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Do males of the Strawberry Poison-dart Frog, *Oophaga pumilio* (Schmidt, 1857), recognize tadpole transport as a cue of reproductive status?

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Sexual interactions, including courtship and territoriality, are ubiquitous and highly variable processes in the animal world. The complexity of sexual behaviours is theorised to reflect a trade-off between costs and benefits. Individuals should optimise mate acquisition while minimising predation and energetic costs (Tinbergen, 1954; Wong and Candolin, 2005). To this end, individuals may use multiple cues to assess the probability of reproductive success and adjust behavioural decisions based on that information (Candolin, 2003; Wong and Candolin, 2005). Some of these cues may reflect the immediate reproductive status of potential mates or rivals (Marler, 1967; Hare and Simmons, 2019). By recognizing these cues, individuals can avoid courting unreceptive mates or challenging rivals that do not pose a threat, thus avoiding associated costs to survival and reproduction.

The Strawberry Poison-dart Frog, *Oophaga pumilio,* exhibits complex sexual behaviours that include territoriality, courtship, and bi-parental care, including tadpole transport and provisioning of tadpoles with trophic eggs by females (reviewed in Dugas, 2018). Males typically emit advertisement calls to defend territories and attract females, and will escalate to aggressive behaviours (e.g., physical confrontations and increased vocal activity) if another male enters their territories (Pröhl, 2005). When a receptive female approaches, the male heads towards her while calling and then guides the female to a suitable oviposition site, using both acoustic signals and physical approaches (Limerick, 1980). The male then tends and moisturizes the eggs until the female carries the newly hatched tadpoles on her back to leaf axil nurseries (often bromeliads) (Weygoldt, 1980; Summers and Tumulty, 2014). Importantly, this species has a promiscuous mating system in which both sexes will mate sequentially with multiple partners. However, since females perform most of the parental care, during which they cannot mate again, males are more likely to benefit from mating sequentially as it will increase their chances of producing more offspring (Pröhl and Hödl, 1999).

From the perspective of a male, both courtship and escalated territorial behaviours may increase energetic costs and the exposure to predators, given the associated displays and increased vocal activity. Moreover, during courtship, males are less likely to engage in territorial defence and could potentially be at risk of losing their territory, a strong predictor of reproductive success (Yang et al., 2018). Therefore, it stands to reason that males would benefit from using cues of reproductive status to reduce the risks associated with misdirected courtship and escalated territorial behaviours. One candidate cue to reveal that another individual is unlikely to be a receptive mate or an immediate threat would be tadpole transport. Typically, this individual would be a female but would unlikely be receptive because mothers take care of their tadpoles up to 45 days after they hatch, during which time they slow down egg production and are less likely to mate (Pröhl and Hödl, 1999; Summers and Tumulty, 2014; Dugas et al., 2016). Alternatively, males have occasionally been seen carrying tadpoles (Weygoldt, 1980, Cossio, 2008; Killius and Dugas, 2014), and while it is not clear whether such observations represent deliberate or accidental acts by males, they may avoid intraspecific competition while carrying a tadpole and would not pose a threat to other males. Therefore, the presence of tadpoles on a carrier's back is likely to be perceived by males as a visual cue of reproductive status.

We visited a population of *O. pumilio* in the Dolphin Bay area of the Bocas del Toro region of Panamá (9.2210°N, 82.2182°W) in May 2022 and observed

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a male displaying for several minutes to a frog that was carrying a tadpole (Fig. 1; video at https://youtu.be/2WkI3QPMmsI). This population, unlike most of the other populations of the species, is polymorphic in dorsal colouration, though in a previous study no evidence of assortative mating based on colour was found (Yang et al., 2016). Interestingly, our observations revealed that the density of individuals is high compared to other populations, with more than five individuals in an area of ca. 3 m^2 that would typically contain one male or a reproductive pair (Pröhl and Berke, 2001). This suggests, first, that the probability of finding available mates may be high, and second, that territories are likely to overlap and reduced aggressiveness via the "dear enemy effect" could occur (Tumulty et al., 2022; but see Bee, 2003). Unfortunately, we avoided any interference to allow the observation and lost sight of the carrying frog, so we could not confirm its sex. Moreover, we could not distinguish between courtship and an aggressive encounter as we did not hear soft courtship calls or antiphonal aggressive calls, typical of these behaviours (Zimmermann, 1990). Therefore, we propose alternative scenarios to explain this observation based on the putative sex of the carrier frog.

Regardless of the tadpole-carrying sex, *O. pumilio* may be unable to discriminate the shape of a tadpole from the dorsal colour pattern of a conspecific. Dorsal patterning in this species is usually in the form of highly variable irregular dots of dark colour, which could easily resemble the shape of a tadpole, as has been suggested for other species in the family Dendrobatidae (Toro-Gómez et al., 2023). Visual acuity or the spatial resolution of the visual system is dependent on eye size, which, in turn, is positively correlated with body size (Caves et al., 2018). The small body size of *O. pumilio* (~2 cm) suggests that these animals have poor visual acuity. Indeed, the larger *Dendrobates auratus* (~4 cm) is hypothesised to have relatively weak visual acuity and be unable to discriminate fine-scale details (e.g., a tadpole vs. dorsal patterning) even at short distances (< 10 cm; Giffin, 2020).

In a scenario where the carrying frog is female, we propose two alternative explanations, in which the male was able to visually recognize that the female was carrying a tadpole. First, the male could be courting the female even though she is unreceptive. It has been hypothesized that unlike males, females are the choosy sex in *O. pumilio*, as females have been observed sampling males (Pröhl and Hödl, 1999; Pröhl and Berke, 2001; Summers and Tumulty, 2014). Moreover, males can mate multiple times on the same day, and they have been known to guard different clutches at the same time (Pröhl and Hödl, 1999; Summers and Tumulty, 2014). Thus, males could be less selective in comparison to females at courting potential mates, and males may be able to make courtship mistakes, as the one observed, without necessarily reducing their reproductive success.

Alternatively, the courtship of *O. pumilio* could be more complex than previously thought. Assuming that the female is carrying the territorial male's tadpole, the male could still be emitting acoustic signals to guide

Figure 1. Male *Oophaga pumilio* on the right displaying to a carrying frog in the Bocas del Toro area of Panama. Photo by Marco González-Santoro.

her to a suitable tadpole deposition site outside of his territory, which occurs in other species of poison frogs (reviewed in Dugas, 2018). However, the polygamous males of *O. pumilio* rarely leave their territories and they continue to advertise to other females even while guarding a clutch (Pröhl and Hödl, 1999), suggesting that they do not typically provide further courtship or parental care after egg moisturizing.

In the scenario of the carrying frog being a male, we propose that the calling male in our study could be defending his territory from a potential intruder. Although it has been an elusive observation in nature, two reports in captivity (Weygoldt, 1980; Killius and Dugas, 2014) and one field observation have described males carrying tadpoles (Cossio, 2008). It has been observed in the species *Allobates femoralis* (Boulenger, 1884) that males performing parental care are more likely to carry tadpoles during times of low intraspecific competition (Ringler et al., 2013). This suggests that the carrying individual observed is unlikely to represent a threat for the territorial male. However, the territorial male may have been unable to visually recognize the tadpole, or the presence of the tadpole may not have conveyed information to the territorial male on the reproductive status of the carrying frog. In either case, the carrying male, acting as an intruder, would represent a threat by the perceived attempt to take over ecological resources in the calling male's territory, which would trigger an aggressive response and the display we observed could be an example of that. It remains unclear if males of *O. pumilio* carry their tadpoles for parental-care purposes or if tadpoles on a male's back are simply due to an opportunistic error of tadpoles attempting to relocate (Killius and Dugas, 2014).

Further work is needed to test our hypothesis that males do not use tadpole transport as a cue of reproductive status. However, our observation may indicate an interesting, heretofore unrecognized variation on the theme of poison frog parental care. Alternatively, our observation may prompt closer scrutiny of what we know about the courtship of *O. pumilio* or the behavioural plasticity in the parental care of this species, a topic that has received much more attention in other species of poison frogs (Summers and Tumulty, 2014; Ringler et al., 2015; Westrick et al., 2023).

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