



Contents lists available at [ScienceDirect](#)

Zoologischer Anzeiger

journal homepage: www.elsevier.com/locate/jcz

Zoologischer
Anzeiger

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

Matthew B. Dugas

Watershed Studies Institute and Department of Biological Sciences, Murray State University, Murray, KY, USA

ARTICLE INFO

Article history:

Received 30 September 2017
Received in revised form
27 November 2017
Accepted 27 November 2017
Available online xxx
Corresponding Editor: Gabriele B Uhl

Keywords:

Begging
Dendrobatidae
Life-history
Parental care
Sex roles
Trophic egg

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.

© 2017 Elsevier GmbH. All rights reserved.

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

E-mail address: matthew.b.dugas@gmail.com

<https://doi.org/10.1016/j.jcz.2017.11.012>

0044-5231/© 2017 Elsevier GmbH. All rights reserved.

Please cite this article in press as: Dugas, M.B., Simple observations with complex implications: What we have learned and can learn about parental care from a frog that feeds its young. *Zool. Anz.* (2017), <https://doi.org/10.1016/j.jcz.2017.11.012>

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



Fig. 1. Reproductive behavior. Male *O. pumilio* call as a component of courtship (A). After successful courtship, a female lays a clutch within the male's territory (B,C), and this clutch hatches within 12 days. Male territorial defense may offer some protection to developing clutches, and males are reported to regularly moisten clutches. Photo credits: Simone Blumenkamp.



Fig. 2. Tadpole transport and extended care. Female *O. pumilio* transport tadpoles to a nursery, usually a bromeliad leaf axil (A) and then visit the tadpole regularly for about 6 weeks (B), laying the tropic eggs upon which tadpoles feed. Frogs may visit leaf axils even when not caring for tadpoles, and multiple females deposit tadpoles in different axils of the same bromeliad (C).

do not care for clutches in this anuran manifestation of bi-parental care.

2.1.2. Why and how is clutch care valuable?

One sex might also specialize in providing care (or a particular form of care) because that sex derives more benefits from doing so than does the other; in other words, one sex might specialize in the tasks at which it is particularly efficient. A potential parallel to clutch care in *O. pumilio* and other frogs is incubation in birds; females are often more efficient at transferring heat to eggs than are males, and this difference in performance can drive the evolution of specialization (Parker et al., 2014). The efficiency-specialization hypothesis is testable with among- and within- species comparisons (Summers et al., 1999a; Pröhl, 2005). Currently, however, such tests are limited by a lack of information about i) the extent to which clutch care actually improves the fitness prospects of embryos, and ii) the proximate mechanisms by which any such value arises.

In the wild, the vast majority of *O. pumilio* clutches (~90%) fail to produce viable tadpoles (Limerick, 1980; Pröhl, 2005); the same is true in captivity (Dugas et al., 2013; Dugas et al., 2016a). The rate of clutch failure can vary temporally (Pröhl, 2005), but remaining unknown is whether variation in the care males provide explains variation in clutch failure. In captivity (under standardized conditions), male population-of-origin explains variation in the success of clutches (Dugas and Richards-Zawacki, 2015), a pattern consistent with differences in the quality of care provided (but also consistent with numerous other hypotheses). If males can influence the fate of clutches in a meaningful way, within-population variation in the extent and the quality of care males are able or willing to offer seems likely. Variation in egg care should be important to female reproductive success (Pröhl, 2005), but as of yet, the importance of a male's potential as an egg tender in female choice remain unexplored in *O. pumilio*. Learning whether and how males improve the fitness prospects of their young through egg care will reveal the relationships between the environmental challenges and

an animal's proximate ability to ameliorate them in driving the evolution of parental care. The current gap in knowledge about egg care is straightforward to address, in part by following Weygoldt's (1980) example of careful observation (e.g., Pröhl and Hödl, 1999; Pröhl, 2005).

The question of whether and why male attendance is necessary for the successful development of eggs is one that can be addressed observationally by comparing the success of clutches that receive different quantities of care, and experimentally by limiting a male's access to the clutch (e.g., via total removal *sensu* Delia et al., 2013a, or by preventing direct contact with a physical barrier). Both observational and experimental studies can be guided by *a priori* considerations of potential mechanisms of male care. Weygoldt's (1980) interpretation of male tending as a means to prevent desiccation, for example, could be tested by comparing the relationship between male attendance and hatching success across circumstances, seasons, or populations that differ in desiccation risk (Pröhl, 2005; Delia et al., 2013a, 2013b; Schulte and Lötters, 2013). Another possible source of mortality identified by Weygoldt (1980) is "spoiling". Weygoldt (1980) points out that males might limit the impact of microbial growth on the clutch as a whole by consuming spoiled eggs. The alkaloids that give poison frogs their toxicity also prevent both bacterial and fungal growth; females provision eggs with alkaloids (Stynoski et al., 2014a,b) and alkaloid delivery via male "moistening" seems at least plausible. Frequent male-clutch contact might also aid in the transfer of beneficial microbial communities (Hughey et al., 2017). Any hypothesis that males do more than simply prevent desiccation could be tested by rearing clutches away from males and manually providing moisture (but not other benefits) to the clutch. Egg predation is also a likely source of mortality, and it is probably the case that the extensive egg consumption by males that Weygoldt (1980) observed in captivity is prevented by territorial behavior in the wild (Ringle et al., 2017). Whether wild males are able or willing to deter predators that do approach the clutch, conspecific or otherwise (e.g., leeches: Pröhl, 2005), remains to be seen.

2.2. Tadpole transport

Weygoldt (1987) hypothesized that the primary adaptive value of regular clutch attendance in dendrobatid frogs (all of which lay terrestrial eggs) might come from the commensurate high probability that a parent will be present when the terrestrial eggs hatch and the tadpoles are ready for transfer to an aquatic nursery. Physical proximity between the members of a newly-hatched clutch and their parent is no doubt of critical importance, but is only the opening scene of a drama that has yet to be fully explored. Referring to the process by which a tadpole leaves the leaf litter and reaches its nursery as “tadpole deposition” (Fig. 2) is convenient, but this phrasing ignores compelling natural history that ties nicely to a rich body of theoretical and empirical literature. A parent does not simply “pick up” a tadpole, a tadpole climbs onto a parent’s back (Weygoldt, 1980; Brust, 1990), accepting the ride that the adult offers. A parent does not simply “deposit” a tadpole; a tadpole retains control over whether it accepts the parent’s offer of a nursery by disembarking. Proximate challenges and opportunities are offered by asking which sex transports tadpoles (2.2.1), a question that can be separated from more general ones about sex roles addressed earlier (Section 2.1.1). Numerous outstanding questions about tadpole transport are largely independent of which parent carries out this task (2.2.2–2.2.4), and this offspring–parent interaction can be viewed through the lenses of family members’ incompletely overlapping fitness interests.

2.2.1. Sex roles, plasticity, and the challenges associated with biparental care

Weygoldt (1980) observed individuals of both *O. pumilio* sexes transporting tadpoles on their back, the method of transport in dendrobatid and other poison frogs (Weygoldt, 1987; Wells, 2007), but also noted that male-transported tadpoles never received maternal provisioning. Males have since been observed carrying tadpoles occasionally (Cossio, 2008; Killus and Dugas, 2015). While there has been no quantitative estimate of how frequent male-transport might be (*sensu* Ringler et al., 2015) and no answer to whether it is always a dead-end for tadpoles (Killius and Dugas, 2014), it now seems nearly certain that females perform the bulk of tadpole transport in *O. pumilio* (Brust, 1990, 1993; Maple, 2002; Stynoski, 2012). Remaining entirely unclear is how a female happens to be present when transport is timely. If an adult is near enough to a clutch that a tadpole can climb on to its back, this tadpole attachment itself is enough to elicit transport behavior in one poison frog (even devoid of any natural context: Pašukonis et al., 2017). Perhaps females can avoid visiting clutches too early (before tadpoles hatch) or too late (well after tadpoles hatch) simply by beginning to visit the clutch several days after laying (the fact that tadpole attachment can, in another frog, elicit transport behavior may explain Weygoldt’s (1980) observation that adult *O. pumilio* avoid new tadpoles from unfamiliar clutches).

The male transport that Weygoldt (1980) observed is not a critical component of parental care in *O. pumilio*, but this fortuitous report offered important hints toward research directions only now being pursued. The starvation of male-transported *O. pumilio* tadpoles (Weygoldt, 1980; Killius and Dugas, 2014) illustrates a puzzle that must have been solved during the evolution of female egg-feeding from an ancestor with male-tadpole transport (Summers et al., 1999a, 2006): females need to know where the tadpoles are if they are to feed them. In an apparently independent evolution of egg-feeding in poison frogs (Summers et al., 1999a), males are responsible for leading females to the tadpoles, and perhaps encouraging trophic egg laying through courtship (Caldwell, 1997; Caldwell and de Oliveira, 1999; Brown et al., 2010). How this problem was solved during the transition to female tadpole transport in *O. pumilio* and its congeners is unknown (Summers et al., 1999a).

The discovery of probably non-functional male tadpole transport in *O. pumilio* also complements more recent discoveries in other poison frogs suggesting that even when one sex is responsible for this task in nature, the necessary neural and motor patterns are present in both (Ringler et al., 2015; Pašukonis et al., 2017). This finding in turn offers an important tool for understanding the proximate mechanisms underlying parental care (Roland and O’Connell 2015). It may even be the case that care can be facultatively expressed in the wild (Ringler et al., 2015, 2017; Pašukonis et al., 2017), a finding that must be incorporated into attempts to re-construct the evolution of parental care (Beck, 1998; Summers et al., 2006; Gomez-Mestre et al., 2012).

2.2.2. Escaping from the leaf litter– potential for within-family conflict

Weygoldt’s (1980) observation that *O. pumilio* adults (usually females) transport tadpoles on their backs was not itself surprising, as this behavior was known in several dendrobatids (Weygoldt, 1987). The observation that tadpoles were typically transported singly (Weygoldt, 1980) was, however, far more remarkable than appreciated at the time, or since. In species with male transport and no female egg-feeding, many, most, or all of the siblings resulting from a clutch are typically transported simultaneously, likely the ancestral state for these lineages (Summers et al., 1999a, 2006; Summers and Tumulty, 2014). One question is why single transport might be adaptive in egg-feeders; presumably the answer to this question is related to the selective advantages of single occupancy of nurseries (Section 2.2.4; Weygoldt, 1980, 1987; Summers and McKeon, 2004; Brown et al., 2010). A separate but related question is how single transport is effected, in other words what proximate differences there are between families with single and multiple tadpole transport. Beyond the proximate level, remaining to be explored is that this evolutionary shift has almost certainly been accompanied by an intensification of conflicts-of-interest within families (Mock and Parker, 1997).

When parents transport tadpoles singly, only one tadpole can receive the first trip away from the clutch. Transport is a valuable and perhaps limited resource, and siblings usually compete over valuable resources (Mock and Parker, 1997), so it stands to reason that tadpoles would compete for transport. To what extent is tadpole transport a limited resource? Parents often, perhaps typically, initially produce more offspring than they can or will provide with the investment required to reach independence (Mock and Forbes, 1995). Consistent with this general pattern in animals, clutches laid by female *O. pumilio* are often larger than the broods that females rear (Weygoldt, 1980; Brust, 1990; Dugas et al., 2016a), and it would not be surprising if a single female occasionally had more than one clutch that overlapped (Dugas et al., 2016a; Section 2.1.1). Female *O. pumilio* make several trips to their clutch to retrieve tadpoles (Brust, 1990), but whether females always transport all the tadpoles from each clutch is unknown (depositing “extra” tadpoles could be a good strategy given that tadpoles often fall victim to predators: Maple, 2002; Stynoski et al., 2014a). Regardless, the probability of transport unavoidably declines each time a female leaves with one tadpole on her back, just as unavoidably setting the stage for competition among brood members to be the first to earn a trip. Females occasionally transport more than one tadpole (Fig. 3), perhaps the result of tadpole competition for primacy. Currently, the potential scope of evolutionary conflict over transport, its proximate manifestations, and whether it has reached a stable resolution, remain unanswered (and largely unasked) questions (Schulte and Mayer, 2017), but are critical to new tests of inclusive fitness theory (Mock and Parker, 1997).



Fig. 3. Variation in tadpole transport behavior.

Female *O. pumilio* typically transport tadpoles singly (A), but occasionally are observed carrying multiple tadpoles (B) in all known populations, including the Aguacate peninsula of Panama (A, B), where these frogs are often blue in body coloration. Photo credit: Yusan Yang (B).

2.2.3. Choosing a nursery: limited choice and asymmetric information

For each tadpole, the value of reaching a parent's back is accrued via the newly gained possibility of reaching a nursery in which development, and eventually metamorphosis, will be possible. A parent is presumably entirely in control of which nurseries it visits with tadpole in tow, but a tadpole may maintain some proximate control over whether and when it leaves its parent's back. There is probably considerable overlap between how parents and offspring assess the quality of a potential nursery; factors like size, desiccation risk, and the presence of potential predators should be of interest to both parents and offspring (Maple, 2002; Lehtinen, 2004; Ryan and Barry, 2011; Schulte et al., 2011; Poelman et al., 2013; but see Rojas, 2014). However, parents and offspring may not agree on whether a particular nursery is "good enough", with offspring selected to have higher standards than parents (Trivers, 1974; Mock and Parker, 1997). Perhaps exacerbating the potential for conflict is an information asymmetry. A tadpole has considerably less information about the availability of and costs of exploring alternative options than does its parent (Kilner and Hinde, 2008).

When an *O. pumilio* female bearing a tadpole enters a potential nursery, it can take upwards of an hour for the tadpole to detach (Pröhl, 2005; personal observations), perhaps a surprisingly long time given the potential costs a tadpole might pay if it misses its only opportunity. This duration might reflect proximate parent-offspring negotiation over nursery quality, but could also be explained by other selective pressures (e.g., a tadpole might be selected to hold on tightly during transit, and that may come at the cost of not being able to detach quickly). Behavioral observations, in the field or captivity, will be useful for distinguishing explanations for variation in tadpole detachment, specifically via testing the prediction that tadpoles reject some offered nurseries (or accept some with more hesitation). The potential for parent-offspring conflict over a tadpole's acceptance of a nursery is perhaps never as apparent as when a candidate nursery is occupied by an older, and potentially cannibalistic, family member. The circumstances under which a parent's fitness interests are served by feeding a new offspring to an older one are considerably broader than those under which a new offspring is best off sacrificing itself (Trivers, 1974; Mock and Parker, 1997). Cannibalism is probably absent in *O. pumilio* (Dugas et al., 2016b, Section 2.2.2), but this best-of-a-bad-job tadpole feeding strategy is hypothesized in other frogs that use small plant-bound nurseries (Poelman and Dicke, 2007), and observations in those species may offer a particularly useful starting place.

2.2.4. Occasionally overcrowded nurseries

While *O. pumilio* typically transport tadpoles singly, typically deposit them one-at-a-time, and typically do not use occupied nurseries (Weygoldt, 1980; Brust, 1990, 1993; Maple, 2002), there is of course variation (Fig. 3). Although Weygoldt (1980) never observed more than one tadpole in a single nursery (leaf axil of a bromeliad), it is not uncommon to find such cases in the wild (Brust 1990; 4–24% in monitored plots in Costa Rica and Panama; M.B. Dugas and E.M. Khazan unpublished data) or in captivity (Dugas et al., 2016a). A central question about the placement of tadpoles in occupied nurseries mirrors the one Weygoldt (1980) asked about the placement of eggs in occupied nurseries: is this an adaptive strategy, or is it a non-adaptive mistake?

How nurseries come to be occupied by multiple tadpoles is unclear: a single female could deliver two offspring simultaneously (Fig. 3) or in different trips, or multiple females could use the same nursery. One possibility is that these secondary depositions are non-adaptive (Rojas, 2014), the unavoidable consequence of a strategy that is on average best (Section 2.2.3). While cannibalism is absent in *O. pumilio*, fatal aggression between nurserymates is not (Brust, 1990; Dugas et al., 2016b), and so adaptive explanations for multiple occupancy (e.g., offering tadpoles as meals to siblings: Poelman and Dicke, 2007) are difficult to imagine, regardless of relatedness between co-occupants. Nonetheless, experimental evidence indicates that mothers experimentally forced to choose among occupied nurseries are more likely to place siblings together (Brust, 1990). Although common, fatal nurserymate aggression is not universal (Dugas et al., 2016b), and so perhaps an already occupied nursery, especially one occupied by a sibling, is sometimes a better option than the others available. In the wild, molecular work is needed to reveal how often nursery co-occupants are siblings (Richards-Zawacki et al., 2012; Muralidhar et al., 2014), as this will shape the fitness outcomes of all players.

2.3. Feeding tadpoles

Weygoldt (1980) motivated his work by noting that *O. pumilio* tadpoles, unlike those of other poison frogs, had proven notoriously difficult to rear in captivity, a challenge that has continued to be of interest with conservation goals in mind (Dugas et al., 2013). The solution to this husbandry problem was the discovery of egg-feeding by mothers. The fact that *O. pumilio* tadpoles could be raised through metamorphosis on frog eggs was known, but Weygoldt (1980) demonstrated that egg feeding is a natural and essential feature of *O. pumilio* reproduction by showing that i) tadpoles starved

when removed from the presence of mothers, ii) trophic eggs were laid only in leaf axils (rearing sites) with tadpole occupants (and only by the female that deposited those tadpoles), and iii) tadpoles that he manually placed in axils (i.e., not transported by parents) were not fed.

2.3.1. Tadpoles require maternally provisioned eggs

Weygoldt (1980) noted that when removed from tanks in which adults are present, captive *O. pumilio* tadpoles starve. A similar experiment in the wild, where alternative food sources (e.g., detritus, invertebrates) are available at natural levels, yielded a similar result, confirming the interpretation that oophagy is obligate in *O. pumilio* (Brust, 1993). Egg-feeding is not just necessary for tadpole survival: the more, and more frequently, a tadpole is fed, the more rapidly it increases in mass (Brust, 1993; Maple, 2002) and the heavier it is at metamorphosis (Dugas et al., 2016a,c). Probably via this effect on metamorphic mass, maternal feeding enhances post-metamorphic offspring survival as well, even in captivity when food provided *ad libitum* (Dugas et al., 2016c). Calories is not all mothers provide via trophic eggs. In captivity, supplementing adults' diet with carotenoids increases the probability of successful metamorphosis by their offspring (Dugas et al., 2013). In the wild, maternally provisioned eggs supply tadpoles with alkaloids, the diet-derived chemicals that give adult *O. pumilio* their toxicity (Stynoski et al., 2014b), and these toxins serve to deter some predators from consuming tadpoles (Stynoski et al., 2014a).

While *O. pumilio* tadpoles starve when they do not receive maternally provisioned trophic eggs (Weygoldt, 1980; Brust, 1993), tadpoles in another poison frog lineage with elaborate parental care only rely on maternal care in small (nutrient-poor) nurseries (Brown et al., 2010). Larval *O. pumilio* will grow when offered other frog eggs as food (Weygoldt, 1980; Stynoski et al., 2014a, 2014b; Dugas et al., 2017), but seemingly not on other potential food items. This finding raises a number of proximate and evolutionary questions, principally regarding what selective pressures and/or constraints have resulted in the evolutionary loss of the ability to eat and/or thrive on food available in their nurseries. It may be informative to explore the extent to which *O. pumilio* tadpoles reject non-egg food items vs. fail to gain nutrition from them; *O. pumilio* tadpoles do not cannibalize nurserymates they kill, demonstrating that some potential food items are rejected (Dugas et al., 2016b). While the costs of such specialization are apparent, the benefits of the traits underlying it have yet to be explored. One possibility is that egg-feeding requires specialized mouth morphology (Wells, 2007), but the ability of *O. pumilio* to kill other tadpoles (Dugas et al., 2016b) and the ability of other tadpoles to eat both eggs and other resources in the nursery (Brown et al., 2010) suggest such specialization is incomplete.

2.3.2. Developmental plasticity and the potential for parent-offspring conflict

Compared with that of other vertebrates in which parental feeding is common (mammals and birds), the growth of amphibian larvae is remarkable for its plasticity. Within species, the duration of the larval period and size at which larvae metamorphose is enormously variable, with larvae generally predicted to delay metamorphosis when resources are abundant in the larval environment (Wilbur and Collins, 1973; Morey and Reznick, 2000; Altwegg and Reyer, 2003). This plasticity could generate an unusually large range of parental care between the minimum level required for offspring viability and the level at which either a parent or offspring's fitness is best served by the parent shifting investment to new offspring (Trivers, 1972; Mock and Parker, 1997; Section 2.4). However, an experiment in captivity suggests little potential for parent-offspring conflict over the duration of care. The extent to which a trophic egg increases the probability a tadpole

will survive through metamorphosis and to adult size increases as tadpoles develop; in other words, the benefits of feeding tadpoles increases as the tadpoles develop (Dugas et al., 2016c). If the marginal benefits of care eventually plateau, they would do so beyond the point at which transitioning to independence (metamorphosis) is a tadpole's optimal strategy (Trivers, 1972). The difference in value between old tadpoles, young tadpoles, and new reproductive opportunities (Section 2.4) is likely to vary predictably across habitats that, among other things, vary in the risks clutches and tadpoles face (Maple, 2002; Pröhl, 2005). Comparative studies among these populations (and species) may be particularly useful to testing life-history theory (Dugas and Richards-Zawacki, 2016).

2.4. The costs of parental care

Parents are selected to optimally allocate parental investment, defined as care that comes at the expense of a parent's ability to care for (invest in) other offspring (Trivers, 1972). In dendrobatid and other poison frogs, the extent to which male care comes at the expense of investing in other offspring has, understandably, received the most attention in species where the male provides all the post-zygotic care (Summers and Tumulty, 2014), leaving males of species like *O. pumilio* understudied (Sections 2.1.1 and 2.1.2). In captivity, *O. pumilio* males held in pairs that reproduce successfully more often die earlier (Dugas et al., 2015a), suggesting that males do invest in care. Females pay similar longevity costs of frequent breeding (Dugas et al., 2015a), and several other lines of evidence also suggest that parental care is costly for females. In captivity, females successfully rear a smaller proportion of their brood to metamorphosis in later reproductive events, an effect independent of maternal age (Dugas et al., 2015b) and one that mirrors reproductive "burn out" sometimes described by hobbyists. In the wild, females have not been observed courting, mating, or transporting tadpoles while caring for a brood (Brust, 1990; Pröhl and Hödl 1999; Pröhl, 2002). Weygoldt (1980) noted similar patterns in captivity, increasing clutch production by experimentally removing a female's brood. More recent studies in a captive breeding colony showed that reproductive attempts decline, but do not cease, while females are feeding tadpoles, and broods often overlap (Dugas et al., 2016a). Although these differing reports suggest opportunities to study female behavior more closely, both support the hypothesis that tadpole feeding is costly for female *O. pumilio*. Finally, there is evidence that females are limited in the number of tadpoles they can feed simultaneously, with meal size (and tadpole survival) declining in larger broods (Dugas et al., 2016a). Understanding the extent to which resource limitations shape wild families will be particularly valuable, especially to efforts to marry poison frog natural history to life-history theory (Dugas and Richards-Zawacki, 2016).

3. Offspring-parent communication

Perhaps chief among Weygoldt's (1980) many exciting observations of his captive frogs was that when an adult *O. pumilio* approached an occupied nursery, "the tadpoles stiffened their tails and rapidly vibrated (p. 330)," in a manner distinct from swimming (supplemental video S1, S2). This tadpole behavior was later interpreted as the first reported (and probably best) potential analog of avian begging in another vertebrate class (Mock and Parker, 1997; Kilner and Johnstone, 1997). Bolstering the interpretation of this behavior as offspring-parent communication were Weygoldt's (1980) reports that he did not observe tadpoles performing this behavior in response to non-adult stimuli (rather they hid), and that females did not lay eggs in nurseries from which he removed tadpoles or in which tadpoles had died (i.e., those without a rapidly

vibrating tadpole). Both tadpole suppression of activity at inappropriate stimuli (Stynoski and Noble, 2012) and a strong relationship between tadpole vibration and maternal feeding (Stynoski, 2012; Dugas et al., 2017) have been subsequently confirmed in the wild.

Perhaps no relevant literature has expanded more since Weygoldt's (1980) report than that regarding the function and evolution of offspring-parent communication (i.e., begging). This topic integrates life-history theory, inclusive fitness theory, and hypotheses for how communication evolves, and has grown from advances in each area (Kilner and Johnstone 1997; Wright and Leonard, 2002; Mock et al., 2011). Matters remaining of considerable debate include the extent to which parents and offspring control the allocation of food, the extent to which it is offspring signals *per se* (rather than correlated traits) that influence parental behaviors, and what information is contained in offspring signals (i.e., to what type of information parents have been selected to attend) (Kilner and Johnstone, 1997; Parker et al., 2002; Royle et al., 2002; Mock et al., 2011). Frogs like *O. pumilio* not only offer the opportunity to test this well-developed theory in a new system, but are also especially tractable model organisms with natural history that allows empirical approaches unavailable in other vertebrates.

3.1. The information content of tadpole displays

Weygoldt's (1980) argument that rapid tadpole vibration probably serves in offspring-parent communication has been, despite a lack of any empirical follow-ups, prominently cited in reviews on the topic of begging (e.g., Kilner and Johnstone, 1997). Only recently have attempts been made to quantify variation in the expression of this putative signal and to use any such variation to test hypotheses for the evolution and function of begging. The most popular suite of hypotheses for why offspring signal is built on the central premise that offspring solicitations evolve because they contain information (Kilner and Johnstone, 1997; Parker et al., 2002; Royle et al., 2002; Mock et al., 2011; but see Section 3.3). Two exclusive hypotheses assume that solicitation intensity reflects current offspring fitness prospects, differing in the direction of the predicted relationship: i) a positive relationship would suggest that intensely vibrating tadpoles advertise high quality, and thus that this signal co-evolved with parents that benefit from diverting resources to offspring progressing best (Section 2.3.2), while ii) a negative relationship would support the hypothesis that tadpoles vibrating rapidly instead advertise their low current fitness prospects (high 'need') and that this signal co-evolved with parents that benefit from correcting such deficits (reviewed by Mock et al., 2011). A non-exclusive hypothesis is that intense tadpole vibration reflects immediate hunger (i.e., an empty gut: Mock et al., 2011).

In *O. pumilio* tadpoles, high intensity begging seems most likely to signal high quality. Several metrics of solicitation intensity are positively associated with tadpole size, developmental stage, and experimentally manipulated body condition (Dugas et al., 2017). The evolution of such a signal is easily explained in *O. pumilio*, as maternal feedings pay higher fitness returns when allocated to more developed offspring (Dugas et al., 2016c). Unlike nearly every other animal reported on (Mock et al., 2011), *O. pumilio* tadpoles display less intensely following food deprivation (Dugas et al., 2017). This result brings focus to the taxonomic limitations to the meaningful use of the term 'hunger'. In birds and mammals, starvation is a constant and immediate risk for developing young reliant on parental care, and experimental short-term food deprivation is ubiquitous in studies of the information content of avian begging (Mock et al., 2011). Tadpole *O. pumilio*, on the other hand, face no such risk, surviving weeks without food (Brust, 1993; Killius and Dugas, 2014). It remains to be seen how deeply the biases associated with studying ectotherms has limited the generality of our understanding about why offspring and parents communicate.

While *O. pumilio* tadpoles decrease the intensity of begging following a period of food deprivation approximating the natural interval between maternal visits (Dugas et al., 2017), they nearly cease begging immediately after eating (Stynoski, 2012). This strategy may help tadpoles avoid predators or at least avoid begging with no chance of reward (Weygoldt, 1980; Stynoski and Noble, 2012). This behavior has parallels in other systems and may prove valuable to testing hypothesized explanations for it. Nestling birds often beg when parents are absent, a behavior hypothesized to be adaptive because it decreases the probability a nestling will miss opportunities to eat (Dor et al., 2007). Missing a potential feeding opportunity might be especially costly for a dependent tadpole given that maternal visits are infrequent (Maple, 2002) and that some tadpoles, including *O. pumilio*, eat nothing else. The costs are even higher assuming that a female that fails to perceive a tadpole's presence eventually stops visiting that nursery (Stynoski, 2009; Section 3.3). Given that the risk of missing meals and/or falling victim to a predator certainly varies among species (e.g., with the extent to which tadpoles depend on trophic eggs) and likely varies among populations (Brown et al., 2010; Dugas and Richards-Zawacki, 2016), comparative studies will be a good way to test whether and why tadpole decisions about when to (not) beg are adaptive.

Some components of *O. pumilio* tadpole vibration displays contain information (Dugas et al., 2017). Future empirical work can help identify the proximate reasons for such relationships, guided by a well-developed theoretical and empirical literature about the evolution of animal signals (Maynard Smith and Harper, 2003). Critical to quantifying variation in the begging displays of tadpoles will also be information about the sensory abilities of adult frogs, for example the extent to which females can discriminate between tadpoles vibrating at different speeds and the sensory systems they use to do so (e.g., while tactile effects of tadpole vibration seems likely to be important, Weygoldt (1980) also reported that females looked into nurseries before entering and feeding, or not feeding, tadpoles). Filling these gaps in system-specific information will help unlock the potential of these frogs to help reveal how and why offspring-parent communication evolves (Section 3.4).

3.2. Maternal favoritism and response to begging

The empirical potential of Weygoldt's (1980) finding that mother *O. pumilio* feed tadpoles while visiting them grew substantially when Brust (1993) observed that, in the wild, mothers that visit their tadpoles do not always feed them. This finding suggests that females are choosy; they might sometimes assess something about a tadpole and use that information to decide not to provide a meal. Weygoldt (1980) never saw females feed multiple tadpoles in quick succession, and assumed that this meant a female always laid all her mature eggs when feeding (i.e., females were limited to yes/no decisions). Weygoldt's (1980) interpretation is, however, perhaps inconsistent with small meal size in the wild and the fact that inter-feeding interval is shorter than the time between reproductive clutch production (Brust, 1990, 1993; Maple, 2002; Pröhl, 2005). If females make yes/no or graded decisions, there is good reason for female *O. pumilio* to favor their more developed offspring (Dugas et al., 2016c; Section 2.3.2), and mothers in captivity (Dugas et al., 2016a) and in the wild (Dugas et al., 2017) have been found to feed larger meals to their older and larger tadpoles. While one observational study in the wild found no such increase in meal size with tadpole development (Brust, 1990), that study included fewer potential predictors of meal size (e.g., begging behavior, brood size), and so it is as of yet unclear whether favoritism towards large offspring is a maternal trait that varies among populations.

Key to testing the hypothesis that *O. pumilio* tadpole displays evolved in the context of communication is demonstrating a link

between the expression of the putative signal (tadpole vibration) and the response of the intended receiver (maternal favoritism). Weygoldt (1980) provided the first piece of evidence suggesting communication when he noted that the mothers he observed never laid trophic eggs in axils from which he had removed tadpoles or in which the tadpole died. An extensive monitoring effort in the wild also suggests that only tadpoles that display are fed by mothers (Stynoski, 2012). However, this signal may not be absolutely necessary to elicit maternal feeding: experimentally cross-fostered non-begging tadpoles are occasionally fed by wild mothers (Dugas et al., 2017). On a finer scale, correlative evidence in the wild suggests that mothers reward particularly rapid vibration with larger meals (Dugas et al., 2017). All the evidence that is currently available suggests that the rapid vibration of *O. pumilio* tadpoles is analogous to the complex begging displays so familiar from birds (Wright and Leonard, 2002), with the signal reliably associated with individual fitness prospects and with mothers responding in a graded fashion to signal intensity (Dugas et al., 2017). However, the only conclusive test of this hypothesis will come from experimental manipulations of tadpole begging effort, ideally in concert with information about other potential constraints on maternal response (e.g., brood size: Dugas et al., 2016a).

3.3. Future directions: unusual natural history and unusual empirical opportunities

When post-zygotic feeding is present, frog families provide excellent opportunities to test hypotheses for how and why offspring-parent communication evolves. Quantifying how much care a free-living offspring receives and comparing this intake to that of others is unusually easy, as care comes only in integer form (Brust, 1993). A connection between the care a parent provides and a loss of other reproductive opportunities (Trivers, 1972) can be made with little ambiguity because tadpoles (sometimes exclusively) eat their mothers' other reproductive opportunities (eggs). The current fitness prospects of tadpoles are relatively easily estimated, as the number of trophic eggs a tadpole has already consumed is straightforward to observe (Maple, 2002; Dugas et al., 2016a) and manipulate (Brust, 1993; Dugas et al., 2016c, 2017). The number of trophic eggs required for a tadpole to reach viability (i.e., amount of further parental investment 'needed') is also readily estimated (Dugas et al., 2016c). Patterns of parental favoritism are more also easily interpreted than they are in other taxa. In endotherms (birds, mammals), resting metabolic demands increase as offspring grow, leaving any evidence that parents favor their larger offspring subject to the criticism that these larger offspring "need" more food. In frogs, there is no such potential for parental preferences for large offspring to be interpreted (fairly or unfairly) as consistent with favoritism for needy individuals: *O. pumilio* tadpoles, for example, can survive weeks without food (Weygoldt, 1980; Brust, 1993).

The natural history of dendrobatids and other poison frogs is exceptionally well-suited to testing hypotheses for the evolution of offspring solicitation displays because mothers rear contemporaneous offspring (i.e., broodmates) in separate nurseries. Animals almost always rear broods of more than one offspring in a single physically confined space (Mock and Parker, 1997), and in these groups assessing the role of signals in resource allocation is difficult. While the bulk of empirical work tends to focus on honest signalling models of begging evolution (Mock et al., 2011; Sections 3.1 and 3.2), honest signalling is not the only way offspring compete for parental investment. Physical competition among offspring, for example, is common in animals (Mock and Parker, 1997), but absent in tadpoles in separate nurseries (the occasional multi-tadpole *O. pumilio* nursery will be valuable to testing for such competition in what is perhaps an intermediate stage in the evolution of elaborate care in poison frogs: Dugas et al., 2016b). Signals

themselves can also evolve through mechanisms other than the more-or-less honest transfer of information (Maynard Smith and Harper, 2003), complicating efforts to test alternative hypotheses for the relationship between information and offspring signal evolution. In a way parallel to physical competition, offspring signals can evolve in a 'signalling scramble' in which offspring produce signals and parents simply allocate resources in proportion to the relative intensity of stimuli offered (Parker et al., 2002; Royle et al., 2002). The distinction between information-driven evolution of offspring displays and these alternatives is non-trivial; only a parent that exerts control over resource allocation can adjust its investment strategy to changing circumstances (Parker et al., 2002; Royle et al., 2002; Mock et al., 2011). Particularly problematic is that information-driven and signalling scramble models often predict identical parental allocation patterns, usually making it difficult to use observations of families to draw conclusions about the selective pressures that shaped offspring signals and parental responses (Parker et al., 2002; Royle et al., 2002). In frogs that rear offspring in individual nurseries, however, these constraints are relaxed substantially, as parents maintain complete proximate control of allocation and interact with (perceive the signals of) only one offspring at a time.

Debates over why offspring solicitations have evolved have begun to give way to comparative efforts allowing for the possibility that offspring solicitations evolved for different reasons in different species (Caro et al., 2016a). Parental feeding and offspring solicitation has evolved in taxonomically diverse frogs (Weygoldt, 1980; Brust, 1993; Jungfer and Weygoldt, 1999; Kam and Yang, 2002; Wells, 2007; Brown et al., 2010). It is entirely plausible that the information content of begging (Yoshioka et al., 2016) varies among systems, perhaps along with the mating system of the frog (relatedness among families: Caro et al., 2016b) or perhaps with the extent to which offspring are dependent on parental care (Smiseth et al., 2003; Brown et al., 2010). Studies in captivity will remain important because of the opportunities they present to comprehensively catalog the reproductive behaviors and outcomes of individuals, but understanding the evolution of parental investment, parental care, and offspring-parent communication will require similar efforts in nature, where families face the same realistic constraints in which their life-history strategies evolved.

4. Parental care, sexual selection, and phenotypic diversity

The strawberry poison frog may be familiar to readers not only for its elaborate parental care, but also for the remarkable phenotypic diversity it displays in and around the Bocas del Toro archipelago of Panama (Daly and Myers, 1967; Wang and Shaffer, 2008; Fig. 4). One popular potential explanation of how this extreme polytypism evolved can trace its roots to Weygoldt's (1980) conclusion that, in *O. pumilio*, "parental investment of the female far exceeds that of the male (p. 331)." In Bocas del Toro, the same region where *O. pumilio* is so diverse, phenotypic and genetic differentiation has not arisen in ecologically similar poison frogs, and it happens that, in those frogs, offspring feeding is absent and males provide tadpole transport (i.e., male and female parental investment are more similar in magnitude: Summers et al., 1997). This among-species difference led Summers et al. (1997) to suggest that the magnitude of female to male investment difference in *O. pumilio* drives stronger sexual selection on male ornamentation than emerges in species with male care, and thus could be responsible for driving color divergence among populations. This hypothesis was particularly timely, as the potential role of sexual selection in driving reproductive isolation was gaining appreciation (Panhuis et al., 2001; Ritchie, 2007). This connection was immediately buoyed by reports that female *O. pumilio* attend to male

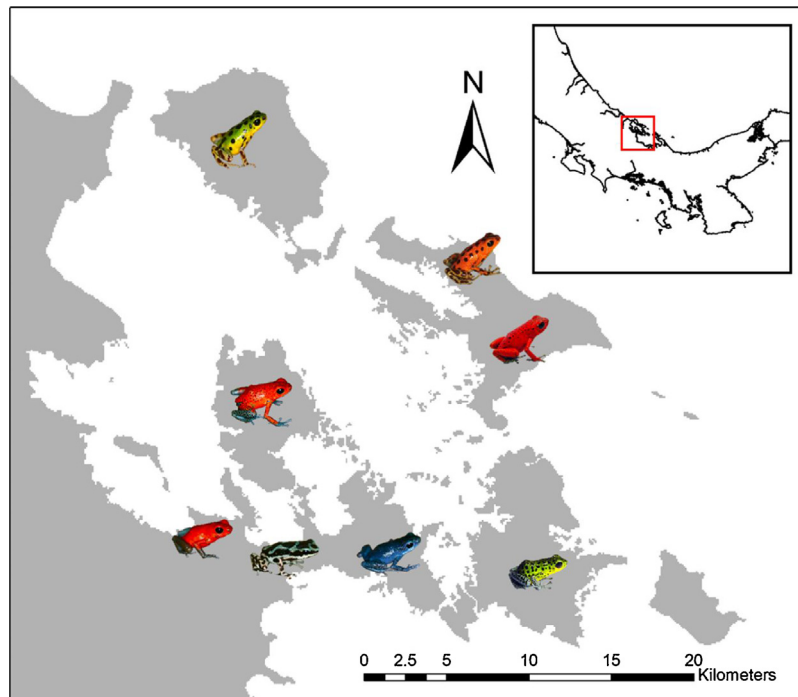


Fig. 4. Phenotypic diversity.

While *O. pumilio* is typically red with blue or black legs throughout most of its Central American range, populations in and around the Bocas del Toro archipelago, Panama, display diverse coloration and patterning, some of which is shown here. This rapid phenotypic diversification is hypothesized to have arisen in part via sexual selection that is in turn hypothesized to be tied to the elaborate parental care that has evolved in this frog. Photo credit: Justin Yeager.

coloration in laboratory preference assays (Summers et al., 1999b; Reynolds and Fitzpatrick, 2007; Maan and Cummings, 2008), and attempts to link this laboratory phenomenon to mate choice and reproductive isolation in the wild continue (Richards-Zawacki et al., 2012; Meuche et al., 2013; Dreher and Pröhl, 2014; Gade et al., 2016; Yang et al., 2016; Dreher et al., 2017).

The hypothesis that the elaborate parental care provided by female *O. pumilio* was the ultimate driver of especially intense sexual selection in this frog (Summers et al., 1997), however, has remained essentially untested. The argument that *O. pumilio* natural history, in particular parental care, should lead to the evolution of females that are choosier than those of other species is one that can only be tested in a comparative framework. The hypothesis that phenotypic divergence (in color or a sexually dimorphic trait like call: Pröhl et al., 2007) is associated with parental care can easily be tested. Remarkable color polytypism has also evolved elsewhere in species with diverse forms of care, including uniparental male care (Noonan and Comeault, 2009; Yeager et al., 2012; Rojas and Endler, 2013; Rojas, 2016), suggesting that this hypothesis may need to be re-visited.

Interrogating the assumptions underlying a hypothetical link between parental care and sexual selection in frogs is also important. The costs of care, be they physiologically (Section 2.4) or socially (Section 2.1) mediated, can be quantified (Dugas et al., 2015a,b; Dugas et al., 2016a,c), and these costs used to test the assumptions that i) females invest more than males, and ii) female *O. pumilio* invest more in each reproductive event than do females of other species. Although substantially higher female than male investment is intuitive in *O. pumilio*, the scant empirical evidence currently available suggests that male investment is non-trivial (Dugas et al., 2015a). The assumption that female *O. pumilio* invest substantially more than non egg-feeding females, in particular, warrants empirical attention. If a female lays a clutch of 10 eggs, carries each resulting tadpole to a nursery, and provides no further care, it is not necessarily the case that she has invested less than a

female that lays 1 egg, carries that tadpole to a nursery, and then feeds it 9 eggs. Trophic egg feeding is common in animals, but it is not commonly assumed that this strategy is equivalent to an overall increase in maternal investment per reproductive event (Perry and Roitberg, 2006). Finally, the parental care, sexual selection, and phenotypic diversity hypothesis likely needs revision in light of subsequent theoretical advances in our understanding of the relationship between parental investment and sexual selection. The assumption that sex differences in care cause intense sexual selection is no longer a consensus (Wade and Schuster, 2002; Kokko and Jennions, 2003; Klug et al., 2013; Royle et al., 2016). Regardless of whether phenotypic diversification is related to elaborate parental care, Weygoldt's (1980) findings underpinned a burst of empirical work that has addressed questions important to our understanding of the generation and maintenance of phenotypic diversity.

5. Conclusions and perspectives

With detailed descriptions of parental behavior in captive individuals, Weygoldt (1980) offered insights into both the biology of a charismatic poison frog and the evolution of parental care. These observations, viewed in the context of an ever-expanding empirical and theoretical literature, highlight the potential for *O. pumilio* to serve in independent tests of hypotheses developed primarily with birds in mind (Mock et al., 2011), and to address questions that may be difficult, if not impossible, to address in more extensively studied animals (Dugas et al., 2016c; Dugas et al., 2017).

There is value to pooling the resources of the scientific community to learn as much as possible about the proximate and ultimate explanations underlying the phenotype (behavioral and otherwise) of common model organisms. Species, however, do not begin as well-studied models, and there is considerable value in describing the basic biology and natural history across as much biological diversity as possible. If existing theory were not consistent with the observations we have, it would presumably not have been

generated in the first place. The literature has shifted away from describing behavior as an end unto itself (Bee et al., 2013), but careful observation, especially in the wild, can be just as useful for hypothesis-testing as laboratory experiments. It was my intention here to illustrate the novel, exciting, and often untrodden paths that could be taken if one were to set out from Weygoldt's (1980, 1987) observations, straightforward experiments, and ideas. I hope that readers will not only be encouraged to follow the signposts laid out by Weygoldt's efforts, but will be also inspired to make their own discoveries. Surely more findings as surprising (and charming) as a frog that feeds its young await those who take the time to watch for them.

Acknowledgements

This manuscript is contained within a special issue honoring Peter Weygoldt, and I offer my thanks to Gabriele Uhl for organizing this issue and inviting me to contribute. Dr. Weygoldt's pioneering contributions to the study of parental care in poison frogs have been central to my own work, and I am grateful for the opportunity to thank him here. This review was strengthened by collaborations, conversations, and the occasional argument with numerous colleagues, including Simone Blomenkamp, Layla Freeborn, Doug Mock, Cori Richards-Zawacki, Ralph Saporito, Stephanie Strickler, Jennifer Stynoski, Yusan Yang, and Justin Yeager. Simone Blomenkamp, Yusan Yang, and Justin Yeager generously allowed me to use their photographs in this manuscript and Nathan Franssen created the map used in Fig. 4. Michael P. Moore, the Whiteman lab, and two anonymous reviewers provided invaluable comments on earlier drafts. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.jcz.2017.11.012>.

References

- Altwegg, R., Reyer, H.U., 2003. Patterns of natural selection on size at metamorphosis in water frogs. *Evolution* 57, 872–882.
- Beck, C.W., 1998. Mode of fertilization and parental care in anurans. *Anim. Behav.* 55, 439–449.
- Bee, M.A., Schwartz, J.J., Summers, K., 2013. All's well that begins wells: celebrating 60 years of *Animal Behaviour* and 36 years of research on anuran social behaviour. *Anim. Behav.* 85, 5–18.
- Birkhead, T.R., Atkin, L., Møller, A.P., 1987. Copulation behaviour of birds. *Behaviour* 101, 101–138.
- Brown, J.L., Morales, V., Summers, K., 2010. A key ecological trait drove the evolution of biparental care and monogamy in an amphibian. *Am. Nat.* 175, 436–446.
- Brust, D.G., 1990. Maternal Brood Care by *Dendrobates pumilio*: A Frog That Feeds its Young. PhD Dissertation. Cornell University, Ithaca, NY.
- Brust, D.G., 1993. Maternal brood care by *Dendrobates pumilio*: a frog that feeds its young. *J. Herpetol.* 27, 96–98.
- Caldwell, J.P., de Oliveira, V.R., 1999. Determinants of biparental care in the spotted poison frog, *Dendrobates vanzolinii* (Anura: Dendrobatidae). *Copeia* 1999, 565–575.
- Caldwell, J.P., 1997. Pair bonding in spotted poison frogs. *Nature* 385, 211.
- Caro, S.M., West, S.A., Griffin, A.S., 2016b. Sibling conflict and dishonest signaling in birds. *Proc. Natl. Acad. Sci. U. S. A.* 113, 13803–13808.
- Caro, S.M., Griffin, A.S., Hinde, C.A., West, S.A., 2016a. Unpredictable environments lead to the evolution of parental neglect in birds. *Nat. Commun.* 7, 1–10.
- Clutton-Brock, T.H., 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton.
- Cossio, R., 2008. *Oophaga pumilio* (strawberry poison frog) parental care. *Herp. Rev.* 39, 462.
- Crump, M.L., 1996. Parental care among the Amphibia. *Adv. Study Behav.* 25, 109–144.
- Daly, J.W., Myers, C.W., 1967. Toxicity of Panamanian poison frogs (*Dendrobates*): some biological and chemical aspects. *Science* 156, 970–973.
- Dawkins, R., Carlisle, T.R., 1976. Parental investment, mate desertion and a fallacy. *Nature* 262, 131–134.
- Delia, J.R.J., Ramirez-Bautista, A., Summers, K., 2013a. Glassfrog embryos hatch early after parental desertion. *Proc. R. Soc. Lond. B.* 67, 557–569.
- Delia, J.R.J., Ramirez-Bautista, A., Summers, K., 2013b. Parents adjust care in response to weather conditions and egg dehydration in a Neotropical glassfrog. *Behav. Ecol. Sociobiol.* 67, 557–569.
- Dor, R., Kedar, H., Winkler, D.W., Lotem, A., 2007. Begging in the absence of parents: a quick on the trigger strategy to minimize costly misses. *Behav. Ecol.* 18, 97–102.
- Dreher, C.E., Pröhl, H., 2014. Multiple sexual signals: calls over colors for mate attraction in an aposematic, color-diverse poison frog. *Front. Ecol. Evol.* 2, 22.
- Dreher, C.E., Rodríguez, A., Cummings, M.E., Pröhl, H., 2017. Mating status correlates with brightness in some but not all poison frog populations. *Ecol. Evol.*, <http://dx.doi.org/10.1002/ece3.3531>.
- Dugas, M.B., Richards-Zawacki, C.L., 2015. A captive breeding experiment reveals no evidence of reproductive isolation among lineages of a polytypic poison frog. *Biol. J. Linn. Soc.* 116, 52–62.
- Dugas, M.B., Richards-Zawacki, C.L., 2016. Conspicuous and cryptic morphs of a polytypic poison frog differ in reproductive output because of differences in tadpole performance not parental effort. *Ethol. Ecol. Evol.* 28, 441–451.
- Dugas, M.B., Yeager, J., Richards-Zawacki, C.L., 2013. Carotenoid supplementation enhances reproductive success in the captive strawberry poison frogs (*Oophaga pumilio*). *Zoo Biol.* 3, 655–658.
- Dugas, M.B., Wamelink, C.N., Richards-Zawacki, C.L., 2015a. Both sexes pay a cost of reproduction in a frog with biparental care. *Biol. J. Linn. Soc.* 115, 211–218.
- Dugas, M.B., Moore, M.P., Wamelink, C.L., Richards-Zawacki, C.L., Martin, R.A., 2015b. An experimental test for age-related improvements in reproductive performance in a frog that cares for its young. *Sci. Nat.* 102, 48.
- Dugas, M.B., Wamelink, C.L., Killius, A.M., Richards-Zawacki, C.L., 2016a. Parental care is beneficial for offspring costly for mothers, and limited by family size in an egg-feeding frog. *Behav. Ecol.* 27, 476–483.
- Dugas, M.B., Stynoski, J.L., Strickler, S.A., 2016b. Larval aggression is independent of food limitation in nurseries of a poison frog. *Behav. Ecol. Sociobiol.* 70, 1389–1395.
- Dugas, M.B., Moore, M.P., Martin, R.A., Richards-Zawacki, C.L., Sprehn, C.G., 2016c. The payoffs of maternal care increase as offspring develop, favouring extended provisioning in an egg-feeding frog. *J. Evol. Biol.* 29, 1977–1985.
- Dugas, M.B., Strickler, S.A., Stynoski, J.L., 2017. Tadpole begging reveals high quality. *J. Evol. Biol.* 30, 1024–1033.
- Evans, J.P., Magurran, A.E., 2000. Multiple benefits of multiple mating in guppies. *Proc. Natl. Acad. Sci. U. S. A.* 97, 10074–10076.
- Gade, M.R., Hill, M., Saporito, R.A., 2016. Color assortative mating in a mainland population of the poison frog *Oophaga pumilio*. *Ethology* 112, 851–858.
- Gomez-Mestre, I., Pyron, R.A., Wiens, J.J., 2012. Phylogenetic analyses reveal unexpected patterns in the evolution of reproductive modes in frogs. *Evolution* 66, 3687–3700.
- Gross, M.R., Sargent, R.C., 1985. The evolution of male and female parental care in fishes. *Am. Zool.* 25, 807–822.
- House, C.M., Walling, C.A., Stamper, C.E., Moore, A.J., 2009. Females benefit from multiple mating but not multiple mates in the burying beetle *Nicrophorus vespilloides*. *J. Evol. Biol.* 22, 1961–1966.
- Hughey, M.C., Delia, J., Belden, L.K., 2017. Diversity and stability of egg-bacterial assemblages: the role of parental care in the glassfrog *Hyalinobatrachium colymbiphylum*. *Biotropica*, <http://dx.doi.org/10.1111/btp.12461>.
- Jennions, M.D., Petrie, M., 2000. Why do females mate multiply? A review of the genetic benefits. *Boil. Rev.* 75, 21–64.
- Jungfer, K.H., Weygoldt, P., 1999. Biparental care in the tadpole-feeding Amazonian treefrog *Osteocephalus oophagus*. *Amphibia-Reptilia* 20, 235–249.
- Jungfer, K.-H., Weygoldt, P., Juraske, N., 1996. *Dendrobates vicentii*, ein neuer pfeilgiftfrosch aus zentral-Panama. *Herpetofauna* 18, 17–26.
- Kam, Y.C., Yang, H.W., 2002. Female-offspring communication in a Taiwanese tree frog, *Chiixalus eiffingeri* (Anura: Rhacophoridae). *Anim. Behav.* 64, 881–886.
- Killius, A.M., Dugas, M.B., 2014. Tadpole transport by male *Oophaga pumilio* (Anura: Dendrobatidae): an observation and brief review. *Herp. Notes* 7, 747–749.
- Kilner, R.M., Hinde, C.A., 2008. Information warfare and parent-offspring conflict. *Adv. Study Behav.* 38, 283–336.
- Kilner, R., Johnstone, R.A., 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol. Evol.* 12, 11–15.
- Klug, H., Bonsall, M.B., Alonzo, S.H., 2013. Sex differences in life history drives evolutionary transitions in maternal, paternal, and bi-parental care. *Evol. Ecol.* 3, 792–806.
- Kokko, H., Jennions, M., 2003. It takes two to tango. *Trends Ecol. Evol.* 18, 103–104.
- Lehtinen, R.M., 2004. Ecology and evolution of phytotelm-breeding anurans. In: *Museum of Zoology, University of Michigan, Ann Arbor (USA)*.
- Limerick, S., 1980. Courtship behavior and oviposition of the poison-arrow frog *Dendrobates pumilio*. *Herpetologica* 36, 69–71.
- Losos, J.B., 2011. Convergence, adaptation, and constraint. *Evolution* 65, 1827–1840.
- Maan, M.E., Cummings, M.E., 2008. Female preferences for aposematic signal components in a polymorphic poison frog. *Evolution* 64, 1748–1761.
- Magrath, M.J.L., Komdeur, J., 2003. Is male care compromised by additional mating opportunity? *Trends Ecol. Evol.* 18, 424–430.
- Maple, M.M., 2002. Maternal Effects on Offspring Fitness in *Dendrobates Pumilio*, the Strawberry Poison Frog. PhD Dissertation. University of Kentucky, Lexington (KY).
- Maynard Smith, J., Harper, D., 2003. *Animal Signals*. Oxford University Press, Oxford.

- Maynard Smith, J., 1977. Parental investment—a perspective analysis. *Anim. Behav.* 25, 1–9.
- McGee, G., 2011. *Convergent Evolution: Limited Forms Most Beautiful*. MIT Press, Massachusetts.
- McVey, M.E., Zahary, R.G., Perry, D., MacDougall, J., 1981. Territoriality and homing behavior in the poison dart frog (*Dendrobates pumilio*). *Copeia* 2011, 1–8.
- Meuche, I., Linsenmair, E., Pröhl, H., 2011. Female territoriality in the strawberry poison frog (*Oophaga pumilio*). *Copeia* 2011, 351–356.
- Meuche, I., Brusa, O., Linsenmair, K.E., Keller, A., Pröhl, H., 2013. Only distance matters—non-choosy females in a poison frog population. *Front. Zool.* 10, 29.
- Mock, D.W., Forbes, L.S., 1995. The evolution of parental optimism. *Trends Ecol. Evol.* 10, 130–134.
- Mock, D.W., Parker, G.A., 1997. *The Evolution of Sibling Rivalry*. Oxford University Press, Oxford (UK).
- Mock, D.W., Dugas, M.B., Strickler, S.A., 2011. Honest begging: expanding from signal of need. *Behav. Ecol. Evol.* 22, 909–917.
- Morey, S., Reznick, D., 2000. A comparative analysis of plasticity in larval development in three species of spadefoot toads. *Ecology* 81, 1736–1749.
- Muralidhar, P., De Sá, F.P., Haddad, C.F.B., Zamudio, K.R., 2014. Kin-bias, breeding site selection and female fitness in a cannibalistic Neotropical frog. *Mol. Ecol.* 23, 423–463.
- Noonan, B.P., Comeault, A.A., 2009. The role of predator selection on polymorphic aposomatic poison frogs. *Biol. Lett.* 5, 51–54.
- Pašukonis, A., Beck, K.B., Fischer, M.-T., Weinlein, S., Stücker, S., Ringler, E., 2017. Induced parental care in a poison frog: a tadpole cross-fostering experiment. *J. Exp. Biol.*, <http://dx.doi.org/10.1242/jeb.165126>.
- Panhuis, T.M., Butlin, R., Zuk, M., Tregenza, T., 2001. Sexual selection and speciation. *Trends Ecol. Evol.* 16, 364–371.
- Parker, G.A., Royle, N.J., Hartley, I.R., 2002. Begging scrambles with unequal chicks: interactions between need and competitive ability. *Ecol. Lett.* 5, 206–215.
- Parker, G.A., Schwagmeyer, P.L., Mock, D.W., 2014. The asymmetric incubation game: a prospective model and a house sparrow investigation. *Anim. Behav.* 93, 37–47.
- Pepperberg, I.M., 2002. *The Alex Studies: Cognitive and Communicative Abilities of Grey Parrots*. Harvard University Press, Cambridge (USA).
- Perry, J.C., Roitberg, B.D., 2006. Trophic egg laying: hypotheses and tests. *Oikos* 112, 706–714.
- Poelman, E.H., Dicke, M., 2007. Offering offspring as food to cannibals: oviposition strategies of Amazonian poison frogs (*Dendrobates ventrimaculatus*). *Evol. Ecol.* 21, 215–227.
- Pröhl, H., Berke, O., 2001. Spatial distributions of male and female strawberry poison frogs and their relation to female reproductive resources. *Oecologia* 21, 215–227.
- Pröhl, H., Hödl, W., 1999. Parental investment, potential reproductive rates, and mating system in the strawberry dart-poison frog, *Dendrobates pumilio*. *Behav. Ecol. Sociobiol.* 46, 215–220.
- Pröhl, H., Hagemann, S., Karsch, J., Höbel, G., 2007. Geographic variation in male sexual signals in strawberry poison frogs (*Dendrobates pumilio*). *Ethology* 113, 825–837.
- Pröhl, H., 2002. Population differences in female resource abundance, adult sex ratio, and male mating success in *Dendrobates pumilio*. *Behav. Ecol.* 13, 175–181.
- Pröhl, H., 2005. Clutch loss affects the operational sex ratio in the strawberry poison frog *Dendrobates pumilio*. *Behav. Ecol. Sociobiol.* 58, 310–315.
- Reynolds, R.G., Fitzpatrick, B.M., 2007. Assortative mating in poison-dart frogs based on an ecologically important trait. *Evolution* 61, 2253–2259.
- Richards-Zawacki, C.L., Wang, I.J., Summers, K., 2012. Mate choice and the genetic basis for color variation in a polymorphic dart frog: inferences from a wild pedigree. *Molec. Ecol.* 21, 3879–3892.
- Ringler, E., Pašukonis, A., Fitch, W.T., Huber, L., Hödl, H., Ringler, M., 2015. Flexible compensation of uniparental care: female poison frogs take over when males disappear. *Behav. Ecol.* 26, 1219–1225.
- Ringler, E., Beck, K.B., Weinlein, S., Huber, L., Ringler, M., 2017. Adopt, ignore, or kill? Male poison frogs adjust parental decisions according to their territorial status. *Sci. Rep.* 7, 43544.
- Ritchie, M.G., 2007. Sexual selection and speciation. *Ann. Rev. Ecol. Evol. System.* 38, 79–102.
- Rojas, B., Endler, J.A., 2013. Sexual dimorphism and intra-specific colour pattern variation in an aposomatic frog *Dendrobates tinctorius*. *Evol. Ecol.* 27, 739–753.
- Rojas, B., 2014. Strange parental decisions: fathers of the dyeing poison frog deposit their tadpoles in pools occupied by large cannibals. *Behav. Ecol. Sociobiol.* 68, 551–5559.
- Rojas, B., 2016. Behavioural, ecological, and evolutionary aspects of diversity in frog colour patterns. *Biol. Rev.* 92, 1059–1080.
- Roland, A.B., O'Connell, L.A., 2015. Poison frogs as a model system for studying neurobiology of parental care. *Curr. Opin. Behav. Sci.* 6, 76–81.
- Royle, N.J., Hartley, I.R., Parker, G.A., 2002. Begging for control: when are offspring solicitation behaviours honest? *Trends Ecol. Evol.* 17, 434–440.
- Royle, N.J., Smiseth, P.T., Kölliker, M., 2012. *The Evolution of Parental Care*. Oxford University Press, Oxford (UK).
- Royle, N.J., Alonzo, S.H., Moore, A.J., 2016. Co-evolution, conflict, and complexity: what have we learned about the evolution of parental care behaviours? *Curr. Opin. Behav. Sci.* 12, 30–36.
- Ryan, M.J., Barry, D.S., 2011. Competitive interactions in phytotelmata-breeding pools of two poison-dart frogs (*Anura: Dendrobatidae*) in Costa Rica. *J. Herp.* 45, 438–443.
- Schulte, L.M., Lötters, S., 2013. The power of the seasons: rainfall triggers parental care in poison frogs. *Evol. Ecol.* 27, 711–723.
- Schulte, L.M., Mayer, M., 2017. Poison frog tadpoles seek parental transportation to escape their cannibalistic siblings. *J. Zool.* 303, 83–89.
- Schulte, L.M., Yeager, J.D., Schulte, R., Veith, M., Werner, P., Beck, L.A., Lötters, S., 2011. The smell of success: choice of larval rearing sites by means of chemical cues in a Peruvian poison frog. *Anim. Behav.* 81, 1147–1154.
- Smiseth, P.T., Darwell, P.T., Moore, A.J., 2003. Partial begging: an empirical model for the early evolution of offspring signaling. *Proc. R. Soc. Lond. B* 270, 1773–1777.
- Strassmann, J.E., Zhu, Y., Queller, D.C., 2000. Altruism and social cheating in the social amoeba *Dictyostelium discoideum*. *Nature* 408, 965–967.
- Stynoski, J.L., Noble, V., 2012. To beg or to freeze: multimodal sensory integration directs behavior in a tadpole. *Behav. Ecol. Sociobiol.* 66, 191–199.
- Stynoski, J.L., Shelton, G., Stynoski, P., 2014a. Maternally derived chemical defences are an effective deterrent against some predators of poison frog tadpoles (*Oophaga pumilio*). *Biol. Lett.* 10, 20140187.
- Stynoski, J.L., Torres-Mendoza, Y., Sasa-Marin, M., Saporito, R.A., 2014b. Evidence of maternal provisioning of alkaloid-based chemical defences in the strawberry poison frog *Oophaga pumilio*. *Ecology* 95, 587–593.
- Stynoski, J.L., 2009. Discrimination of offspring by indirect recognition in an egg-feeding dendrobatid frog, *Oophaga pumilio*. *Anim. Behav.* 78, 1351–1356.
- Stynoski, J.L., 2012. *Behavioral Ecology of Parental Care in a Dendrobatid Frog (Oophaga pumilio)*. PhD Dissertation. University of Miami, Miami (FL).
- Summers, K., McKeon, C.S., 2004. The evolutionary ecology of phytotelmata use in neotropical poison frogs. In: Lehtinen, R.M. (Ed.), *Ecology and Evolution of Phytelm-breeding Anurans*, vol. 193. Misc. Publ. Mus. Zool. Uni. Mich., pp. 55–73.
- Summers, K., Tumulty, J., 2014. Parental Care, Sexual Selection, and Mating Systems in Neotropical Poison Frogs. In: Macedo, R., Machado, G. (Eds.). Academic Press, London (UK), pp. 191–199.
- Summers, K., Bermingham, E., Weigt, L., McCafferty, S., Dahlstrom, L., 1997. Phenotypic and genetic divergence in three species of dart-poison frogs with contrasting parental behavior. *J. Herid.* 88, 8–13.
- Summers, K., Weigt, L.A., Boag, P., Bermingham, E., 1999a. The evolution of female parental care in poison frogs of the genus *Dendrobates*: evidence from mitochondrial DNA sequences. *Herpetologica* 55, 254–270.
- Summers, K., Symula, R., Clough, M., Cronin, T., 1999b. Visual mate choice in poison frogs. *Proc. R. Soc. Lond. B: Biol. Sci.* 266, 2141–2145.
- Summers, K., McKeon, C.S., Heying, H., 2006. The evolution of parental care and egg size: a comparative analysis in frogs. *Proc. R. Soc. Lond. B: Biol. Sci.* 273, 687–692.
- Trivers, R.L., 1972. Parental investment and sexual selection. In: Campbell, B. (Ed.), *Sexual Selection and the Descent of Man*. Aldine, Chicago, pp. 136–179.
- Trivers, R.L., 1974. Parent-offspring conflict. *Amer. Zool.* 14, 249–264.
- Ursprung, E., Ringler, M., Jehle, R., Hödl, W., 2011. Strong male/male competition allows for nonchoosy females: high levels of polygamy in a territorial frog with parental care. *Mol. Ecol.* 20, 1759–1771.
- Wade, M.J., Schuster, S.M., 2002. The evolution of parental care in the context of sexual selection: a critical reassessment of parental investment theory. *Am. Nat.* 160, 285–292.
- Wang, I.J., Shaffer, H.B., 2008. Rapid color evolution in an aposomatic species: a phylogenetic analysis of color variation in the strikingly polymorphic strawberry poison-dart frog. *Evolution* 62, 2742–2759.
- Wells, K.D., 2007. *The Ecology and Behavior of Amphibians*. The University of Chicago Press, Chicago.
- Weygoldt, P., 1980. Complex brood care and reproductive behaviour in captive poison-arrow frogs, *Dendrobates pumilio*. *Behav. Ecol. Sociobiol.* 7, 329–332.
- Weygoldt, P., 1987. Evolution of parental care in dart poison frogs. *Z. Zool. Syst. Evol. Forsch.* 25, 51–67.
- Wilbur, H.M., Collins, J.P., 1973. Ecological aspects of amphibian metamorphosis. *Science* 182, 1305–1314.
- Wright, J., Leonard, M. (Eds.), 2002. *The Evolution of Begging*. Kluwer Acad. Publ., Dordrecht.
- Yang, Y., Richards-Zawacki, C.L., Devar, A., Dugas, M.B., 2016. Poison frog color morphs express assortative mate preferences in allopatry but not sympatry. *Evolution* 70, 2778.
- Yeager, J., Brown, J.L., Morales, V., Cummings, M., Summers, K., 2012. Testing for selection on color and pattern in a mimetic radiation. *Curr. Zool.* 58, 668–677.
- Yoshioka, M., Meeks, C., Summers, K., 2016. Evidence for begging as an honest signal of offspring need in the biparental mimic poison frog. *Anim. Behav.* 113, 1–11.