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RESEARCH PAPER

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Climate and mating systems as drivers of global diversity of parental care in frogs

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Abstract

Aim: Amphibians exhibit unusually diverse reproductive modes, including a wide array of parental care strategies. The evolutionary drivers of this diversity, however, remain unclear. Here, we investigate three major factors that might predict interspecific variation in parental care strategies: climate, intrasexual selection and social environment. We hypothesize that some forms of care evolved to cope with harsh conditions, such as dry or unpredictable habitats. We contrast this prediction with the hypothesis that parental roles have co-evolved with the social environment and mating systems.

Location: Global.

Major taxa studied: Frogs and toads (Amphibia: Anura).

Time period: Extant taxa that represent *c.* 220 Myr of evolutionary history.

Methods: Using geographical and behavioural data for 971 species of frogs and toads that represent 45 anuran families, we quantified the global distribution of four forms of parenting separately for males and females: nest building, nest and/or tadpole attendance, carrying and nourishment. We used phylogenetic comparative analyses to investigate whether climate, social environment and mating systems predicted interspecific variation in parental care.

Results: Our results showed that climatic effects contribute to parental care diversity: in cool and humid climates the males provide offspring attendance, whereas in predictable temperatures endotrophy occurs, whereby the female provides all nutrients for the offspring until metamorphosis. In addition, we found other associations between mating systems and forms of parental care: uniparental clutch attendance by males is present in species with territorial defence, whereas cooperative nest building co-occurs with sperm competition. The type of parental care is not associated with adult sex ratios.

Main conclusions: No specific form of care is associated with hostile environments; in fact, some forms of care occur in beneficial conditions, whereas others are used

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independently from the climate. Instead, parenting diversity has co-evolved closely with mating systems in frogs.

KEYWORDS

climate, frogs, mating systems, parental care, phylogenetic comparative methods, social environment

1 | INTRODUCTION

Parental care is one of the most diverse social behaviours (Balshine, 2012; McGraw, Székely, & Young, 2010; Royle, Smiseth, & Kölliker, 2012; Wilson, 1975). In some groups, such as mammals and birds, parental care appears to have a limited set of forms (Remes, Freckleton, Tökölyi, Liker, & Székely, 2015; West & Capellini, 2016), whereas in other clades, such as bony fish or amphibians, a remarkable diversity of care behaviours has evolved (Furness & Capellini, 2019; Mank, Promislow, & Avise, 2005; Vági, Végvári, Liker, Freckleton, & Székely, 2019). The causes of this diversity are not fully understood, and the role of abiotic or social environmental factors in creating a plethora of parental care strategies has rarely been investigated in detail (Balshine, 2012; Trumbo, 2012).

Understanding the ecological causes of parenting is important, because in many organisms, reproductive success (and thus individual fitness) depends crucially on the type and duration of care and on whether one or two parents look after the young (Clutton-Brock, 1991; Royle et al., 2012; Székely, Webb, Houston, & McNamara, 1996). Parental care has evolved to increase offspring survival in adverse environmental conditions (Martin & Carter, 2013; Vági et al., 2019; Vincze et al., 2017), and among the abiotic environmental factors, the influence of the climate may be crucial. Unfavourable climatic conditions can alter the ideal time of reproduction (Visser, van Noordwijk, Tinbergen, & Lessels, 1998) and lead to increased (AlRashidi, Kosztolányi, Shobrak, Küpper, & Székely, 2011; Hopkins, Moss, & Gill, 2011) or decreased parenting (Bustnes & Erikstad, 1991; Öberg et al., 2015; Suski & Ridgway, 2007) or to the evolution of alternative caring strategies (Schulte & Lötters, 2013).

Variation in climate, however, does not explain the full diversity of forms of parental care across species. Parental roles have co-evolved with other aspects of reproductive biology, such as mating patterns or pair bonds (these, together with care, are referred to as breeding systems; Reynolds, 1996). Spatial and temporal variations in habitat influence the distribution of females, which, in turn, acts on male mating strategies (Emlen & Oring, 1977). When resources and/or female distribution are aggregated in space, males are able to monopolize them by territorial defence (Clutton-Brock, 1991; Emlen & Oring, 1977); in turn, territoriality can promote male parental care owing to the opportunity to defend multiple broods (Reynolds, Goodwin, & Freckleton, 2002; Williams, 1975). Temporal patterns are also important: for example, limited availability of receptive females may lead to direct male competition (Arak, 1983).

Recent theoretical models predict that mate choice, pair bonding and parental roles are related to adult sex ratios. Traits associated with sexual selection are likely to be influenced by adult sex ratios because the rarer sex in the population has an upper hand in driving social interactions (i.e., in making decisions about mate choice or clutch abandonment; Kokko & Jennions, 2008; McNamara, Székely, Webb, & Houston, 2000). Consistent with theoretical expectations, field-based studies show that changes in adult sex ratios influence mating systems (Grant & Grant, 2019; Le Gaillard, Fitze, Ferriere, & Clobert, 2005). Phylogenetic comparative analyses have produced results highly consistent with field-based studies (Liker, Freckleton, & Székely, 2013, 2014), and theory is also supported by experimental manipulation of adult sex ratios (Aronsen, Berglund, Mobley, Ratikainen, & Rosenqvist, 2012).

Therefore, the abiotic and the social environment together shape mating systems and parental roles. In contrast to birds, in mammals and ectothermic vertebrates, uniparental care is more widespread (Balshine, 2012), possibly because in the ancestors of these clades, no care or uniparental care was the ancestral state (Furness & Capellini, 2019; Reynolds et al., 2002; Sutton & Wilson, 2019). However, it is still unclear why uniparental care remained the dominant form, because in harsh environments both parents are often needed to raise the offspring, leading to parental cooperation (Brown, Morales, & Summers, 2010; Vincze et al., 2017). In contrast, when the care provided by one parent is sufficient, one of the parents may desert (Liker et al., 2013, 2014), leading to uniparental care.

In frogs and toads (Anura; hereafter, frogs), parental strategies exhibit variation that is remarkable among the tetrapods (Crump, 1996; Vági et al., 2019; Wells, 2007). It seems likely that alternative forms of care have evolved in response to different environmental challenges. For example, both nest building and egg (or offspring) attendance might have evolved to decrease predation and/or the risk of desiccation (Chuang et al., 2017; Delia, Bravo-Valencia, & Warketin, 2017; Pereira et al., 2017; Poo & Bickford, 2013), while increased nourishment of tadpoles enabled reproduction in nutrient-scarce environments (Brown et al., 2010). Although nest building, egg/tadpole attendance and carrying can be performed by both parents, tadpole nourishment is typically provided by the female (Brown et al., 2010; Vági et al., 2019). In frogs, care is predominantly uniparental; however, biparental care with cooperation between the sexes also occurs (Brown et al., 2010; Furness & Capellini, 2019).

In this study, we investigate the role of climate, mating systems and social environment as potential drivers of parental care in 971 frog species. We predict that harsh environmental conditions, such as low precipitation, or large seasonal variation and between-year fluctuations in climatic factors favour the evolution of parental care (Vincze et al., 2017) or increase the number of caring parents (Rubenstein & Lovette, 2007). In addition, we expect that mating systems influence the forms of parental care. On the one hand, competition for mating partners in males selects for reduced care, because the most successful males can increase their reproductive success by mating with multiple females instead of taking care of the young; moreover, the paternity can be uncertain in competitive breeding because of sperm competition (Rausch, Sztatecsny, Jehle, Ringler, & Hödl, 2014; Roberts, Standish, Byrne, & Doughty, 1999). On the other hand, territoriality in males might promote egg or offspring guarding (Reynolds et al., 2002; Williams, 1975), either because males can take care of multiple broods or because of their high confidence of siring (Beck, 1998; Sutton & Wilson, 2019). We also hypothesize that male-biased populations show male parental care, because the opportunity for males of multiple mating is low (Kokko & Jennions, 2008; Liker et al., 2013). Additionally, we tested climatic effects on biparental care and parental roles, in addition to associations between different forms of care, to examine task division and cooperation between anuran parents.

2 | METHODS

2.1 | Data collection

Data on parental care were extracted from primary publications, books and reviews; for detailed information, see Vági etal. (2019). We aimed to include all frog species with adequate information on their parental care, sampled from each family and most genera, to cover the diversity of parental care strategies in each anuran clade. See parental care dataset in Supporting Information file S1.

We used the same set of species as Vági et al. (2019), but applied a modified coding system for caring behaviour. Here, we investigate three forms of protective parental care in frogs: nest building, attendance and carrying, assessed separately for both males and females. We also considered two characteristic forms of nourishing: endotrophy and trophic egg feeding provided by females. We used a binary coding for all these care variables (presence versus absence). Nest building was defined as the construction of structures serving for the defence of the offspring: constructed burrow or subterranean chamber, attached leaves and, most importantly, foam around the eggs. Attendance was defined as any case when both or either of the parents was observed staying next to the eggs or developing larvae, regardless of whether they actively defend their clutch or offspring. Carrying was defined for cases when one or both parents carry their eggs, larvae or juveniles for any time interval. Endotrophy included all cases when the mother provides all nutrients in the egg yolk necessary to reach the (metamorphosed) juvenile phase (including species skipping the larval phase by direct development), whereas in trophic egg feeding, the mother supplies the developing tadpoles by feeding them with additional unfertilized eggs. All these forms of care have evolved several times independently (Furness & Capellini, 2019; Vági et al., 2019). We defined two further care variables derived from the previous ones: the number of caring parents (0 = no care; 1 = uniparental care; 2 = biparental care); and sexual bias in care (−1 = the female cares more; 0 = equal contributions; 1 = the male cares more). For calculating these indices, we considered all the above-mentioned forms of care in males and females in addition to internal brooding and viviparity, excluding endotrophy, which is considered to be an increased investment to gametes but not an active care provision.

To calculate potential climatic predictors of the variation in care, we computed the annual mean temperature and the annual sum of precipitation, their between-year variances and within-year variances calculated from monthly values, and climatic extremities, defined as the upper and lower quartiles of temperature and lower quartiles of precipitation, calculated for the whole of the year (Lothka, Kyselý, & Farda, 2018). To compute annual climatic parameters, first we extracted species ranges, available in shapefile format at iucnredlist.org for 5,791 anuran species. In the next step, we excluded range polygons that include introduced and unconfirmed populations, to exclude evolutionarily irrelevant or unconfirmed records. Next, we retrieved global rasters at 2.5° × 2.5° resolution of monthly temperature and precipitation data from WorldClim (wordclim.org). In the following step, we cropped the climate rasters by the species ranges and derived temperature means and annual precipitation totals averaged for each 2.5° × 2.5° raster grid cell of the distribution shapefile throughout the past 50 years. In the next step, we calculated the within-year variance of monthly values, the between-year variance of annual values, and the upper and lower quartiles of annual temperature means and lower quartiles of precipitation totals.

To assess the association of certain forms of male–male competition with forms of parental care, we adapted binary states (presence versus absence) for three types of male social behaviours (male combat, male scramble competition and male territory defence) from Han and Fu (2013). In addition, we added further male territory defence data from Wells (2007). We collected data on testes mass and body mass from previous comparative literature (Byrne, Roberts, & Simmons, 2002; Kusano, Toda, & Fukuyama, 1991; Zamudio, Bell, Nali, Haddad, & Prado, 2016). Adult sex ratio (ASR) data were collected from the literature by entering the “adult sex ratio” and anuran species and genus names as search terms into literature databases of Web of Science and Google Scholar. Given that available ASR data were scarce, we considered all data with ≥ 20 individuals originating from the same population using standardized collection methods. These methods included sampling by visual observation, capturing by nets, and included censuses of whole populations, such as collection of migrating individuals by drift fence and pitfall traps. In this dataset, ASR values were independent of the collection method [sampling versus census; general linear model (GLM) m; $F_{1,128} = .03$; $p = .862$] and the sample size ($F_{1,136} = 0.681$; $p = .411$). Whenever we calculated a species-level average from multiple ASR data, the within-species variance was independent of mean ASR values (GLM; $F_{1,39} = 0.009$; $p = .927$) and the mean sample size (GLM; $F_{1,39} = 0.58$; $p = .451$; see ASR dataset in Supporting Information File S2.

2.2 | Phylogeny

We applied a comprehensive amphibian phylogenetic tree: the consensus tree constructed by Jetz and Pyron (2018), which contained most of the species (971 of 1,044; 93%) in our dataset. Considering this good coverage, in phylogenetic analyses we used the original tree and did not supplement it with the missing species.

2.3 | Phylogenetic comparative analyses

Climatic variables and male intrasexual selection were analysed using phylogenetic GLM models, applying the "phyloGLM" function available in the "phylolm" package, considering maximum penalized likelyhood estimation and computing the parametric bootstrap on 1,000 fitted replicates (Ho et al., 2018). This method allows a binary response variable and controls for the phylogenetic non-independence of species. We developed separate phyloGLM models for each binary parental care variable, whereas climatic and intrasexual selection variables were entered as predictors. Owing to multicollinearity between some variables ($r > 0.7$), in the next step we excluded the lower and upper quartiles of annual temperature (correlated with annual mean temperature), variation in annual precipitation and lower precipitation quartiles (correlated with annual precipitation) and male combat (correlated with male scramble competition and territory defence) from the final analyses.

Given that the central role of terrestrial reproduction is well known in predicting parental care (Gomez-Mestre, Pyron, & Wiens, 2012; Vági et al., 2019) and its connections to abiotic factors are also well documented (Gomez-Mestre et al., 2012; Liedtke et al., 2017; Lion et al., 2019), we included terrestrial reproduction as a predictor. Where insufficient variation in terrestrial reproduction (i.e., when all species with the focal type of care reproduced on land) made it impossible for us to use this control variable, we ran analyses without control for terrestrial reproduction. We performed these latter analyses both for the whole species pool and by excluding species with aquatic reproduction. To test for the robustness of potential climatic effects, we repeated climatic analyses with the exclusion of male intrasexual selection variables, which allowed a substantially larger sample size.

We also tested which forms of care are associated with each other, using phyloGLM models. We entered the three male forms of care (nest building, attending and carrying) as the dependent variables into three separate models, and the five female forms of care (nest building, attending, carrying, endotrophy and trophic egg feeding) as predictors. We performed similar analyses to test for relationships between different aspects of female care: protective female forms of care (nest building, attending and carrying) and nourishment types (endotrophy and trophic egg feeding).

In analyses on the number of caring parents, sexual bias in care and testes size, we used phylogenetic least squares (PGLS; Freckleton, Harvey, & Pagel, 2002; Martins & Hansen, 1997; Pagel, 1999). This approach controls for the non-independence among species by incorporating a variance–covariance matrix that represents their phylogenetic relationships. In all analyses, we set the phylogenetic dependence (λ) to the maximum likelihood value (Freckleton et al., 2002).

We conducted two PGLS analyses on climate and male intrasexual selection using the number of caring parents and sexual bias in care as response variables. As a sensitivity test, we repeated these analyses using the "phylolm" function using the "lambda" model specification. In the analyses of testes size, we entered testes mass as the dependent variable, and each form of parental care (excluding carrying by males, because for species with this form of care we did not have testes size data) and male body mass as predictors in a single PGLS model. In analyses of adult sex ratios, we used the "phylolm" function with "lambda" model, entering sexual bias in care as the response and ASR as the predictor. The limited frequency of care occurrence data in our original care categories did not allow separate analyses for each form of care within the ASR dataset.

All analyses were carried out using R v.3.1.0 (R Core Team, 2019) with the packages "caper" (Orme, 2018), "phylolm" (Ho et al., 2018), "maptools" (Lewin-Koh & Bivand, 2019), "raster" (Hijmans, Etten, & Cheng, 2019) and "rgdal" (Bivand et al., 2015).

3 | RESULTS

3.1 | Geographical distributions and climatic effects

Most species with some forms of parental care are concentrated in tropical and subtropical areas, with peaks in diversity being observed in South and Central America, where all types of parental care co-occur (Figure 1). However, the large zoogeographical realms show substantial differences in the presence or absence of parental care forms; for instance, attendance and carrying are almost absent in the Indian subcontinent and the Indo-Malayan region (for detailed description, see Figure 1).

Clutch or offspring attendance by male frogs was more common in cooler and wetter climates, whereas endotrophic nourishment occurred in stable temperature conditions (i.e., where between-year and within-year temperature fluctuation were low; Table 1). In contrast to our expectations, other forms of care were not associated with any of the climatic variables (Table 1). Moreover, when we ran these models with the exclusion of sexual selection variables, only the negative association between male attendance and annual mean temperature remained significant with the larger species sample (Supporting Information Table S1). Precipitation stochasticity was negatively associated with the number of caring parents, indicating

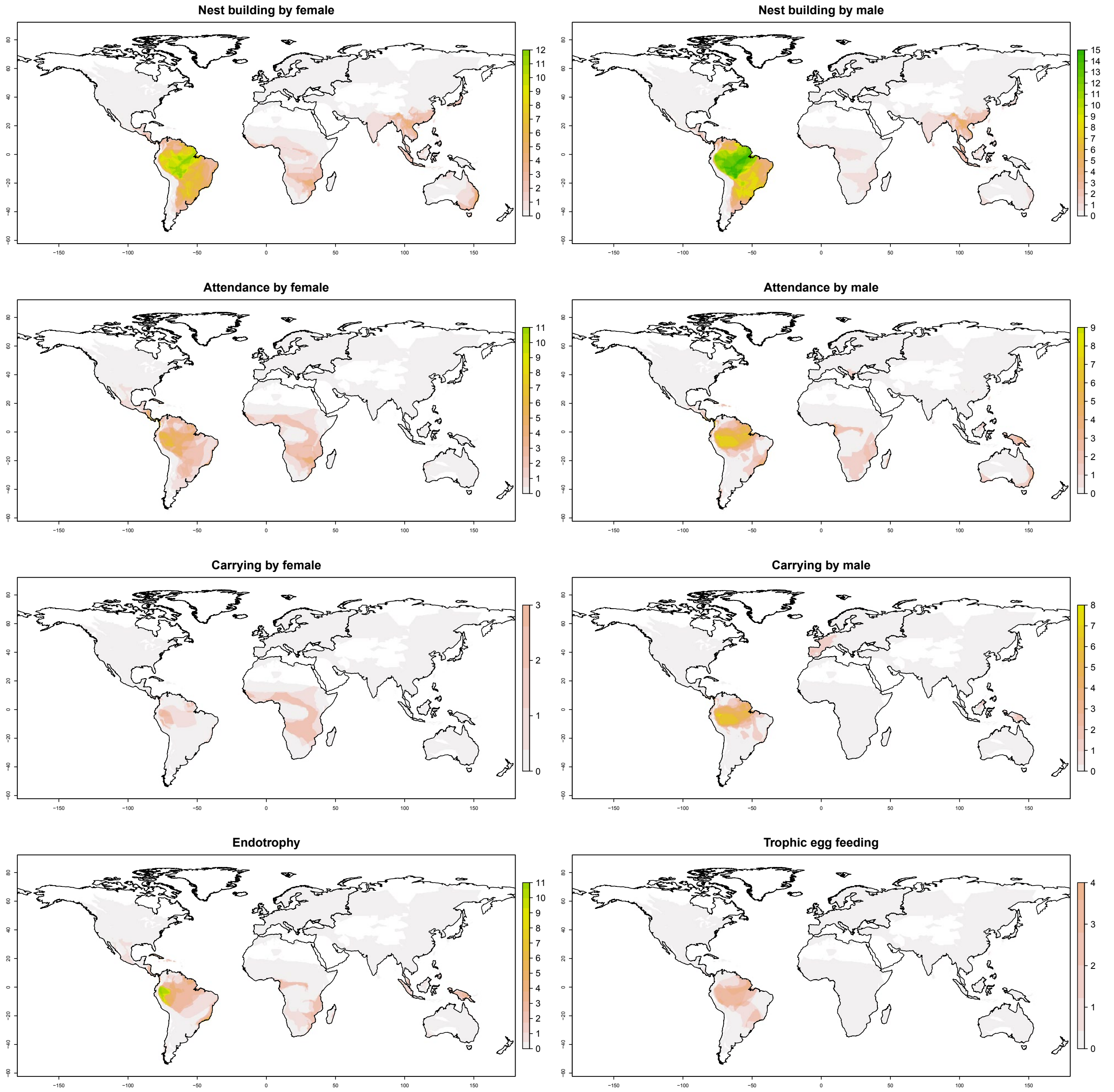

FIGURE 1 Global distribution of forms of parental care in Anura. Nest building by females and/or males occurs in almost every tropical or subtropical area, whereas female and/or male attendance is almost completely lacking in the Indian subcontinent and Southeast Asia. Apart from South America, where carrying by either sex is widespread (especially in the families Dendrobatidae and Hemiphractidae), carrying by females occurs in the Afrotropical realm (*Hemisus* spp.), whereas carrying by males occurs in Southwestern Europe (*Alytes* spp.), Borneo (*Limnonectes*) and New Guinea (Microhylidae: *Aphantophryne*, *Liophryne*, *Pseudocallulops* and *Sphenophryne*). Species with carrying by the female include sooglossids in the Seychelles, and species with carrying by the male are represented by *Leiopelma* spp. in New Zealand. Species with endotrophic nourishment can be found in every tropical or subtropical zoogeographical realm, whereas trophic egg feeding is concentrated in the Neotropics, with isolated occurrences on the islands of Madagascar (*Mantella laevigata*) and Taiwan (*Kurixalus eiffingeri*). Grey shading shows areas where all species in our database lack the focal type of care. The colour scale represents the number of species performing the focal type of care in our database

that more parents are involved in care in climates with more evenly distributed precipitation among years. Additionally, analyses on the sexual bias in care showed that male care is more common with lower precipitation stochasticity, whereas species with female care are associated with larger variance in between-year precipitation (Supporting Information Table S2).

3.2 | Male intrasexual selection and social environment

Egg and/or offspring attendance was more common among male frogs that defend territories (Figure 2; Table 1), whereas female attendance was negatively associated with male territoriality. Male

TABLE 1 Forms of parental care in relationship to male social behaviour and climatic predictors in Anura by phylogenetic generalized linear models (phyloGLM) using climatic variables, male territory defence (presence/absence), male scramble competition (presence/absence) and terrestrial reproduction (presence/absence) as explanatory variables and, in each model, the presence/absence of one form of parental care as the response variable

Predictor	β ± *SE*	*z*	*p*	β ± *SE*	*z*	*p*
Nest building	**By females (*n* = 126)**			**By males (*n* = 378)**		
Annual T_{mean}	−0.022 ± 0.185	−0.120	.905	−0.420 ± 0.305	−1.380	.168
Within-year T_{mean} variance	−0.016 ± 0.164	−0.099	.921	−0.280 ± 0.239	−1.172	.241
T_{mean} stochasticity	0.034 ± 0.161	−0.211	.833	−0.264 ± 0.280	−0.885	.376
Prec$_{ann}$	0.012 ± 0.205	−0.057	.955	−0.318 ± 0.358	−0.887	.375
Prec$_{ann}$ stochasticity	−0.003 ± 0.136	0.020	.984	0.022 ± 0.236	0.092	.926
Male territory defence	−0.027 ± 0.217	−0.126	.900	0.706 ± 0.455	1.553	.120
Male scramble competition	0.005 ± 0.364	−0.014	.987	−0.003 ± 0.472	−0.007	.994
Terrestrial reproduction	Aquatic reproducing species excluded*			*1.290 ± 0.754*	*1.710*	*.087*
Attendance	**By females (*n* = 378)**			**By males (*n* = 378)**		
Annual T_{mean}	*0.493 ± 0.279*	*1.770*	*.077*	**−0.354 ± 0.145**	**−2.446**	**.015**
Within-year T_{mean} variance	−0.265 ± 0.192	−1.381	.167	0.000 ± 0.102	−0.001	.999
T_{mean} stochasticity	0.241 ± 0.233	1.032	.302	0.012 ± 0.133	0.091	.928
Prec$_{ann}$	−0.247 ± 0.227	−1.089	.276	**0.616 ± 0.200**	**3.078**	**.002**
Prec$_{ann}$ stochasticity	0.062 ± 0.154	0.406	.685	−0.180 ± 0.133	−1.352	.176
Male territory defence	*−0.870 ± 0.448*	*−1.942*	*.052*	**0.787 ± 0.256**	**3.078**	**.002**
Male scramble competition	−0.066 ± 0.430	−0.148	.883	**−0.948 ± 0.379**	**−2.503**	**.012**
Terrestrial reproduction	**1.587 ± 0.633**	**2.506**	**.012**	**0.626 ± 0.314**	**1.993**	**.046**
Carrying	**By females (*n* = 378)**			**By males (*b* = 126)**		
Annual T_{mean}	0.343 ± 0.306	1.122	.262	−0.100 ± 0.175	−0.568	.570
Within-year T_{mean} variance	0.216 ± 0.189	1.143	.253	−0.025 ± 0.137	−0.184	.854
T_{mean} stochasticity	0.319 ± 0.259	1.233	.217	−0.006 ± 0.135	−0.047	.963
Prec$_{ann}$	0.020 ± 0.265	0.075	.941	0.003 ± 0.169	0.022	.983
Prec$_{ann}$ stochasticity	−0.031 ± 0.207	−1.149	.881	0.003 ± 0.112	0.024	.981
Male territory defence	−0.198 ± 0.370	−0.536	.592	−0.159 ± 0.216	−0.733	.563
Male scramble competition	−0.208 ± 0.445	−0.467	.640	−0.185 ± 0.350	0.526	.599
Terrestrial reproduction	1.054 ± 0.706	1.493	.135	Aquatic reproducing species excluded*		
Nourishment by females	**Endotrophy (*n* = 383)**			**Trophic egg feeding (*n* = 383)**		
Annual T_{mean}	−0.235 ± 0.156	−1.832	.132	−0.459 ± 0.431	−1.064	.287
Within-year T_{mean} variance	**−0.235 ± 0.136**	**−2.529**	**.036**	0.037 ± 0.338	0.111	.912
T_{mean} stochasticity	**−0.348 ± 0.165**	**−1.325**	**.035**	−0.482 ± 0.460	−1.048	.295
Prec$_{ann}$	*−0.337 ± 0.185*	*−0.103*	*.068*	0.399 ± 0.339	1.175	.240
Prec$_{ann}$ stochasticity	0.139 ± 0.117	1.325	.234	0.248 ± 0.251	0.989	.323
Male territory defence	0.316 ± 0.216	0.087	.143	**1.101 ± 0.561**	**1.964**	**.050**
Male scramble competition	*−0.662 ± 0.357*	*−0.567*	*.064*	0.257 ± 0.764	0.034	.973
Terrestrial reproduction	0.324 ± 0.287	3.653	.259	0.159 ± 0.657	0.242	.809

Note: Climatic predictors were standardized. *In tests for nest building by females and carrying by males, we included only terrestrially reproducing species. For similar analyses on all species, see the Supporting Information (TableS3). We provide parameter estimates with the standard error (β±*SE*), *z* and *p*-values. Bold text indicates significant (p<.05) and italic text marginally significant (p<.1) statistics. Abbreviations: prec$_{ann}$ = annual precipitation; T_{mean} = mean temperature.

territory defence also predicted trophic egg feeding by females (Table 1). Scramble competition was significantly less frequent among male frogs that attend their progeny and had a marginally significant negative association with endotrophy (Table 1). In frog species where females participate in nest building, the males had relatively larger testes, whereas the presence of other forms of care

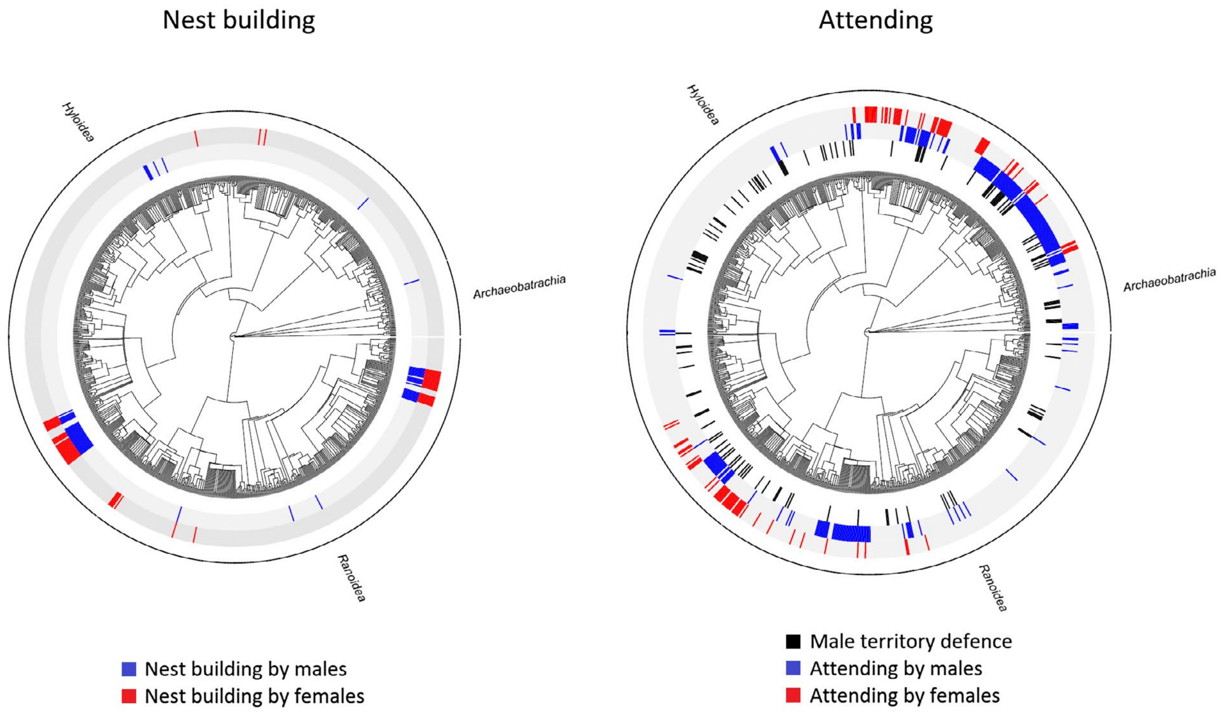

FIGURE 2 Phylogenetic distribution of nest building and attendance by male and female frogs. *n* = 948 species in both panels. In the right panel, we also indicate the presence of male territoriality (note that not all species in the figure have territoriality data). See also Tables 1, 3 and 4 for statistics

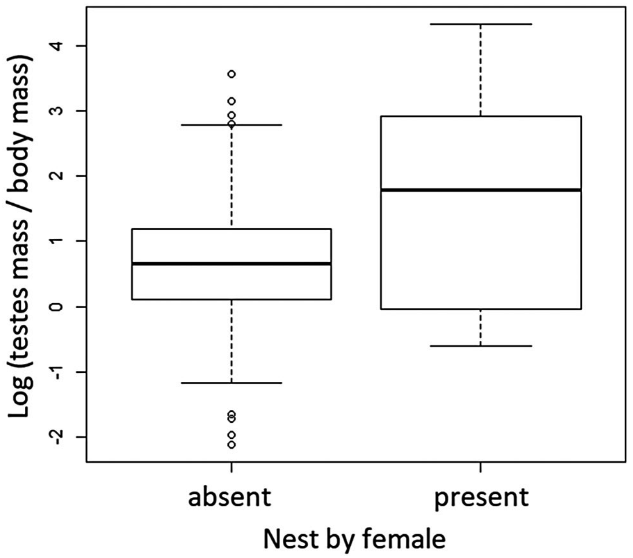

FIGURE 3 Relative mass of testes of male frogs in relationship to nest building by females. Number of species is 953 and 68 in species with the absence and the presence of female nest building, respectively. See statistics in Table 2

had no association with relative testes size (Figure 3; Table 2). Adult sex ratio was unrelated to parental roles in care (Figure 4), either when we included species with no care (*n* = 72 species; phyloLM; *p* = .87) or when we included only care-providing species (*n* = 25 species; phyloLM; *p* = .71).

3.3 | Parental roles: Task division and cooperation

Nest building by male and female frogs frequently co-occurred, implying that nests are often built in cooperation by the parents (Figure 2; Table 3). In contrast, male and female attendance was negatively associated, implying that uniparental attendance is the predominant form of attendance in frogs (Figure 2; Table 3). Interestingly, male attendance often co-occurred with female carrying (Table 3). When we investigated associations between female protection and nourishment, we found that female frogs tend to attend eggs and juveniles with endotrophic development (e.g., when females also provide food for the juveniles; Table 4).

4 | DISCUSSION

Our key result is that two out of eight forms of parental care in frogs were predicted by macroclimatic factors (Table 5), indicating strong links only between cooler temperatures and male attendance. In contrast, nearly all forms of parental care were closely associated with predictors describing sexual selection and breeding systems, including interactions with other forms of parenting performed by the same or the other parent (Tables 1, 4 and 5). Therefore, although the evolution of terrestrial reproduction was a key step towards parental care (Vági et al. 2019), and the opportunity of terrestrial egg laying is indeed predicted by the climate (Gomez-Mestre et al., 2012; Lion et al., 2019), it seems that evolution of breeding systems (including

TABLE 2 Parental care in relationship to size of testes in frogs by phylogenetic least squares (PGLS)

Characteristic	*β* ± *SE*	*t*	*p*
Nest building by males	12.82 ± 49.86	0.257	.798
Nest building by females	**164.04 ± 42.06**	**3.900**	**< .001**
Attendance by males	−12.17 ± 50.59	−0.240	.810
Attendance by females	12.07 ± 68.72	0.176	.861
Carrying by females	−30.31 ± 134.4	−0.226	.822
Endotrophy	3.25 ± 79.51	0.041	.967
Trophic egg feeding	−16.83 ± 81.46	−0.207	.837
Male body mass	**3.078 ± 0.682**	**4.512**	**< .001**
Model*	Adj. R^2 = 0.207	*F* = 4.838 (d.f. = 110)	**< .001**

Note: We entered the size of the testes as the dependent variable and binary care variables and male body mass (in grams) as predictors in the model. Carrying by males was not tested owing to the lack of testes mass data in species with this type of care. We provide parameter estimates with the standard error (β ± *SE*), *t* and *p*-values. *In the Model row, we present adjusted R^2 and the *F*-value and corresponding degree of freedom. Bold text indicates significant ($p < .05$) statistics.

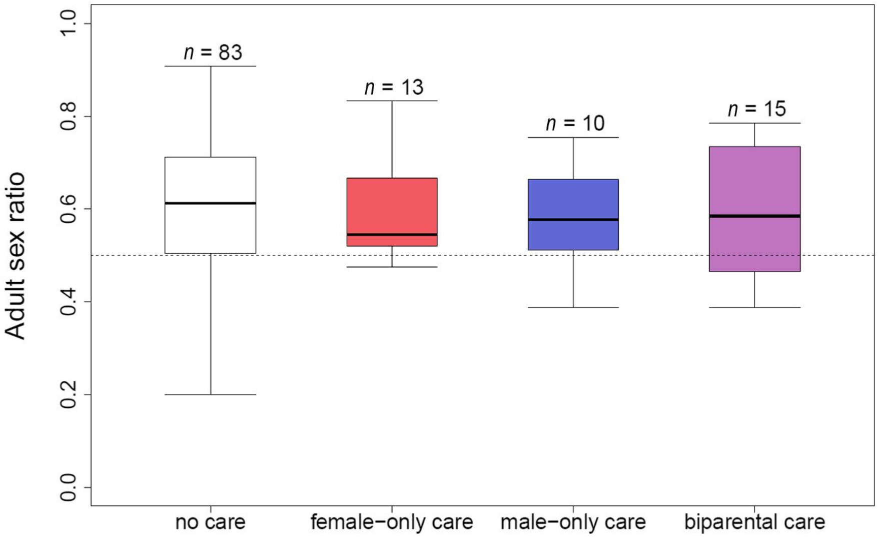

FIGURE 4 Adult sex ratios (the proportion of males in the adult population) in frog species with different types of parenting. Dashed line represents an even sex ratio. *n* refers to the number of species

parental conflicts and cooperation) was more important in shaping the current diversity of anuran parental care.

4.1 | Parental care and climatic conditions

In contrast to our expectations, climatic factors were found to be less important predictors of forms of parental care in frogs than those describing mating systems. This is surprising, because adult amphibians, in addition to amphibian eggs and larvae, are sensitive to several environmental factors, such as temperature and humidity (Martin & Carter, 2013; Wells, 2007). The less amplified contribution of climate is mirrored by the global distribution of forms of care, which does not reflect global climatic patterns, except for the general rule that most care is restricted to tropical and subtropical areas, where amphibian diversity is higher and terrestrial reproduction more common (Gomez-Mestre et al., 2012; Lion et al., 2019). Given that most forms of care are stable within a frog lineage (Clough & Summers, 2000; Meegaskumbura et al., 2015; Pereira et al., 2017), historical causes might have made a larger contribution to current care distributions. This can explain why the large zoogeographical realms (Udvardy, 1975), which are populated by characteristically different assemblages of amphibian clades (Pyron, 2014), show substantial differences in the presence or absence of certain types of parental care. The diversity hotspots of care in the tropics can be attributed to both climatic effects on terrestrial reproduction and global amphibian species richness distributions. The spatial evolution of different forms of care calls for a comprehensive historical phylogenetic and biogeographical analysis.

Care may provide protection against hostile environmental conditions in other vertebrate groups (AlRashidi et al., 2011; Vincze et al., 2017), but in frogs the case seems to be different: surprisingly, none of the forms of care are associated with a drier climate or less predictable precipitation (i.e., high within- and between-year variance in monthly and yearly sums), which is difficult for amphibians to cope with. Male attendance emerged as the only form of care

TABLE 3 Associations between male and female types of care in Anura

Female care	Male care $\beta \pm SE$	z	p
	Nest building		
Nest building	**1.956 ± 0.901**	**2.159**	**.031**
Attendance	*−0.886 ± 0.476*	*−1.864*	*.062*
Carrying	−0.064 ± 0.886	−0.072	.943
Endotrophy	−0.016 ± 0.445	−0.037	.971
Trophic egg	−0.905 ± 0.685	1.321	.187
	Attendance		
Nest building	−0.043 ± 0.229	−0.188	.851
Attendance	**−1.660 ± 0.364**	**−4.559**	**< .001**
Carrying	**1.324 ± 0.478**	**2.769**	**.006**
Endotrophy	−0.293 ± 0.272	1.079	.281
Trophic egg	0.687 ± 0.496	1.385	.166
	Carrying		
Nest building	−0.004 ± 0.127	−0.028	.977
Attendance	−0.285 ± 0.176	−1.624	.104
Carrying	−0.052 ± 0.322	0.160	.873
Endotrophy	0.238 ± 0.231	1.032	.302
Trophic egg	−0.852 ± 0.611	−1.394	.163

Note: We entered the occurrence of male types of care as the dependent variable and the occurrence of five female types of care as explanatory variables into the phylogenetic generalized linear models (phyloGLM). $n = 940$ species. We provide parameter estimates with the standard error ($\beta \pm SE$), t and p-values. Bold text indicates significant ($p < .05$) and italic text marginally significant ($p < .1$) statistics.

TABLE 4 Associations between female protective care and types of nourishment in Anura

Female nourishment	Female protective care $\beta \pm SE$	z	p
	Nest building		
Endotrophy	0.243 ± 0.524	0.464	.643
Trophic egg	0.044 ± 0.566	0.077	.938
	Attending		
Endotrophy	**1.370 ± 0.688**	**1.993**	**.046**
Trophic egg	1.564 ± 0.982	1.593	.111
	Carrying		
Endotrophy	2.408 ± 1.781	1.352	.176
Trophic egg	2.777 ± 2.107	1.318	.188

Note: We entered the occurrence of female types of protective care as the dependent variable and the occurrence of nourishment types as explanatory variables into the phylogenetic generalized linear models (phyloGLM). $n = 940$ species. We provide parameter estimates with the standard error ($\beta \pm SE$), z and p values. **Bold** text indicates significant ($p < .05$) statistics.

TABLE 5 Summary for all significant predictors of forms of frog parental care

Type of care	By females	By males
Nest building	Male relative testes mass (+)	Female nest building (+)
	Male nest building (+)	
Attendance	Male attendance (−)	Annual T_{mean} (−)*
	Endotrophy (+)	Annual precipitation (+)*
		Male territory defence (+)
		Male scramble competition (−)
		Female attendance (−)
		Female carrying (+)
Carrying	Male attendance (+)	–
Endotrophy	T_{mean} variance (−)*	(Does not exist in males)
	T_{mean} stochasticity (−)*	(Does not exist in males)
	Female attendance (+)	
Trophic egg feeding	Male territory defence (+)	(Does not exist in males)

Note: Direction of association is marked by (+) and (−) signs in parentheses. Climatic predictors are marked with an asterisk.
Abbreviation: T_{mean} = mean temperature.

positively associated with annual precipitation sums. This suggests that wetter climates allow for the emergence of attendance, because more actively attending frogs decrease the risk of desiccation (Bickford, 2004; Wells, 2007). In humid environments the risk of desiccation is lower (Simon, 1983), but predation or pathogens (e.g., fungal infections) are more frequent in wetter conditions, and attending frogs may successfully defend their progeny against these threats by deterring predators (Delia, Bravo-Valencia, & Warkentin, 2017; Poo & Bickford, 2013) or by excreting antimicrobial substances against pathogens (Salthe & Mecham, 1974; but see Simon, 1983; Wells, 2007). Therefore, increased attendance in cool and humid conditions can be caused by both decreased costs and increased benefits of this form of care.

Interestingly, only paternal attendance, and not maternal attendance, is associated with climatic factors. It is possible that male frogs, which are usually smaller (Han & Fu, 2013; Monnet & Cherry, 2002), are more sensitive to adverse conditions, such as dry environments, owing to their higher surface-to-body mass ratios. Moreover, male attendance seems to have co-evolved with territorial defence (see below), and this prolonged activity might be more dependent on environmental conditions than attendance in females, which might be restricted to a shorter, external brooding of the clutch (Delia et al., 2017; Wells, 2007). The positive association between female attendance and endotrophy implies that, in female frogs, larger maternal investment in individual offspring can predict a longer duration of parental care (Kolm & Ahnesjö, 2005; Shine, 1978, 1989; Summers, McKeon, & Heying, 2006; but see Gilbert & Manica, 2010).

Nest building is not related to dry climates, although it is hypothesized to provide passive protection against desiccation

(Duellman & Trueb, 1986; Heyer, 1969; Salthe & Mecham, 1974). In contrast to attendance, nest building is not associated with humid environments. Nesting often co-evolves with egg laying in or near water bodies (Pereira et al., 2017; Schäfer et al., 2019), where the water supply is plentiful, and this fact also highlights that its main advantage could have been protection from predators. However, nests can be constructed in various climatic conditions, which might have enabled the occupation of less hospitable habitats (Meegaskumbura et al., 2015; Pereira et al., 2017). Therefore, nest building, as a form of care that is often cooperative, might have enhanced niche expansions, as demonstrated in other vertebrates (Cornwallis et al., 2017).

Among forms of nourishment, endotrophy is associated with more stable temperatures. Endotrophic offspring tend to spend a longer time at the egg-laying site, because they often complete their development there (Gomez-Mestre et al., 2012; Wells, 2007). We hypothesize that this longer-term placement of eggs and offspring is possible only in predictable environments.

4.2 | Intrasexual selection and parental roles

Our findings show that the mating system influences both the type of parental care and related parental roles. Male territoriality predicts male egg and offspring attendance, as was suggested previously for fish (Reynolds et al., 2002; Williams, 1975). Based on our results, we cannot exclude the possibility that the main role of territory defence in frogs is directed to the protection of the eggs or the offspring, and not to obtaining food, mating partners or other resources. On the contrary, territoriality and egg/offspring attendance are not related to nest building by males or females. To explain this pattern, we propose that anuran nests provide an efficient passive protection, which would not be increased substantially by active attendance. The association between trophic egg feeding and male territoriality can be explained by the finding that trophic egg feeding often co-occurs with paternal attendance as a form of cooperation between parents (Brown et al., 2010); however, we could not detect this relationship in our analyses of parental cooperation, possibly because trophic egg feeding has evolved only a few times in the anuran phylogeny. Nonetheless, territoriality and trophic egg feeding both need well-developed spatial orientation and might share some underlying physiological mechanisms.

Scramble competition between males is rare in species where the male parent is involved in attendance of the clutch, suggesting that competition for mates decreases in the caring sex, a general pattern demonstrated in other vertebrate groups (Clutton-Brock, 1991; Liker et al., 2013). Additionally, scramble competition in frogs is often accompanied by sperm competition (Rausch et al., 2014; Roberts et al., 1999), raising the uncertainty of paternity, whereas controlled and certain paternity seems to have crucial importance in the evolution of parental care in external fertilizers (Beck, 1998; Sutton & Wilson, 2019). Female nest building is associated with larger testes size (indicating intense sperm competition; Byrne et al., 2002), but not direct fights between the males. A possible explanation is that in these species, the males value the females not only for their gametes, but also for their dominant contribution to nest building (both in terms of secreted materials and building job). Given that females can be found where conditions are ideal for nest building, for males it is not beneficial to be territorial. As larger nests might be more robust against threats, it is worthwhile for males to cooperate not only with the female, but also with each other, and to avoid direct fights (which might lead to nest destruction). The result is polyandrous mating with cooperative nest building; however, the males' sperm may compete for the fertilization of the eggs during the process.

Although nest building is a form of cooperation between parents, attendance in frogs seems to be predominantly uniparental. Attendance also seems to be a more flexible behaviour (Furness & Capellini, 2019). Switches in parental roles are common among frog lineages with egg or tadpole attendance, such as poison frogs (Dendrobatidae; Ringler et al., 2015), rainfrogs (Eleutherodactylidae and Strabomantidae; Wells, 2007) or glassfrogs (Centrolenidae; Delia et al., 2017). Parental roles in attendance can be a hot ground for sexual conflicts, because one of the parents may abandon the clutch (Liker et al., 2014). The widespread uniparental attendance and within-lineage variance in the care-providing parent suggest that similar evolutionary games might have shaped the parental division of labour in frogs (Ringler et al., 2015).

4.3 | Limitations

We could not detect correlations between adult sex ratios and parental strategies. Adult sex ratio data are limited for frogs, especially for tropical species with diverse parental strategies. Another limitation is that separation of ASR and operational sex ratio (OSR) raises difficulties, although this distinction is fundamental in our understanding of breeding systems (Székely, Weissing, & Komdeur, 2014). The ASR can differ greatly between populations or breeding seasons, which can also act on breeding strategies and may affect parental care, which is known to show within-species plasticity (Martins, Pombal, & Haddad, 1998; Ringler et al., 2015). Thus, population-level data might be more suitable to test the association of parental behaviour with ASR in anurans.

Another limitation is that we have restricted information for the breeding systems of the species. Breeding season length seems to be a key factor linking abiotic and social predictors, because it is often governed by environmental conditions and is strongly associated with the breeding system (Arak, 1983; Machado, Buzatto, García-Hernández, & Macías-Ordóñez, 2016; Wells, 1977). For example, species with extremely short (explosive) breeding periods usually have breeding aggregations with a strongly male-biased OSR, where males are involved in scramble competition with each other for possession of females, and female choice is dominated by male coercion (Davies & Halliday, 1978; Hettyey et al., 2014; Vági & Hettyey, 2016). In contrast, in species with prolonged, sometimes year-round breeding, males often defend permanent territories and resources, and the variation of male mating success is higher in the population (Arak, 1983; Wells, 2007). However, species-level data on breeding months are often aggregated for populations of the entire range of the species (see Amphibiaweb, 2020). On this scale, it is challenging to distinguish between explosive and prolonged breeders, because explosive breeders can have several bouts of breeding in different parts of their range (Matsui, 1989; Terhivuo, 1988) and the cumulative breeding period seems to be longer than the breeding season for the populations. A potential future direction is to evaluate the association between mating systems and the real length of the breeding season based on population-level studies.

Additionally, despite our increasing knowledge, details of the reproduction of many anuran species are still unexplored. A recent study discovered possible parental care in the largest anuran, the charismatic and well-known goliath frog (*Conraua goliath*), but the details of this behaviour are unknown (Schäfer et al., 2019). This clearly shows that parental care can remain unnoticed even in familiar species and in species with non-caring close relatives.

4.4 | Conclusions

In conclusion, sexual selection and climatic conditions contributed to the evolution of different forms of parental care in Anura, creating an extraordinary behavioural diversity in the > 7,000 anuran species (Amphibiaweb.org). Sexual selection played an important role (comparable to that in warm-blooded vertebrates) in shaping the complex behaviours observed today; therefore, the potential of anurans as model organisms of parental care evolution cannot be overestimated. The risk of extinction of many anurans (González-del-Pliego et al., 2019) will not only prune the amphibian tree of life (Jetz & Pyron, 2018), but also depauperate this behavioural diversity. Population-level field studies and comparative research are both warranted as soon as possible to recognize the most endangered species and reproductive forms.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All relevant data analysed in the paper and in the Supporting Information are available in a public Dryad repository: https://doi.org/10.5061/dryad.m905qftxs. Species distributions are available as shapefiles from IUCN databases: https://www.iucnredlist.org/resources/spatial-data-download. WorldClim variables are available at: http://www.worldclim.org/bioclim

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REFERENCES

AlRashidi, M., Kosztolányi, A., Shobrak, M., Küpper, C., & Székely, T. (2011). Parental cooperation in an extreme hot environment: Natural behaviour and experimental evidence. *Animal Behaviour*, *82*, 235–243. https://doi.org/10.1016/j.anbehav.2011.04.019

Amphibiaweb (2020). Retrieved from https://amphibiaweb.org. Berkeley, CA: University of California.

Arak, A. (1983). Male-male competition and mate choice in anuran amphibians. In P. Bateson (Ed.), *Mate choice* (pp. 181–205). Cambridge, UK: Cambridge University Press.

Aronsen, T., Berglund, A., Mobley, K. B., Ratikainen, I. I., & Rosenqvist, G. (2012). Sex ratio and density affect sexual selection in a sex-role reversed fish. *Evolution*, *67*, 3243–3257. https://doi.org/10.1111/evo.12201

Balshine, S. (2012). Patterns of parental care in vertebrates. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care* (pp. 62–80). Oxford, UK: Oxford University Press.

Beck, C. W. (1998). Mode of fertilization and parental care in anurans. *Animal Behaviour*, *55*, 439–449. https://doi.org/10.1006/anbe.1997.0619

Bickford, D. P. (2004). Differential parental care behaviors of arboreal and terrestrial microhylid frogs from Papua New Guinea. *Behavioral Ecology and Sociobiology*, *55*, 402–409. https://doi.org/10.1007/s00265-003-0717-x

Bivand R., Lewin-Koh, N. (2019). *maptools: Tools for Handling Spatial Objects. R package version 0.9-9*. Retrieved from https://CRAN.R-project.org/package=maptools

Bivand, R., Keitt, T., Rowlingson, B., Pebesma, E., Sumner, M., Hijmans, R., … Bivand, M. R. (2015). *Package "rgdal". Bindings for the geospatial data abstraction library*. Retrieved from https://cran.r-project.org/web/packages/rgdal/index.html

Brown, J. L., Morales, V., & Summers, K. (2010). A key ecological trait drove the evolution of biparental care and monogamy in an amphibian. *The American Naturalist*, *175*, 436–446. https://doi.org/10.1086/650727

Bustnes, J. O., & Erikstad, K. E. (1991). Parental care in the common eider (*Somateria mollisima*): Factors affecting abandonment and abortion of the young. *Canadian Journal of Zoology*, *68*, 1538–1545.

Byrne, P. G., Roberts, J. D., & Simmons, L. W. (2002). Sperm competition selects for increased testes mass in Australian frogs. *Journal of Evolutionary Biology*, *15*, 347–355. https://doi.org/10.1046/j.1420-9101.2002.00409.x

Chuang, M.-F., Lee, W.-H., Sun, J.-S., You, C.-H., Kam, Y.-C., & Poo, S. (2017). Predation risk and breeding site value determine behavior and indirectly affect survivorship of their offspring. *Behavioral Ecology and Sociobiology*, *71*, 122.

Clough, M., & Summers, K. (2000). Phylogenetic systematics and biogeography of the poison frogs: Evidence from mitochondrial DNA sequences. *Biological Journal of the Linnean Society*, *70*, 515–540. https://doi.org/10.1111/j.1095-8312.2000.tb01236.x

Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton: Princeton University Press.

Cornwallis, C. K., Botero, C. A., Rubenstein, D. R., Downing, P. A., West, S. A., & Griffin, A. S. (2017). Cooperation facilitates the colonization of harsh environments. *Nature Ecology and Evolution*, *1*, 0057. https://doi.org/10.1038/s41559-016-0057

Crump, M. L. (1996). Parental care among the Amphibia. *Advances in the Study of Behavior*, *25*, 109–144.

Davies, N. B., & Halliday, T. R. (1978). Deep croaks and fighting assessment in the toad *Bufo bufo*. *Nature*, *274*, 683–685.

Delia, J., Bravo-Valencia, L., & Warkentin, K. M. (2017). Patterns of parental care in Neotropical glassfrogs: Fieldwork alters hypotheses of sex-role evolution. *Journal of Evolutionary Biology*, *30*, 898–914. https://doi.org/10.1111/jeb.13059

Duellman, W. E., & Trueb, L. (1986). *Biology of amphibians*. New York, NY: McGraw-Hill.

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection and the evolution of mating systems. *Science*, *197*, 215–223. https://doi.org/10.1126/science.327542

Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic analysis and comparative data: A test and review of evidence. *The American Naturalist*, *160*, 712–726. https://doi.org/10.1086/343873

Furness, A. I., & Capellini, I. (2019). The evolution of parental care diversity in amphibians. *Nature Communications*, *10*, 4709. https://doi.org/10.1038/s41467-019-12608-5

Gilbert, J. D. J., & Manica, A. (2010). Parental care trade-offs and life-history relationships in insects. *The American Naturalist*, *176*, 212–226. https://doi.org/10.1086/653661

Gomez-Mestre, I., Pyron, R. A., & Wiens, J. J. (2012). Phylogenetic analyses reveal unexpected patterns in the evolution of reproductive modes in frogs. *Evolution*, *66*, 3687–3700. https://doi.org/10.1111/j.1558-5646.2012.01715.x

González-del-Pliego, P., Freckleton, R. P., Edwards, D. P., Koo, M. S., Scheffers, B. R., Pyron, R. A., & Jetz, W. (2019). Phylogenetic and trait-based prediction of extinction risk for data-deficient amphibians. *Current Biology*, *29*, 1557–1563. https://doi.org/10.1016/j.cub.2019.04.005

Grant, P. R., & Grant, B. R. (2019). Adult sex ratio influences mate choice in Darwin's finches. *Proceedings of the National Academy of Sciences USA*, *116*, 12373–12382. https://doi.org/10.1073/pnas.1903838116

Han, X., & Fu, J. (2013). Does life history shape sexual size dimorphism in anurans? A comparative analysis. *BMC Evolutionary Biology*, *13*, 27. https://doi.org/10.1186/1471-2148-13-27

Hettyey, A., Vági, B., Kovács, T., Ujszegi, J., Katona, P., Szederkényi, M., … Hoi, H. (2014). Reproductive interference between *Rana dalmatina* and *R. temporaria* affects reproductive success in natural populations. *Oecologia*, *176*, 457–464.

Heyer, H. R. (1969). The adaptive ecology of the genus *Leptodactylus* (Amphibia, Leptodactylidae). *Evolution*, *23*, 421–428.

Hijmans, R. J. (2019). *raster: Geographic Data Analysis and Modeling. R package version 3.0-7*. R package. https://CRAN.R-project.org/package=raster

Ho, L. S. T., & Ane, C. & van der (2018). A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology*, *63*, 397–408. https://cran.r-project.org/web/packages/phylolm2018

Hopkins, K., Moss, B. R., & Gill, A. B. (2011). Increased ambient temperature alters the parental care behaviour and reproductive success of the three-spined stickleback (*Gasterosteus aculeatus*). *Environmental Biology of Fishes*, *90*, 121–129. https://doi.org/10.1007/s10641-010-9724-8

Jetz, W., & Pyron, R. A. (2018). The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature Ecology and Evolution*, *2*, 850–858. https://doi.org/10.1038/s41559-018-0515-5

Kokko, H., & Jennions, M. D. (2008). Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology*, *21*, 919–948. https://doi.org/10.1111/j.1420-9101.2008.01540.x

Kolm, N., & Ahnesjö, I. (2005). Do egg size and parental care coevolve in fishes?*Journal of Fish Biology*, *66*, 1499–1515. https://doi.org/10.1111/j.0022-1112.2005.00777.x

Kusano, T., Toda, M., & Fukuyama, K. (1991). Testes size and breeding systems in Japanese anurans with special reference to large testes in the treefrog, *Rhacophorus arboreus*. *Behavioral Ecology and Sociobiology*, *29*, 27–31.

Le Galliard, J. F., Fitze, P. S., Ferriere, R., & Clobert, J. (2005). Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences USA*, *102*, 18231–18236. Retrieved from https://www.pnas.org/content/102/50/18231.short

Lhotka, O., Kyselý, J., & Farda, A. (2018). Climate change scenarios of heat waves in Central Europe and their uncertainties. *Theoretical and Applied Climatology*, *131*, 1043–1054. https://doi.org/10.1007/s00704-016-2031-3

Liedtke, H. C., Müller, H., Hafner, J., Penner, J., Gower, D. J., Mazuch, T., … Loader, S. P. (2017). Terrestrial reproduction as an adaptation to steep terrain in African toads. *Proceedings of the Royal Society London B: Biological Sciences*, *284*, 20162598.

Liker, A., Freckleton, R. P., & Székely, T. (2013). The evolution of sex roles in birds is related to adult sex ratio. *Nature Communications*, *4*, 1587. https://doi.org/10.1038/ncomms2600

Liker, A., Freckleton, R. P., & Székely, T. (2014). Divorce and infidelity are associated with skewed adult sex ratios in birds. *Current Biology*, *24*, 880–884. https://doi.org/10.1016/j.cub.2014.02.059

Lion, M. B., Mazzochini, G. G., Garda, A. A., Lee, M. T., Bickford, D., Costa, G. C., & Fonseca, C. R. (2019). Global patterns of terrestriality in amphibian reproduction. *Global Ecology and Biogeography*, *28*, 744–756. https://doi.org/10.1111/geb.12886

Machado, G., Buzatto, B. A., García-Hernández, S., & Macías-Ordóñez, R. (2016). Macroecology of sexual selection: A predictive conceptual framework for large-scale variations in reproductive traits. *The American Naturalist*, *188*(S1), S8–S27.

Mank, J. E., Promislow, D. E. L., & Avise, J. C. (2005). Phylogenetic perspectives in the evolution of parental care in ray-finned fishes. *Evolution*, *59*, 1570–1578. https://doi.org/10.1111/j.0014-3820.2005.tb01806.x

Martin, K. L., & Carter, A. L. (2013). Brave new propagules: Terrestrial embryos in anamniotic eggs. *Integrative and Comparative Biology*, *53*, 233–247. https://doi.org/10.1093/icb/ict018

Martins, E. P., & Hansen, T. F. (1997). Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist*, *149*, 646–667. https://doi.org/10.1086/286013

Martins, M., Pombal, J. P., & Haddad, C. F. B. (1998). Escalated aggressive behaviour and facultative parental care in the nest building gladiator frog, *Hyla faber*. *Amphibia-Reptilia*, *19*, 65–73. https://doi.org/10.1163/156853898X00331

Matsui, M. (1989). Breeding strategy in the Japanese common toad, *Bufo japonicus*. In M. Matsui, H. Hikida, & R. C. Goris (Eds.), *Current herpetology in East Asia* (pp. 332–341). Kyoto, Japan: Herpetological Society of Japan.

McGraw, L., Székely, T., & Young, L. J. (2010). Pair bonds and parental behaviour. In T. Székely, A. J. Moore, & J. Komdeur (Eds.), *Social behaviour: Genes, ecology and evolution* (pp. 271–301). Cambridge, UK: Cambridge University Press.

McNamara, J. M., Székely, T., Webb, J. N., & Houston, A. I. (2000). A dynamic game-theoretic model of parental care. *Journal of Theoretical Biology*, *205*, 605–623.

Meegaskumbura, M., Senevirathne, G., Biju, S. D., Garg, S., Meegaskumbura, S., Pethiyagoda, R., … Schneider, C. J. (2015).

Patterns of reproductive mode evolution in old world tree frogs (Anura, Rhacophoridae). *Zoologica Scripta*, *44*, 509–522. https://doi.org/10.1111/zsc.12121

Monnet, J. M., & Cherry, M. I. (2002). Sexual size dimorphism in anurans. *Proceedings of the Royal Society B: Biological Sciences*, *269*, 2301–2307.

Öberg, M., Arlt, D., Pärt, T., Laugen, A. T., Eggers, S., & Low, M. (2015). Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. *Ecology and Evolution*, *5*, 345–356. https://doi.org/10.1002/ece3.1345

Orme, D., Freckleton, R. P., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2018). *caper: Comparative Analyses of Phylogenetics and Evolution in R. R package version 1.0.1*. R package v.5. Retrieved from https://CRAN.R-project.org/package=caper

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*, 877–884. https://doi.org/10.1038/44766

Pereira, E. B., Pinto-Ledesma, P. N., Gomez de Freitas, C., Villalobos, F., Garcia Colevatti, R., & Medeiros Marciel, N. (2017). Evolution of anuran foam nest: Trait conservatism and lineage diversification. *Biological Journal of the Linnean Society*, *122*, 814–823.

Poo, S., & Bickford, D. P. (2013). The adaptive significance of egg attendance in a South-East Asian tree frog. *Ethology*, *119*, 671–679. https://doi.org/10.1111/eth.12108

Pyron, R. A. (2014). Biogeographical analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. *Systematic Biology*, *63*, 779–797.

R Core Team (2019). *R: A language and environment for statistical computing*, Vienna, Austria: R Foundation for Statistical Computing. Version 3.1.0. Retrieved from http://www.R-project.org/

Rausch, A. M., Sztatecsny, M., Jehle, R., Ringler, E., & Hödl, W. (2014). Male body size and parental relatedness but not nuptial colouration influence paternity success during scramble competition in *Rana arvalis*. *Behaviour*, *151*, 1869–1884.

Remes, V., Freckleton, R. P., Tökölyi, J., Liker, A., & Székely, T. (2015). The evolution of parental cooperation in birds. *Proceedings of the National Academy of Sciences USA*, *112*, 12603–13608.

Reynolds, J. D. (1996). Animal breeding systems. *Trends in Ecology and Evolution*, *11*, 68–72. https://doi.org/10.1016/0169-5347(96)81045-7

Reynolds, J. D., Goodwin, N. B., & Freckleton, R. P. (2002). Evolutionary transitions in parental care and live bearing in vertebrates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*, 269–281. https://doi.org/10.1098/rstb.2001.0930

Ringler, E., Pašukonis, A., Tecumseh Fitch, W., Huber, L., Hödl, W., & Ringler, M. (2015). Flexible compensation of uniparental care: Female poison frogs take over when males disappear. *Behavioural Ecology*, *26*, 1219–1225. https://doi.org/10.1093/beheco/arv069

Roberts, J. D., Standish, R. J., Byrne, P. G., & Doughty, P. (1999). Synchronous polyandry and multiple paternity in the frog *Crinia georgiana* (Anura: Myobatrachidae). *Animal Behaviour*, *57*, 721–726. https://doi.org/10.1006/anbe.1998.1019

Royle, N. J., Smiseth, P. T., & Kölliker, M. (2012). The evolution of parental care: Summary, conclusions and implications. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care* (pp. 327–343). Oxford, UK: Oxford University Press.

Rubenstein, D. R., & Lovette, I. J. (2007). Temporal environmental variability drives the evolution of cooperative breeding in birds. *Current Biology*, *17*, 1414–1419. https://doi.org/10.1016/j.cub.2007.07.032

Salthe, S. N., & Mecham, J. S. (1974). Reproduction and courtship patterns. In B. Lofts (Ed.), *Physiology of the Amphibia* (Vol. 2, pp. 309–521). New York, NY: Academic Press.

Schäfer, M., Tsekané, S. J., Tchassem, F. A. M., Drakulić, S., Kameni, M., Gonwouo, N. L., & Rödel, M.-O. (2019). Goilath frogs build nests for spawning – the reason for their gigantism?*Journal of Natural History*, *53*, 1263–1276.

Schulte, L. M., & Lötters, S. (2013). The power of the seasons: Rainfall triggers parental care in poison frogs. *Evolutionary Ecology*, *27*, 711–723. https://doi.org/10.1007/s10682-013-9637-z

Shine, R. (1978). Propagule size and parental care: The "safe harbour" hypothesis. *Journal of Theoretical Biology*, *75*, 417–424.

Shine, R. (1989). Alternative models for the evolution of offspring size. *The American Naturalist*, *134*, 311–317. https://doi.org/10.1086/284982

Simon, M. P. (1983). The ecology of parental care in a terrestrial breeding frog from New Guinea. *Behavioral Ecology and Sociobiology*, *14*, 61–67. https://doi.org/10.1007/BF00366657

Summers, K., McKeon, C. S., & Heying, H. (2006). The evolution of parental care and egg size: A comparative analysis on frogs. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 687–692.

Suski, C. D., & Ridgway, M. S. (2007). Climate and body size influence nest survival in a fish with parental care. *Journal of Animal Ecology*, *76*, 730–739. https://doi.org/10.1111/j.1365-2656.2007.01242.x

Sutton, F. B., & Wilson, A. B. (2019). Where are all the mums? External fertilization predicts the rise of male parental care in bony fish. *Evolution*, *72*, 2451–2460.

Székely, T., Webb, J. N., Houston, A. I., & McNamara, J. M. (1996). An evolutionary approach to offspring desertion in birds. In V. Nolan, & E. D. Ketterson (Eds.), *Current ornithology* (Vol. 13, pp. 271–330). Boston, MA: Springer.

Székely, T., Weissing, F. J., & Komdeur, J. (2014). Adult sex ratio variation: Implications for breeding system evolution. *Journal of Evolutionary Biology*, *27*, 1500–1512. https://doi.org/10.1111/jeb.12415

Terhivuo, J. (1988). Phenology of spawning of the common frog (*Rana temporaria* L.) in Finland from 1846 to 1986. *Annales Zoologici Fennici*, *25*, 165–175.

Trumbo, S. T. (2012). Patterns of parental care in invertebrates. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care* (pp. 81–100). Oxford, UK: Oxford University Press.

Udvardy, M. D. F. (1975). A classification of the biogeographical provinces of the world. In: *Man and the biosphere programme*. Project N.8. IUCN Occasional Paper N.18. Morges, Switzerland: International Union for Conservation of Nature and Natural Resources.

Vági, B., & Hettyey, A. (2016). Intraspecific and interspecific competition for mates: *Rana temporaria* males are effective satyrs of *Rana dalmatina* females. *Behavioral Ecology and Sociobiology*, *70*, 1477–1484. https://doi.org/10.1007/s00265-016-2156-5

Vági, B., Végvári, Z., Liker, A., Freckleton, R. P., & Székely, T. (2019). Terrestriality and the evolution of parental care in frogs. *Proceedings of the Royal Society B: Biological Sciences*, *286*, 20182737.

Vincze, O., Kosztolányi, A., Barta, Z., Küpper, C., Alrashidi, M., Amat, J. A., … Székely, T. (2017). Parental cooperation in a changing climate: Fluctuating environments predict shifts in care division. *Global Ecology and Biogeography*, *26*, 347–385. https://doi.org/10.1111/geb.12540

Visser, M. E., vanNoordwijk, A. J., Tinbergen, J. M., & Lessells, C. M. (1998). Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society B: Biological Sciences*, *265*, 1867–1870. https://doi.org/10.1098/rspb.1998.0514

Wells, K. D. (1977). The social behaviour of anuran amphibians. *Animal Behaviour*, *25*, 666–693. https://doi.org/10.1016/0003-3472(77)90118-X

Wells, K. D. (2007). *The ecology and behaviour of amphibians*. Chicago, IL and London, UK: Univ. of Chicago Press.

West, H. E. R., & Capellini, I. (2016). Male care and life history traits in mammal. *Nature Communications*, *7*, 11854.

Williams, G. C. (1975). *Sex and evolution*. Princeton, NJ: Princeton University Press.

Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge, MA: Harvard University Press.

Zamudio, K. R., Bell, R. C., Nali, R. C., Haddad, C. F. B., & Prado, C. P. A. (2016). Polyandry, predation and the evolution of frog reproductive modes. *The American Naturalist*, *188*, S41–S61. https://doi.org/10.1086/687547

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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