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Kin cannibals: recently hatched *Philoria pughi* tadpoles consume unhatched siblings in isolated terrestrial nests

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ABSTRACT

Cannibalism is a behaviour exhibited across amphibian life history stages; however, there are few records that involve cannibalism between siblings. Here, we describe observations of recently hatched tadpoles of the frog *Philoria pughi* consuming sibling embryos with delayed or failed development. Our observations indicate that additional nutrition is obtained from the ingested embryos, despite tadpoles of species of *Philoria* being capable of endotrophic development. This discovery should be considered when establishing captive breeding colonies for *Philoria* species and needs further investigation in wild populations.

Keywords: Anura, asynchronous development, behaviour, captive management, diet, predation, siblicide, threatened species.

Introduction

The embryos of oviparous species are vulnerable to external threats, such as predation, given that they are laid directly into the environment and confined to an immobile egg (Niehaus *et al.* 2006; Refsnider and Janzen 2010). Parents can reduce the chances of their offspring succumbing to predation prior to or after hatching by providing some form of parental care (Furness and Capellini 2019), depositing in structures that reduce exposure (Gould 2021), or by choosing deposition sites that allow eggs to be isolated (Resetarits and Wilbur 1989; Buxton and Sperry 2017; Gould *et al.* 2021).

The transition of egg deposition from permanent to ephemeral waterbodies is a behavioural tactic that has evolved among some amphibians to isolate eggs from predators, such as fish, which cannot regularly colonise these systems due to their shortened hydroperiods (Skelly 1996; Buxton and Sperry 2017). However, this strategy may not reduce exposure of offspring to the threat of predation by conspecifics (Polis and Myers 1985; Gould *et al.* 2020). Parents can further isolate their offspring to protect against conspecifics by depositing in much smaller waterbodies (Lehtinen 2004; Poelman and Dicke 2007), or in terrestrial chambers (Magnusson and Hero 1991; Touchon and Worley 2015). Yet even here, offspring are possibly still faced with the risk of predation by siblings if egg hatching is not synchronous (Poelman and Dicke 2007).

The killing of one's own siblings is referred to as siblicide (Mock 1984), and can carry direct fitness benefits by reducing competition and/or providing nutrition via cannibalism, but at the potential cost of indirect fitness losses (Crump 1990; Pfennig 1997; Mock and Parker 1998). Sibling cannibalism, which may or may not involve siblicide, has been observed widely between amphibian tadpoles (Pfennig *et al.* 1993, 1994; Walls and Blaustein 1995), and may arise under conditions of food scarcity (Pfennig 1992). There is, however, limited indication in the literature of amphibian siblicide and/or cannibalism involving interactions between tadpoles and earlier life stages (Poelman and Dicke 2007).

The Pugh's mountain frog (*Philoria pughi*) is an Australian ground frog (Anura: Limnodynastidae) that deposits its eggs within a frothed bubble egg mass or 'nest' that is laid within a subterranean chamber (Knowles *et al.* 2004). Here, the offspring complete embryogenesis and larval development through to metamorphosis alongside their siblings, away from the offspring of other conspecifics (Anstis 2017). *Philoria* tadpoles are capable of endotrophic development but have been observed feeding on silt and detritus within the nesting chamber (Debavay 1993; Anstis 2017). Herein, we report on the predation of unhatched *P. pughi* embryos that have delayed or halted development by recently hatched sibling tadpoles within a terrestrial chamber prior to their emergence.

Materials and methods

As part of a study investigating captive husbandry protocols, we collected a newly deposited *P. pughi* egg mass from a chamber at the headwaters of a stream in north-east NSW, Australia, in spring of 2020. Substrate material was also collected from nearby and stored in a sealed container. The egg mass was transported to the laboratory with water sourced from a nearby creek in a 5 cm × 5 cm × 5 cm plastic container. The embryos were in transit for approximately 36 h before being transferred to a plastic aquarium, where they were placed within a small artificial depression (3 cm round × 1.5 cm deep) made with the collected substrate. The nest was supplied with a slow seepage of aerated water to mimic the natural watering offspring would be exposed to in the nest chamber and covered with black cloth to mimic underground conditions.

Observations were made of the developing embryos under subdued lighting and photographs taken with a macro lens and flash. Checks of the embryos were made every few hours. Staging of embryonic and larval development followed Gosner (1960), as modified by Debavay (1993).

Results

At the time of collection, the *P. pughi* egg mass was approximately 30 mm in diameter and contained 28 similarly sized unpigmented eggs (3 mm yolk diameter). Each egg was contained within an independent capsule and embedded throughout the egg mass that was aerated with large air bubbles. The majority of eggs (26 of 28; 93%) were fertilised, with embryos at Gosner Stage 16–17. The remaining two eggs were either unfertilised or had become non-viable.

A majority of the embryos (19 of 26; 73%) had synchronous development and hatched within a period of 5 days after collection at Gosner Stage 20. However, there was a small number of embryos (7 of 26; 27%) whose development had slowed or stalled at Gosner Stage 16–17 (Fig. 1*a*). The capsule around these embryos remained clear and there was no sign of fungal infection.

The tadpoles were unpigmented and contained a large amount of yolk within their stomachs upon hatching. They remained relatively static in the egg mass but were capable of active movement, and showed keratinised jaws 5 days after hatching (10 days after collection) (Gosner Stage 24) (Fig. 1*b*). By this time, the frothed mucus of the nest had begun to break down (10 days after collection). The first observation of tadpoles feeding occurred 6 days after hatching, with individuals found attached to the mucus with their mouthparts and engaged in active chewing. After much of the mucus had been eaten or dissolved away, we observed several of the more advanced tadpoles chewing on the capsules of those embryos that had not hatched, which occured 7 days after hatching had commenced. Total consumption of the embryos occurred over a 5-day period, with several of the tadpoles observed ingesting small parts of the yolky contents of the embryos. Only non-viable eggs and unhatched embryos were cannibalised, and we did not observe any cannibalistic behaviour among the tadpoles themselves.

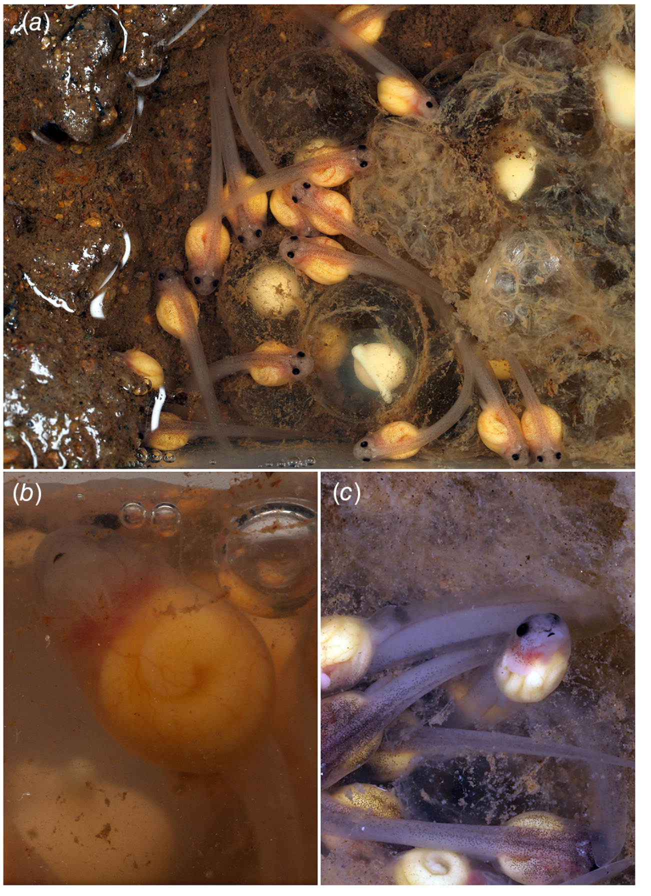

Fig. 1. Recently hatched *Philoria pughi* tadpoles from a single clutch collected from the field in NSW, Australia. Images show (*a*) tadpoles concentrated around their unhatched siblings within a terrestrial chamber (tadpoles approximately 8 mm in total length), (*b*) and (*c*) tadpoles from the same clutch, presenting with keratinised mouthparts at Gosner Stage 24, 5 days after hatching.

Discussion

Our observations indicate that recently hatched *P. pughi* tadpoles consume nest material and unhatched sibling embryos prior to emergence from the terrestrial chamber. This is a surprising finding as *Philoria* tadpoles are capable of endotrophic development and have been recorded feeding only on silt or detritus within the nesting chamber (Debavay 1993; Anstis 2017). We do not believe that the adult female of this clutch had deliberately deposited unfertilised 'trophic' eggs as food for her offspring upon hatching (e.g. Poelman and Dicke 2007). Indeed, most of these consumed eggs were fertilised, indicating that tadpoles were opportunistically exploiting embryos. The most similar predatory interaction is found in *Dendrobates ventrimaculatus*, where tadpoles are provisioned fertilised eggs from subsequent breeding events (Poelman and Dicke 2007). We believe this is the first record of within-clutch sibling predation between embryo and tadpole life stages within *Philoria*, representing a form of siblicide rarely described among amphibians.

Occurrences of asynchronous embryo development and death within-clutch have been reported in the nest chambers of other *Philoria* species (e.g. Seymour *et al.* 1995). This could be caused by oxygen starvation if embryos within frothed nests become distant from the embedded air bubbles that act as an oxygen store, which may occur during froth nest breakdown (Gould 2021). We currently do not have an explanation for the slower development exhibited by several embryos in the clutch we observed. What is apparent is that synchronised hatching would be advantageous in preventing sibling predation.

Although the unhatched *P. pughi* embryos were still alive when consumed, it remains to be determined if they were viable and would have continued developing if protected from their siblings. If the embryos are assumed to be non-viable, cannibalism of sibling detritus rather than siblicide has occurred. This represents an opportunistic recycling of maternal nutrients within the clutch, improving the odds of a female's viable offspring surviving by (1) allowing them to reach metamorphosis more rapidly or at a larger size (Babbitt and Meshaka 2000), and (2) preventing disease transmission (Pfennig 1997; Polis 1981). If the embryos are viable but have poorer fitness prospects than their faster developing siblings, this is a predatory interaction and a form of siblicide that could otherwise suggest that there is a payoff in selfishly cannibalising relatives as opposed to being altruistic and allowing the relatives to continue developing (Dugas *et al.* 2016). Both scenarios would mean that the loss of the siblings does not come at the cost of reducing the genetic fitness of the parents.

The unique circumstances of premetamorphic development among *Philoria* may be more conducive to this form of sibling predation when compared to other amphibians. *Philoria* eggs hatch within a terrestrial chamber where the larval period is completed (Knowles *et al.* 2004). While isolated from non-conspecific predators, the siblings are a predatory threat to each other, concentrated in a small space where there is limited means of avoidance for unhatched embryos that are likely the most nutritional food resource available (Crump 1990; Fleming *et al.* 2009). We thus hypothesise that this could be an under-reported form of siblicide among the amphibians, despite terrestrial froth nesting and delayed tadpole emergence occurring across several amphibian genera (Gould 2021).

Our observations show that *P. pughi* tadpoles opportunistically feed on unhatched siblings. This could be exploited in captive breeding programs currently underway for several threatened species in the genus (Scheelings 2015; Heard *et al.* 2021), as it suggests the fitness of captive offspring could be improved by providing additional nutrition, such as yolk granules, very early on during tadpole development. However, it must be noted that the observations presented in this study are from a single clutch. Further investigation is required on wild populations to determine the frequency of occurrence of this phenomenon, including the fitness benefits for individuals in terms of its impact on their developmental rates or size at metamorphosis. Additionally, our observations highlight the need to explore predator–prey interactions between amphibian siblings at all developmental stages, as these interactions are likely to play a role in shaping the evolution of maternal egg investment strategies and development synchrony.

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