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NATURAL HISTORY NOTE

Proximate determinants of family size in an obligate egg-feeding frog

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Abstract

The number of offspring parents rear varies considerably among closely related lineages, individuals, and even reproductive events by one individual. Constraints can come at any point, from the costs of producing a large clutch to the cost of caring for a large brood of dependent young. We report here on observations of the early phase of a reproductive cycle in a captive colony of *Oophaga pumilio*, a poison frog with offspring entirely dependent on maternally provisioned trophic eggs. We tracked reproductive clutches, and found that while clutch and egg size were variable, neither predicted the success of a clutch; there was also no evidence of a trade-off between clutch and egg size. Larger eggs did, however, produce larger tadpoles, and when parents transported only a subset of the brood to nurseries, the tadpoles they moved were larger than the ones they did not. Adaptive adjustment of parental investment is a key life-history trait, and a complete accounting of the way families are constructed is key to understanding the evolution of parental care, parental favoritism, and cooperation and conflict among closely related individuals.

Keywords Clutch size · Dendrobatidae · Parental investment · Transportation

Introduction

Families come in all sizes: some parents produce hundreds of millions of eggs a year and others produce a single offspring every few years (Stearns 1992). The way an individual distributes effort among and within reproductive events is a result of inescapable constraints (Smith and Fretwell 1974), myriad selective pressures and adaptations that shaped the lineage (Furness et al. 2022), and the individual's plastic response to circumstances (Houston and McNamara 1992). Particularly when parents provide post-zygotic care, constraints that limit family size result from constraints operating at several points during a reproductive

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cycle. Clutch size, for example, is limited by the energetic demands of producing an egg (Monaghan and Nagler 1997; Warne and Charnov 2008). But even if mothers could afford the energetic costs of producing eggs, the size of their clutch can still be limited, for example, by the size and shape of their body (Shine 1992), the locomotor costs of carrying eggs (Cox and Calsbeek 2010), or the demands of incubation (Thomson 1998; Węgrzyn et al. 2023). When parents provide exogenous food to offspring, limitations on family size might have little to do with the egg, driven instead by the costs of providing food to rapidly developing offspring, especially as they approach independence and their demands peak (Martin 1987; Monaghan and Nagler 1997; Martin et al. 2000).

Numerous incentives select for parents to set initial family size somewhat higher than the number they typically rear to independence (Mock and Forbes 1995). In large clutches, for example, individual eggs may be better protected against desiccation or predation (Mappes et al. 1997; Clark and Faeth 1998), and with more siblings, dependent mammals and birds may pay lower per-capita costs of thermoregulation (Zepeda et al. 2019). An initial family size that would typically push parents past their limits can also be optimal if circumstances are sometimes good enough to allow these extra offspring to be reared at low expense (Forbes and Mock 1996). Initial overproduction can also offer parents a backup in the event of early mortality of some offspring (Cash and Evans 1986; Forbes 1990), and in a related vein, may offer parents the opportunity to select from the full brood a subset of young promising enough to warrant the bulk of parental attention (Forbes and Mock 1998). Important to shaping the benefits of this entire suite of potential advantages of overproduction are an expense of initial production and whether, how, and at what cost parents bring family size from its optimistic starting point to one aligned with their current reality (Mock and Forbes 1995; Forbes and Mock 1996, 1998).

We studied how parents shape family size early in a reproductive cycle in the dendrobatid poison frog *Oophaga pumilio*. The natural history of this frog and its close relatives offer parents opportunities to adjust family size, and perhaps reasons to play favorites (Dugas 2018). Like other dendrobatids, *O. pumilio* lay terrestrial clutches cared for by males. Most clutches fail, but if the clutch is successful, mothers must transport newly hatched tadpoles to small water-filled nurseries, typically in plants (Pröhl 2005). While transport of tadpoles in groups is common in dendrobatids (Summers et al. 1999, 2006), O. *pumilio* mothers usually make several trips and move tadpoles one-at-a-time (Brust 1990; Khazan et al. 2019), allowing them substantial proximate control over brood size. Some factors shaping optimal brood size may be knowable at the time a clutch is laid; female *O. pumilio* feed their tadpoles with unfertilized eggs, and per-capita meal size is smaller in the largest broods, suggesting a constraint (Dugas et al. 2016a). Other constraints might be apparent only later, demanding that mothers make adjustments. The number of nurseries that are water-filled and unoccupied is, for example, contingent on weather and the actions of other parents, and so may change between egg laying and embryo hatching (Schulte and Lötters 2013; Pröhl et al. 2019).

We used observations of reproduction in a captive colony of *O. pumilio* to identify the ways in which constraints and parental behaviors shape family size in this frog that feeds its young. We used observations of reproductive clutches to test the hypothesis that initial investment constrains this outcome, testing the predictions that clutch and egg size trade-off and are positively associated with clutch success (Crump 1984; Dziminski and Roberts 2006). We then followed a subset of successful clutches through tadpole deposition, allowing us to assess the extent to which parental care in the form of transport is a limited resource at this life stage and how it is allocated among offspring. A complete accounting of how parents construct and care for families will allow us to continue to leverage this complex and tractable study animal to learn about cooperation and conflict among relatives.

Methods

Study animals

Oophaga pumilio is a small (14–19 mm snout-vent length) terrestrial frog native to Central America, occurring in lowland forests from Nicaragua to Panama. Females lay clutches of ~5 eggs in the leaf litter following successful courtship by a territorial male, and the male tends and hydrates the clutch (Pröhl & Hödl 1999). Females transport newly hatched tadpoles (stage 25, sensu Gosner 1960) to nurseries, typically water-filled leaf axils within ~2 m of the ground (Maple 2002), although females may deposit tadpoles much higher in the canopy (Young 1979). Parents rear broods of up to four tadpoles, but typically transport tadpoles individually and rear each in a separate nursery (Brust 1990; Dugas 2018). Females offer unfertilized trophic eggs to their tadpoles about every two days for the next month and a half, with these eggs serving as the sole source of nutrition for developing larvae (Dugas 2018).

We studied *O. pumilio* in a captive breeding colony at Illinois State University (Normal, IL, USA). These animals are descended from wild-caught frogs from four populations in the Bocas del Toro Region of Panama. The pairs used here contain within- and between-population pairs as well as various backcrosses, and there is no evidence of differences in reproductive success among types of pairs (Dugas and Richards-Zawacki 2015). We fed adults three times weekly with nutrient-dusted *Drosophila melanogaster* or *D. hydei* reared on a carotenoid-supplemented media (Dugas et al. 2013). We housed breeding pairs in plastic tanks (37×22×25 cm) held within an environmental chamber maintained on a 12 L:12D photoperiod and at 23–27 °C and ~ 40–80% relative humidity; an automated system misted tanks four times daily. Each tank was lined with sphagnum moss and contained live plants (*Epipremnum aureum*), and we provided four water-filled PVC tubes (~20 mL) that served for tadpole deposition. We provided two plastic film canisters that adults used for depositing reproductive clutches. We longitudinally split and then taped closed each canister, a modification that allowed us to temporarily "unfold" the canister and capture photographs of developing clutches. By pulling the sides of the split canister away from one another, we also temporarily flattened the walls of the hollow cylinder so that each egg became equidistant from the camera (Fig. 1). In these, and all photographs described below, we included a size standard, and the camera was fixed 30 cm above the egg or tadpole. We took digital photographs using a Canon EOS 800D Digital SLR camera fit with a 100 mm f/2.8 macro lens (Canon, Inc., Lake Success, NY, USA) and a macro flash (Neewer NW-14EXT, Neewer, Inc., Shenzhen, China).

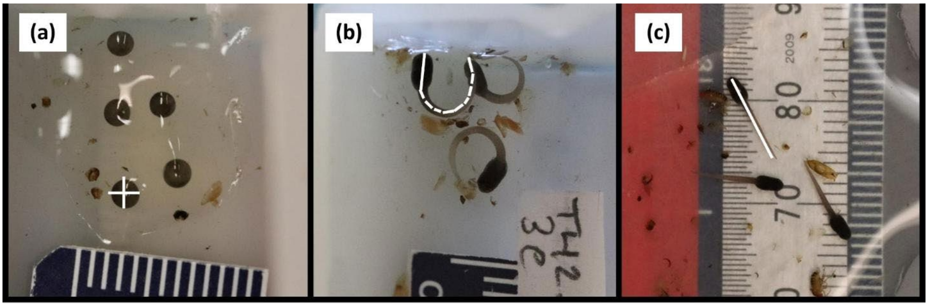

Fig. 1 White lines illustrate measurements we used to quantify the diameter of newly laid *O. pumilio* egg yolks (**a**) and the total length of nearly developed embryos (**b**) and newly free-swimming or deposited tadpoles (**c**)

Monitoring reproduction and statistical analyses

We monitored reproduction of 19 *O. pumilio* pairs Aug 2022–Jan 2023. Three times a week, we inspected the two film canisters in each tank for the presence of developing eggs. If a new clutch was present, we temporarily (<5 min) removed it from the tank and photographed it, unfolding the canister so that the clutch was on a flat surface. We then returned the canister to its original position in the tank. We began re-photographing clutches if and when embryos reached about stage 19 (Gosner 1960), and continued every 2–3 days until tadpoles were transported by parents or were free-swimming. Any clutch that failed we classified as “dried” or “spoiled”.

We monitored 100 clutches from Aug–Nov 2022. Using photographs of these clutches, we tested for a trade-off between clutch size and egg size. In a linear mixed model, we entered the mean yolk diameter of eggs in a clutch as the dependent variable, and the clutch size as a fixed effect; we included the random effect of parent pair. We then used generalized linear mixed models to ask whether clutch size and mean egg size predicted several clutch outcomes. We tested as dependent variables the binary responses of the clutch producing at least one fully developed tadpole or one tadpole deposited in a nursery by parents. Using only the subset of clutches that produced at least one developed embryo (or transported tadpole), we asked if clutch size and yolk diameter were associated with the number of developed or transported tadpoles. Finally, using the subset of clutches that failed, we asked if these predictors were associated with the binary response of clutches failing due to drying (y/n), as hydration seems the primary function of male clutch care in this frog (Pröhl and Hödl 1999; Pröhl 2005).

In a subset of 18 clutches produced by 9 unique pairs, we were able to use within-clutch physical position to match embryos to eggs (n = 56 embryos from 18 clutches). We used these reproductive events to test for a predicted positive relationship between egg size and tadpole size. We used the initial clutch photograph and the last available photograph of the developing clutch. For each developing tadpole, we recorded developmental stage (Gosner 1960) and measured total length; the mean ± SD developmental stage of tadpoles used in this analysis was 23.4 ± 1.8 (range 18–25). We assessed the relationship between tadpole size and yolk diameter using a linear mixed model. We entered tadpole total length as the dependent variable and yolk diameter as a fixed effect. As random effects, we included parent pair and clutch nested within parent pair.

For a subset of 37 clutches produced by 10 unique pairs in Oct 2002–Jan, 2023 we monitored clutches daily when they approached hatching. If tadpoles were missing from the clutch, we inspected the four rearing sites in each tank for the presence of newly-deposited tadpoles (if parents were transporting tadpoles, we checked the tank again later in the day). We temporarily moved to a petri dish and photographed any newly deposited tadpoles and any tadpoles remaining in the container housing the clutch, and used these to measure the total length of each tadpole. We repeated this daily until any un-transported tadpoles died. In some events, parents transported only a subset of their tadpoles on the first day of transport. We compared the total length of these transported and not transported tadpoles in the subset of 24 broods in which not all tadpoles were moved on the first day (i.e., the broods in which we had two groups of tadpoles to compare). We used a linear mixed model with status (transported or not) as the fixed effect and random effects of parent pair and clutch nested within parent pair; we specified clutch as a repeated subject effect.

We measured egg yolk and tadpole size using the ‘straight’ tool in imageJ (Schneider et al. 2012). For eggs, we measured the yolk diameter twice with lines perpendicular to one another (Fig. 1a), and used means for further analyses. For tadpoles, we measured total length, defined as the distance between the tip of the nose and tip of the tail (Fig. 1b,c). For developed embryos still in the egg, we summed several straight lines to measure total length (Fig. 1b); free-swimming tadpoles could typically be measured with a single line (Fig. 1c). In all statistical models, we used Kenward-Roger degrees of freedom for fixed effects and tested both compound symmetry and variance components covariance structure. Variance components typically produced better model fit, assessed with –2 residual log likelihood (linear mixed models) or chi-square / df (generalized linear mixed models).

Results

In the 100 newly laid clutches we photographed, mean egg size within a clutch was not associated with clutch size ($F_{1,94.5} = 0.28$, $p = 0.599$; Fig. 2a), and parent pair explained 14% of the residual variance in mean egg size. At least one embryo completed development in 39 clutches. Whether at least one embryo completed development was not related to clutch size ($F_{1,97} = 0.22$, $p = 0.642$), or the mean size of eggs in clutch ($F_{1,97} = 0.42$, $p = 0.516$). These patterns were similar if we instead asked if at least one tadpole from a clutch was deposited in a nursery by parents (clutch size: $F_{1,97} = 0.37$, $p = 0.546$; mean egg size: $F_{1,97} = 0.52$, $p = 0.473$). The number of developed tadpoles produced by a clutch was not significantly associated with clutch size in the subset of clutches that produced at least one fully developed tadpole ($\beta \pm SE$: 0.09 ± 0.06, $F_{1,25} = 2.2$, $p = 0.149$), a result that was similar if we substituted deposited tadpoles as the dependent variable ($F_{1,37} = 0.15$, $p = 0.703$). In the subset of clutches that failed, neither clutch nor mean egg size predicted whether a clutch dried (clutch size: $F_{1,58} = 0.46$, $p = 0.500$; mean egg size: $F_{1,58} = 0.79$, $p = 0.378$). The total length of embryos/tadpoles in clutches nearing the end of development was positively associated with the size of the yolk from which they developed ($F_{1,36.9} = 9.6$, $p = 0.004$; Fig. 2b) and with their developmental stage ($\beta \pm SE$: 0.043 ± 0.007, $F_{1,22.7} = 32.9$, $p < 0.001$). Parent pair explained 18% of the residual variance in embryo/tadpole size, and clutch explained 4%.

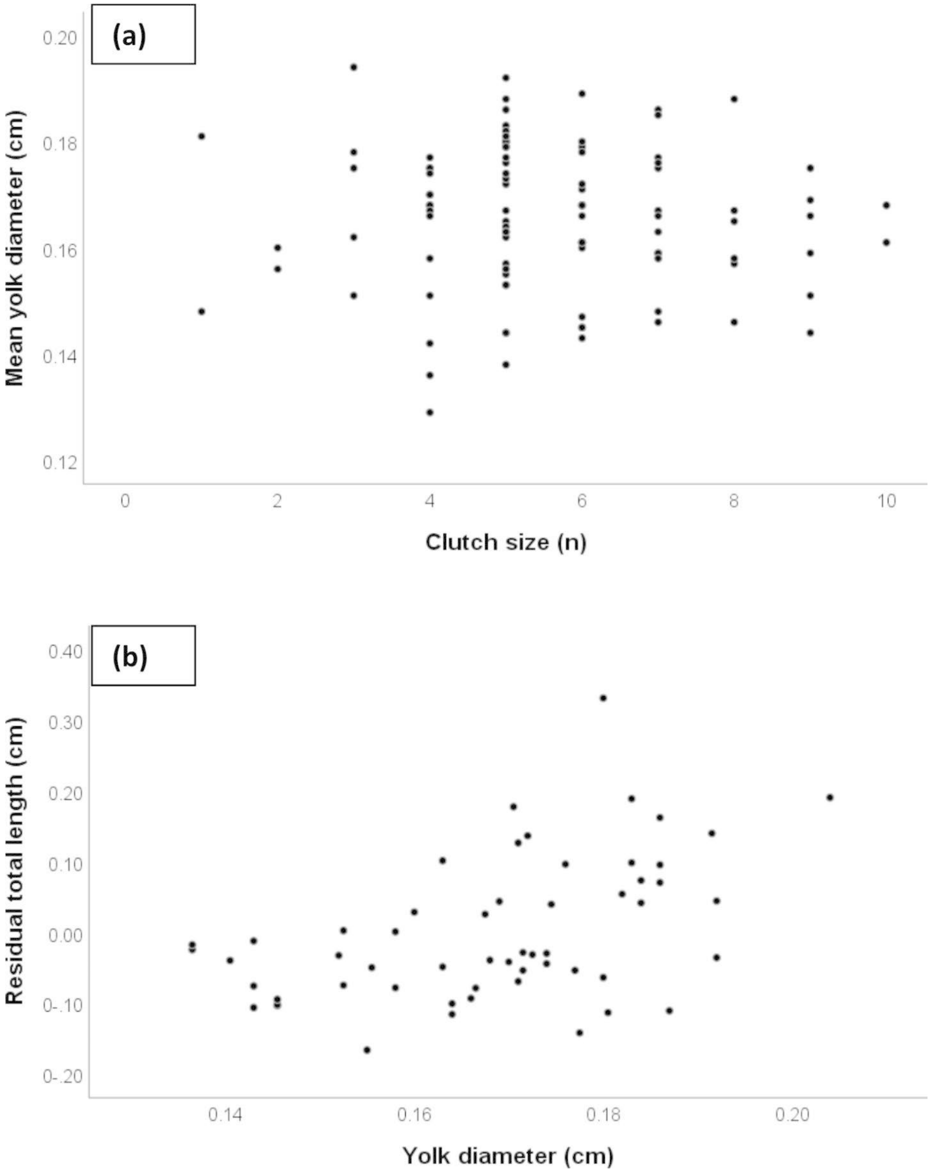

Fig. 2 The relationships between clutch size and mean yolk diameter of reproductive clutches produced by captive *O. pumilio* (**a**) and between yolk diameter of individual eggs and the total length of embryos nearing the end of development, corrected for developmental stage

Parents transported at least one tadpole to a nursery in 32 of the 37 clutches from the subset we monitored daily near the completion of development. In these 32 clutches, we followed the fate of 128 tadpoles: 76 were deposited in a nursery, and 29 were unequivocally abandoned (died in the clutch container). The remaining 26 tadpoles were simply missing, not present with the remainder of the clutch or in a nursery. Parents transported tadpoles with 1.7 ± 0.9 d (mean ± SD) transport days (range 1–5). In 8 of the 32 clutches that produced tadpoles deposited in nurseries, parents transported all tadpoles from the clutch to nurseries on the first transport day. In 24, parents transported a portion of the brood on the first day and abandoned all other tadpoles (n = 8) or moved portions of the brood on different days (n = 16), which allowed us to compare the size of tadpoles transported and not on that first day. Tadpoles transported by their parents on the first transport day were larger than those they did not transport ($F_{1,77.1} = 43.4$, $p < 0.001$; Fig. 3). Parent pair explained 37% of the residual variance in tadpole size, while brood explained 13%.

Discussion

Captive *O. pumilio* pairs produce clutches that vary considerably in the number of eggs they contain and the size of these eggs. However, we found no evidence of a trade-off between the size and number of eggs in a clutch. To the extent egg production is limited by raw materials (e.g., food intake), a trade-off between quantity and quality should be unavoidable (Smith and Fretwell 1974). Food is presumably more limiting in the wild than in captivity, and consistent with the hypothesis that food intake limits egg production, captive *O. pumilio* seem to lay more and larger clutches than frogs in the wild (Pröhl and Hödl 1999; Pröhl 2005; Dugas et al. 2016a). Even in captivity, however, tadpoles in larger broods are fed smaller trophic meals, suggesting some limitation (Dugas et al. 2016a). Other potential constraints on clutch production include water balance in the egg (Brown and Shine 2009), presumably via investment in the jelly capsule (Delia et al. 2020), female body size, and the

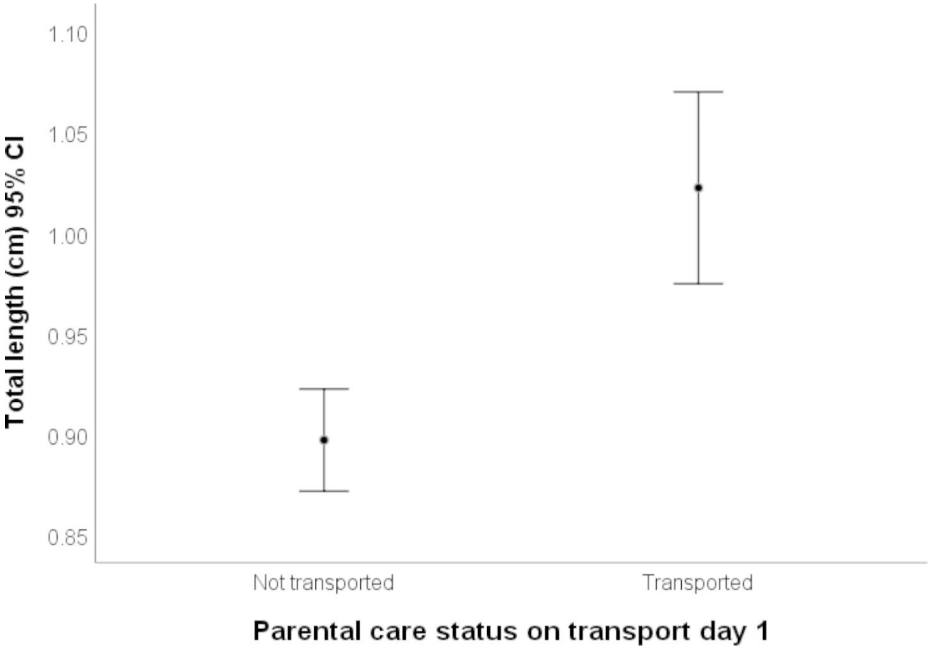

Fig. 3 Total length of tadpoles transported to nurseries by captive *O. pumilio* parents and their clutch-mates not transported on the first day parents began moving tadpoles

physiological costs associated with oocyte recruitment and development (Jørgensen 1981; Shine 1992). Even in captivity, producing reproductive clutches carries a longevity cost for female *O. pumilio*, a finding consistent with this latter hypothesis (Dugas et al. 2015).

Large *O. pumilio* clutches or those with eggs with large yolks were no more likely to produce viable tadpoles, suggesting that, at least under captive conditions, investing heavily in a clutch affords no benefit to parents. If clutches fail in the wild primarily for reasons unrelated to clutch size, like predation, this could select for variable investment in eggs like that we observed (Farnsworth and Simons 2001; Olofsson et al. 2009). A line of inquiry that may still warrant attention is assessing the role males play in clutch outcomes. By hydrating or otherwise tending the clutch, males could buffer any physical constraints on clutch size (e.g., water loss). Our captive males had access only to the clutches of a single female, but wild *O. pumilio* males mate multiply and presumably could allocate care non-randomly (Pröhl and Hödl 1999; Pröhl 2005). If males provide more or better quality care to larger clutches or those they otherwise perceive as high quality, this could select for females that produce larger clutches than they intend to rear (Sargent 1988; Manica 2002; Moreno and Osorno 2003).

Despite the lack of a relationship between mean yolk size and clutch success, individual tadpoles from eggs with large yolks were larger, a relationship that could reflect resource limitation and/or how developing tadpoles allocate these resources. Fitness effects of egg (and resulting tadpole) size in amphibians are often inconsistent across environments that differ in food availability or competition (Olofsson et al. 2009; Moore et al. 2015). While *O. pumilio* most often occupy nurseries alone, they do occasionally find themselves with roommates (Khazan et al. 2019) and are subject to aggression in these cases, during which large size is likely an advantage (Dugas et al. 2016b). Large size at hatching might also allow tadpoles to more readily consume trophic eggs, often deposited when mothers deposit tadpoles (Maple 2002) and, of course, roughly the same size as the tadpole itself. Finally, tadpole size at hatching can, like any maternal effect, shape how parents treat offspring post-hatching (Dugas 2015).

Completing embryonic development did not prove sufficient for tadpoles to continue their progress toward independence: only about 6 in 10 tadpoles were transported to a nursery. About half of failed tadpoles were abandoned, with the other half's fate unknown. Many amphibians, including dendrobatid frogs, consume conspecific eggs (Spring et al. 2019) and male *O. pumilio* may consume spoiled eggs in their own clutches (Weygoldt 1980), so it seems entirely plausible that parents might have consumed these tadpoles. Another possibility is that these missing tadpoles left the clutch on the back of a parent and disembarked prematurely (after this experiment, we found a tadpole dead on the top of a film canister, and expect it did not get there by itself). The transport common in dendrobatids demands much of tadpoles, including, for example, specialized mouthparts and the ability to identify appropriate circumstances to climb on an adult frog, move to the correct location on its body, hold on, and let go (Schulte and Mayer 2017; Peignier et al. 2022). A tadpole mistake at any point could result in failed transport, as might parent behaviors. Experimental findings in *Allobates femoralis* suggest that transport can be triggered simply by placing a tadpole on the back of an adult frog (Pašukonis et al. 2017), but parents presumably share control over the endpoint of transport with their young. In our captive colony, *Ranitomeya imitator* fathers use their hind limbs to dislodge tadpoles from their backs once in the nursery (O. L. Brooks *personal observations*). Although we have not seen the same in *O. pumilio*, tadpoles do seem to fall from the back of a transporting female when she is handled or even disturbed, perhaps suggesting she can control a tadpole's attachment (M. B. Dugas *personal observations*). Transportation offers numerous opportunities for conflicts-of-interest to shape poison frog family size, and both proximate and ultimate interactions will be of interest in future work.

The *O. pumilio* tadpoles that did reach a nursery were larger than their siblings that were not transported. A preference for large offspring is nearly universal in avian parents allocating prey (Caro et al. 2016), and *O. pumilio* mothers also feed larger meals to older tadpoles (Dugas et al. 2016a, 2017). Biased transport, however, is interpretable as a parental strategy only to the extent parents control which subset of larvae they carry. While *O. pumilio* and some other dendrobatids usually transport tadpoles singly to single-occupancy nurseries, the ancestral state in this lineage is probably group transport and deposition (Summers et al. 1999, 2006; Summers and Tumulty 2014). How single transport is effected by parents is unknown, but studying occasional transport of multiple tadpoles by *O. pumilio* females may offer some insights (Khazan et al. 2019). A neat and orderly tadpole queue seems unlikely given the obvious incentive for each tadpole to secure a ride, but even scramble competition among tadpoles does not necessarily leave parents unable to influence outcomes. Parent birds can bias resources towards their most competitive offspring by feeding from certain locations in the nest (Kölliker and Richner 2004). Parents offering transport to larvae could similarly set the stage for competition with variation in their body position relative to the clutch and/or the time they allow tadpoles to find a place to settle. Establishing a clutch that hatched asynchronously might also allow parents more control over transport (Węgrzyn et al. 2023). Especially in captivity, manipulating the composition of hatched clutches should offer opportunities to identify the mechanisms underlying biased transport, offering insights into the proximate and ultimate opportunities for within-family conflict over this care.

All kinds of parents produce more offspring than they rear to independence (Mock and Forbes 1995). Even in the presumably benign conditions of captivity, parent *O. pumilio* deposit more tadpoles than they rear (Dugas et al. 2016a), and we now have evidence that they lay more eggs than hatch, and continue to care for only a subset of the offspring that hatch. Future efforts can explicitly test the hypothesized benefits of initial overproduction. Optimistic clutch sizes might, for example, allow parents to occasionally take advantage of better than expected nursery availability (e.g., after high rainfall), a benefit perhaps higher in lineages with maximum family size unconstrained by trophic egg-feeding (Schulte and Lötters 2013). If caring for tadpoles and producing new reproductive clutches are temporally separated (Pröhl and Hödl 1999; Pröhl 2005), these extra offspring might serve as replacements in the event of early mortality, maximizing the output of a bout of caring. Parents might encourage competition so as to select only their best offspring for limited nurseries (Kozloski & Stearns 1989; Mock and Forbes 1998). A tadpole's journey from a terrestrial clutch to a water-filled nursery is filled with opportunities for selection and adaptation, and for incompletely overlapping fitness interests of family members to manifest in directly observable interactions (Trivers 1974). Studying the earliest stages of family construction in poison frogs, animals with diverse modes of care and potential constraints, will offer exceptional opportunities to test foundational theory about within-family conflict and cooperation.

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Author contributions All authors conceived and designed the study. T. C. S., M. E. C., E. E. V.-D., and M. D. H. collected the data. T. C. S. prepared an early draft of the manuscript. M.B.D. analyzed the data and drafted the final manuscript. All authors approved the final version.

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Data Availability All data generated or analyzed during this study are included in the supplementary information.

Code Availability Not applicable.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethics approval All animal handling and research in this study was approved by the Illinois State University Institutional Animal Care and Use Committee (2019 – 1087, 2021 – 1187).

Consent to participate Not applicable.

Consent for publication Not applicable.

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