



Adult poison frogs can capture and consume aquatic tadpoles

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Abstract

Cannibalism is common in animals, and its expression is shaped by a suite of costs and benefits beyond the caloric content of meals made of conspecifics. We report here on fortuitous observations of cannibalism of tadpoles by unrelated adult *Oophaga pumilio* made during experimental assays of tadpole begging. This cannibalism was rare, but performed by adults of both sexes and from six populations in the Bocas del Toro archipelago. Only tadpoles at the earliest free-living stages were cannibalized, and those that were cannibalized begged more often than tadpoles at the same developmental stages that were not eaten by adults. This newly documented proficiency at capturing and consuming food in water is impressive given that *O. pumilio* adults are terrestrial and not known to consume aquatic prey. This ability, if employed in nature, may also afford additional reproductive opportunities to adults. The nurseries used for tadpole deposition are often limiting, and a parent could make an occupied nursery more hospitable for its young (or attractive to a potential mate) by consuming the occupant, or could even parasitize the parental investment of another mother by replacing her tadpole.

Keywords Cannibalism · Dendrobatidae · Nursery · Parental care

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Introduction

The benefits of foraging most often come in the form of nutrients that can be devoted to maintenance, growth, and reproduction (Perry and Pianka 1997). Foragers also, on occasion, consume things that offer benefits not strictly, or even primarily, about energy. Devoting time and gut space to consuming calorie-poor foods might, for example, help foragers fight pathogens and parasites (de Roode et al. 2013) or offer access to pigments required for ornamentation (Negro et al. 2002). Many predators consume individuals of the same species, a habit that carries myriad fitness costs and benefits (Elgar and Crespi 1992). Tadpoles, for example, often develop in a spatially confined habitat, and by eating one another gain direct benefits, are exposed to direct and indirect fitness costs, and shape their own future competitive environment (Mock and Parker 1998; Griffin and West 2002). Adults kill and consume unrelated juveniles, and can benefit from doing so if it increases access to reproductive opportunities or shapes the competitive environment for their offspring (Ebensperger 1998). Some adults even consume their own young, a behavior that might contribute positively to a parent's fitness if offspring survival is density dependent or if lower quality offspring can be sacrificed early, reducing the total cost of care (Manica 2002; Klug and Bonsall 2007). The best way to understand why an animal might eat something, especially when that something is a conspecific, may not, therefore, always be nutrient content.

We report here on fortuitous observations of cannibalism in the strawberry poison frog (*Oophaga pumilio*). Mother *O. pumilio* transport larvae from terrestrial clutches to small water-filled nurseries, and then return regularly to offer the unfertilized trophic eggs that serve as tadpoles' only source of nutrition. Tadpoles usually develop alone, but do occasionally encounter another tadpole deposited in the nursery (Khazan et al. 2019), a circumstance under which they are aggressive, but not cannibalistic (Dugas et al. 2016). In a study of offspring-parent communication, we exposed tadpoles to unrelated adult frogs in an effort to stimulate their vibratory begging display. During these assays, several of the adult stimulus frogs consumed the focal tadpole, a behavior reported anecdotally in captive *O. histrionica* (Zimmerman and Zimmerman 1982) and *O. pumilio* (E. Zimmerman personal communication cited in Haase and Pröhl 2002), but to our knowledge not one previously documented or described in any detail. This observation is surprising not least because *O. pumilio*, like other dendrobatids, are entirely terrestrial and not known to consume aquatic prey. These observations, perhaps more importantly, may help explain why females that care for tadpoles are aggressive toward other frogs (Haase and Pröhl 2002), and suggest the potential for diverse reproductive tactics in this frog.

Methods

We made the observations reported here while studying *O. pumilio* offspring-parent communication. We collected frogs and tadpoles from eight localities in and around the Bocas del Toro Archipelago, Panama (Table 1), catching adults by hand and collecting tadpoles by searching plant leaf axils and, in some populations, cups we placed several weeks before collection. We captured about two thirds females to use as stimulus frogs, but tadpoles beg equivalently to both sexes (Stynoski and Noble 2012). We did not capture or use in trials any adults that appeared by-eye to be in poor condition. We moved all animals to the Smith-

Table 1 Collection localities of *O. pumilio* used in this study, and the number of cannibalism events and tadpoles sampled from each population

Locality	Latitude	Longitude	Cannibalized / Tadpoles
Isla Popa	9.22818	-82.12037	1 / 19
Isla Colón	9.39300	-82.26911	1 / 17
Isla Solarte	9.33240	-82.21856	1 / 27
Isla Bastimentos	9.34970	-82.21259	0 / 10
Mainland (Bahía Delfines)	9.22138	-82.21833	1 / 17
Mainland (Tierra oscura)	9.19707	-82.25063	1 / 19
Isla Pastores	9.23647	-82.33661	1 / 14
Mainland (Almirante)	9.24440	-82.36732	0 / 29

sonian Tropical Research Institute Bocas del Toro field station shortly after collection. We held tadpoles individually in glass vials, and did not feed them. We housed adults in small groups (4–8 individuals) in plastic terraria (37×22×25 cm) lined with leaf litter. We placed small pieces of fruit in the terraria to attract insects that frogs ate, and supplemented this diet with termites. Typically, adults were in captivity no more than two days prior to being used in begging assays.

Starting the morning after tadpoles were collected, we conducted assays of begging. We first moved tadpoles to begging arenas, flat-sided, transparent, acrylic tanks in which we used styrofoam inserts to reduce the size to ~1.5 cm × 1.5 cm × 3 cm (~10 ml), the approximate size of a large leaf axil (Maple 2002). After allowing tadpoles 10 min to acclimate, we stimulated their begging display by trapping an adult in the arena, using a gas-permeable foam plug to prevent its escape. We recorded interactions using a commercial action camera recording at 120 fps (Sony HDR-AS20). We started the recording immediately after introducing the stimulus adult or when the tadpole was first active (swimming or begging), and continued it for 10 min after the tadpole first begged. If a tadpole did not perform at least one bout of rapid vibration (a behavior distinct from swimming) after 10 min, we attempted the assay again the following morning; most tadpoles that did beg were not assayed a second time. Following these assays, we returned adult frogs to their point of capture and euthanized tadpoles for another study.

On a few occasions, the adult stimulus frog ate the focal tadpole during these trials (see Results). While these events were rare and unexpected, we made some effort to assess their distribution across our observations. We first compared descriptive statistics about the developmental stages (Gosner 1960) of tadpoles consumed and not consumed during assays. We then used a Fisher's Exact test to compare the proportion of tadpoles that begged in trials during which the tadpole was cannibalized and those in which it was not; we limited the 'not cannibalized' sample to initial begging assays, as we primarily assayed tadpoles again only if they did not beg the first time.

Results

We assayed the begging of 152 tadpoles, with 86 assayed on consecutive days. In seven of these 239 trials, the adult stimulus frog ate the tadpole, an interaction we captured on video six times (Fig. 1; *Supplementary videos*). Two males and five females consumed tadpoles, and these were from six populations. Tadpoles were from seven populations; in all but one

Fig. 1 Image of an adult *O. pumilio* after consuming a tadpole, the tail of which can be seen protruding from its mouth (indicated by white arrow). Videos of six events are available in electronic supplementary materials



assay, the stimulus adult and tadpole were from the same population (this one case was the only trial in which we used a stimulus frog from a different population). Our assays included tadpoles at Gosner stage 25, when tadpoles are deposited by females, through stage 43, when front limbs emerge. The seven tadpoles consumed by adults (mean $SD \pm 25.9 \pm 0.9$; range: 25–27) were at earlier developmental stages than those not consumed (30.4 ± 5.7 ; range: 25–43) during trials. Six of the seven tadpoles eaten by stimulus adults begged at least once prior to being eaten, a proportion of begging higher than in the tadpoles from the same developmental stage range that were not eaten (16 of 66 ‘not eaten’ begged; Fisher’s Exact $p = 0.006$). In the six cannibalism events we recorded, three adults consumed tadpoles near the water surface as tadpoles swam or begged near the adult’s mouth. The other three adults were oriented toward the tadpole when the tadpole was not moving near the bottom of the tank ($n = 2$) or in the water column ($n = 1$) and consumed it when it began swimming. We observed all adults for at least 24 h and saw no apparent ill effects.

Discussion

We observed cannibalism of tadpoles by adult *O. pumilio* of both sexes and from multiple populations in the Bocas del Toro region. Although adults in the wild routinely spend a length of time in a nursery similar to (or longer) than the duration of our experimental assays, we certainly put stimulus adults in a novel situation by not allowing them to escape the proxy nursery during these assays. Nonetheless, our observations seem consistent with adults intentionally consuming tadpoles. Both extensive monitoring of nurseries visited by free-living frogs (Stynoski 2012) and identical assays of begging (Dugas et al. 2017) in a Costa Rica population resulted in no observed cannibalism of tadpoles. Genetic divergence (Hagemann and Pröhl 2007), perhaps driven by selection (Wang and Summers 2010), between Costa Rica and Bocas del Toro *O. pumilio* populations suggest behavioral divergence is plausible. Cannibalism may be absent, rare, or cryptic in the wild, or the populations most observed may simply not be the ones in which the behavior is most common.

Tadpoles that fell victim to stimulus adults were at the very earliest stages at which *O. pumilio* develop outside the egg, and had more frequently begged during the assay than tadpoles that were not eaten. Could cannibalism by adults be an unappreciated cost of beg-

ging for *O. pumilio* tadpoles? Adults other than parents routinely visit occupied nurseries and are greeted with begging (Stynoski 2012), so some of the conditions under which cannibalism occurred in our trials are common in nature. Parents likely recognize their offspring by location rather than direct mechanisms (Stynoski 2009), but whether and how *O. pumilio* tadpoles might recognize their mothers, presumably less likely to eat them, is unknown. Tadpoles do seem able to use tactile, visual, and chemical information to distinguish between conspecific and heterospecific adults or invertebrate predators when deciding to beg (Stynoski and Noble 2012), so the mechanism by which recognition of mothers might occur are clear. A tadpole ability to distinguish mothers from other conspecifics visiting the nursery may also be important to the hypothesis that *O. pumilio* form mate preferences for the phenotype of their mothers, potentially driving reproductive isolation among phenotypically distinct populations (Yang et al. 2019). Even if cannibalism were a rare risk of begging, however, the costs of missing a parent (and potential meal) might still leave ‘beg to any *O. pumilio* adult’ an on-average winning strategy for tadpoles (Dor et al. 2007).

Despite the different morphology and behavioral repertoire required to capture prey on land and in water (O’Reilly et al. 2002), some terrestrial frogs do consume aquatic prey, including tadpoles (Measey et al. 2015). Aquatic prey, tadpole or otherwise, seem unlikely to make up a substantial portion of the adult *O. pumilio* diet given what we currently know (Donnelly 1991), although the apparent ease with which adults captured and consumed tadpoles perhaps suggests the possibility merits some attention. Among animals, cannibalism is often more likely when food is limited, and so experimental approaches might be employed that increase the frequency of this rare event (Elgar and Crespi 1992; Dugas et al. 2016). Perhaps more exciting for our understanding of poison frog reproductive ecology is the possibility that parents could employ this skill in a way that pays fitness dividends beyond those offered by the nutrition contained in a young tadpole (Haase and Pröhl 2002). Nurseries seem to be a limiting resource for *O. pumilio* (Donnelly 1989; Pröhl and Berke 2001), and nurseries unsuitable because they are occupied could be made suitable by cannibalistic mothers-to-be. Poison frogs eat each other’s reproductive clutches (Spring et al. 2019), so this arena of intraspecific competition seems plausible (Haase and Pröhl 2002). Because adults seem to remember nurseries and not identify individual tadpoles (Stynoski 2009), parents could also replace a tadpole with their own, parasitizing the reproductive effort of a conspecific. Increased aggression by female *O. pumilio* rearing tadpoles and near their rearing sites is at least consistent with predation on tadpoles by conspecific females being a salient risk in the wild (Haase and Pröhl 2002). Asking how many mothers care for unrelated young in the wild, while logistically imposing, could test for this potential reproductive strategy (Ursprung et al. 2011), as perhaps could experimental manipulations, for example of nursery availability.

While *O. pumilio* are terrestrial frogs that specialize on ants and mites (Donnelly 1991), our observations demonstrate that adults can also capture prey in water, a tendency that is perhaps rare but present in multiple populations, including allopatric ones. Interesting in its own right, this capacity could, if employed in nature, shape selection on territoriality (Haase and Pröhl 2002), parent-offspring recognition (Stynoski 2009), and offspring-parent communication. Understanding how resource limitation and inter- and intraspecific competition shape reproductive ecology in poison frogs promises to introduce these charismatic model organisms to an even broader suite of topics in evolutionary ecology.

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Author contributions All authors participated in the collection of animals in the field, and RC established field sites. MBD and OLB conducted the begging assays. MBD prepared the manuscript, which was approved by all authors prior to submission.

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Data Availability All data generated or analyzed during this study are included in this manuscript.

Code Availability Not applicable.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethics approval All procedures were approved by the STRI AUCUC (2019-0701-2022) and the Ministerio de Ambiente (Panama) issued the required permit (ARB-010-2022).

Consent to participate Not applicable.

Consent for publication Not applicable.

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