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Simple observations with complex implications: What we have learned and can learn about parental care from a frog that feeds its young

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ABSTRACT

The discovery of a trait in a new lineage, especially one distantly related to those already known to express the trait, affords the opportunity to test and refine existing hypotheses for that trait's evolution and to develop new ideas. Peter Weygoldt made such a discovery, reporting the first instance of a frog that feeds its young and, even more remarkably, the first instance of dependent tadpoles that perform solicitation displays before being fed (*1980. Behav. Ecol. Sociobiol. 7, 329–332*). This discovery has featured prominently in taxonomic surveys of parental care and offspring-parent communication, but more importantly has expanded the questions that are and can be asked about these topics. I review the advances in knowledge of the natural history of the frog Weygoldt studied as well as the theoretical frameworks that inform and are informed by these advances. I highlight ideas and information about parental care in *O. pumilio* that are central to broadly understanding the evolution of parental care. Our understanding of the evolution of sex roles will, for example, improve by following Weygoldt's finding that male *O. pumilio* care for clutches with detailed accounting of the costs and benefits mothers and fathers might pay for performing this task. When a parent transports tadpoles from a terrestrial clutch to an aquatic nursery, it sets the stage for sibling competition for this resource (transport), and proximate and ultimate tests for such conflict will inform more general ideas about how conflict and cooperation shape nuclear families. That the begging displays of tadpole *O. pumilio* are performed in solitary nurseries makes this species uniquely suited to test honest-signaling models for the evolution of offspring-parent communication. By detailing the implications and possibilities stemming from Weygoldt's work, I hope to inspire readers to follow Weygoldt's lead and his example of careful and detailed observation.

1. Introduction

The first report of a behavior or phenomenon in a species (or group of species) often arrives to much fanfare and excitement, in particular when the phenomenon was thought to be the exclusive purview of "higher" organisms (e.g., Caldwell, 1997; Strassmann et al., 2000; Pepperberg, 2002). Novel findings in new organisms are important and interesting for at least two reasons. First, the independent evolution of similar traits in multiple lineages offers the opportunity to rigorously test adaptive hypotheses for the trait's evolution (Losos, 2011; McGee, 2011). Beyond confirming or refining any one particular theory, the discovery of a new instance of a well-studied phenomenon offers a test of the general hypothesis that evolution is predictable. Second, unusual or unique natural history features of this newly discovered model system might happen to fit well a body of theory awaiting empirical test and/or allow an empiricist a way around some constraint inherent to already well-studied lineages (e.g., if two traits are always or never expressed together).

Peter Weygoldt (1980) discovered that a small terrestrial frog provides elaborate care to its tadpoles, detailing the reproductive behavior of the first frog known to feed its young. Observing and working with strawberry poison frogs (*Oophaga pumilio*, formerly *Dendrobates pumilio*) purchased at a nearby pet store (this frog is native to the Caribbean slope of Central America), Weygoldt (1980) also discovered that *O. pumilio* belongs to the even more exclusive set of animals in which parental feedings are preceded by offspring solicitation displays (commonly called 'begging' in birds). As one of few examples of elaborate parental care in amphibians, and one

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of even fewer potential begging analogs outside birds, Weygoldt's (1980) description of the *O. pumilio* nuclear family became a standard citation in reviews of parental care and offspring-parent communication (Clutton-Brock, 1991; Kilner and Johnstone, 1997; Mock and Parker, 1997; Royle et al., 2012).

In the nearly 40 years since Weygoldt (1980) first reported parental care and offspring-parent communication in the strawberry poison frog, the number and diversity (i.e., independent evolutionary events) of frogs known to provide post-zygotic care to their young have grown, an expansion in knowledge in which Weygoldt himself played no small part (Weygoldt, 1987; Jungfer et al., 1996; Jungfer and Weygoldt, 1999). I refer readers interested in the diversity of parental care in frogs to authoritative reviews available elsewhere (Crump, 1996; Beck, 1998; Summers and McKeon, 2004; Summers et al., 2006; Wells, 2007; Brown et al., 2010; Gomez-Mestre et al., 2012; Summers and Tumulty, 2014). Here, my focus is on reviewing the empirical and theoretical progress made via follow-ups to each of Weygoldt's (1980) many findings. I emphasize aspects of parental care in frogs that are especially appropriate for testing existing theory in behavioral and evolutionary ecology and/or puzzling given what is currently known. This review is centered around the progress made in *O. pumilio*, but findings of other ecologically similar frogs are incorporated when especially relevant (there is thus much excellent empirical work that I do not review here). I encourage others to follow Weygoldt's (1980, 1987) example, highlighting still incompletely understood features of natural history and evolution that remain of particular importance to answering questions about the evolution of sex roles, parental care, and offspring-parent communication. Before closing the review, I consider one notable way in which Weygoldt's (1980) findings have motivated work and progress outside the immediate scope of parental care.

2. Parental care

It may be useful to broadly summarize a reproductive cycle in *O. pumilio* before exploring the details (especially the uncertain ones) and placing each in a comparative and hypothesis-driven framework. Like other toxic and conspicuously colored frogs, *O. pumilio* is diurnal and terrestrial. In the wild, both male and female *O. pumilio* are territorial, and the larger home ranges of females overlap the smaller territories of multiple males (McVey et al., 1981; Pröhl and Berke, 2001; Meuche et al., 2011). Both sexes mate multiply (Pröhl and Hödl, 1999). Following successful courtship (Fig. 1, mate choice is discussed further in Section 4), a female lays a clutch of ~5 eggs in the leaf litter (Pröhl and Hödl, 1999). Weygoldt (1980) described three phases of parental care that follow oviposition. The clutch is attended by males until tadpoles hatch (Fig. 1). Females then transport each tadpole to a nursery, a small body of water usually contained within plant tissue (e.g., leaf axil, tree hole; Fig. 2). Then, for about six weeks, mothers return to these rearing sites periodically (Fig. 2) to lay the unfertilized eggs upon which tadpoles feed (supplemental video S1).

2.1. Caring for eggs

Weygoldt (1980) observed the development of clutches laid by captive females. While he suggested that neither sex guards eggs, he did note that males called from near the clutch. Weygoldt (1980) notably reported that males tend the clutch, moistening it daily, a report that has been confirmed with observations in the wild (Pröhl and Hödl, 1999). It is this attendance and daily warding off of dehydration that seems to entirely comprise *O. pumilio* male behaviors that are uniquely paternal. Although egg tending has been treated as a relatively minor contribution compared with female care (e.g., Summers et al., 1997, 1999a), the questions that remain about how and why this behavior evolved are central to testing broader hypotheses about the evolutionary causes and consequences of sex-specific parental care in animals.

2.1.1. Why do males, and not females, care for eggs?

Exclusive male care is the most common mode of parental care in *O. pumilio*'s close relatives (Weygoldt, 1987; Summers et al., 1999a, 2006), common in frogs overall (Wells, 2007), and the dominant form of care in fishes that, like *O. pumilio* and other frogs, have external fertilization (Gross and Sargent, 1985). Numerous hypotheses explain why one parent or the other may end up caring for young. One well known hypothesis is that the parent with the best opportunity to desert does, placing the other in a 'cruel bind', forced to chose between abandoning the new zygotes (presumably to poor fitness prospects) or caring for them alone (Trivers, 1972). In fish, it is typically the male that releases gametes last (Gross and Sargent, 1985), a potential explanation for why exclusive male care is so common in this group (Dawkins and Carlisle, 1976). Weygoldt (1980) reported that just the opposite seems to be the case in *O. pumilio*, with males depositing gametes on some substrate (e.g., a leaf) before the female oviposits (also reported in the wild: Limerick, 1980). Females in egg feeding species, including *O. pumilio*, do not abandon offspring entirely (Summers et al., 1999a; Wells, 2007; Brown et al., 2010), and so provide an imperfect analog to other external fertilizers like fish. However, female desertion (male-only care) is common in related frogs (Weygoldt, 1987; Wells, 2007), and comparing the order and timing of gamete release among those that divide sex roles differently may shed light on how this aspect of breeding reflects and shapes the evolution of each sex's contribution to parental care.

Most hypothesized explanations for division of labor among parents rests on sex differences in the costs and benefits of providing care. One commonly predicted cost of care is reduced access to alternative mating opportunities (Maynard Smith, 1977; Wade and Schuster, 2002; Kokko and Jennions, 2003). Exclusive male care of clutches in *O. pumilio* may have evolved because these costs are particularly low for males (Magrath and Komdeur, 2003; Royle et al., 2016). Males are already present in close proximity to the clutch because they are territorial, and since once daily attendance requires little time (Pröhl and Hödl, 1999), males are unlikely to miss out on other mating opportunities by providing clutch care (Magrath and Komdeur, 2003). Could the potential loss of alternative mating opportunities explain why female *O. pumilio* do not tend clutches? Weygoldt (1980) observed that eggs took 10–12 days to hatch. What a female does during this time is unknown, but she could produce 2–3 additional clutches (Pröhl, 2005). Given that most clutches fail (Limerick, 1980; Pröhl, 2005; Dugas et al., 2016a), it seems unlikely that mating once and then optimistically awaiting that clutch's successful hatching is the strategy by which females maximize reproductive success. Laying overlapping clutches seems a better route to producing tadpoles, a prediction that parallels the 'fertility assurance hypothesis' for why female animals mate multiply (Birkhead et al., 1987). Staying in close proximity to any one clutch would require staying in close proximity to one male, which would in turn likely limit mating opportunities with other males. Behavioral observations in the wild (perhaps along with molecular work: Ursprung et al., 2011; Richards-Zawacki et al., 2012) will be required to reveal the extent to which females mate multiply during reproductive bouts (e.g., Pröhl, 2002; Pröhl,2005). Observational and experimental work can reveal whether female *O. pumilio* benefit from mating with multiple males vs multiply with the same male (Evans and Magurran, 2000; Jennions and Petrie, 2000; House et al., 2009) and thus whether the costs of forgoing these opportunities can explain why females

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