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What are the contributions of maternal and paternal traits to fecundity and offspring development? A case study in an amphibian species, the spined toad *Bufo spinosus*

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Abstract

Assessing the determinants of reproductive success is critical but often complicated because of complex interactions between parental traits and environmental conditions occurring during several stages of a reproductive event. Here, we used a simplified ecological situation—an amphibian species lacking post-oviposition parental care—and a laboratory approach to investigate the relationships between parental (both maternal and paternal) phenotypes (body size and condition) and reproductive success (fecundity, egg size, embryonic and larval duration, larval and metamorphic morphology). We found significant effects of maternal phenotype on fecundity, hatching success, and tadpole size, as well as on the duration of larval development. Interestingly, and more surprisingly, we also found a potential contribution of the paternal phenotype occurring during early (embryonic development duration) offspring development. Although our study focused on life-history traits such as body size and development duration, additional mechanisms involving physiological costs of development may well mediate the relationships between parental phenotypes and offspring development. Future studies are required to decipher the mechanisms underlying our findings in order to clarify the mechanistic basis of the links between parental phenotypes and offspring development.

Key words: clutch quality, embryonic development, larval development, phenotype, reproductive success.

Assessing the determinants of fecundity and offspring quality, and thus reproductive success, remains an essential question in evolutionary ecology (Pianka 2011). This is especially the case at a time when natural (ancestral) environmental conditions for most species are disrupted by novel, additional anthropogenic sources of perturbations (Moore and Waring 2001; Rhind 2009; Seress and Liker 2015). Indeed, reproductive success often depends on a variety of parameters which include both parental traits and environmental conditions where the reproductive event occurs. It is thus critical to thoroughly investigate determinants of reproductive success across a variety of taxa if we are to understand the consequences of anthropogenic global change on the persistence of populations (Dahlhoff et al. 2008; Massot et al. 2008; Loarie et al. 2009; Auer and Martin 2013).

Reproductive success is known to be particularly dependent on the quality (with both genetic and environmental components, Berg et al. 2019; Salles et al. 2020) of parental organisms (Kölliker et al. 2014; Ratikainen et al. 2018). Such parental quality is expressed through complex interactions between ecology, physiology, and behavior during reproduction (Moczek 1998; Bradshaw and McMahon 2008; Cauchard et al. 2013). For instance, parental quality can influence reproductive success through processes that include the selection of suitable reproductive sites, the selection of suitable mates, the production of gametes, and the energetic investment during embryonic development (Amos et al. 2001;

Refsnider and Janzen 2010; Cauchard et al. 2013; Kölliker et al. 2014; Ratikainen et al. 2018). In addition to these traits which occur relatively early during reproduction, other determinants of reproductive success can occur later and are often expressed through the parental care to the progeny and the quality of the environment where reproduction takes place (Clutton-Brock 2019). In many cases, both environmental characteristics and parental traits interact to determine reproductive success, sometimes during several stages of a reproductive event (Hoy et al. 2016). As a consequence, it is often difficult to tease apart the relative contributions of parental (including both maternal and paternal organisms) and environmental factors on reproductive success (Ridley 2007; Hoy et al. 2016). All of these sources of variation of reproductive success and offspring development have been grouped within the concept of parental effects with a strong focus on their evolutionary consequences (Rollinson and Hutchings 2013; Lynch and Lynch 2017). Accordingly, this corpus of literature has highlighted that phenotypic correlations between parents and offspring can reflect both parental effects and direct genetic correlations between parents and offspring (Amos et al. 2001; Fan et al. 2015).

Some ecological situations offer relevant opportunities to simplify such complex interactions between environmental and parental characteristics. This is typically the case for species lacking post-oviposition parental care and that breed communally (Heisswolf et al. 2005; Refsnider and Janzen

2010). Indeed, such a situation allows to reduce the influence of parental organisms to a few simple factors of the reproductive investment, such as the quality of the gametes and the energetic investment in the eggs (Ratikainen et al. 2018). In such a context, it is thus possible to directly assess how maternal and paternal traits (proxies of individual quality, Wilson and Nussey 2010) can affect fecundity and offspring quality, and thus reproductive success (Ratikainen et al. 2018).

Amphibians are one such taxa allowing to simplify complex interactions between environmental and parental traits. Indeed, many amphibian species lack parental care (Wells 2010) and lay their eggs communally (i.e., in the same breeding pond, Doody et al. 2009). In these taxa, maternal phenotype (e.g., body size, mass, and condition) has been shown to positively affect fecundity and egg size (Castellano et al. 2004) which, in turn, positively affect the subsequent larval quality (Laugen et al. 2002; Loman 2002). Interestingly, as in most vertebrate species, the influence of paternal phenotype on reproductive success has been overlooked to date (Moiron et al. 2020; but see Lange et al. 2021), presumably because of the predominant role of females for reproduction in most systems (Parker and Begon 1986; Caro et al. 2008). Yet, it is widely recognized that reproductive success depends on both maternal and paternal traits, even in species in which the contribution of paternal organisms to reproduction is reduced to the fertilization of the eggs (Brommer and Rattiste 2008; Germain et al. 2016). It is thus essential to include paternal phenotypes in addition to maternal traits to thoroughly assess the effects of parental traits on fecundity and offspring quality, and thus reproductive success.

In this study, we used a common garden experiment to investigate the relationships between parental (both maternal and paternal) phenotypes (body size and condition) and reproductive success in an amphibian species that breed communally and lacks post-oviposition parental care, the spined toad *Bufo spinosus*. Pairs of breeding toads (amplexus) were captured in the field after that mate selection occurred and brought back to the laboratory before egg laying, which allowed us to monitor the whole reproductive event (from egg laying to metamorphosis) under controlled conditions. With such a design, we were able to assess whether maternal and paternal phenotypes relate to each other (i.e., indicating assortative mating, Chajma and Vojar 2016; but see Green 2019), and to assess how maternal and paternal phenotypes influenced fecundity (number and size of the eggs), embryonic development traits (duration, hatching success), and larval development traits (duration, body size across key developmental stages) up to metamorphosis (body size, mass, and condition). It is important to emphasize that parental trait variation can have both a genetic and an environmental component and that our study design did not allow to separate these effects.

Material and Methods

Study species and sampling

Spined toad *B. spinosus* is one of the most common amphibian species in western Europe (Trujillo et al. 2017). Breeding occurs between late winter and early spring (mid-January to late March) depending on the climatic conditions. During breeding, adults converge to reproductive ponds where they pair and lay their eggs (Brischoux et al. 2018). Both embryonic and larval developments occur in reproductive ponds.

Sampling took place in February 2020 in western France. Three typical breeding sites (ponds surrounded by a mixture of woods and arable lands) were monitored from the onset of the breeding season (mid-January). These sites were situated close to the laboratory (CEBC, 46°8′ 48.64″N; 0°25′30.86″W) and considered as a single population (unpublished microsatellites data). Captures were conducted at night using a headlamp and toad pairs (hereafter amplexus) were caught using a net. We collected a total of 23 amplexus which were brought back to the laboratory until laying.

Parental traits and fecundity

At the laboratory, each amplexus was separated and males and females were individually weighed (with an electronic scale, ± 0.01 g). Each pair was reunited in plastic containers (59 × 36 × 28 cm) containing 30 L of dechlorinated tap water, a rock, and a branch (for egg attachment). Each amplexus was monitored several times a day until the completion of egg laying (all pairs successfully laid eggs), which occurred after 0–7 days (2.54 ± 0.38).

When egg laying was completed, males and females were individually weighed and the body size (snout-to-vent length, SVL) was measured using a caliper (±0.01 mm). All individuals were released at the site of capture within 1 day after laying.

The clutch of *B. spinosus* is formed by elongated egg strings containing 3,000–5,000 eggs (Cheron et al. 2021a). In order to assess the fecundity of each amplexus, each egg string was placed in a container (35 × 20 × 25 cm) containing 2 cm of dechlorinated tap water and a scale (graph paper). A picture was taken in order to measure the total length of the egg string using ImageJ software (Schneider et al. 2012). For each clutch, we randomly selected 5 segments of 10 cm long and individually counted the number of eggs within each segment. The mean number of eggs per 10-cm segment was calculated and used to assess fecundity (number of eggs) for each clutch based on the length of the egg strings.

Embryonic and larval development

For each clutch, we randomly subsampled 4 pieces containing 34 eggs that were kept for our experiment. The remaining eggs were released at their site of origin. Each piece was placed in a Petri dish above the graph paper and a picture was taken in order to measure the egg size (diameter) using the ImageJ software (Schneider et al. 2012). We collected a total of 136 values of egg diameter per clutch (34 eggs measured for each of the 4 segments of each clutch). Each segment was then individually transferred in glass tanks (18 × 13 × 18 cm) containing 2 L of dechlorinated tap water (changed every week) until hatching. Hatching occurred at Gosner stage 25 (Gosner 1960) and for each segment, we recorded the duration of embryonic development and the number of live and undeveloped embryos. The 2 later variables were used to assess hatching success for each of the 4 segments of each clutch.

Upon hatching, we randomly selected 6 tadpoles per clutch to monitor the larval development until metamorphosis (*N* = 138 tadpoles). The remaining individuals were released at their site of origin. Tadpoles were raised individually in glass tanks (18 × 13 × 18 cm) containing 2 L of dechlorinated tap water. During the larval development, tadpoles were fed *ad libitum* with organic chopped spinach, and the water was changed every week. We used morphological features to

classify developmental stages according to Gosner (1960). We selected Gosner stages 25, 30, 37, 41, and 42 (hereafter, GS 25, GS 30, GS 37, GS 41, and GS 42, respectively) in order to monitor larval development (Cheron et al. 2021a). For each stage, we measured the total length and tail length following Cheron et al. (2021a). Each tadpole was put into a Petri dish placed above graph paper with the water from its own tank, and photographs were taken from above the Petri dish. Morphological measurements were performed with the software ImageJ (Schneider et al. 2012).

At metamorphosis (Gosner stage 46, Gosner, 1960), toadlets were individually transferred to a plastic box (17 × 15 × 9 cm) with a damp paper towel as substrate and a shelter. Toadlets were measured (SVL) and weighed 5 days after metamorphosis and individuals were then released at their site of origin.

All the experiments took place in a thermally controlled room with the temperature set at 17°C (both air and water). The photoperiod was controlled (12 h dark–12 h light).

Statistical analyses

All data were tested for homogeneity of variance, residual independence, and normality with the Bartlett test, Dubin–Watson test, and Shapiro–Wilks test, respectively. We also checked the residue normality using diagnostic plots. All statistical analyses were carried out with R v.4.0.3 (R Core Team 2019). For variables following normal distribution (fecundity, morphological traits, development duration), we used linear mixed models (LMER, lm4 package), and for variables following binomial distribution (hatching success), we used generalized mixed models (GLMER, lme4 package).

Body size and body mass were highly correlated in adult individuals as well as in metamorphic toadlets. As a consequence, we quantified a body condition index (BCI) using residual scores from the linear regressions between body size and body mass independently in males, females, and metamorphic toadlets. In all cases, BCI was not correlated to body size (all $P > 0.355$).

First, to quantify the relationships between parental traits (SVL and BCI), we used linear models with female traits as dependent variables and male traits as explanatory variables.

Second, to study the relation between fecundity (clutch size, egg size) and parental traits (SVL, mass, and BCI), we fitted linear models with clutch size or egg size as dependent variables and parental measurements (body size and body condition) as explanatory variables.

Third, for embryonic development duration (assessed as the time elapsed between the date of egg laying and the date of hatching), we fitted linear mixed models (LMER, lm4 package) with development duration as dependant variable and parental measurements as explanatory variables (SVL and BCI). We used generalized mixed models (GLMER, lme4 package) to investigate the relationships between hatching success (binomial distribution) and parental traits. In all cases, we used clutch identity as a random effect.

Fourth, to test whether there was a relation between parental traits and larval development, we used repeated measures analyses. Larval development traits (total length or days elapsed between Gosner stages) were used as dependant variables and egg size or parental traits (female or male SVL, female or male BCI) as explanatory variables in interaction with Gosner stages. In all models, we used tadpole identity nested within clutch identity as a random effect. We performed post hoc analyses using emmeans package (emtrends function) to test for statistical differences in slope at each stage.

Finally, to test whether there was a relation between parental traits and toadlet life-history traits, we fitted several linear mixed models with toadlet SVL, BCI, or body mass as dependent variables and egg size or parental traits (SVL and BCI) as explanatory variables.

Results

Relationships between parental traits

We did not find any relationship between male and female body size ($F_{1,21}= 0.016$, $P = 0.969$), body mass ($F_{1,21}= 0.122$, $P = 0.730$), or body condition ($F_{1,21}= 0.018$, $P = 0.966$).

Parental determinants of fecundity and egg size

SVL and BCI were positively related to clutch size in females (SVL $F_{1,21}= 9.782$, $r^2 = 0.285$, $P = 0.005$ and BCI $F_{1,21}= 10.46$, $r^2 = 0.332$, $P = 0.004$, Figure 1), but not in males (SVL $F_{1,21}= 0.318$, $P = 0.579$ and BCI $F_{1,21}= 9.99$, $P = 0.881$, Figure 1).

The size of the eggs was neither related to female or male traits (all $P > 0.307$) nor to clutch size $P = 0.286$.
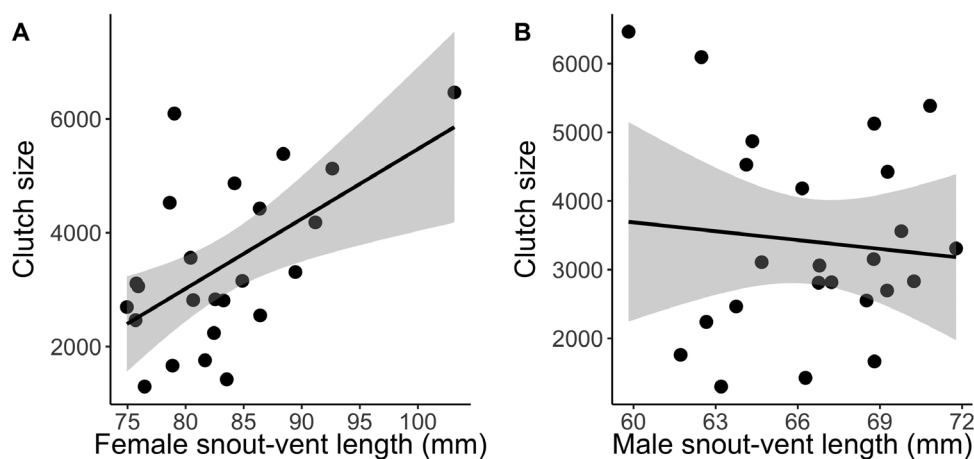

Figure 1. Relationships between (A) female or (B) male body size (SVL, mm) and fecundity (clutch size). Gray shading indicates 95% confidence intervals.

Parental influences during embryonic development

Hatching success varied between clutches (χ^2 = 379.50, df = 22, P < 0.001, range 0.35–0.99) but not within clutches (χ^2 = 0.740, df = 3, P = 0.864). Eggs size and embryonic development duration were not related to hatching success (respectively, $F_{1,3126}$ = 2.158, P = 0.141 and $F_{1,3126}$ = 1.035, P = 0.307). Finally, we found no relationship between eggs size and embryonic development duration ($F_{1,21}$ = 0.304, P = 0.587).

Hatching success was not related to female or male SVL (respectively, χ^2 =0.439, df = 1, P = 0.598; χ^2 =3.053, df = 1, P = 0.081). Hatching success was marginally positively linked to female BCI (χ^2 =3.579, df = 1, P = 0.059, Figure 2), but not to male BCI (χ^2 =1.249, df = 1, P = 0.264, Figure 2).

Embryonic development duration was not related to female SVL ($F_{1,22}$ = 2.166, P = 0.155, Figure 3) but was marginally negatively correlated to male SVL ($F_{1,22}$ = 3.585, P = 0.072, Figure 3). Neither female nor male BCI influenced embryonic development duration (respectively, $F_{1,22}$ = 1.015, r^2 = 0.046, P = 0.325; $F_{1,22}$ = 1.811, r^2 = 0.046, P = 0.193).

Parental influences during larval development

Overall, the total length of tadpoles increased through time ($F_{2,274}$ = 7139.2, P < 0.001). We did not find any relation between tadpole total length and egg size, female and male SVL, or male body condition (all P > 0.109). However, we found that female BCI was related to tadpole size throughout ontogeny (BCI × Stages: $F_{2,271}$ = 10.09, P < 0.001, Figure 4). Post hoc analyses showed that female BCI was negatively related to the total length of tadpoles at GS30 ($F_{1,30}$ = 5.324, P = 0.028, Figure 4) and GS37 ($F_{1,30}$ = 8.420, P = 0.007, Figure 4) but not GS25 ($F_{1,30}$ = 1.121, P = 0.298, Figure 4).

Neither female SVL, male SVL, nor egg size was related to the total duration of larval development (from GS 25 to GS 46, all P > 0.660). However, female BCI was positively related to the total duration of larval development (from GS 25 to GS 46, $F_{1,20}$ = 5.763, P = 0.026). When focusing our analysis to the days between stages, we found a similar result (BCI × Stage: $F_{4,535}$ = 3.72, P = 0.006, Figure 5). More specifically, post hoc analyses showed that females in better condition produced tadpoles that developed less rapidly between GS 30 to GS37 ($F_{1,192}$ = 6.355, P = 0.013, Figure 5) and between GS41 and GS42 ($F_{1,19}$ = 14.525, P = 0.002 Figure 5). Other parental traits were not correlated to either total duration of larval development or duration of each Gosner stage (all > 0.660).

Parental influences on toadlets

Toadlet SVL was not influenced by parental traits (all P > 0.445). Parental traits did not influence the body mass of metamorphic individuals (all P > 0.410). We found a marginal
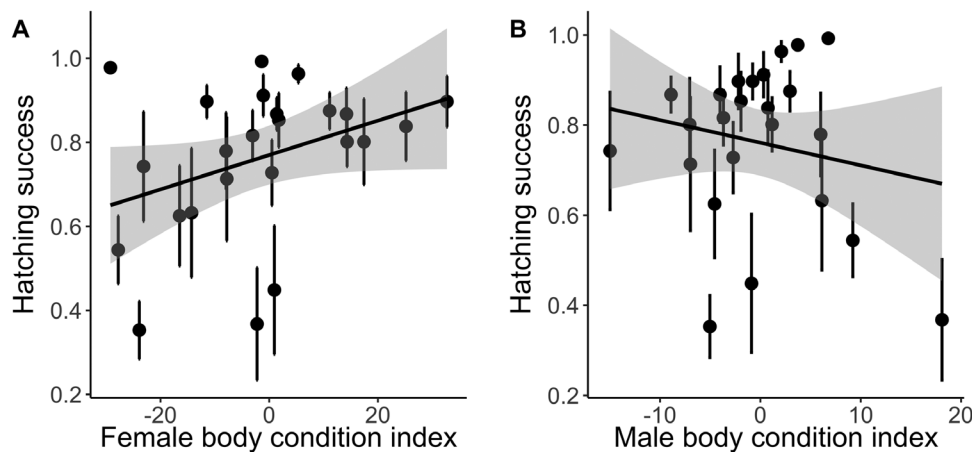

Figure 2. Relationships between (A) female or (B) male body condition and hatching success. Grey shading indicates 95% confidence intervals.
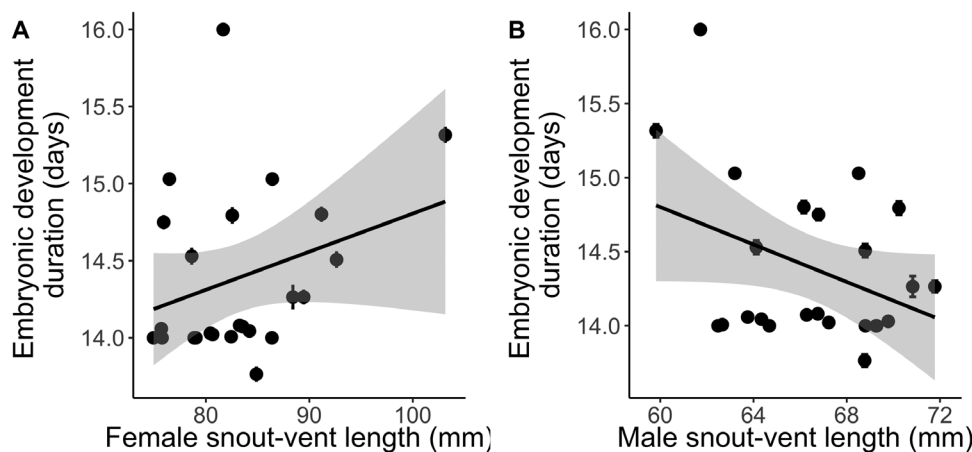

Figure 3. Relationships between (A) female or (B) male body size (SVL, mm) and embryonic development duration (days). Gray shading indicates 95% confidence intervals.
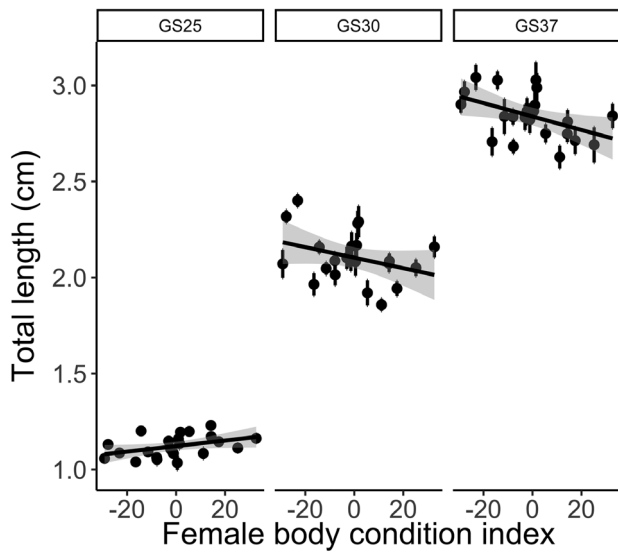
Figure 4. Relationships between female body condition and tadpole size (total length, cm) across 3 main developmental stages (GS25, GS30, and GS37 according to Gosner [1960]). Gray shading indicates 95% confidence intervals.
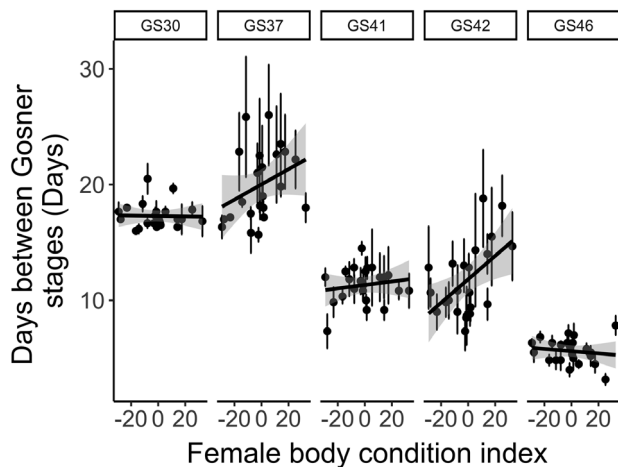

Figure 5. Relationships between female body condition and duration of larval development between key developmental stages according to Gosner (1960). GS30 indicates the time elapsed between GS25 and GS 30; GS37 indicates the time elapsed between GS30 and GS 37; GS41 indicates the time elapsed between GS37 and GS 41; GS46 indicates the time elapsed between GS41 and GS 46. Gray shading indicates 95% confidence intervals.

Figure 6. Relationship between egg size (mm) and toadlet body condition. Gray shading indicates 95% confidence intervals.

positive relation between egg size and toadlet body mass ($F_{1,89}$ = 3.358, P = 0.070). Toadlet BCI was not related to parental traits (all P > 0.753) but we found a positive relation between egg size and toadlet BCI ($F_{1,70}$ = 4.618, P = 0.035 Figure 6).

Discussion

In this study, we investigated the effects of both maternal and paternal phenotypes on embryonic and larval development in an amphibian species. Importantly, we did not find size-related assortative mating in our study species (see also Marco and Lizana 2002). As expected, we found significant effects of maternal phenotype on fecundity, hatching success, and tadpoles size, as well as on the duration of larval development.
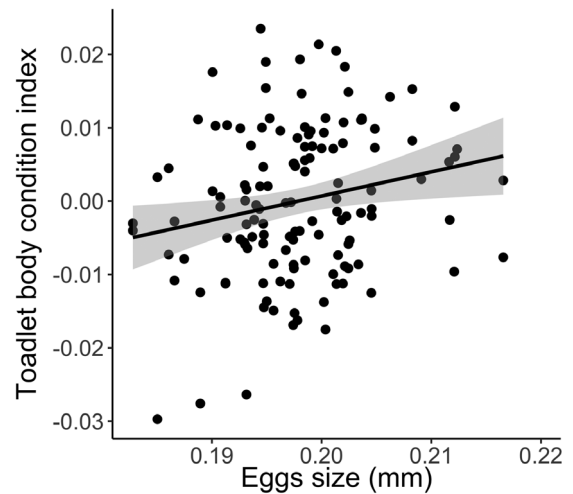
Interestingly, and more surprisingly, we also found a marginally significant contribution of the paternal phenotype occurring during early (embryonic development duration) offspring development. It is also important to highlight that phenotypic correlations between parents and offspring can reflect both parental effects and direct genetic correlations between parents and offspring. Although the effects of parental phenotype are likely influenced by the environment, part of the variation related to offspring traits can be of genetic origin. Parental trait variation can have both a genetic and an environmental component, and our study design did not allow to separate these effects. In addition, maternal (or paternal) phenotypic effects in the current study (where adults are not reared in a common garden and offspring are full sibs) can reflect genetic dominance and/or parental effects (Hunt and Simmons 2002; Wolf and Wade 2009; Martin and Pfennig 2010; Hwang et al. 2020). Future common garden studies are required in order to disentangle genetic and environmental sources of parental phenotype effects (Rowiński et al. 2020).

We found that fecundity was strongly linked with maternal life-history traits (size and condition). As expected, clutch size was positively related with female body size and body condition, indicating that larger and bigger females laid a higher number of eggs. Such positive effect of female size and condition on fecundity is a widespread relationship that has already been highlighted in amphibians (Gibbons and McCarthy 1986; Castellano et al. 2004) as well as in other taxa (Hines 1988; Blackmore and Lord 2000).

Egg size was, however, not related to parental phenotypes and not related to clutch size. Such a result contrasts with the classical trade-off between egg number and egg size that has been found in amphibians (Gould et al. 2022) as well as in other taxa (Jørgensen 1984; Berven 1988; Elgar 1990). The lack of relationships between parental phenotypes or fecundity and egg size can plausibly be related to the fact that our methodology did not allow to capture subtle but significant variations in egg size (but see the relationship between egg size and toadlet condition in Figure 6). Future studies are required to investigate the determinants of egg size in this species and to complement our approach which failed to identify such factors.

We found that females in better condition produced clutches with greater hatching success. In this species and its close relative *B. bufo* (Trujillo et al. 2017), hatching success has been either related to fertilization success (Touzot et al. 2020) or to embryonic mortality (Cheron et al. 2021b). Our result demonstrates that the quality (body condition) of females positively influenced embryonic survival while our analyses revealed that male phenotype does not significantly affect hatching success. This result also reinforces the fact that, in this species, hatching success can be used as an index of clutch quality (Cheron et al. 2021b).

Interestingly, although our analysis does not reveal an influence of male traits on fertilization success (see above), we found that the eggs fertilized by larger males produced embryos that tend to develop quicker. The mechanisms underlying such intriguing result remain unknown and deserve specific investigations. Yet, it is likely that this effect is mediated through the quality of the sperm produced by larger—presumably older—males (Gasparini et al. 2010; Roth et al. 2010). Although age-dependent sperm quality in amphibian species is expected to decrease through senescence (Hettyey et al. 2012), a study found that older males displayed the same fertilization capacity (e.g., motility and concentration) as younger males (Watt et al. 2021). In addition, it has also been shown that younger males produced more atypical spermatozoa than older males (Watt et al. 2021). Other complementary mechanisms could potentially involve size-specific macromolecular composition of spermatozoa affecting the duration of the first steps of fertilization (e.g., acrosome composition, chromatin unpacking) and/or the embryonic development (Gusseck and Hedrick 1971; Lohka and Masui 1983; Carroll Jr et al. 1991). Finally, we cannot rule out possible genetic effects (Rowiński et al. 2020) as our study did not allow to disentangle environmental parental effects from direct genetic effects. Future studies are required to precisely identify the mechanisms that link paternal size, sperm quality, and embryonic development duration. Such paternal influence on embryonic development duration may be critical to the survival of minute and immobile embryos that are susceptible to predation (Zamudio et al. 2016). Furthermore, longer embryonic development may also induce carry-over effects on the following larval stage duration, a potentially deleterious consequence if spawning takes place in ephemeral water bodies.

Parental phenotypes continued to influence offspring development during larval stages. Specifically, female body condition was positively related to the total duration of larval development. This suggests that larvae originating from larger clutch took more time to successfully develop up to metamorphosis. Stage-specific durations demonstrated that these effects occurred at 2 different key stages of larval development, namely somatic growth (GS30 to GS37, Cheron et al. 2021a) and onset of metamorphosis (GS41 to GS42, Cheron et al. 2021a). Interestingly, this effect was supported by the negative relationship we found between female body condition and tadpole size during larval somatic growth (GS30 and GS 37, Cheron et al. 2021a). Again, tadpoles that originated from larger clutch were smaller during somatic growth. Surprisingly, we failed to detect such effects during later phases of larval development, and 2 different but nonmutually exclusive hypotheses could explain this lack of longer term effects. First, later larval phases correspond to critical phases dedicated to the onset of metamorphosis. The remarkable modifications of tadpole morphology, behavior,

and physiology (Cheron et al. 2021a) during such stages may have obscured such effect. Second, it is plausible that mechanisms of compensatory growth may have allowed smaller tadpoles to reach similar body size than their counterpart originating from smaller clutch (Hector et al. 2012). Such compensatory growth is likely to occur, as tadpoles need to reach a minimal size to successfully complete metamorphosis (Wilbur and Collins, 1973). Although we lack behavioral data (e.g., feeding rates, activity level, Cheron et al. 2021a) to test for this hypothesis, future studies should usefully investigate whether tadpole behavior could compensate for lower growth rates during early phases of larval development and whether such putative effects are mediated by parental phenotypes and/or genotypes.

Finally, we failed to detect any link between parental traits and the life-history traits of toadlets during their first days of terrestrial life. As stated above, the remarkable modifications of tadpole morphology, behavior, and physiology (Cheron et al. 2021a) during and following metamorphosis may have negatively affected our ability to detect such effects. It is also plausible that the characteristics of embryonic and larval development may carry over later in life (Bouchard et al. 2016; Garcia et al. 2017; DiGiacopo and Hua 2020; Ruthsatz et al. 2020; Zeitler et al. 2021), and future studies investigating longer term effects of parental phenotypes on young toadlets up to adult life may usefully reveal functional links between parental quality and offspring development (Parker and Begon 1986; Ensminger et al. 2018). In contrast, we found a strong relationship between egg size and toadlet body condition (and to a lesser extent body mass). This relation is puzzling in light of the lack of relationship we highlighted between egg size and embryonic and larval development traits. This further indicates that egg size can bear long-term consequences in this study species as the body size of metamorphic individuals can affect their survival (Semlitsch et al. 1988). Future studies are required to investigate the determinants of egg size in this species and to complement our approach which failed to identify such factors.

To conclude, our study sheds light on the contribution of both maternal and paternal phenotypes on fecundity and offspring phenotype and performance in a study species lacking parental care. As expected, we found significant effects of maternal phenotype on fecundity, hatching success, and hatchling size, as well as on the duration of larval development. Interestingly, we also found a potential contribution of the paternal phenotype occurring during early (embryonic development duration) offspring development. This is especially interesting as, in amphibians, the role of fathers has often been reduced to egg fertilization (Kouba et al. 2009; Byrne and Silla 2020). Although our study focused on life-history traits such as body size and development duration, additional mechanisms involving physiological costs of development (e.g., telomere attrition, oxidative status, Saino et al. 2005; Burraco et al. 2017) may well mediate, at least in part, the relationships between parental phenotypes and offspring development (Wells 2014; Van Leeuwen et al. 2015). The potential underlying costs of development may bear strong consequences later in life (Burraco et al. 2020). Clearly, future studies should investigate the mechanisms underlying our findings in order to clarify the mechanistic basis of the links between parental phenotypes and offspring development.

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