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Benefits and costs of female and male care in amphibians: a meta-analytical approach

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The origin of parental care is a central question in evolutionary biology, and understating the evolution of this behaviour requires quantifying benefits and costs. To address this subject, we conducted a meta-analysis on amphibians, a group in which parental care has evolved multiple times. We found that both male and female parents increase egg survival, regardless of whether the breeding site is concealed or exposed. Parental care also increases survival and growth of tadpoles and juveniles, independent of the caring sex. However, parental care reduces parental body condition, particularly when parents remain stationary near the offspring. Females tend to experience higher reproductive costs, but sample size is restricted to few species. In some frog species, paternal care increases male reproductive success because females prefer caring males. The benefits of parental care in amphibians resembles those reported for arthropods but differ from fish, in which parental care does not improve offspring survival. Moreover, the decrease in body condition, which is not found in fish, is influenced by the form of parental care, suggesting a trade-off between caring and foraging, as already reported for certain arthropods. Finally, the reproductive costs of parental care for both sexes remain unexplored and deserve further research.

1. Introduction

Why do parents of some animal species care for the offspring while others leave eggs and juveniles unattended? This question has been extensively explored in evolutionary biology, with verbal and mathematical models providing valuable insights. One influential verbal model proposed by Wilson [1] emphasizes the role of four key factors in the evolution of parental care: stable and structured environments, harsh abiotic conditions, use of specialized food resources and intense offspring mortality due to natural enemies. Subsequent mathematical models proposed that other factors such as adult death rate, egg maturation rate, resource availability and spatial clumping among parents and offspring may also influence the evolution of parental care [2]. However, both verbal and mathematical models predict that parental care evolves only when the benefits of this behaviour outweigh the costs [2]. Therefore, a solid empirical understanding of the benefits and costs of parental care in different taxa is crucial for comprehending its evolution.

Parental care in invertebrates and vertebrates exhibits remarkable diversity [3,4], but it primarily serves two short-term benefits for the offspring: protection against natural enemies and harmful abiotic conditions, and provision of food resources essential for survival and development [5]. Protection can be provided by females, males or both. Empirical studies with arachnids [6], insects [7] and frogs [8,9] show that in closely related species living in the same habitat but differing in the identity of the caring sex, males are as efficient as females in preventing egg mortality. Efficient food provisioning can also be accomplished by both males and females, as observed in most monogamous bird species [10].

However, food provisioning is usually a sex-specific task, exemplified by milk production in mammals and trophic egg production in certain frog species [4].

Parental care may incur short-term non-reproductive costs borne by the parents. These costs can be classified into two main categories: increased mortality risk due to harsh biotic or abiotic conditions, and reduced food intake and/or increased energy expenditure leading to deteriorated body condition during the caring period [5]. Among arthropods and birds, evidence of increased mortality during the caring period is inconclusive. Mark-recapture studies indicate that survival probabilities of caring individuals may be lower, equal or even higher than those of non-caring individuals (e.g. [7,11–15]). Deterioration of body condition is also not a universal pattern, as demonstrated by a meta-analysis of fish [16]. The analysis revealed that, although uniparental care negatively impacts males' body condition in nearly 50% of the species analysed, the average across all species is non-significant. Although a decrease in body condition may negatively affect both the caring quality and parental survival after the caring period, the long-term impact of this non-reproductive cost on the lifetime fitness of the parents is poorly explored.

In contrast to the non-reproductive costs, the reproductive costs of parental care are usually sex dependent. In species with exclusive paternal care, such as certain arachnids [17], insects [17], fish [16] and frogs [18], females exhibit strong mating preferences for caring males. When paternal care is a sexually selected behaviour, it confers reproductive benefits rather than costs, and males' reproductive success are not negatively affected [19,20]. However, in other species, caring males may be limited in their ability to mate multiple times or have a reduced number of partners due to physical constraints of carrying eggs. Examples are water bugs, in which males carry eggs on their back [21], seahorses and pipefishes, in which males carry eggs inside brood pouches [22], and some frogs in which males carry eggs on their back or inside pouches, vocal sac or stomach [23]. Similarly, females of most species are physiologically prevented from mating while caring [24,25]. Consequently, the time and energy invested in current offspring trade-off with future reproductive events, thereby reducing females' future fecundity [5]. Thus, except for a few exceptions, reproductive costs of parental care are expected to be higher for females than for males.

Amphibians represent a highly diversified clade in which maternal, paternal and biparental care have independently evolved multiple times [26]. The forms of parental care in amphibians vary widely, from egg attendance to trophic egg feeding during tadpole development ([26–28], figure 1). A recent comparative study has shown that male and female egg attendance in amphibians primarily occurs when eggs are laid in concealed places like subterranean burrows, tree holes, or underneath rocks, logs or leaf litter [29]. The authors suggest that oviposition in concealed places, which precedes the evolution of egg attendance, enhances egg survival, particularly in terrestrial environments. In the case of females, terrestrial eggs with direct development also favour the evolution of egg attendance, probably because the eggs are large and few in number. Therefore, they represent a significant maternal investment, and the loss of a clutch would entail a high cost to the females [29]. Finally, tadpole feeding with trophic eggs is associated with oviposition in phytotelmata where predation pressure is low, but food resources for tadpole development are scarce [30]. Consequently, while the costs of protecting offspring against predation are minimized, the offspring becomes highly reliant on maternal provisioning.

In this study, we employ a meta-analytical approach to quantify the benefits and costs of parental care in amphibians. We aim to address the following questions: (i) does egg attendance enhance offspring survival, and is the effect influenced by the caring sex? (ii) Does the type of breeding site (concealed or exposed) affect egg survival? (iii) Does long-term association with offspring, including tadpole attendance, juvenile and tadpole feeding, and tadpole transport, increase offspring survival and development, and are the effects sex dependent? (iv) Does parental care impose non-reproductive costs on parents, and are these costs similar between females and males? (v) Does the form of parental care influence the non-reproductive costs incurred by parents? (vi) Does parental care impose reproductive costs on parents, and are these costs higher for females than for males?

2. Methods

(a) Data collection and selection criteria

The literature search was based on Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA; electronic supplementary material, figure S1). We first used the following combination of key words in the *Web of Science* (up to January 2022): (('parental care' or 'paternal care' or 'maternal care' or 'egg care' or 'male care' or 'female care' or 'egg guard*' or 'brood guard*' or 'tadpole feeding' or 'tadpole transport' or 'tadpole attend*' or 'juvenile feeding' or 'juvenile transport' or 'juvenile attend*) and (cost* or benefit*) and (amphibia* or anura* or frog* or salamander* or newt* or caudata or caecilian* or urodela)). Using *Google Scholar*, we also performed backward and forward searches in three review papers [28,31,32] and backward search in the references of the chapter 'Parental Care' of the book *The Ecology and Behaviour of Amphibians* [23]. Finally, since many cases of parental care in amphibians occur in the Neotropical region, where the most common idioms are Spanish and Portuguese, we used the following combination of keywords in *Google Scholar*: ['cuidado parental' amphibia beneficios costos custos].

From the resultant list of documents (papers and theses), we used their titles to identify studies of interest, and scanned their abstracts searching for information on costs and benefits of parental care. When some information was found in the abstract, we consulted the main text. If a study was selected, we performed backward and forward searches for other studies that could provide additional data. Complementarily, we contacted authors when we needed additional information to calculate effect sizes or used WebPlotDigitizer (https://apps.automeris.io/wpd/) to retrieve data reported in figures. In total, we screened 1480 studies, and the final dataset includes 224 effect sizes extracted from 86 studies, across 48 species (2 caecilians, 8 salamanders and 38 frogs) encompassing 16 families distributed in all continents, except Antarctica (electronic supplementary material, table S1).

(b) Benefits: egg survival

We found 41 studies (76 effect sizes; 31 species) exploring the benefits of parental care in terms of egg survival. The dataset includes only cases of egg attendance in which parental presence may decrease mortality by predation and dehydration. In total, we have data for 9 species with maternal care (29 effect sizes), 21 with paternal care (44 effect sizes) and 2 with biparental care (3 effect sizes) in which the identification of the caring sex was determined by the egg-tending sex (females: 29 effect sizes, 9 species; males: 47 effect sizes, 23 species). Negative

Figure 1. (*a*) Male of the glass frog *Centrolene savagei* guarding eggs on the vegetation. Males remain close to the eggs until hatching, and tadpoles drop off into the water below the oviposition site. (*b*) Female of the strawberry poison frog *Oophaga pumilio* carrying two tadpoles on her back. Eggs are laid in phytotelma, and after hatching, females feed the tadpoles with trophic eggs for several weeks. Eventually, females transport the tadpoles from the phytotelma where they were raised to a pond where they will metamorphose into froglets. (*c*) Male of the common midwife toad *Alytes obstetricans* carrying eggs attached to his back legs. Males keep eggs moist and secrete a substance through the skin that protects the eggs from infection. When eggs are about to hatch, the male detaches them in ponds. (*d*) Female of the western slimy salamander *Plethodon albagula* guarding eggs inside a rock cavity. The species has no aquatic larval stage, so juveniles hatch from the eggs and then disperse. (*e*) Female of the marbled salamander *Ambystoma opacum* guarding eggs laid under a fallen log. Females remain with their eggs until the nest floods and the larvae hatch. (*f*) Female of an unidentified caecilian curled around her eggs in a dump pocket. Females remain close to the eggs until they hatch, either as larvae or already metamorphosed juveniles. All images are licensed under Creative Commons Attributions: (*a*) Juan Camilo Manquillo Franco; (*b*) Pavel Kirillov; (*c*) Laurent Lebois; (*d*) Stanley Trauth; (*e*) Glenn Bartolotti; (*f*) Davidvraju.

values of effect sizes indicate that parental care decreases egg survival whereas positive values indicate that parental care increases egg survival.

(c) Benefits: development and survival of juveniles and tadpoles

We found 17 studies (44 effect sizes; 11 species) exploring the benefits of parental care in terms of development and survival of juveniles and tadpoles. The dataset includes cases of tadpole attendance (10 effect sizes, 4 species), juvenile or tadpole survival and/or growth due to food provisioning of trophic eggs or sloughed off skin (23 effect sizes, 4 species), tadpole transport (5 effect sizes, 1 species) and selection of suitable places for tadpole deposition (6 effect sizes, 3 species). In total, we have data for 2 species with maternal care (3 effect sizes), 7 with paternal care (22 effect sizes) and 3 with biparental care (19 effect sizes) in which the identification of the caring sex was based on the sex responsible for parental activities that contribute to the enhanced development and survival of juveniles and tadpoles (females: 25 effect sizes, 5 species; males: 15 effect sizes, 7 species). Negative values of effect sizes indicate that parental care decreases offspring development and survival whereas positive values indicate that parental care increases offspring development and survival.

(d) Non-reproductive costs

We found 22 studies (68 effect sizes, 15 species) exploring the non-reproductive costs of parental care, from which we extracted several measurements commonly employed to evaluate body condition in amphibians (reviewed and discussed in [33]): (a) different indices of body condition, usually residuals of a regression between body size and body mass; (b) fat content, usually comparing parental and non-parental individuals; (c) body mass, usually measured at the beginning and end of the caring period; (d) gut content, usually comparing parental and non-parental individuals; (e) growth or mass change in species with continuous growth during the breeding season (such as some salamanders included in our dataset); and (f) locomotor performance while carrying eggs or tadpoles on the dorsum, a behaviour that increases parental expenditure and may affect body condition. Given that the number of studies quantifying mortality risk during the caring period was small (e.g. [34,35]), this cost has not been included in our analysis. In addition, because we only obtained data on two species (five effect sizes) with exposed breeding sites, we could not answer whether the type of breeding site influences the non-reproductive costs incurred by parents. The final dataset includes 9 species with maternal care (36 effect sizes) and 6 with paternal care (32 effect sizes). Negative values of effect sizes indicate that parental care incurs a reduction in body condition, whereas positive values indicate that parental care incurs an increase in body condition.

(e) Reproductive costs

We found 18 studies (36 effect sizes, 13 species) exploring reproductive costs of parental care from which we extracted three measurements: (a) mating success, including estimates of mating frequency, number of mates, reproductive rates and attractiveness (22 effect sizes, 10 species); (b) future fecundity (8 effect sizes, 3 species) and (c) time-out (6 effect sizes, 2 species), i.e. a measure that refers to the period during which parental individuals are outside the mating pool and is generally negatively correlated with the reproductive rate [36]. Given that the number of studies quantifying paternity loss was small (e.g. [37,38]), this cost has not been included in our analysis. The dataset includes 2 species with maternal care (5 effect sizes), 10 with paternal care (23 effect sizes) and 1 with biparental care (a total of 8 effect sizes; 6 on costs incurred by females and 2 on costs by males). The most common form of parental care among these species is egg attendance ($n = 9$), but there are also species showing egg brooding (*sensu* [27]), and tadpole feeding and transport ($n = 1$, each). Negative values of effect sizes indicate that parental care imposes reproductive costs to the parents (i.e. a reduction in mating success and future fecundity, or an increase in the time-out), whereas positive values indicate that parental care incurs reproductive benefits to the parents (i.e. an increase in mating success and future fecundity, or a reduction in the time-out).

(f) Statistical analyses

We performed meta-analytical models based on four different sets of response variables: *benefits* of egg attendance for egg survival; *benefits* of parental care at tadpole and juvenile stage for development and survival; *non-reproductive costs* of parental care, and *reproductive costs* of parental care. As all effect sizes were *z*-transformed, the respective sampling variances equated to 1/(sample size − 3) [39]. Because some studies provided more than one effect size, some species provided more than one effect size, and species are phylogenetically related, the effect sizes are not independent. To account for data dependency and include random effects in our analyses, we ran multilevel models [40]. We included three random effects in all models: study identity, effect size identity and phylogeny (based on [41], electronic supplementary material, figure S2). The phylogeny was included as a correlation matrix with values ranging from 0.00 to 1.00, indicating the degree of phylogenetic closeness between species (data from the same species have a correlation of 1). The incorporation of this correlation matrix as a random effect is a standard procedure to control for species identity in meta-analyses [39].

Before testing whether parental care is beneficial to offspring and costly to parents, we tested whether effect sizes in our dataset differ according to the methodological procedures (experimental or observational) and type of data (field, mesocosm or laboratory) used in the studies. Because these analyses inform how predictor variables influence effect sizes, we ran multilevel meta-regressions [42,43], with methodological procedures and type of data as moderators. We found that none of our response variables is influenced by the methodological procedures or the type of data (electronic supplementary material, table S2). Complimentarily, when it comes to non-reproductive costs, we tested whether removing effect sizes based on locomotor performance changes results, but results do not differ if these effect sizes are included or not (electronic supplementary material, table S3). Consequently, to test our hypotheses regarding benefits and costs, we conducted models that pooled all effect sizes.

Models to calculate the overall mean estimate for benefits, non-reproductive and reproductive costs had no moderators. To test whether the magnitude of benefits and costs differ according to the caring sex, we ran models with sex (female or male) as moderator. To test whether egg survival is affected by the type of breeding site (concealed or exposed sites, following classification in [29]), we ran models with this moderator. We also tested whether non-reproductive costs are affected by the form of parental care. Because the number of effects sizes we found for certain forms of parental care is limited, we created two broad types that may influence the foraging opportunities or the energy expenditure of the parents, and consequently their body condition. The first type includes all forms of parental care in which parents remain stationary close to the offspring (i.e. egg, tadpole or juvenile attendance, *sensu* [27]). The second type includes all forms of parental care in which parents are mobile or carry a load (i.e. egg or tadpole brooding, tadpole transport or feeding, *sensu* [27]). We ran models with type of parental care (stationary or mobile) as moderator.

To test for the occurrence of publication bias, we performed Egger's regressions [43]. For each model, we also estimated data heterogeneity by calculating I^2 estimates [42–44]. To assess the potential occurrence of phylogenetic effects on data heterogeneity, we report the contribution of each random effect (including phylogeny) to the magnitude of I^2. To fit all models (via restricted maximum likelihood), we used the function *rma.mv* of the *metafor* package [44,45]. Throughout the study, we only ran models when there were at least 10 effect sizes for each level of each moderator.

3. Results

(a) Benefits: egg survival

Across amphibians, egg attendance has a mean positive effect on egg survival ($Zr = 0.54$, 95% CI = 0.29 to 0.80; $p < 0.01$; effect sizes: 76; species: 31). The magnitude of the benefits does not differ whether eggs are concealed or exposed (concealed: 0.56, 95% CI = 0.00 to 1.13, effect sizes: 42, species: 15; exposed: 0.63, 95% CI = 0.02 to 1.24, effect sizes: 34, species: 16; $p = 0.65$; figure 2). Moreover, the magnitude of the benefits is not sex dependent (maternal: 0.66, 95% CI = 0.02 to 1.31, effect sizes: 29, species: 9; paternal: 0.47, 95% CI = −0.18 to 1.13, effect sizes: 47, species: 23; $p = 0.28$; figure 2). We found no publication bias ($Zr_{\text{intercept}} = 0.05 \pm 0.06$ s.e., $t = 0.85$; $p = 0.40$), data heterogeneity is high ($I^2 = 95.41\%$) and phylogeny poorly explains data variation (phylogeny: 16.89%; study identity: 47.39%; effect size identity: 31.14%).

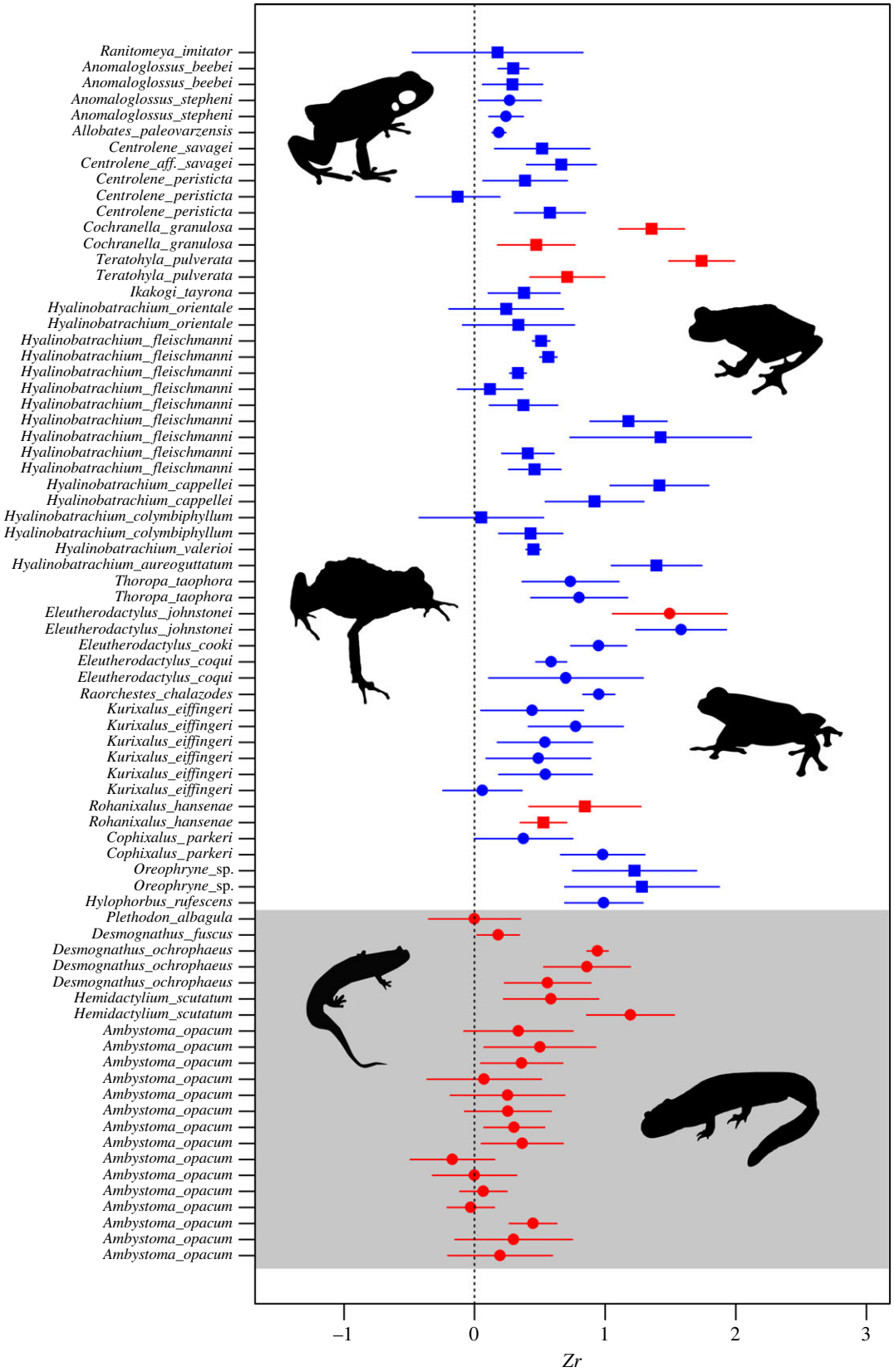

Figure 2. Benefits of parental care in terms of egg survival across amphibians. Effect sizes are shown as *Zr* values (with 95% confidence intervals); positive values indicate that parental care increases egg survival, whereas negative values indicate that parental care decreases egg survival. Frogs: 26 species; salamanders (in grey): 5 species. Blue: males; red: females. Circles: concealed breeding sites; squares: exposed breeding sites. All images are licensed under Creative Commons Attributions (CC0 1.0; from the top to the bottom): 于川云 (Chuanxin Yu); Vijay Karthick, Beth Reinke; José Carlos Arenas-Monroy.

(b) Benefits: development and survival of juveniles and tadpoles

Across amphibians, parental care at the tadpole and juvenile stages has a mean positive effect on development and survival of the offspring ($Zr = 0.62$, 95% CI = 0.39 to 0.85; $p < 0.01$; effect sizes: 40; species: 11). The magnitude of the benefits is not sex dependent (maternal: 0.80, 95% CI = 0.50 to 1.10, effect sizes: 25, species: 5; paternal: 0.41, 95% CI = 0.09 to 0.74, effect sizes: 15, species: 7; $p = 0.09$;

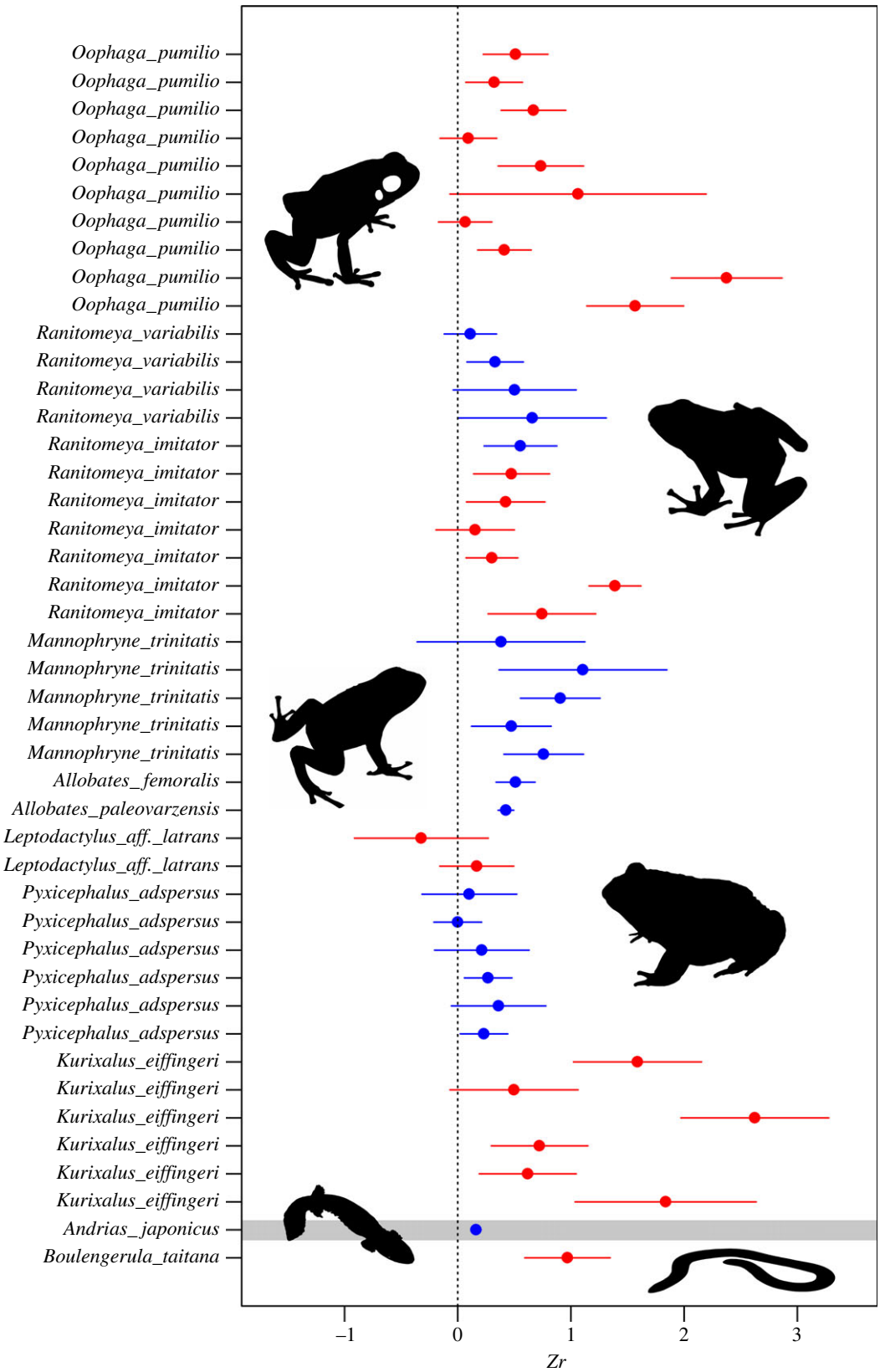

Figure 3. Benefits of parental care in terms of development and survival of juveniles and tadpoles. Effect sizes are shown as *Zr* values (with 95% confidence intervals); positive values indicate that parental care increases offspring performance, whereas negative values indicate that parental care decreases offspring performance. Frogs: 9 species; salamanders (in grey): 1 species; caecilians (bottom): 1 species. Blue: males; red: females. All images are licensed under Creative Commons Attributions (CC0 1.0; from the top to the bottom): 于川云 (Chuanxin Yu); Margot Michaud; Steven Traver; Chuanxin Yu; José Carlos Arenas-Monroy.

figure 3). We found no publication bias ($Zr_{intercept} = 0.05 \pm 0.10$ s.e., $t = 0.53$, $p = 0.60$), data heterogeneity is high ($I^2 = 95.45\%$) and phylogeny poorly explains data variation (phylogeny: <0.01%; study identity: 53.25%; effect size identity: 42.19%).

(c) Non-reproductive costs: body condition

Across amphibians, parental care has a mean negative effect on the body condition of parental individuals ($Zr = -0.24$, 95% CI = −0.44 to −0.03; $p = 0.02$; effect sizes: 68; species: 15). The magnitude of the costs does not differ whether parental

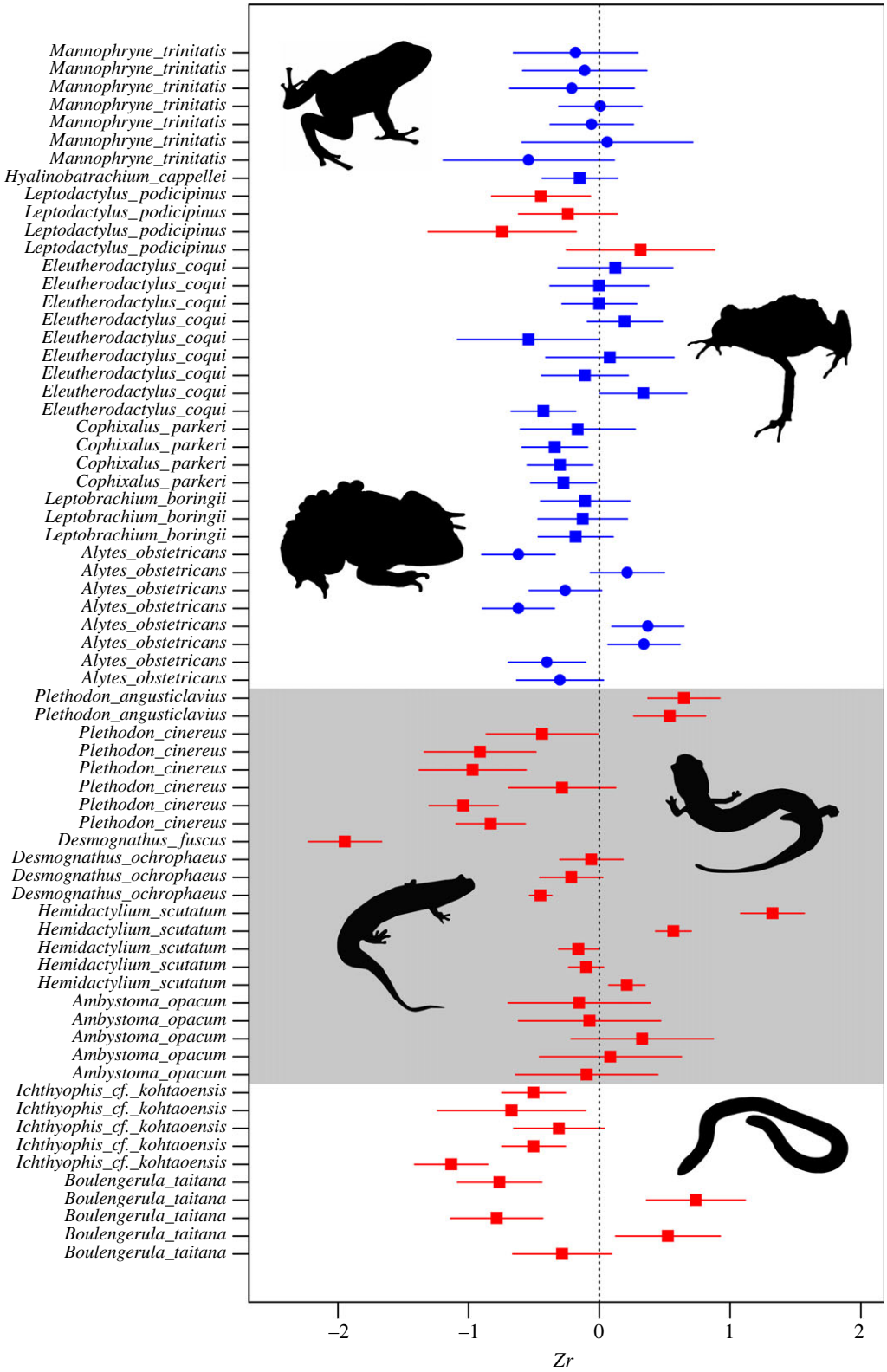

Figure 4. Non-reproductive costs of parental care across amphibians. Effect sizes are shown as *Zr* values (with 95% confidence intervals); negative values indicate that parental care incurs a reduction in body condition, whereas positive values indicate that parental care incurs an increase in body condition. Frogs: 7 species; salamanders (in grey): 6 species; caecilians (bottom): 2 species. Blue: males; red: females. Circles: parents are mobile during parental care; squares: parents are stationary during parental care. All images are licensed under Creative Commons Attributions (CC0 1.0; from the top to the bottom): Steven Traver; Beth Reinke; Beth Reinke; José Carlos Arenas-Monroy.

individuals are stationary or mobile ($p = 0.77$; figure 4). However, parental care reduces the body condition only when parents are stationary, as the mean effect size is negative, and the confidence interval does not overlap zero (mean = −0.26, 95% CI = −0.49 to −0.02, effect sizes: 53, species: 13). When parents are mobile, the mean effect size is also negative, but the confidence interval overlaps zero (mean = −0.17, 95% CI = −0.66 to 0.31, effect sizes: 15, species: 2). The magnitude of the costs is not sex dependent (females: −0.29, 95% CI = −0.56 to −0.02, effect sizes: 36, species: 9; males: −0.16, 95% CI = −0.50 to 0.18, effect sizes: 32, species: 6; $p = 0.57$; figure 4). We found no publication bias ($Zr_{\text{intercept}} = 0.03 \pm 0.08$ s.e., $t = 0.45$; $p = 0.65$), data heterogeneity is high ($I^2 = 93.64\%$) and phylogeny poorly

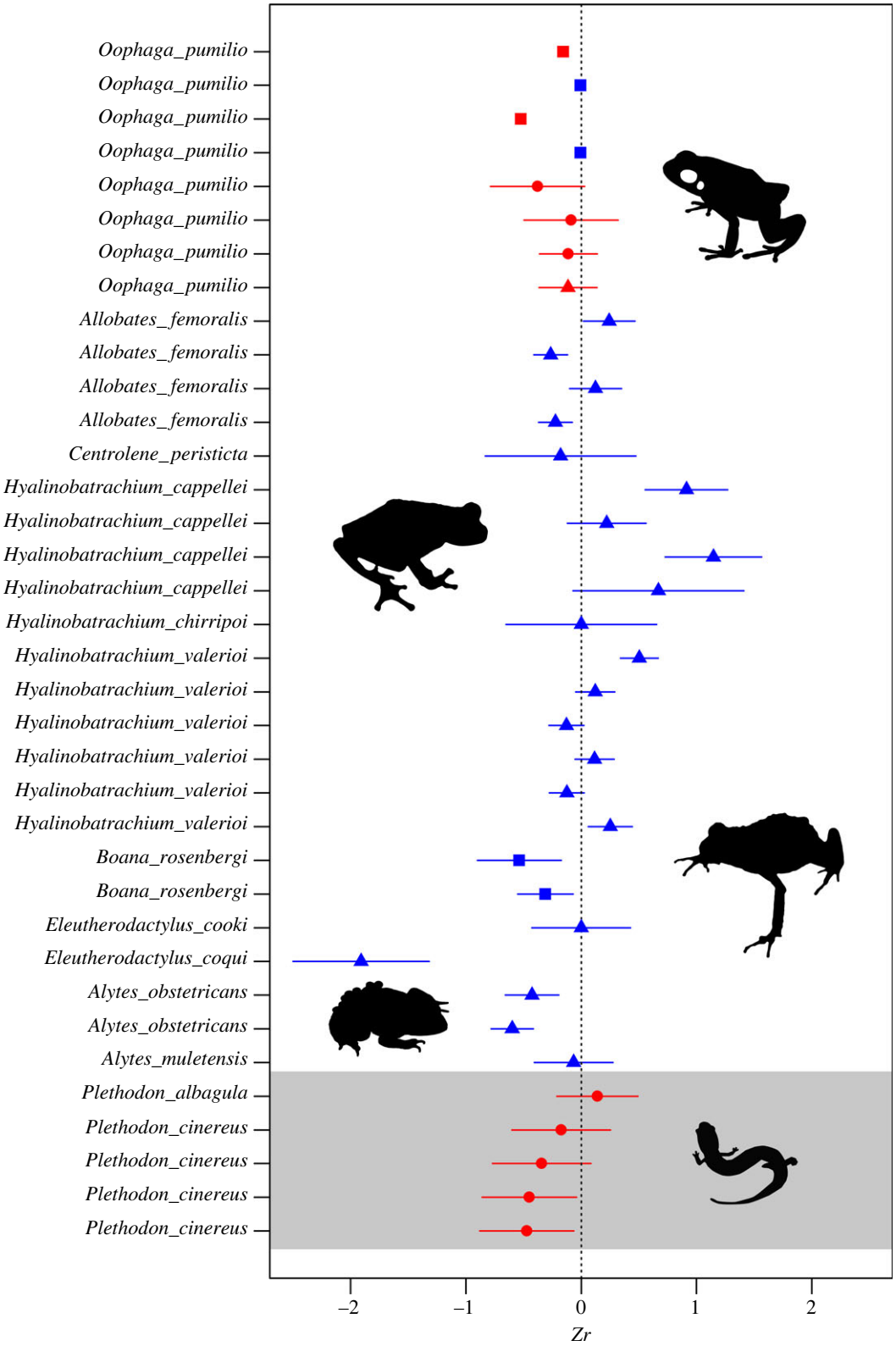

Figure 5. Reproductive costs of parental care across amphibians. Effect sizes are shown as *Zr* values (with 95% confidence intervals); negative values indicate that parental care imposes reproductive costs to the parents, whereas positive values indicate that parental care incurs reproductive benefits to the parents. Frogs: 11 species; salamanders (in grey): 2 species. Blue: males; red: females. Circles: future fecundity; squares: time out; triangles: mating success. All images of amphibian individuals are licensed under Creative Commons Attributions (CC0 1.0; from the top to the bottom): 于川云 (Chuanxin Yu); José Carlos Arenas-Monroy; Beth Reinke.

explains data variation (phylogeny: <0.01%; study identity: 60.96%; effect size identity: 32.68%).

(d) Reproductive costs

When considering all species, regardless of the caring sex, parental care incurs no clear reproductive costs ($Zr = -0.29$, 95% CI = −2.21 to 1.63; $p = 0.77$; effect sizes: 36; species: 13). However, when considering each sex separately, there is a non-significant tendency that females pay higher costs than males (females: −0.46, 95% CI = −2.25 to 1.34, effect sizes: 11, species: 3; males: −0.16, 95% CI = −1.95 to 1.63, effect sizes: 25, species: 11; $p = 0.06$; figure 5). While

we obtained estimates from various amphibian taxa, most of our estimates come from anurans (85.3%). In addition to the taxonomic bias, when it comes to the magnitude of reproductive costs, we found a possible publication bias ($Zr_{intercept} = 0.21 \pm 0.09$ s.e., $t = 2.31$, $p = 0.03$), with fewer than expected low negative values and small sample sizes. Data heterogeneity is high ($I^2 = 99.88\%$), and phylogeny explains much of the data variation (phylogeny: 97.90%; study identity: 0.47%; effect size identity: 1.52%; electronic supplementary material, table S4).

4. Discussion

In this study, we used a meta-analytical approach to investigate the benefits and costs of parental care in amphibians. First, we asked if egg attendance increases offspring survival and whether this benefit is influenced by the caring sex. We found that both male and female parents increase egg survival. Additionally, we examined if the effect of parental care on egg survival is dependent on the type of breeding site and found similar egg survival in concealed and exposed sites. The third question focused on survival and growth experienced by tadpoles and juveniles. Parental care increases offspring survival and growth, but this positive effect does not depend on the caring sex. Moreover, we explored if parental care incurs non-reproductive costs. Irrespective of the caring sex, parental care decreases the body condition of the parents. The negative effect of parental care on body condition is more pronounced when parents remain stationary near the offspring during embryonic development or until tadpole or juvenile dispersal. Finally, we explored reproductive costs, and our results suggest that females tend to experience higher costs than males. To enrich the discussion of these patterns, we will draw comparisons with two recently published meta-analyses—one focused on arthropods [46] and another on fish [16]—which also investigated the benefits and costs of parental care. Just like in those two meta-analyses, our dataset includes quantitative information for a limited number of species. Although it is not possible to determine if our results can be extrapolated to all amphibians with parental care, they represent the state of the art on the subject.

The finding that egg attendance increases egg survival in amphibians is similar to findings in egg-tending arthropods [46]. However, parental care in fish does not increase offspring survival [16]. We obtained data on egg survival from 32 species, and all of them lay eggs in non-aquatic habitats (e.g. bamboo stumps, cave crevices, leaf litter, rock shore and vegetation). The prevailing explanation for the evolution of terrestrial and arboreal oviposition in amphibians is that eggs and early hatched larvae in non-aquatic habitats are more protected from predation by aquatic organisms [27,47]. Although eggs laid in non-aquatic habitats are also vulnerable to predators, high offspring survival can be achieved through terrestrial and arboreal oviposition coupled with parental care [23,27,28], as demonstrated in our study. This same reasoning can be applied to arthropods, as 44 out of 45 species included in the meta-analysis lay eggs in non-aquatic habitats [46]. By contrast, in fish, it appears that even with parental protection, high predation pressure in aquatic habitats negates the benefits of parental care on offspring survival. Alternatively, taxonomic differences in the benefits of egg attendance could be attributed to filial cannibalism, which is widespread in fish [48] but has been rarely reported in the meta-analyses of arthropods (1 out of 45 species [46]) and amphibians (6 out of 32). The consumption of eggs for clutch sanitation, improving body condition and sustaining parental activities leads to a decrease in clutch size, which can obscure the positive effects of egg protection in fish [16], but not in arthropods and amphibians.

The benefits of egg attendance in amphibians do not depend on the caring sex. This comparison has not been made in previous meta-analyses, and only a few studies compared the efficiency of uniparental egg protection provided by females or males [6–9]. In all these studies, the benefits of egg attendance are not sex dependent. Given that egg attendance is a simple form of parental care involving protective behaviours that can be performed by males and females [49], it makes sense that both sexes are equally efficient in increasing egg survival. Our findings also show that the benefits of egg attendance are not dependent on the type of breeding site. A comprehensive comparative study has found that the emergence of both male and female egg attendance in amphibians is associated with egg deposition in concealed sites [29]. There are two non-mutually excluding hypotheses to explain this association: (i) eggs laid in exposed sites may be easier for predators to find [23,28] and (ii) concealed sites may decrease parental mortality imposed by predators [29].

While originally proposed to elucidate evolutionary transitions between non-care and egg attendance in amphibians, hypothesis (i) can also be employed to compare the benefits of egg attendance in terms of egg survival. According to this hypothesis, when parents are experimentally removed from their clutches in an exposed site, egg mortality should be higher, as eggs are more visible to predators and are likely more exposed to dehydration. Conversely, when parents are removed from their clutches in a concealed site, egg mortality should be lower, as eggs are better protected from predation and dehydration. Thus, considering that protection against predation and dehydration are the two main benefits of egg attendance in amphibians [8,23,28,32], the magnitude of the benefit conferred by parental presence should be greater for species that lay eggs in exposed sites. However, the results of our meta-analysis do not support this prediction. The absence of a difference between the two types of breeding sites may be partially explained by the identity of the egg predators. If the primary predators are not visually oriented, such as certain snakes, arthropods and leeches (see references in [23]), eggs in exposed sites should not experience higher predation rates than those in concealed sites. Moreover, if parents select oviposition sites with suitable abiotic conditions (e.g. [8,50,51]), eggs should not be at a greater risk of dehydration. Although our results offer insights into the role of the type of breeding site in influencing the benefits of egg attendance, it is important to emphasize that we lack quantitative information to test whether egg concealment in terrestrial and aquatic habitats can still increase egg survival in *non-caring* species. This is an open question that deserves attention in future experimental studies.

Parental care in amphibians also increases survival and growth of tadpoles and juveniles. Our dataset includes frog species in which parents attend tadpoles, transport them to suitable sites for development and provide trophic eggs. Additionally, one caecilian species has juveniles that feed on the mother's skin. When offspring require constant parental

assistance in early stages (as observed in certain arthropods, many birds and all mammals), the absence of parents usually leads the young to death by predation, dehydration or starvation [3,4,52]. For instance, in most frog species in which females feed the offspring with trophic eggs, tadpoles grow in small ponds or phytotelma with limited food availability and intense intraspecific competition. In such circumstances, continuous food provisioning by females is crucial for offspring development [30]. Female caecilians are also solely responsible for juvenile feeding, an intermediate stage in the evolution of viviparity [26,53]. Juveniles that feed on mother's skin and those born from viviparous species attain independence at a larger size, potentially reducing their mortality risk [53]. Other forms of parental care in our dataset can be performed by both sexes [27,28], such as tadpole transport. Despite the low taxonomic representativeness of the species analysed, our results show similar overall benefits provided by females and males. This finding aligns with our previous results on egg attendance and suggest that both sexes effectively increase the performance of tadpoles in juveniles.

We used body condition to assess short-term non-reproductive costs associated with reduced food intake and/or increased energy expenditure during the caring period [5]. Our measures are similar to those used in the fish meta-analysis [16], albeit only amphibians exhibit a decrease in body condition during the caring period. We hypothesize that the trade-off between parental care and foraging is more intense in amphibians, regardless of the caring sex. During the caring period, parents of fish can feed on various food items (e.g. zooplankton, phytoplankton, benthic invertebrates, algae and weeds growing close to the nests) without leaving the offspring unattended. Among the 19 species included in the fish meta-analysis, at least 15 feed on these items [16], which may explain why parental care does not compromise their condition. By contrast, egg, juvenile and tadpole attendance—the most common forms of parental care in our dataset—constrain the foraging opportunities of the parents (females or males) and impact their body condition. In fact, we found that forms of parental care in which parents remain stationary close to their eggs, juveniles or tadpoles impose an average negative effect on body condition while there is no average negative effect in forms of parental care in which parents are mobile, such as egg or juvenile brooding and tadpole transport or feeding. Thus, we propose that a marked reduction in foraging opportunities while caring for the offspring at a fixed location may explain why parental care negatively affects body condition in amphibians (and also certain arthropods [13,54]), but not in fish (see exceptions in [16,55]).

We found no reproductive costs when considering both sexes collectively, although there was a marginally significant trend suggesting that females may face higher costs than males. However, due to the limited sample size of only 3 species (1 frog and 2 salamanders) for quantifying female reproductive costs, the implications of our findings are certainly constrained. In the case of males, our sample size is larger, encompassing 11 frog species, which is the same number included in the fish meta-analysis examining the relationship between paternal care and male reproductive success [16]. Among the 25 effect sizes we obtained, 13 are negative (6 of them with 95% CI overlapping zero), while 11 are positive (6 of them with 95% CI overlapping zero). This pattern suggests two distinct response groups: one in which paternal care incurs reproductive costs (negative values) and another in which paternal care provides reproductive benefits (positive values). Given the even distribution of effect sizes across these two groups, the mean effect size for males approaches zero. Notably, some of the highest costs in our dataset are observed in species in which males carry eggs attached to their body (*Alytes obstetricans* [56]), limiting or even precluding the males from acquiring multiple clutches. Additionally, species in which males cease sexual advertisement while caring for the eggs (*Eleutherodactylus coqui* [57] and *Boana rosenbergi* [58]) also pay high reproductive costs. Conversely, greater benefits arise when parental care is a sexually selected trait, enhancing the attractiveness of parental males to females, as documented for arthropods [17] and fish [16]. Examples in our dataset include *Hyalinobatrachium capellei* [18] and *H. valerioi* [59]. Taken together, these findings reinforce the understanding that parental care may or may not entail reproductive costs for males [19,20].

In conclusion, our study demonstrates the beneficial effects of parental care on the survival and development of eggs, juveniles and tadpoles in amphibians. These benefits are consistent regardless of the caring sex or the type of breeding site (in the case of egg attendance). Given that our dataset on the benefits of egg attendance encompasses numerous species from diverse lineages in which parental care has independently evolved [26], we propose that these patterns may be widespread among amphibians. Despite the benefits, parental care results in a reduction in the body condition of both parents, and this negative effect is more pronounced when parents remain stationary in proximity of their offspring compared to when they have the possibility to move around and search for food. This finding suggests a trade-off between caring and foraging, as previously reported for some arthropods. However, the link between this short-term cost and the long-term fitness of parents remains largely unexplored in amphibians (but see [60]). Lastly, our understanding of the evolution of paternal care would greatly benefit from studies exploring the interplay between natural selection, which increases offspring fitness, and sexual selection, which increases reproductive success for parents. Currently, this aspect of amphibian biology is still understudied and warrants further investigation.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data and R code supporting this article are included in the electronic supplementary material [61].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. G.M.: conceptualization, investigation, methodology, project administration, validation, visualization, writing—original draft, writing—review and editing; R.C.M.-R.: data curation, formal analysis, methodology, validation, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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