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Parental care and the evolution of terrestriality in frogs

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Frogs and toads (Anura) exhibit some of the most diverse parental strategies in vertebrates. Identifying the evolutionary origins of parenting is fundamental to understanding the relationships between sexual selection, social evolution and parental care systems of contemporary Anura. Moreover, parenting has been hypothesized to allow the invasion of terrestrial habitats by the ancestors of terrestrial vertebrates. Using comprehensive phylogenetic analyses of frogs and toads based on data from over 1000 species that represent 46 out of 55 Anura families, we test whether parental care is associated with terrestrial reproduction and several life-history traits. Here, we show that both the duration of care and offspring protection by males and females have coevolved with terrestrial reproduction. Sexual size dimorphism is also related to care, because the large male size relative to female size is associated with increased paternal care. Furthermore, increased egg size and reduced clutch volume are associated with increased care in bivariate but not in multivariate analyses, suggesting that the relationships between care, egg size and clutch volume are mediated by terrestrial reproduction. Taken together, our results suggest that parenting by males and females has coevolved, and complex parenting traits have evolved several times independently in Anura in response to breeding in terrestrial environments.

1. Introduction

Parental care is a highly diverse social behaviour that has evolved to increase offspring survival, although it tends to be costly to the care giving parent [1–3]. Frogs and toads (Anura, hereafter frogs) are characterized by a remarkable diversity of care [4,5] that is rivalled among vertebrates only by the older and more speciose bony fishes [6]. Approximately 10–20% of extant frog species exhibit parental behaviour, with the duration of care, the sex of the care provider and the type of care all showing unique diversity and phylogenetic plasticity [5,7,8].

Understanding the evolutionary origin and maintenance of frog reproductive diversity is important for understanding the adaptive significance of parental care both on evolutionary and ecological time scales. Firstly, parental care tends to increase offspring survival especially in hostile environments [9,10], and thus, it may have played a key role in the colonization of terrestrial habitats, i.e. not only in the evolution of recent amphibians but also in early tetrapods, opening the way to the subsequent radiation into terrestrial niches [11]. Because parenting is one of the traits linked to expansion into non-aquatic niches [12,13], identifying correlates of care in extant taxa will help us to understand major transitions such as the occupation of terrestrial niches by

early tetrapods. Secondly, parental care is an ideal system to understand interactions between individuals that have been extensively investigated in experimental and game-theoretic analyses of social interactions [14–16]. Because parenting influences offspring survival and reproduction, parental decisions often impact on reproductive success and population dynamics [14]. Third, phylogenetic comparative analyses are important to uncover ecological and life-history predictors of parenting: they add a time axis to social interactions and link ecological and evolutionary time scales [8,17,18], although these studies rarely cover a whole order of organisms (but see [19,20]).

Frog parental care is immensely diverse, and it includes simple types of care such as constructing a foam nest or attending the eggs, as well as more elaborated forms such as internal brooding of offspring [4,5,12], or cooperation between parents to attend and provide food for the growing offspring [18]. Reproductive modes, i.e. the variation in nesting sites and the environment where tadpoles develop, are also linked to care [5,7,21], although it is not clear whether these associations hold for different care types, e.g. male-only, female-only and/or biparentally caring species, or are relevant only at certain stages of reproduction [13].

Terrestrial environments are hostile for anamniotic eggs, given the high risks of desiccation and exposure to diseases, parasites and predators although predation risk tends to be high in aquatic environments as well. Therefore, egg attendance and egg protection, including urination on the eggs to keep them moist, may considerably increase offspring survival in terrestrial environments [10,22]. In addition, several frogs show extensive post-hatch care by carrying the tadpoles (or froglets) on their backs or in specialized brooding organs [21,23]. Terrestrially reproducing frogs may have endotrophic larvae that develop in a protected chamber, or directly developing embryos which skip larval phase and hatch as fully developed froglets [5,13]. These offspring rely upon parental provisions until they reach the next stage of their development (e.g. metamorphosis, hatching or birth). Consequently, anurans may enhance offspring care by extending the duration of care, by providing more protection for the offspring and/or by increasing nutrient provisioning in nutrient-scarce environments. These behaviours enable the offspring to spend a longer period of their development in a safe place [18,24,25].

Here we investigate three hypothesized drivers of parental care. We focus on the evolution of care by scoring aspects of care on a finer scale and, to our knowledge, we present the most detailed phylogenetic analyses of parenting in any major taxa. First, we test whether terrestrial versus aquatic reproduction relates to different care types, since caring is expected to provide protection against hostile environments [5,10,13]. Second, we investigate whether life-history variables including egg size and clutch size correlate with the duration of care, protection and nourishment provided by any of the parents. Specifically, we hypothesize that large eggs are associated with longer care and more protection than small eggs [1,5,26]. Third, sexual selection has been linked to parental care since Trivers' [27] seminal idea (reviewed by [1,9,28]), therefore we also investigate whether intense sexual selection is associated with reduced care provisioning [29–31]. We use sexual size dimorphism (SSD) as a proxy for the intensity of sexual selection [30,31]. Note that SSD as an indicator of sexual selection has been debated in

frogs, since SSD may reflect selections acting on females, e.g. to increase fecundity [32–34]. Nonetheless, large size in males is associated with high reproductive success in several species of frogs (reviewed by [5,35]) owing to competition for mates or female choice [36–39], with the latter processes being clearly linked to sexual selection.

To address these objectives, we use a comprehensive dataset that represents 46 out of 55 extant anuran families. We analyse three main components of care: duration of care, protection of eggs and/or offspring, and nutrient transfer to offspring. We consider these separately, because complex social traits such as caring may have multiple components that evolve independently, or traded off against each other and thus respond to different selection pressures [40–43]. Second, instead of combining male-only care, female-only care and biparental care into a single variable (for instance, presence or absence of care by either parent), we treat care by males and females separately, since ecological and life-history variables may exert stronger effects on one sex than on the other. For instance, a reproductive effort such as egg size and clutch volume may be an important constraint of female care, whereas the intensity of sexual competition may be an important constraint of male care [8,42,43]. Our work demonstrates that these distinctions are important since some of the relationships between care components and ecological and life-history variables differ between males and females.

2. Material and methods

(a) Data collection

We compiled the initial dataset from comprehensive phylogenetic comparative publications which contain information on parental care in frogs [8,13,18,26,42,44,45]. Next, we augmented this dataset with data from primary research publications (electronic supplementary material, S3 supplementary data), online databases [46,47] and peer-reviewed books [5,48,49]. Our final database holds information from 1044 species; 399 of these species exhibit some form of care. Forty-six of 55 Anura families are represented in our database that holds approximately 95% of extant species (electronic supplementary material, table S1).

(b) Parental care variables

We used four variables for coding parental care. First, type of care was scored on a five-point scale: 0—no care; 1—male-only care; 2—female-only care; 3—biparental care; 4—care either by the male or the female. Because the latter (i.e. uniparental care either by male or female) was reported only from seven species, we excluded these species from the analyses. We considered biparental care if both parents participate in offspring care. In the analysis of the number of care-providing parents, male-only care and female-only care (scores 1 and 2) were combined as uniparental care, whereas score 3 was kept as biparental care.

Second, we scored the duration of care based on discrete ontogenetic stages of the offspring (egg, tadpole and juvenile care) and recorded the most advanced stage when a particular caring behaviour has been reported. Care duration was defined as 0—no care; 1—egg care; 2—tadpole care; 3—juvenile care. Care duration was scored separately for males and females.

Third, we scored offspring protection as a separate variable on a six-point scale: 0—no protection; 1—offspring protected in a nest but not attended by parent(s); 2—parental attendance; 3—carrying on the back of parent(s); 4—carrying in a closed organ (brooding pouch, dermal invagination, stomach or vocal

sack) of parent(s); 5—viviparity. This scoring was based on the logic that protection is more effective when eggs or offspring are enclosed (e.g. in a brooding pouch, stomach, vocal sac, skin invagination) rather than exposed on the back of the parent(s). The highest level of protection appears to be in viviparous species because in these species, the offspring only leave the reproductive tract of the mother in a well-developed stage. Protection was scored separately for males and females.

Fourth, nourishment was categorized as follows: 0—exotrophic tadpoles feed mainly on external food sources after depleting their yolk provided in the egg; 1—feeding tadpoles by trophic eggs or skin secretion; 2—endotrophic tadpoles and directly developing species (which complete metamorphosis inside the egg) reach metamorphoses nourishing only upon the egg's yolk. Nourishment was only provided by the female except in two species in which the males provision the offspring (*Ecnomiohyla rabborum*, *Rhinoderma darwini* [5,50]). Consequently, the latter two species were excluded from the analyses of nourishment.

In order to investigate the consistency of our parental care scores with three published datasets that scored parenting as a binary variable (presence/absence) [13,26,44], we calculated the correlations between these four datasets. The association between our dataset and the three independent datasets were highly significant (electronic supplementary material, table S2).

(c) Life-history variables

Egg size was defined as the diameter of the egg (vitelline) in millimetres, excluding the gelatinous capsule. Clutch size was defined as the number of eggs laid during one egg-laying event. We use clutch volume (calculated as egg volume in cm^3 multiplied by clutch size) instead of clutch size in bivariate analyses, because clutch volume appears to be a more appropriate indicator of female reproductive expenditure than clutch size alone. However, to separate the potential effects of egg size and clutch size in multivariate analyses, we included egg size and clutch size in the models. Snout-vent length (SVL) was calculated separately for males and females, computed as mean values across all available data for a given species. Body size (mean SVL) was calculated as the average of male and female SVLs (in mm) for each species, whereas SSD was $\log_{10}(\text{SVL}_{\text{male}}/\text{SVL}_{\text{female}})$. Clutch size, clutch volume and egg size were transformed to a logarithmic scale to ensure homoscedasticity. If several data points were available for a given species, we calculated their arithmetic mean.

Terrestrial reproduction and direct development were treated as binary variables (present or absent), following previous classifications [13,21]. Terrestrial reproduction included floating foam nest on water, as in this case the eggs themselves are included in an air-filled chamber, and also viviparity and egg-brooding in different organs (pouches, stomach, vocal sac) provided by terrestrial parents. By contrast, members of the genus *Pipa* which lay eggs in water and broods by aquatic parents were considered aquatic breeders. We established these categories because anuran eggs are adapted primarily to aquatic development and placing them outside water exposes them to hostile conditions, and we considered the strategy for this challenge as an important aspect of parental care.

(d) Phylogeny

We used a comprehensive amphibian phylogenetic tree (the consensus tree from [51]) which included the majority of species in our database. Archaeobatrachians were treated as all anurans outside the Neobatrachia clade, and basal Neobatrachians as all Neobatrachians outside the Hyloidea and Ranoidea clade (figure 1; electronic supplementary material, figure S1). In

figure 1*a–c*, we used Grafen-transformed branch lengths for better visualization.

Anuran phylogenies tend to hold consistent patterns, at least in the topology of deeper nodes [51,52]. Because most variation in care is between genera and families, our results appear to be robust to different phylogenetic hypotheses. Nonetheless, to check the sensitivity of our results to alternative phylogenies, we re-analysed the major models using an alternative tree: a composite tree based on [53]. We augmented the latter tree [53] with 145 additional species inserted next to their closest species (whenever known), based on recent phylogenetic information. Nodes were collapsed to polytomies when no further information was available on the phylogenetic relationships within a genus. The species we added manually are listed in the electronic supplementary material, table S7, along with the references for their phylogenetic relationships. We use the branch lengths of the original trees [51,53]. In composite phylogeny, we assumed half branch length for the new species we included using 'phytools' package [54] in R v. 3.1.0 [55]. Importantly, the results using the alternative phylogeny were highly consistent with those of the main phylogeny (table 1; electronic supplementary material, tables S3–S6).

(e) Comparative analyses

We tested associations between parental care and life-history variables using phylogenetic least squares (PGLS) [56–58]. This approach controls for the non-independence among species by incorporating a variance–covariance matrix that represents their phylogenetic relationships. All analyses incorporated phylogenetic dependence by estimating Pagel's λ [58]. We built separate multi-predictor PGLS models for each parental care variable (i.e. care duration by females, care duration by males; protection by females, protection by males, nourishment by females) in which one of the care variables was the dependent variable, and log clutch size, log egg size, average SVL, sexual dimorphism, terrestrial reproduction and direct development were the predictors.

We also included the higher nodes (i.e. superfamily identity, see the electronic supplementary material, S2) as a factor in PGLS models [53,59]. This was to control for the lack of variation in key traits within higher taxa: for traits that do not vary within higher nodes, the effective level of replication and appropriate degrees of freedom can be questioned. Owing to the lack of variation within clades, three species-poor lineages ('Crown Hyloidea' that includes Alsodidae, Ceratophryidae, Hylodidae, Odontophrynidae and Rhinodermatidae, 12 species in total; Heleophrynidae, two species; and Sooglossioidea, three species) were excluded from analyses that included higher node as factor. Higher nodes were not included in analyses on trophic egg feeding (nourishment excluding species in nourishment category 2)—in this case, most of the clades showed little variance to the trait.

We tested multicollinearity between predictors using the variance inflation factor (VIF) analysis: all predictors had VIF values of less than 5 ($\text{VIF}_{\text{max}} = 2.02$). In multiple regression models, we included six predictor variables (table 1) except in models of nourishment we did not include developmental mode because nourishment and developmental mode were correlated by definition. All analyses were carried out using R v. 3.1.0 [55] with the 'caper' package [60].

3. Results

Types of care varied across Anura, with each type of care occurring in several clades (figure 1; electronic supplementary material, table S1). Major clades exhibited substantial variations in sex of care provider, protection and nourishment (figure 1): exceptional diversity was exhibited by five

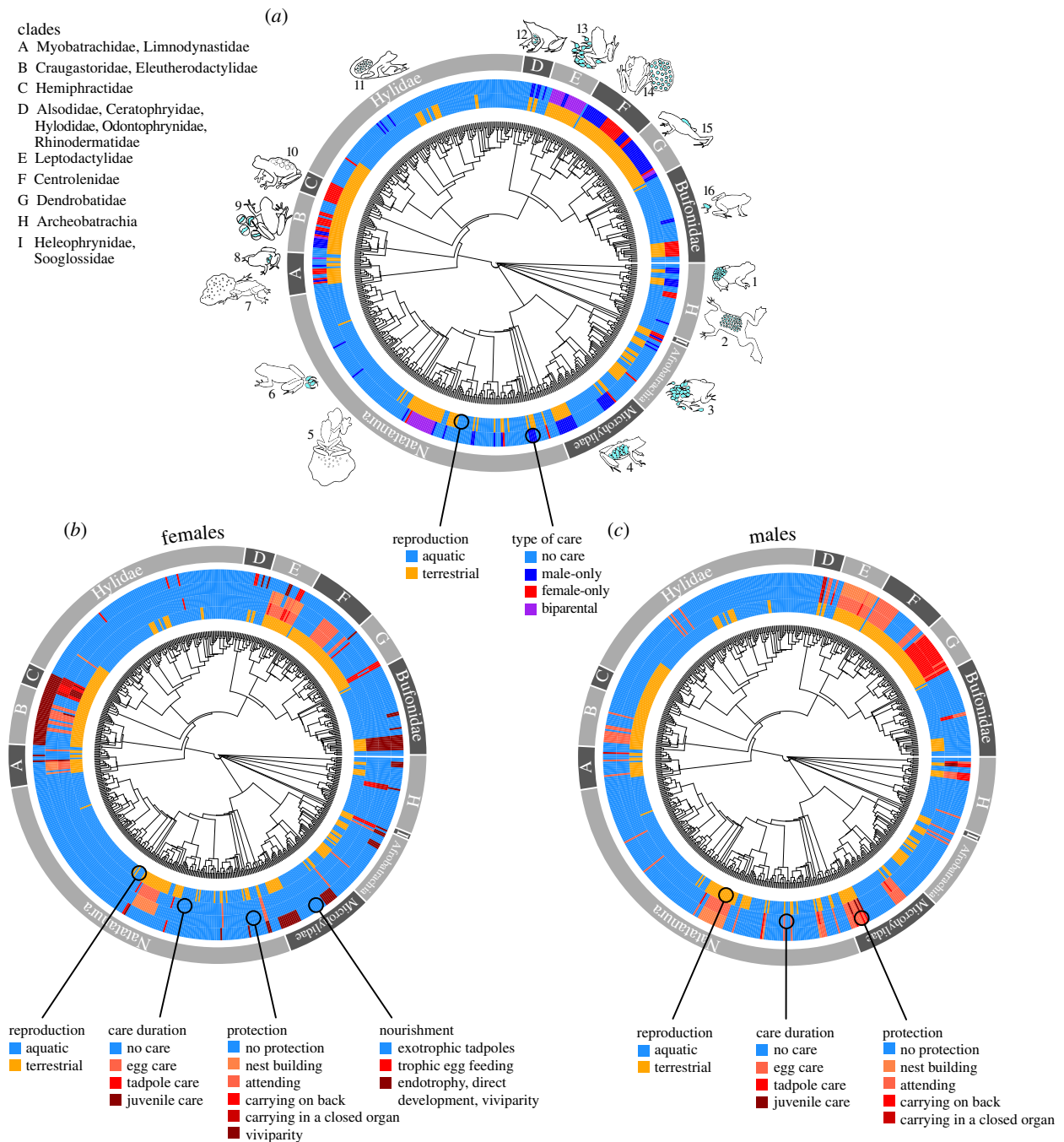


Figure 1. Phylogenetic distribution of parental care and breeding habitat in frogs. (a) Type of care (592 species). (1) Alytidae (*Alytes* sp., male egg transport), (2) Pipidae (*Pipa* sp., eggs embedded in the dorsal skin of female), (3) Hemisotidae (*Hemisus* sp., tadpole guarding by the female), (4) Microhylidae (*Sphenophryne cornuta*, juvenile transport by the male), (5) Rhacophoridae (*Rhacophorus* sp., foam nest made by both parents), (6) Dicroglossidae (*Limnonectes larvaepartus*, viviparity: live birth to larvae), (7) Limnodynastidae (*Limnodynastes peronii*, foam nest made by the female), (8) Myobatrachidae (*Assa darlingtoni*, male carry tadpoles in inguinal pouches), (9) Eleutherodactylidae (*Eleutherodactylus coqui*, direct developing eggs guarded by the male), (10) Hemiphractidae (*Flectonotus* sp., eggs carried in dorsal pouch of the female), (11) Hylidae (*Hypsiboas boans*, male guard eggs in constructed mud pool), (12) Rhinodermatidae (*Rhinoderma darwini*, tadpoles reared in vocal sac of the male), (13) Leptodactylidae (*Leptodactylus podicipinus*, the pair constructs the foam nest, the female guards the tadpoles), (14) Dendrobatidae (*Ranitomeya imitator*, the male transports tadpoles, the female feeds tadpoles in cooperation with the male), (16) Bufonidae (*Nimbaphrynoides* sp., viviparity: live birth to toadlets). (b) Diversity of female care (care duration, protection and nourishment, 594 species). (c) Diversity of male care (care duration and protection, 593 species). Grafen-transformed branch lengths are shown.

clades that include Eleutherodactylidae, Dendrobatidae, Leptodactylidae, Rhacophoridae and Microhylidae (electronic supplementary material, figure S1).

Care duration, protection and nourishment were not different between species with female-only care, male-only care and biparental care (PGLS, care duration: electronic supplementary material, figure S2, $F_{2,379} = 0.716$; $p = 0.489$; protection: $F_{2,375} = 0.502$; $p = 0.610$; nourishment:

$F_{2,370} = 0.502$; $p = 0.426$), nor between uniparental and biparental species (PGLS, care duration: $F_{1,387} = 0.415$; $p = 0.520$; protection: $F_{1,382} = 0.788$; $p = 0.375$; nourishment: $F_{1,378} = 1.694$; $p = 0.194$). Thus, males and females provide similar extents of care in anurans. Interestingly, the extent of parental care by males was associated with the extent of female care both in care duration (PGLS; $F_{1,1006} = 8.674$; $p < 0.0001$) and protection ($F_{1,1005} = 54.58$; $p < 0.0001$).

Table 1. Parental care in relation to ecology, life-history and sexual dimorphism in Anura using phylogenetically corrected generalized linear squares (PGLS) models. (Multi-predictor PGLS models for each care variable are provided separately for males and females; note that only females provide nourishment. Higher node was included in the models except for nourishment (see Material and methods). Italics indicate significant predictors. Egg size is provided as diameter in mm. Clutch volume is calculated as egg volume \times clutch size and provided as mm³. Clutch volume and egg size were log-transformed prior to the analyses. Body size refers to the average snout-vent length (SVL) in mm. Sexual size dimorphism was calculated as $\log_{10}(SVL_{\text{male}}/SVL_{\text{female}})$. We provide parameter estimates with standard error ($\beta \pm \text{s.e.}$), the corresponding t and p -values and the adjusted R^2 for the model including $F(\text{d.f.}_{\text{effect}}, \text{d.f.}_{\text{error}})$ and p -values, respectively.)

care duration	by females			by males		
	$\beta \pm \text{s.e.}$	t	p -value	$\beta \pm \text{s.e.}$	t	p -value
terrestrial reproduction	<i>0.227 ± 0.103</i>	2.209	<i>0.028</i>	<i>0.278 ± 0.093</i>	3.000	<i>0.003</i>
direct development	-0.386 ± 0.224	1.721	0.087	-0.015 ± 0.197	0.077	0.938
clutch size	0.007 ± 0.056	0.130	0.897	-0.006 ± 0.053	0.110	0.913
egg size	0.011 ± 0.177	0.061	0.951	0.009 ± 0.166	0.052	0.959
body size	-0.001 ± 0.001	0.407	0.685	0.002 ± 0.001	1.421	0.157
sexual dimorphism	-0.110 ± 0.388	0.282	0.778	<i>1.070 ± 0.376</i>	<i>2.842</i>	<i>0.005</i>
model	0.155	2.961 (18, 175)	0.0001	0.175	3.254 (18, 174)	<0.0001

protection	by females			by males		
	$\beta \pm \text{s.e.}$	t	p -value	$\beta \pm \text{s.e.}$	t	p -value
terrestrial reproduction	<i>0.426 ± 0.137</i>	3.113	<i>0.002</i>	<i>0.414 ± 0.158</i>	2.626	<i>0.009</i>
direct development	0.452 ± 0.295	1.532	0.127	0.086 ± 0.332	0.261	0.795
clutch size	0.045 ± 0.087	0.524	0.601	-0.016 ± 0.097	0.168	0.867
egg size	-0.059 ± 0.285	0.209	0.835	0.084 ± 0.310	0.272	0.786
body size	0.000 ± 0.001	0.038	0.969	0.001 ± 0.002	0.656	0.513
sexual dimorphism	-0.208 ± 0.640	0.325	0.746	<i>2.156 ± 0.701</i>	<i>3.075</i>	<i>0.002</i>
model	0.282	5.231 (18, 176)	<0.0001	0.125	2.539 (18, 176)	<0.001

nourishment	by females			by females excluding species with endotrophic tadpoles, direct development and viviparity		
	$\beta \pm \text{s.e.}$	t	p -value	$\beta \pm \text{s.e.}$	t	p -value
terrestrial reproduction	0.018 ± 0.098	0.186	0.853	0.014 ± 0.055	0.265	0.792
clutch size	<i>-0.180 ± 0.053</i>	3.389	<i><0.001</i>	<i>-0.066 ± 0.030</i>	2.162	<i>0.032</i>
egg size	0.119 ± 0.169	0.706	0.481	<i>-0.195 ± 0.097</i>	<i>2.010</i>	<i>0.046</i>
body size	<i>0.003 ± 0.001</i>	<i>2.043</i>	<i>0.042</i>	<i>0.003 ± 0.001</i>	<i>3.513</i>	<i>0.001</i>
sexual dimorphism	-0.148 ± 0.373	0.398	0.691	0.162 ± 0.347	0.208	0.437
model	0.194	3.781 (17, 179)	<0.0001	0.060	3.283 (5, 174)	0.007

Terrestrial reproduction was a key factor associated with parental care (figure 1). All forms of care were more common in terrestrial taxa than in aquatic ones (figure 2) including protection by males (5.5% and 46.5% of aquatic and terrestrial taxa, respectively), protection by females (1% and 39.0%) and nourishment (5.0% and 34.5%). Terrestrial reproduction was associated with increased levels of care by both males and females (figure 2; electronic supplementary material, table S3). Consequently, the number of caring parents was significantly higher in terrestrial frogs than in aquatic ones (PGLS; $F_{1,591} = 80.47$; $p < 0.0001$).

Large eggs and small clutches were associated with extended parenting and protection by both sexes, and

provisioning by the female (figure 3; electronic supplementary material, table S4). However, since egg size and clutch volume often depend on body size, we also investigated the relationships between egg size, clutch volume and care by including body size as an explanatory variable in phylogenetically corrected models (electronic supplementary material, table S5). When body size was statistically controlled for, neither egg size nor clutch volume remained correlated with care with the exception of nourishment, and small clutch volume remained associated with male care (electronic supplementary material, table S5).

SSD was associated with male care but not female care (electronic supplementary material, table S4 and figure S3).

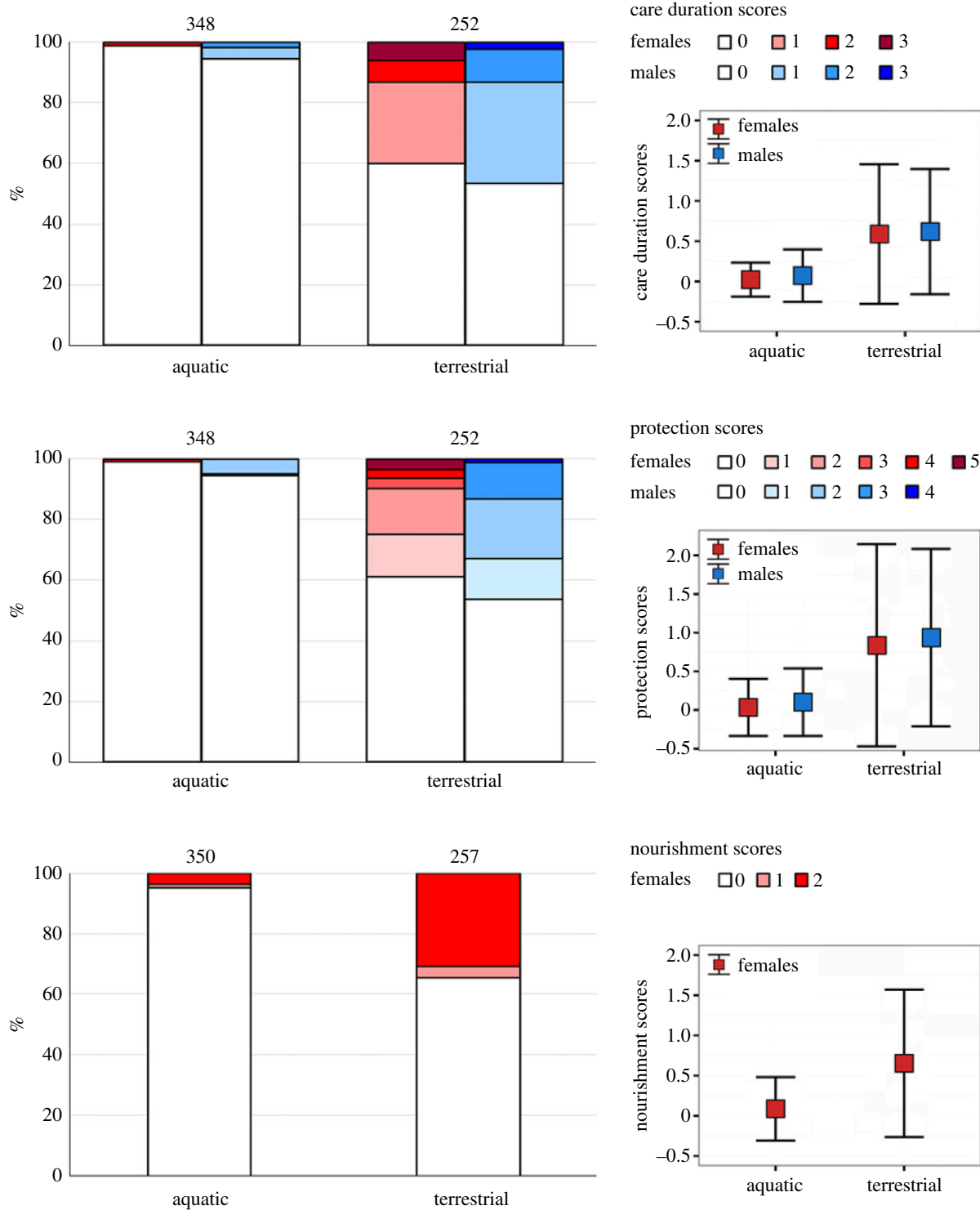


Figure 2. Care duration, offspring protection and nourishment in relation to aquatic and terrestrial reproduction in frogs. Number of species exhibiting different extent of care duration, offspring protection and nourishment (on the left) and the extent of female and male parental care in aquatic and terrestrial species (mean + s.d.; on the right). Red shades represent female care, blue shades represent male care.

However, male care was associated with increased male size relative to female size (electronic supplementary material, table S4). The latter relationship remained significant when absolute body size was controlled for in the analysis (electronic supplementary material, table S5). The latter relationship between size dimorphism and body size suggests that Anura exhibit an allometric relationship between sizes of males and females known as Rensch's rule [44,61] (PGLS; $F_{1,430} = 7.39$; $p = 0.007$).

Terrestrial reproduction remained the main predictor of both care duration and offspring protection in multi-

predictor analyses, but not for nourishment (table 1). These results suggest that the relationships between life history and care we uncovered using bivariate analyses (electronic supplementary material, table S4) may be mediated by terrestrial reproduction. Nevertheless, in multi-predictor models, male-biased size dimorphism remained associated with male care (table 1), and nourishment remained associated with clutch size and body size.

Trophic feeding (i.e. exotrophic tadpoles feed on external food sources versus tadpoles fed by trophic eggs or skin secretion) was associated with sexual dimorphism and clutch

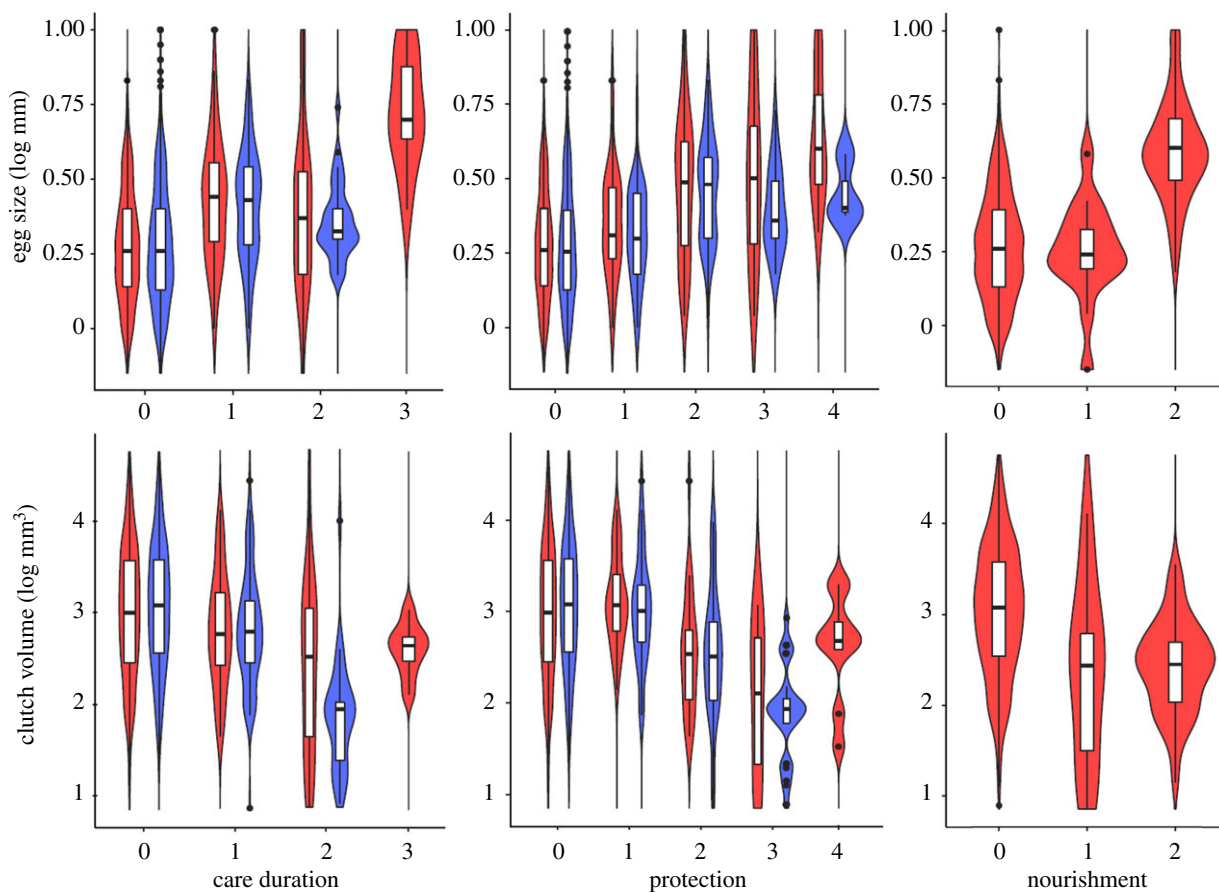


Figure 3. Parental care in relation to life histories in frogs. Egg size and clutch volume are plotted against offspring care, protection and nourishment in females (red) and males (blue, see statistics in the electronic supplementary material, tables S4 and S5). The variables were scored as follows. Care duration: 0—no care; 1—egg care; 2—tadpole care; 3—juvenile care; protection: 0—no protection; 1—nest building; 2—attending; 3—carrying on back; 4—carrying in a closed organ; 5—viviparity; nourishment: 0—exotrophic tadpoles; 1—trophic egg feeding; 2—endotrophic tadpoles, direct development or viviparity.

volume (electronic supplementary material, tables S3 and S4), and these relationships remained significant after controlling for body size (electronic supplementary material tables, S5 and S6).

4. Discussion

Our comprehensive phylogenetic analyses of the extent of male and female care show that care is extremely variable both within and among major clades of frogs. Not only the presence or absence of care varies—that has been uncovered by previous studies [18,26]—but also the type and duration of care are highly variable. In contrast to reptiles and mammals, in which the females are the main care provider, or to birds in which biparental care is the predominant form of care [9,62], in frogs female-only, male-only and biparental care are all widespread among various lineages, and the involvement of males and females in care is comparable. Because in approximately 20% of newts and salamanders (urodeles) one of the parents guards the eggs or the offspring [5,9,63,64], and caecilians in which females may feed their offspring using an excretion of their skin [65,66], the overall richness of caring is spectacular in amphibians. This suggests that over the course of amniote evolution, the phylogenetically younger tetrapod clades (e.g. reptiles, birds and mammals) became specialized to a limited set of care patterns [62].

Consistently with previous studies [11–13], we found that the transition towards terrestrial reproduction facilitated parental care. Moreover, our work advances the understanding of evolutionary relationships by showing that terrestrial reproduction is related to all forms of both male and female care, except nourishment. Thus, when early tetrapods invaded terrestrial niches, both males and females may have been under selective forces to improve the survival of their offspring, so that both males and females evolved various forms of care provisioning in response to terrestrial reproduction. Therefore, the subsequent canalization of parental care largely towards females (e.g. in reptiles and mammals) and cooperation by both sexes (in birds) may have been the result of additional selective pressures that the ancestors of these clades faced during their radiation into various ecological niches. This implies that the predominance of maternal care coevolved with internal fertilization ([67], but see [68]). In urodeles, where internal fertilization is more frequent, only phylogenetically basal external fertilizers with aquatic reproduction appear to provide paternal care [5,63], although clutch attending by females is widespread especially in those with terrestrial reproduction [63].

We also found that egg size and clutch volume are related to parental care, although these associations became non-significant by including terrestriality in the models. On the one hand, terrestrial egg-layers have larger eggs and smaller clutches than aquatically reproducing frogs [8,13,26], which may be predicted by other factors besides parental care,

such as selection on offspring size [69] or protection against the hostile environment [11]. However, egg size and clutch size were no longer associated with care duration and protection when body size was statistically controlled. Therefore, the associations between egg size, clutch size and parenting showed by previous studies [8,13,26] may have been mediated by other factors, e.g. body size and/or terrestrial reproduction. On the other hand, increased nutrient transfer to the offspring is associated with reduced clutch size, which seems to be the result of an increased investment to individual offspring [3] traded off against fecundity. Moreover, trophic egg feeding is also associated with reduced egg size (electronic supplementary material, table S6), implying that mothers may reduce the cost of egg production using this type of nourishment.

Finally, the evolutionary relationship between male care and size dimorphism has been debated [32–34], and our results using fine-scaled care variables, multi-predictor models and more extensive taxonomic coverage than previous studies, confirm that male care is associated with SSD [44]. We suggest two mutually non-exclusive explanations for the increased male size (relative to female size) with the extent of male care. On the one hand, sexual selection may favour larger males in male caring species if females prefer large males and/or large males are more successful in coercive mating [38,39], provided that these males are more successful in nursing the offspring. On the other hand, male care may reduce the fecundity selection pressure on females, so that female size decreases in those species in which the males provide care [44,61]. To distinguish between these scenarios, further experimental and phylogenetic analyses are warranted [9,17].

Here, we treat parental care as an invariable trait for a given species, although this assumption suits some species better than others. For example, *Allobates femoralis* exhibits variation in parenting since females transport tadpoles but this behaviour is only provoked by the absence of the father that is normally the care-providing parent [41]. Therefore, future phylogenetic analyses should pay attention to

the flexibility of care provisioning [41,70]. Care provision can be further tuned by variation in the ecological [25,71,72] or social environment [41], and this plasticity not only enables better adaptation to seasonal and unpredictable changes of the environment, but it may also act as the origin of evolutionary changes in the extent of care [41,45] or in parental roles [41,43,45]. Field-based and laboratory-based studies will probably add more examples for this plasticity and would help in identifying environmental factors which provokes shifts.

In summary, parental care is predicted by ecological and life-history variables in frogs. Care is a complex social trait and specific aspects of care have different predictors in males and females. Further analyses are needed to investigate the impacts of climate, reproductive modes and mating systems on care strategies. Since new forms of parental care are cropping up [71,72], field-based studies of yet unstudied species are needed to explore breeding systems (including parenting) in frogs that live in remote areas and/or inhabit extreme environments. Taken together, studies of anuran parental care provide important contributions to the understanding of reproduction, evolution and diversification in the most threatened vertebrate class of the Anthropocene.

Data accessibility. All relevant data are within the paper and its electronic supplementary material and are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8c4092n> [75].

Authors' contributions. B.V. and T.S. conceived the study. B.V., Z.V., R.P.F. and T.S. designed the analyses, B.V. collected the data, B.V. and Z.V. conducted the analyses. All authors wrote the paper.

Competing interests. We declare we have no competing interests.

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