The pay-offs of maternal care increase as offspring develop, favouring extended provisioning in an egg-feeding frog

M. B. DUGAS*[1], M. P. MOORE*[1], R. A. MARTIN*, C. L. RICHARDS-ZAWACKI†‡ & C. G. SPREHN†

*Department of Biology, Case Western Reserve University, Cleveland, OH, USA
†Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA, USA
‡Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, USA

Abstract

Offspring quantity and quality are components of parental fitness that cannot be maximized simultaneously. When the benefits of investing in offspring quality decline, parents are expected to shift investment towards offspring quantity (other reproductive opportunities). Even when mothers retain complete control of resource allocation, offspring control whether to allocate investment to growth or development towards independence, and this shared control may generate parent–offspring conflict over the duration of care. We examined these predictions by, in a captive colony, experimentally removing tadpoles of the strawberry poison frog (*Oophaga pumilio*) from the mothers that provision them with trophic eggs throughout development. Tadpoles removed from their mothers were no less likely to survive to nutritional independence (i.e. through metamorphosis) than were those that remained with their mothers, but these offspring were smaller at metamorphosis and were less likely to survive to reach adult size, even though they were fed *ad libitum*. Tadpoles that remained with their mothers developed more slowly than those not receiving care, a pattern that might suggest that offspring extracted more care than was in mothers' best interests. However, the fitness returns of providing care increased with offspring development, suggesting that mothers would be best off continuing care until tadpoles initiated metamorphosis. Although the benefits of parental investment in offspring quality are often thought to asymptote at high levels, driving parent–offspring conflict over weaning, this assumption may not hold over natural ranges of investment, with selection on both parents and offspring favouring extended durations of parental care.

Introduction

The evolution of parental investment is mediated by the trade-off between investing in offspring quality and offspring quantity (Stearns, 1992; Roff, 2002). For a parent, the fitness pay-offs of each additional offspring are, *ceteris paribus*, expected to accrue linearly (Stearns, 1992; Roff, 2002). The fitness pay-offs of investing in the quality of a particular offspring, however, are more complex. A minimum threshold of investment is required for offspring to be viable, and the benefits of increased investment are generally assumed to asymptote at high levels of investment (Godfray, 1991, 1995; Mock & Parker, 1997; but see Schwagmeyer & Mock, 2008). The optimal balance between alternative routes to fitness will differ among species and among contexts, driving the evolution and plastic expression of diverse parental investment strategies (Clutton-Brock, 1991; Stearns, 1992; Roff, 2002; Royle *et al.*, 2012).

When the benefits of investment in offspring quality decline, it becomes in a parent's best interest to shift investment towards offspring quantity, a shift that can

Correspondence: Matthew B. Dugas, Department of Biology, Case Western Reserve University, 2080 Adelbert Rd., Cleveland, OH 44106, USA.
Tel.: +1216 368 2177; fax: +1216 368 4672;
e-mail: matthew.b.dugas@gmail.com
[1]These authors contributed equally to this work.

manifest as the cessation of investment in a particular offspring. A parent that terminates investment too late (i.e. invests too much) misses the opportunity to invest in offspring quantity, gaining less from the higher quality of an offspring than it would have from instead producing an additional one (Sinervo & DeNardo, 1996; Einum & Fleming, 2000; Allen *et al.*, 2008). A parent that terminates investment too early can produce young unlikely to survive to independence (Zink, 2003; Huang, 2006), deficient in traits that shape survival post-independence (e.g. body size: Rius *et al.*, 2010; Mitchell *et al.*, 2015) and/or lacking in traits not under selection until maturity (e.g. sexual attractiveness: McGraw *et al.*, 2005; fecundity: Marshall & Monro, 2012). Further complicating parental investment evolution is the fact that offspring will usually benefit more from longer durations of care than will their parents, with such conflict strongest as offspring approach independence (Trivers, 1974; Mock & Parker, 1997). Offspring use myriad traits to shape the level and share of investment they receive (Mock *et al.*, 2011), and retain substantial control over how the investment they receive is allocated. Investment could, for example, be saved as fat, put towards growing larger or spent on development towards independence (Kaplan, 1992; Allen & Marshall, 2013; Moore *et al.*, 2015). Yet, while assessing how offspring allocate finite parental investment to multiple fitness-related traits is critical to evaluating the fitness consequences of parental investment strategies (Marshall & Morgan, 2011; Sheriff & Love, 2013), longitudinal experiments remain rare.

Amphibians make especially good models for studying the relationship between parental investment and dependent offspring's transition to independence. Relative to the more often studied avian and mammalian young, amphibian larvae grow and develop along astoundingly flexible trajectories. Developmental time and size at metamorphosis can span an order of magnitude even within the same population and are both sensitive to variable nutritional conditions like those created by variation in parental investment (Wilbur & Collins, 1973; Morey & Reznick, 2000; Altwegg & Reyer, 2003). Prolonged post-zygotic parental investment is rare but taxonomically widespread in frogs, and can come in the form of maternally provisioned trophic eggs (Crump, 1996; Perry & Roitberg, 2006). Trophic egg feeding is often hypothesized to have evolved (and be facultatively expressed) because it facilitates successful development in the tiny leaf axils or tree holes in which these caring frogs typically rear their young, perhaps supplementing the few resources present in these nurseries and/or permitting faster development than would be possible without these additional nutrients (Summers & McKeon, 2004; Poelman & Dicke, 2007; Brown *et al.*, 2010; Schulte & Lötters, 2013). While intuitively appealing, this latter proximate explanation is at odds, especially for the presumably ancestral

facultative egg feeder (Summers *et al.*, 2006), with the well-established prediction that amphibian larvae experiencing high nutrient availability will delay development and prioritize growth (Wilbur & Collins, 1973; Morey & Reznick, 2000).

We studied the relationships among maternal investment duration, offspring growth, development and fitness prospects in the trophic egg-feeding strawberry poison frog (*Oophaga pumilio*). Unlike most other egg-feeding frogs (Perry & Roitberg, 2006), *O. pumilio* tadpoles seem entirely dependent on mothers for nutrients (Brust, 1993). Post-hatching maternal investment is thus required for tadpole viability, but several lines of evidence suggest that *O. pumilio* females face selection on maximum investment as well. Even in presumably benign captive conditions, reproduction is negatively associated with the success of later reproductive events (Dugas *et al.*, 2015a) and survival (Dugas *et al.*, 2015b). Tadpoles in larger broods are fed less at each meal, and tadpole survival declines in the largest broods (Dugas *et al.*, 2016). Perhaps because of these costs, mothers sometimes abandon tadpoles (Maple, 2002; Dugas *et al.*, 2016).

We manipulated the duration of maternal provisioning in a captive *O. pumilio* colony by removing tadpoles from their mothers at a range of developmental stages and tracking tadpole survival, growth and development both pre- and post-metamorphosis. We also considered how tadpoles respond to the cessation of parental care, comparing the prediction that developmental speed is limited by nutrient availability in egg-feeding frogs (Poelman & Dicke, 2007; Schulte & Lötters, 2013) to the more general prediction that amphibian larvae should delay metamorphosis in nutrient-rich habitats (Wilbur & Collins, 1973; Morey & Reznick, 2000). Finally, by testing for an effect of reduced maternal investment both pre- and post-independence, we could assess the fitness consequences of variation in the timing of maternal shifts from investing in current and future offspring. Together, these tests will help reveal the complex biological and social relationships shaping the evolution of parental care and frame the potential scope of parent–offspring conflict over the duration of care in the families of egg-feeding frogs.

Materials and methods

Study species

Oophaga pumilio is a small terrestrial frog native to Central America. In the wild, males defend territories from which they court females and, when courtship is successful, females lay clutches of ~5 eggs in leaf litter (Pröhl & Hödl, 1999). Males hydrate clutches daily until hatching (stage 25, *sensu* Gosner, 1960), after which females transport tadpoles to rearing sites, typically water-filled leaf axils (Brust, 1993; Pröhl & Hödl,

1999). For the next ~45 days, females visit tadpoles about every 2 days, delivering meals of unfertilized trophic eggs from which tadpoles seem to derive all their nutrition (Brust, 1993; Maple, 2002). While there is considerable variation among mothers, tadpoles that eventually complete metamorphosis generally receive ~1 egg per day in the wild (Brust, 1993; Maple, 2002) and in captivity (Dugas *et al.*, 2016).

Animal maintenance

We studied a captive breeding colony of *O. pumilio* housed at Tulane University (New Orleans, USA). This colony was established in August 2009 with wild-caught individuals from four populations in the Bocas del Toro Region of Panama (Tranquilo Bay, Isla Basti-mentos: 9°15′8.03″N, 82°8′43.30″W; Cemetery, Isla Bastimentos: 9°20′48.48″N, 82°12′23.04″W; Isla Popa: 9°8′25.98″N, 82°7′39.11″W; and Aguacate Peninsula: 9°12′47.13″N, 82°12′49.29″W), and now contains both wild- and captive-born breeding adults. Tadpoles used in this study were produced by both within- and between-population pairs as well as F1 backcross pairs, but there is no evidence that pair make-up influences tadpole success (Dugas & Richards-Zawacki, 2015).

We housed breeding pairs in plastic enclosures (37 × 22 × 25 cm) maintained in an environmental chamber at 22–27°C and ~40% relative humidity under a 12L/12D light cycle. Each tank was lined with sheet moss and filled with live plants, and water-filled PVC tubes (10 × 3.8 cm, ~20 mL) in each corner of the tank provided tadpole deposition and rearing sites. Tanks were automatically misted twice daily, and we fed adult frogs three times weekly with vitamin-dusted *Drosophila melanogaster* (details in Dugas *et al.*, 2013). We monitored breeding with twice-weekly censuses during which we confirmed the survival of adults and checked each of the four rearing sites for tadpoles.

Experimental design

We selected tadpoles for inclusion in this experiment in five colonywide 'sweeps'. We randomly assigned the first tadpole encountered from a parent pair to a 'parents-present' or 'parents-absent' treatment, with subsequent tadpoles from each family alternately assigned to treatments. Overall, we included tadpoles at Gosner stages 35–42 (mean ± SD = 39 ± 2.4; Gosner, 1960), and initial stage did not differ between treatments (t_{62} = 0.6, P = 0.575). To minimize the number of individuals that starved, we ran our first trials with only well-developed tadpoles, including tadpoles at earlier developmental stages only after confirming that well-developed tadpoles could complete metamorphosis without maternal feedings. This approach resulted in an overrepresentation of late Gosner stages in the study.

We removed all tadpoles briefly from their rearing sites for staging and then returned them to PVC tubes. When tadpoles were assigned to the parents-present treatment, we returned this PVC tube to the parents' breeding tank. When tadpoles were assigned to the parents-absent treatment, we instead placed this entire PVC tube in a tank identical to breeding tanks, but without adults present; this tube was replaced with a new one in the parents' tank. We checked each tadpole every other day, switching to daily monitoring as individuals neared metamorphosis. We considered a tadpole to have died when (i) we did not find the tadpole on two consecutive checks, or (ii) we found remains (about half the cases). Our previous monitoring efforts suggested that frequent handling results in high mortality, so we did not remove and stage tadpoles again.

When a tadpole completed metamorphosis and left the water of its rearing site (Gosner stage 46), we weighed it to the nearest 0.001 g on an electronic balance, taking three separate measurements and using the mean for further analysis (repeatability, *sensu* Lessells & Boag, 1987, was high: r = 0.995, $F_{50,102}$ = 609.6, P < 0.001). We then moved this new metamorph to a rearing tank with 0–2 other, phenotypically distinct juveniles. We fed juveniles with *D. melanogaster* and supplemented with springtails (Collembola), a smaller prey item. There was no evidence that juvenile density in rearing tanks influenced growth (linear mixed model of mass at 90 days with random effects as described below: juvenile density, $F_{1,15.1}$ = 1.7, P = 0.209) or survival (generalized linear mixed model on survivorship to 90 days with random effects as described below: juvenile density, χ^2_1 = 0.2, P = 0.660). We reweighed each juvenile at 16, 30, 60 and 90 days post-metamorphosis; by 90 days, most individuals reach adult size in the colony.

Statistical analyses

We began by comparing larval survival, growth and development of parents-present and parents-absent treatment groups. To compare survival to metamorphosis, we used a generalized linear mixed model with binomial error structure, including the fixed effects of treatment, the Gosner stage at which we began observations (hereafter 'initial stage'), and their interaction. As fixed effects, we also fit a quadratic effect of initial stage and the interaction between treatment and this term, allowing for the possibility that the value of maternal presence was unequal across developmental stages (e.g. asymptotes at late stages). This interaction term was never significant (all P > 0.349) and so we dropped it from all models presented in Results, and for clarity, we present models including the quadratic term only when it was significant (P < 0.05). We included three random effects: (i) parent pair identity, which addresses the nonindependence of siblings, (ii) mother

population-of-origin, and (iii) father population-of-origin; the latter two effects account for potential population-level differences in tadpole success (Dugas & Richards–Zawacki, in press). We next used linear mixed models, with fixed and random effects described above, to assess treatment effect on the continuous response variables mass at metamorphosis (g) and time to metamorphosis (days).

We then compared the survival and growth of juveniles from parents-present and parents-absent treatments through 90 days post-metamorphosis. We compared survival using a mixed-effects Cox regression in which we included the fixed effects of treatment and initial stage. We included the random effects of parent pair, mother population-of-origin, father population-of-origin and juvenile rearing tank in each model. We assessed variation in juvenile growth through 90 days post-metamorphosis using a linear mixed model. This model included the fixed effects of treatment, the linear and quadratic effects of measurement day (0, 16, 30, 60, 90) and the interactions between these terms; we also included initial stage as a covariate. We included random effects as above. We first ran this model including all juveniles and then performed a supplemental analysis in which we only included individuals that survived through 90 days; this model served to ensure that any treatment differences in growth did not simply result from differential mortality (see Results).

Finally, we asked whether and how the influence of parental care on offspring fitness prospects changed during development, as these relative benefits will determine optimal parental allocation patterns. We began by estimating the probability, at each initial stage, that tadpoles in the parents-absent treatment would survive to 90 days post-metamorphosis, integrating pre- and post-metamorphic survival (we used a generalized linear mixed model with initial stage as a fixed effect and random effects as described above). We then calculated the benefits of care across developmental stages (e.g. 35–36, 36–37) as the difference in survival probability between tadpoles removed from parents at stage x and stage $x - 1$. We then divided these benefits by costs of care, operationally defined as the number of eggs mothers provided tadpoles during this stage range. To estimate the number of eggs tadpoles were fed, we used predicted days to metamorphosis at each stage (from a new model that included only parents-absent tadpoles) along with estimates of per-day feeding rates drawn from previous work in this captive colony (Dugas *et al.*, 2016; Appendix S1). Feeding rates are lower in larger broods, and we used this variation to generate upper and lower estimates of cost (Dugas *et al.*, 2016; Appendix S1).

We used the 'lme4' package (Bates *et al.*, 2014) in R v.3.1.2 (R Core Team, 2014) for all generalized linear mixed models and linear mixed models, and the 'coxme' package (Therneau, 2015) for Cox regressions. We tested the significance of fixed effects in generalized linear mixed models using a Wald's test (Bolker *et al.*, 2009), and degrees of freedom for fixed effects in linear mixed models were calculated using the Kenward–Roger approximation (Kenward & Roger, 1997). We natural log-transformed mass in all models in which it was the dependent variable, and after transformation all models met the assumption of residual normality.
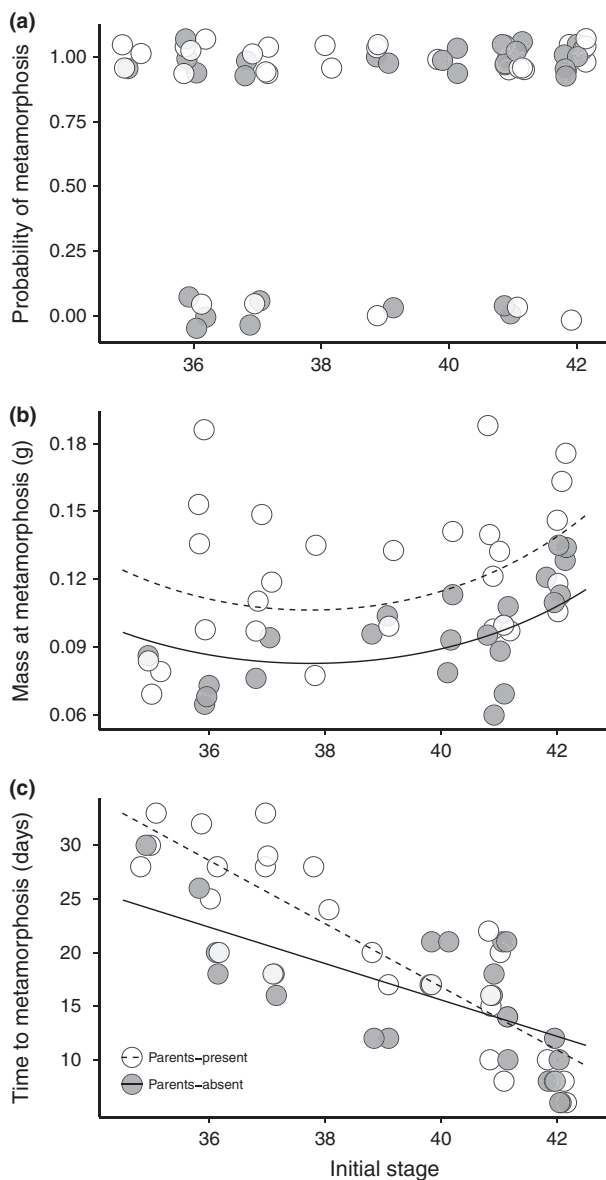
Results

Survival and development through metamorphosis

Most tadpoles survived through metamorphosis (28/33 parents-present; 23/31 parents-absent). Survivorship models including the quadratic effect of initial stage did not converge. In a model without this effect or its interaction with treatment, survivorship did not differ between parents-present and parents-absent treatments ($\chi_1^2 = 1.8$; $P = 0.277$) and was not associated with initial stage ($\chi_1^2 = 2.1$, $P = 0.146$), and the treatment × initial stage interaction was nonsignificant ($\chi_1^2 = 2.1$, $P = 0.151$; Fig. 1a). The main effects of treatment and initial stage remained nonsignificant (both $P > 0.126$) with the interaction term removed. Parent pair explained 3% of residual variation in larval survival, and mother and father population-of-origin explained 10 and < 0.1%, respectively.

In the model of mass at metamorphosis, the interaction between treatment and initial stage was nonsignificant ($F_{1,34.7} = 0.3$, $P = 0.568$). A model with this term removed revealed that tadpoles in the parents-absent treatment were lighter than controls at metamorphosis ($F_{1,30.7} = 25.3$, $P < 0.001$; Fig. 1b). Tadpoles that began treatments later were also heavier at metamorphosis: mass at metamorphosis was positively associated with both the linear and quadratic effects of initial stage (linear: $F_{1,41.5} = 4.7$, $P = 0.036$; quadratic: $F_{1,41.4} = 5.0$, $P = 0.031$), with the slope increasing closer to metamorphosis (Fig. 1b). Parent pair explained 22.9% of residual variation in mass at metamorphosis, mother population-of-origin explained 5.2% and father population-of-origin explained 36.8%.

Parent removal significantly shortened time to metamorphosis ($F_{1,43.2} = 5.2$, $P = 0.028$), and tadpoles that began treatments at later initial stages also took less time to reach this milestone ($F_{1,43.5} = 51.1$, $P < 0.001$), but there was a significant interaction between these effects ($F_{1,43.2} = 4.8$, $P = 0.035$). Time to metamorphosis was negatively and significantly associated with initial stage in both treatments (both $F > 8.63$, $P < 0.02$), but treatments differed only when tadpoles began treatment at early developmental stages (Fig. 1c). Parent pair and mother population-of-origin explained < 0.1% of residual variation in time to metamorphosis, and father population-of-origin accounted for 6.7%.
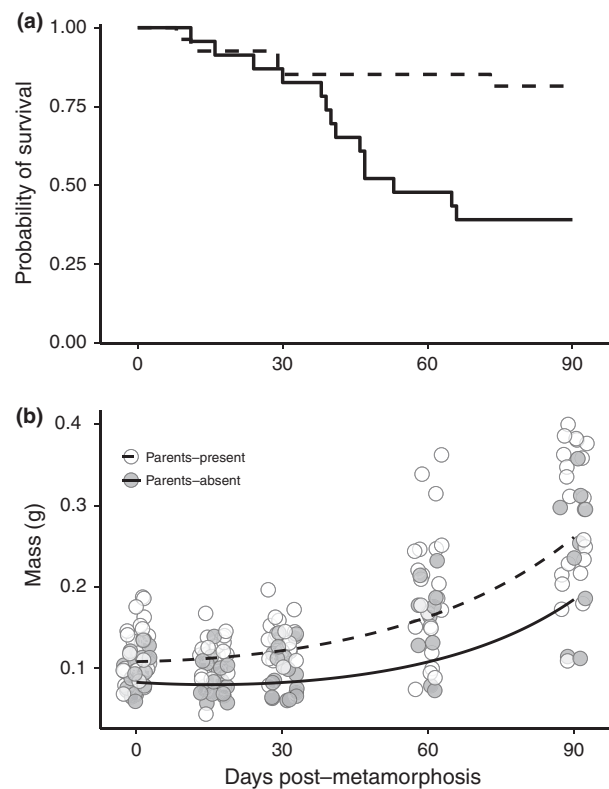
Fig. 1 Results of generalized linear mixed models with which we estimated the survival to metamorphosis (a), mass at metamorphosis (b) and time to metamorphosis (c) of *Oophaga pumilio* tadpoles that were monitored (open circles) or removed from their mothers and monitored (filled circles) at a range of Gosner developmental stages.

Fig. 2 Survival (a) through 90 days post-metamorphosis of *Oophaga pumilio* tadpoles that remained with their mothers throughout larval development (dashed lines) or removed from their mothers earlier in development (solid lines), and growth (b) of control (open circles) and experimentally removed (filled circles) tadpoles over the same time period.

Post-metamorphic growth and survival

As indicated by the hazard ratio of treatment ($\exp(\beta)$) from the Cox regression), juveniles from the parents-present treatment were 3.7 times as likely to survive through 90 days than those from the parents-absent treatment ($\beta \pm SE = 1.31 \pm 0.55$, $\chi_1^2 = 6.2$, $P = 0.013$; Fig. 2a), but initial stage was not a significant predictor of survival ($\beta \pm SE = -0.06 \pm 0.11$, $\chi_1^2 = 0.3$,

$P = 0.601$). Consistent with this treatment effect being mediated primarily by mass at metamorphosis, this treatment effect was not present ($\beta \pm SE = 0.35 \pm 0.62$, $\chi_1^2 = 0.3$, $P = 0.592$) when we included mass at metamorphosis in the model ($\beta \pm SE = -3.95 \pm 1.53$, $\chi_1^2 = 7.3$, $P = 0.007$); the effect of initial stage remained nonsignificant ($\beta \pm SE = 0.19 \pm 0.15$, $\chi_1^2 = 1.8$, $P = 0.185$).

Juveniles from the parents-absent tadpole treatment weighed less than those from the parents-present treatment throughout development ($F_{1,109.9} = 13.9$, $P < 0.001$; Figs 2b and 3), and the lack of interactions between treatment and either the linear or quadratic effect of measurement day indicates that growth was similar for juveniles from both tadpole treatments (treatment × day: $F_{1,157.1} = 2.2$, $P = 0.137$; treatment × day × day: $F_{1,154.7} = 1.6$, $P = 0.205$). Juvenile mass was associated with the quadratic ($F_{1,154.6} = 36.8$, $P < 0.001$), but not the linear ($F_{1,157.1} = 0.9$, $P = 0.334$), effect of post-metamorphic day: juveniles gained little mass in the first 30 days post-metamorphosis and then gained mass more rapidly in the next
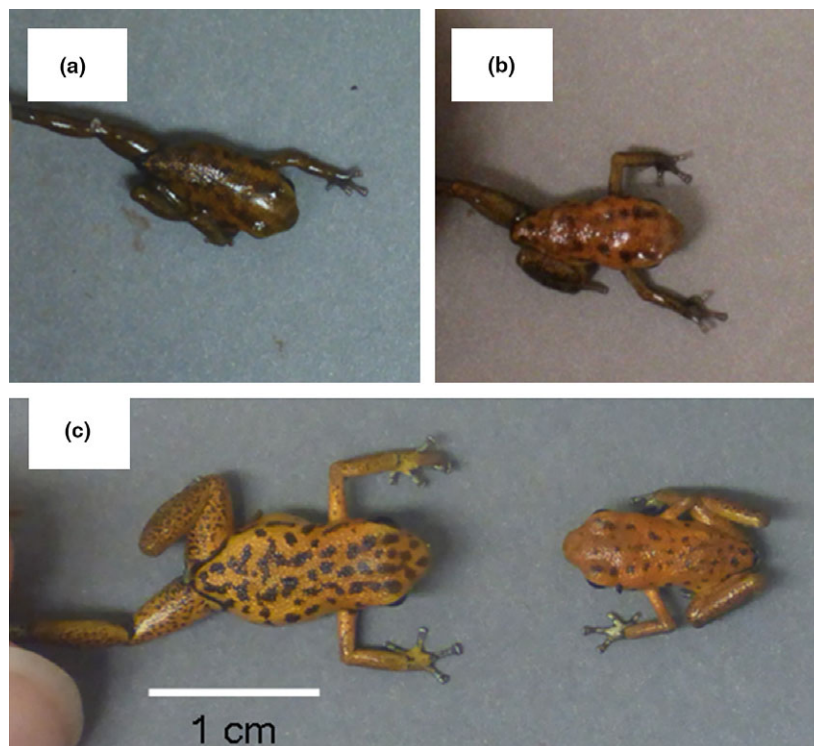
Fig. 3 Sibling *Oophaga pumilio* juveniles from the same brood, one of which remained with parents throughout development (panel (a) and left in panel (c)) and one of which was removed from parents at Gosner stage 42 (panel (b) and right in panel (c)). Photographs illustrate size at metamorphosis (a, b) and 90 days post-metamorphosis (c).
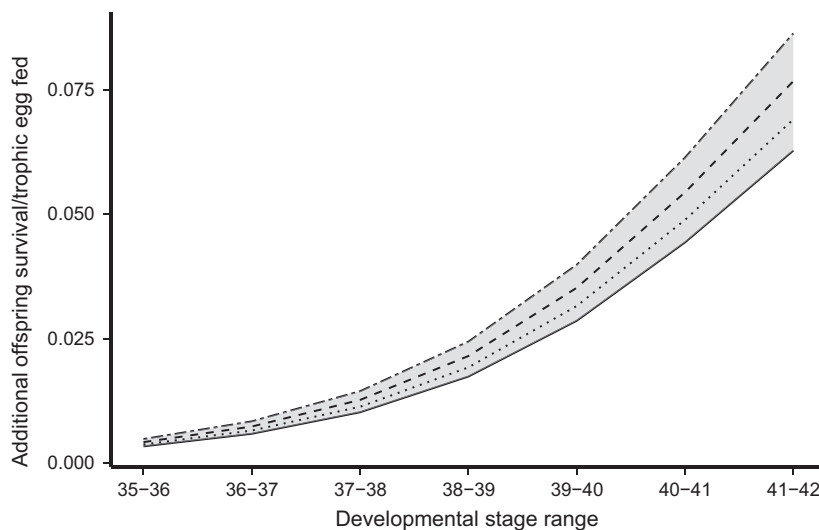
Fig. 4 Predicted value of maternal provisioning across a range of developmental stages. The value of care was estimated as the difference in estimated survival probability of tadpoles removed from mothers at a developmental stage and the stage immediately before divided by the estimated number of eggs mothers provide during that developmental period.

60 days (Fig. 2b). Throughout development, mass was positively associated with the initial stage at which tadpole observations began ($\beta \pm$ SE = 0.05 $\pm$ 0.01, $F_{1,32.6}$ = 17.9, $P < 0.001$). Parent pair, mother population-of-origin and father population-of-origin accounted for 12.2%, 12.1% and 14.5% of residual variance, respectively. None of these results were qualitatively different when we removed nonsignificant interaction effects, and a model that included only individuals that

survived 90 days post-metamorphosis also yielded similar results (Appendix S2).

Relative value of parental care across development

The value of parental care to *O. pumilio* tadpoles was higher later in development (Fig. 4). Although the costs of care (eggs provided) increase over developmental ranges (Appendix S1), the survival difference between

offspring that remained with their parents and those that were taken away from them increased more quickly. This pattern was clear regardless of whether we used high or low estimates of provisioning rates.

Discussion

Longer durations of parental investment are better for *O. pumilio* tadpoles, with the positive effects of care manifesting primarily after metamorphosis. Within the range of developmental stages we considered, tadpoles removed from their mothers were just as likely to complete metamorphosis as controls. Observational work in the wild, where predation is common, similarly suggests that maternal care (number of trophic eggs provisioned) is unassociated with survival to metamorphosis (Maple, 2002), although these same metrics are associated in captivity when tadpoles are followed through all of development (Dugas *et al.*, 2016). This evidence suggests that maternal provisioning to *O. pumilio* tadpoles is most important to larval survival early in development, a result consistent with the hypothesis that anuran larval development includes a threshold at which metamorphosis becomes possible (Wilbur & Collins, 1973; Morey & Reznick, 2000). The evolution of maternal provisioning that extends beyond this minimum in *O. pumilio*, on the other hand, seems most likely explained by benefits accrued post-metamorphosis.

Tadpoles that remained with their parents weighed more at metamorphosis than those experimentally removed from parents, and the earlier in development tadpoles were removed, the less they weighed. The stage at which we began monitoring was also associated with mass at metamorphosis in controls; this unexpected pattern might have resulted from disturbance caused by monitoring, or tadpoles at later developmental stages may have been a high-quality subset of all tadpoles alive at earlier stages. *Oophaga pumilio* juveniles from the parents-absent treatment were less likely to survive to adult size than were controls and did not grow more quickly post-metamorphosis, effects likely mediated via the direct influence of parental investment on mass at metamorphosis. Although caution is appropriate when interpreting patterns like this in captivity, it seems likely that selection on size at metamorphosis is relaxed relative to nature when food is provided *ad libitum*, emphasizing the potential importance of parental investment in the wild. Size at metamorphosis in amphibians and similar life-history traits in other organisms frequently correlate with adult reproductive success (Taylor *et al.*, 1998; Altwegg & Reyer, 2003), and are often shaped by both pre- and post-zygotic parental investment (Rauter & Moore, 2002; Schwagmeyer & Mock, 2008). Selection on body size at crucial developmental milestones may have important yet understudied consequences for the evolution of parental investment (Coulson *et al.*, 2003; Marshall & Monro, 2012).

Tadpoles completed metamorphosis more quickly when we experimentally removed them from their mothers and the exogenous nutrients mothers provide. This result supports the hypothesis that amphibian larvae should prioritize growth over development when food is abundant in the larval habitat (Wilbur & Collins, 1973; Morey & Reznick, 2000), and reveals that larval developmental rate is not strictly limited by nutrient availability in phytotelm nurseries (i.e. tadpoles are not developing as quickly as physiologically possible). Our results instead suggest that general inviability of small juveniles might be an important source of post-metamorphic mortality and drive the evolution of parent and offspring life-history strategies.

When phytotelm-bound larvae are at risk of desiccation, some dendrobatids without obligate maternal feeding deposit eggs or even new tadpoles with existing larvae, a behaviour hypothesized to provide nutrients that allow tadpoles to develop quickly and escape their disappearing nurseries (Poelman & Dicke, 2007; Schulte & Lötters, 2013). Whereas this explanation for these maternal behaviours remains untested, it reflects the hypothesized role of parental care in shaping the proportion of time offspring spend in relatively vulnerable vs. relatively safe life stages (e.g. egg vs larvae: Klug & Bonsall, 2014). Whereas an *O. pumilio* mother could perhaps delay offspring development by withholding food, increased provisioning will result in faster development only if faster development is also in the tadpole's interest (e.g. if the nursery is drying).

Parent frogs could seemingly force faster tadpole development only by terminating care, and mother *O. pumilio* do sometimes abandon tadpoles (Maple, 2002; Dugas *et al.*, 2016). However, our exploration of the relative benefits of caring for tadpoles across development suggests that abandonment is unlikely to be an adaptive maternal response to exploitation by offspring. Even in captive conditions that presumably maximize the survival of low-quality metamorphs, we identified no conditions under which it would be in a mother's best interest to shift investment from a well-developed tadpole to a less developed, or new, one. Overall, the results of this study suggest that the duration of care in *O. pumilio* does not reflect an expensive resolution of parent–offspring conflict (Trivers, 1974; Trillmich & Wolf, 2008); both a mother's and a tadpole's fitness are maximized when the mother continues to provision as long as the tadpole is willing and able to eat (mouthparts may atrophy at late stages: Gosner, 1960). Maternal abandonment of tadpoles may instead be driven by the costs of trophic egg production, which might increase with declines in female condition or at high production levels (Dugas *et al.*, 2015a,b, 2016).

Even when a mother and tadpole agree that care should extend throughout development, any costs of egg production might drive parent–offspring conflict and sibling rivalry over the size and frequency of meals

a tadpole receives. Consistent with the prediction that investing in more developed offspring pays higher fitness dividends, mothers in this captive colony feed larger meals to older tadpoles (Dugas *et al.*, 2016). Intriguingly, *O. pumilio* tadpoles perform behavioural displays when mothers visit rearing sites (Stynoski, 2012), and these displays might contain information mothers use to make allocation decisions. However, despite the apparent benefits of high levels of investment, captive *O. pumilio* mothers often divide limited care among several concurrent offspring, investing submaximally in each (Dugas *et al.*, 2016). Studies of families in the wild will be necessary to identify the full suite of intrinsic (e.g. egg production costs) and extrinsic (e.g. nursery desiccation and predation risk) factors shaping optimal initial and final family size and within-brood allocation of resources.

The evolution of parental investment strategies is shaped by the relative pay-offs of investing in offspring quantity and quality. *Oophaga pumilio* mothers invest more in offspring than is required for viability, and the fitness benefits of this strategy accrue via increased post-metamorphic survival. Whereas offspring's ability to control their own development rate might allow them to force parents into providing above optimal durations of care, this is not the case in *O. pumilio*, where mothers instead benefit more from providing care to more developed offspring. These and other empirical results (Schwagmeyer & Mock, 2008) suggest that it is not safe to assume a plateau in the relationship between parental investment and offspring fitness (Godfray, 1991; Stearns, 1992) across natural ranges of investment. Obligate and facultative egg-feeding frogs remain an exceptional and largely untapped model with which to study the evolution of parental investment (Crump, 1996; Summers *et al.*, 2006). Of particular value will be the enormous range over which parental investment might vary, with the minimum required for viability far below the levels at which the benefits of parental investment asymptote. Comparisons both among species and among populations (Dugas & Richards–Zawacki, in press) promise to offer insights into the fitness consequences of parental investment and the social and ecological forces that shape them.

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Supporting information