

Tadpole transport by male *Oophaga pumilio* (Anura: Dendrobatidae): An observation and brief review

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Across taxonomic groups, parents provide post-zygotic care to offspring, most commonly by offering protection (e.g., from predators, parasites, or harsh environments) and/or by delivering exogenous food (Smiseth et al., 2012). The extent of such post-zygotic parental investment is a key life-history trait (Stearns, 1992), and in sexually reproducing organisms, the relative investment that each sex makes has broad evolutionary consequences (Trivers, 1972). Specifically, sexual selection is typically more intense in the sex that invests less in parental care, resulting most often in showy males and choosy females (Trivers, 1972). In amphibians, as in most animals, females produce nutrient-rich eggs in which they presumably invest far more than males do in sperm, but the sum of investment made by each sex can be further shaped by post-zygotic care (Duellman and Trueb, 1986; Dugas et al. *in press*).

Clutch attendance is relatively common in amphibians, and it is usually the male that performs this task (Duellman and Trueb, 1986; Beck, 1998). Species of the genus *Leptodactylus* deposit fertilized eggs in foam nests that protect larvae, often along with unfertilized eggs upon which tadpoles feed while they develop (Shepard and Caldwell, 2005). In frogs that lay terrestrial eggs, even more elaborate care has evolved (Crump, 1996). For example, in *Hyalinobatrachium valerioi* (Centrolenidae), males guard and moisten eggs, and male removal results in a significantly higher mortality rate (Vockenhuber et al., 2009); analogous behaviour appears to be present in other frogs as well (Wells 1977; Duellman and Trueb, 1986; Brust, 1993; Beck, 1998). Elaborate post-zygotic parental care is especially common in dendrobatid frogs, where one

or both parents often contribute egg tending, tadpole transport, and continued feeding of tadpoles throughout development (Savage, 1968; Weygoldt, 1980; Beck, 1998; Pröhl and Hödl, 1999). These behaviours are generally presumed to be costly, and thus the relative behavioural roles of parents are thought to be a useful proxy for predicting the strength of sexual selection (e.g., Summers et al., 1997). Establishing the extent of parental roles is, therefore, a key part of generating and testing predictions about the evolution of parental care (e.g., Beck, 1998).

Oophaga pumilio (Schmidt, 1857) is a dendrobatid native to Central America, ranging from southern Nicaragua to western Panama (Guyer and Donnelly, 2005). Females lay terrestrial eggs that are tended by males (Weygoldt, 1980; Crump, 1996; Pröhl and Hödl, 1999). Female *O. pumilio* provision growing tadpoles with unfertilized eggs regularly throughout their development (Brust, 1993), and are typically reported as the sex that transports tadpoles to rearing sites (Young, 1979; Weygoldt, 1980; Pröhl and Hödl, 1999; Stynoski, 2009). We report here on an observation of tadpole transport by a male *O. pumilio* (Figure 1) in a captive breeding colony at Tulane University, LA, USA (see Dugas et al. 2013 for details). On May 15, 2014, while performing routine censusing, we observed a male with a tadpole on its back (Figure 1). We replaced the lid of the enclosure and attempted to observe the male's behaviour, but because of the dense vegetation in the tank, we were unable to do so in a way that did not disturb the male. On the following day, we re-checked tadpole deposition sites (PVC tubes) and found two new tadpoles. We are unaware of any instances of adult frogs transferring tadpoles or of females picking up tadpoles from anywhere other than the reproductive clutch, and so this observation is most consistent with deposition by the male (also reported by Weygoldt, 1980). Both tadpoles died by the next census, one week later.

This observation of tadpole transport by a male



Figure 1. A male *Oophaga pumilio* transporting a newly hatched tadpole. Inset (bottom right) is a photograph showing the male-typical dark vocal sac of this individual. This observation was made in a captive breeding colony at Tulane University (LA, USA), where male-female pairs were held together in plastic enclosures.

O. pumilio joins three previous reports of this behaviour, two published (Weygoldt, 1980; Cossio, 2008) and one anecdotal (cited in Wells, 1997 without further details). Two observations were made in a captive population of unknown origin (probably Costa Rica: Weygoldt, 1980), and one in the field on Isla Popa, Bocas del Toro, Panama (Cossio, 2008). The male we observed was captured on Isla Bastimentos, a Bocas del Toro population genetically distinct from the one in which the previous observation was made (Wang and Shaffer, 2008), suggesting that male tadpole transport may be widespread in this species. Although parental care behaviours are typically described as male or female, overlap in sex roles is not unusual (Smiseth et al., 2012). For example, male *Allobates femoralis* (Dendrobatidae) predominantly transport tadpoles, but females performed this task in 10 of 129 cases observed in the wild (Ringler et al., 2013). Because male *O. pumilio* (and other dendrobatids) moisten eggs and are thus in regular contact with developing embryos, opportunities for tadpoles to climb on their fathers' backs are presumably frequent in both the laboratory and the wild. Of interest in future work will be the tadpole and parent traits that

mediate which sex primarily transports offspring.

This overlap in sex roles is interesting for a number of reasons, especially if this phenomenon turns out to be widespread in frogs with parental care. First, comparative studies assigning care to one sex (e.g., Beck, 1998) may be improved by accommodating such variation, especially with respect to correctly identifying the number of times a behaviour evolved de novo (Shepard and Caldwell, 2008). This lack of complete specialization by the sexes also raises questions about coevolved traits. For example, when females provision tadpoles, the need to repeatedly visit sites presumably requires derived cognitive abilities, and it is unclear how a female would find a tadpole deposited by a male without complex behavioural traits (e.g., Caldwell and de Oliveira, 1999), which are apparently absent in *O. pumilio* (Stynoski, 2009). It is, however, difficult to attribute the death of the male-transported tadpole we observed to maternal neglect; in our lab colony 57% of all tadpoles die before metamorphosis, and we have recorded 15 tadpoles that survived 27.3 ± 14 (mean \pm SD) days without ever being fed (unpublished data).

We detected male tadpole transport in *O. pumilio* only because it occurred in a captive pair in which the male and female were from phenotypically distinct populations, and another observation was made because the male was calling (Cossio, 2008). For justifiable ethical reasons, it is unusual for observers to capture and inspect frogs carrying tadpoles and instead most simply assume the behaviour was being executed by the sex reported to perform it. However, the documentation of variation in this behaviour may provide valuable insights into the evolutionary causes (Ringler et al., 2013) and consequences (Summers et al., 1997) of parental care.

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