individuals were still alive. We were not able to observe interactions with tadpoles in older stages at this time due to tadpole mortality.

Then, during the first week of the rainy season (May to November annually) on 23 May 2018, we collected approximately 300 *Rhinophrynus dorsalis* tadpoles

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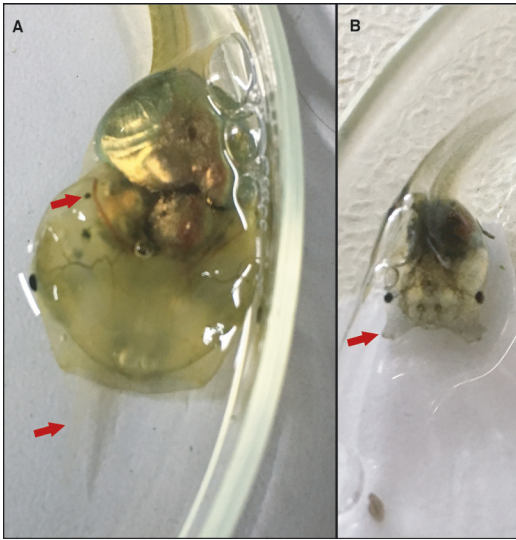


Figure 1. (A) Tail of small *Rhinophrynus dorsalis* tadpole is visible outside of the mouth of a larger *R. dorsalis* tadpole in the process of cannibalism. Eyespot of the smaller tadpole is also visible through the transparent ventral surface of the larger tadpole. (B) After one month of living in the same container with large tadpoles, small tadpoles grew extended soft structures on their head, which could function in gape limiting the large tadpoles and thus reduce cannibalism. Photos by Jennifer L. Stynoski.

in a net from a rain-filled pool (3 m radius, 0.5 m depth) inside of a dry riverbed at the Rio Cuajiniquil in Sector Santa Rosa, Área de Conservación Guanacaste, Provincia de Guanacaste, Costa Rica (10.8767°N, 85.6095°W). The pool contained what we estimate to be hundreds of thousands of *R. dorsalis* tadpoles, all Stage 24 or less according to Gosner (1960). No other species of tadpoles were observed in this pool, although calling males of *Incilius luetkenii* Boulenger, 1891, *Hypopachus variolosus* Cope 1875, *Smilisca baudinii* Duméril and Bibron, 1841, *Engystomops pustulosus* Cope 1864, *Incilius coccifer* Cope, 1866, and *Trachycephalus typhonius* [=venulosus] Linnaeus, 1758, were heard calling within 100 m of the collection site. We transported tadpoles to the laboratory at the Instituto Clodomiro Picado in 10 1-gallon Ziploc bags inside of a large cooler. We poured the tadpoles into two open clear plastic containers (30 x 50 cm, approximately 150 tadpoles per container), maintaining 5–10 cm of fresh rainwater and removing waste at the bottom of the container with a turkey baster several times per week.

We fed tadpoles 2–3 times weekly with 1 crushed Spirulina tablet (Spirunat, Santa Ana, Costa Rica) and 4–6 ReptoMin food pellets (Tetra, Blacksburg, VA, USA). We maintained tadpoles in these conditions until they died naturally, were removed for sampling in a concurrent project, or metamorphosed 6–12 weeks later.

Results and Discussion

In each container, we observed between two and six tadpoles at any given time that were significantly larger than the rest, as described by Starrett (1960). These “large morph” tadpoles (approximately 40–50 mm) swam at a faster velocity and were frequently observed “bumping” the mostly stationary smaller tadpoles (approximately 20–25 mm) with their mouths, to which the small tadpoles generally turned in the other direction and swam in a short burst away from the large tadpoles. In one case when we removed three of six large tadpoles for sampling purposes as part of another study, within 1 week there were again six large tadpoles present in that container, suggesting that small tadpoles grew rapidly to replace the removed large tadpoles.

On six occasions, a large tadpole was observed successfully ingesting a small tadpole rather than merely bumping into it. In one case, the large tadpole swam for over two hours with the tail of the small live tadpole sticking out of its mouth, until we removed the large tadpole from the container to take a ventral photograph (Fig. 1A). Within one hour of being placed back in the container, the large tadpole swallowed the remainder of the small tadpole.

After one month in captivity, the large tadpoles reached Stage 38, whereas the small tadpoles remained at Stages 26–33. The small tadpoles grew extended soft protuberant structures on the anterior edges of their heads just medial to the eyes (Fig. 1B), as depicted in Starrett (1960). The protuberances were lost as tadpoles matured. Although we do not have experimental data to support this hypothesis, based on observations, we suggest that these structures may serve to interrupt the gaping ability of large tadpoles while cannibalizing small tadpoles, especially considering extremely common failed “bump” attempts by large tadpoles.

Based on these observations, we speculate that *Rhinophrynus dorsalis* may in fact exhibit polyphenic morphotypes (*i.e.* multiple discrete phenotypes for a given genotype) – a large carnivorous and cannibalistic morphotype and a smaller omnivorous filter-feeding morphotype – as seen in tadpoles of Spadefoot toads

Spea multiplicata Cope, 1863 and *S. bombifrons* Cope, 1863 (reviewed in Pfennig et al., 2007). We concur with Starrett (1960) in observing that the morphology (protuberances, size, growth rate, behaviour, digestive tracts, etc.) of these morphotypes is distinct and consistent. Phenotypic plasticity could be responsible for the rapid development of new large tadpoles when we removed existing large tadpoles from containers. Such plasticity could allow tadpoles to optimise the use of available resources while living in dense aggregations in ephemeral pools following explosive breeding, as facultative cannibalism is a strategy employed to enhance growth and differentiation in many anuran groups (see Pfennig et al., 2007; Crossland et al., 2011).

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