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Research

Parental care and the evolution of terrestriality in frogs

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1   Frogs and toads (Anura) exhibit some of the most diverse parental strategies in vertebrates. Identifying

2   the evolutionary origins of parenting is fundamental to understanding the relationships between sexual

3   selection, social evolution and parental care systems of contemporary Anura. Moreover, parenting has

4   been hypothesized to allow the invasion of terrestrial habitats by the ancestors of terrestrial vertebrates.

5   Using comprehensive phylogenetic analyses of frogs and toads based on data from over 1000 species that

6   represent 46 out of 55 Anura families, we test whether parental care is associated with terrestrial

7   reproduction and several life history traits. Here we show that both the duration of care and offspring

8   protection by males and females have co-evolved with terrestrial reproduction. Sexual size dimorphism is

9   also related to care, since large male size relative to female size is associated with increased paternal care.

10   Furthermore, increased egg size and reduced clutch volume are associated with increased care in bivariate

11   but not in multivariate analyses, suggesting that the relationships between care, egg size and clutch volume

12   are mediated by terrestrial reproduction. Taken together, our results suggest that parenting by males and

13   females has co-evolved, and complex parenting traits have evolved several times independently in Anura in

14   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 caregiving 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 has been extensively investigated in experimental and game-theoretic analyses of social interactions [14–16]. Since 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

48 addition, several frogs show extensive post-hatch care by carrying the tadpoles (or froglets) on their

49 backs or in specialized brooding organs [21,23]. Terrestrially reproducing frogs may have endotrophic

50 larvae that develop in a protected chamber, or directly developing embryos which skip larval phase and

51 hatch as fully-developed froglets [5,13]. These offspring rely upon parental provisions until they reach

52 the next stage of their development (e.g., metamorphosis, hatching or birth). Consequently, anurans

53 may enhance offspring care by extending the duration of care, by providing more protection for the

54 offspring and/or by increasing nutrient provisioning in nutrient-scarce environments. These behaviours

55 enable the offspring to spend a longer period of their development in a safe place [18,24,25].

56   Here we investigate three hypothesized drivers of parental care. We focus on the evolution of

57 care by scoring aspects of care on a finer scale and, to our knowledge, we present the most detailed

58 phylogenetic analyses of parenting in any taxa. First, we test whether terrestrial vs aquatic reproduction

59 relates to different care types, since caring is expected to provide protection against hostile

60 environments [5,10,13]. Second, we investigate whether life history variables including egg size and

61 clutch size correlate with the duration of care, protection and nourishment provided by any of the

62 parents. Specifically, we hypothesize that large eggs are associated with longer care and more

63 protection than small eggs [1,5,26]. Third, sexual selection has been linked to parental care since

64 Trivers' [27] seminal idea (reviewed by [1,9,28]), therefore we also investigate whether intense sexual

65 selection is associated with reduced care provisioning [29–31]. We use sexual size dimorphism (SSD)

66 as a proxy for the intensity of sexual selection [30,31]. Note that SSD as an indicator of sexual selection

67 has been debated in frogs, since SSD may reflect selections acting on females, e.g. to increase

68 fecundity [32–34]. Nonetheless, large size in males is associated with high reproductive success in

69 several species of frogs (reviewed by [5,35]) due to competition for mates or female choice [36–39], with

70 the latter processes being clearly linked to sexual selection.

71   To address these objectives, we use a comprehensive dataset that represents 46 out of 55 extant

72 anuran families. We analyse three main components of care: duration of care, protection of eggs and

73 young, and nutrient transfer to offspring. We consider these separately, because complex social traits

74 such as caring may have multiple components that evolve independently, or traded off against each

75 other and thus respond to different selection pressures [40–43]. Second, instead of combining male-only

76 care, female-only care and biparental care into a single variable (for instance, presence or absence of

77 care by either parent), we treat care by males and females separately, since ecological and life-history

78 variables may exert stronger effects on one sex than on the other. For instance, reproductive effort such

79 as egg size and clutch volume may be an important constraint of female care, whereas the intensity of

80 sexual competition may be an important constraint of male care [8,42,43]. Our work demonstrates that

81   these distinctions are important, since some of the relationships between care components and

82   ecological and life history variables differ between males and females.

83

2. Methods

(a) Data collection

86   We compiled the initial dataset from comprehensive phylogenetic comparative publications which

87   contain information on parental care in frogs [8,13,18,26,42,44,45]. Next, we augmented this dataset

88   with data from primary research publications (see Supporting Information), online databases [46,47],

89   and peer-reviewed books [5,48,49]. Our final database holds information from 1044 species; 399 of

90   these species exhibit some form of care. 46 of 55 Anura families are represented in our database that

91   hold approximately 95% of extant species (electronic supplementary material, table S1).

92

(b) Parental care variables

94   We used 4 variables for coding parental care. First, type of care was scored on a five point scale: 0–no

95   care; 1–male-only care; 2–female-only care; 3–biparental care; 4–care either by the male or the female.

96   Because the latter (i.e, uniparental care either by male or female) was reported only from seven

97   species, we excluded these species from the analyses. We considered biparental care if both parents

98   participate in offspring care. In the analysis of the number of care-providing parents, male-only care and

99   female-only care (scores 1 and 2) were combined as uniparental care, whereas score 3 was kept as

100 biparental care.

101   Second, we scored the duration of care based on discrete ontogenetic stages of the offspring

102 (egg, tadpole and juvenile care), and recorded the most advanced stage when a particular caring

103 behaviour has been reported. Care duration was defined as 0–no care; 1–egg care; 2–tadpole care; 3–

104 juvenile care. Care duration was scored separately for males and females.

105   Third, we scored offspring protection as a separate variable on a 6 point scale: 0–no protection;

106 1–offspring protected in a nest but not attended by parent(s); 2–parental attendance; 3–carrying on the

107 back of parent(s); 4–carrying in a closed organ (brooding pouch, dermal invagination, stomach or vocal

108 sack) of parent(s); 5–viviparity. This scoring was based on the logic that protection is more effective

109 when eggs or offspring are enclosed (e.g., in a brooding pouch, stomach, vocal sack, skin invagination)

110 rather than exposed on the back of the parent(s). The highest level of protection appears to be in

111 viviparous species because in these species the offspring only leave the reproductive tract of the mother

112 in a well-developed stage. Protection was scored separately for males and females.

113   Fourth, nourishment was categorized as follows: 0–exotrophic tadpoles feed mainly on external

114   food sources after depleting their yolk provided in the egg; 1–feeding tadpoles by trophic eggs or skin

115   secretion; 2–endotrophic tadpoles and directly developing species (which complete metamorphosis

116   inside the egg) reach metamorphoses nourishing only upon the egg's yolk. Nourishment was only

117   provided by the female except in two species in which the males provision the offspring (*Ecnomiohyla*

118   *rabborum, Rhinoderma darwini* [5,50]). Consequently the latter two species were excluded from the

119   analyses of nourishment.

120   In order to investigate the consistency of our parental care scores with three published datasets

121   that scored parenting as a binary variable (presence/ absence) [13,26,44], we calculated the

122   correlations between these four datasets. The association between our dataset and the three

123   independent datasets were highly significant (electronic supplementary material, table S2).

124

(c) Life-history variables

126   Egg size was defined as the diameter of the egg (vitelline) in millimetres, excluding the gelatinous

127   capsule. Clutch size was defined as the number of eggs laid during one egg-laying event. We use clutch

128   volume (calculated as egg volume in cm^3 multiplied by clutch size) instead of clutch size in bivariate

129   analyses, because clutch volume appears to be a more appropriate indicator of female reproductive

130   expenditure than clutch size alone. However, to separate the potential effects of egg size and clutch

131   size in multivariate analyses, we included egg size and clutch size in the models. Snout-vent length

132   (SVL) was calculated separately for males and females, computed as mean values across all available

133   data for a given species. Body size (mean SVL) was calculated as the average of male and female

134   SVLs (in mm) for each species, whereas sexual size dimorphism was log_{10} (SVL_{male} / SVL_{female}). Clutch

135   size, clutch volume and egg size were transformed to logarithmic scale to ensure homoscedasticity. If

136   several data points were available for a given species, we calculated their arithmetic mean.

137   Terrestrial reproduction and direct development were treated as binary variables (present or

138   absent), following previous classifications [13,21]. Terrestrial reproduction included floating foam nest on

139   water, as in this case the eggs themselves are included in an air-filled chamber, and also viviparity and

140   egg-brooding in different organs (pouches, stomach, vocal sac) provided by terrestrial parents. In

141   contrast, members of the genus *Pipa* which lay eggs in water and brood by aquatic parents were

142   considered aquatic breeders. We established these categories because anuran eggs are adapted

143   primarily to aquatic development and placing them outside water exposing them to hostile conditions,

144   and we considered the strategy for this challenge as an important aspect of parental care.

145

(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 and electronic supplementary material, figure S1). In figure 1a–c we used Grafen-transformed branch lengths for better visualisation.

Anuran phylogenies tend to hold consistent patterns, at least in the topology of deeper nodes [51,52]. Since 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 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 3.1.0 [55]. Importantly, the results using the alternative phylogeny were highly consistent with those of the main phylogeny (see 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 multipredictor 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 ID, see supporting data 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. Due to the lack of variation within clades, three species-poor lineages ('Crown Hyloidea' that includes Alsodidae, Ceratophryidae, Hylodidae, Odontophrynidae and

179 Rhinodermatidae, 12 species in total; Heleophrynidae, 2 species; and Sooglossoidea, 3 species) were

180 excluded from analyses that included higher node as factor. Higher nodes were not included in analyses

181 on trophic egg feeding (Nourishment excluding species in Nourishment category 2) – in this case, most

182 of the clades showed little variance to the trait.

183   We tested multicollinearity between predictors using variance inflation factor (VIF) analysis: all

184 predictors had VIF values less than 5 (VIF_{max} = 2.02). In multiple regression models, we included six

185 predictor variables (see table 1) except in models of nourishment we did not include developmental

186 mode since nourishment and developmental mode were correlated by definition. All analyses were

187 carried out using R 3.1.0 [55] with 'caper' package [60].

188

189 # 3. Results

190 Types of care varied across Anura, with each type of care occuring in several clades (figure 1; electronic

191 supplementary material, table S1). Major clades exhibited substantial variations in sex of care provider,

192 protection and nourishment (figure 1): exceptional diversity was exhibited by five clades that include

193 Eleutherodactylidae, Dendrobatidae, Leptodactylidae and Microhylidae, figure S1).

194   Care duration, protection and nourishment were not different between species with female-only

195 care, male-only care and biparental care (Phylogenetic Generalised Least Squares PGLS, care

196 duration: figure S2, $F_{2,379}$ = 0.716; p = 0.489; protection: $F_{2,375}$ = 0.502; p = 0.610; nourishment: $F_{2,370}$ =

197 0.502; p = 0.426), nor between uniparental and biparental species (PGLS, care duration: $F_{1,387}$ = 0.415;

198 p = 0.520; protection: $F_{1,382}$ = 0.788; p = 0.375; nourishment: $F_{1,378}$ = 1.694; p = 0.194). Thus, males and

199 females provide similar extents of care in anurans. Interestingly, the extent of parental care by males

200 was associated with the extent of female care both in care duration (PGLS; $F_{1,1006}$ = 8.674; p < 0.0001)

201 and protection ($F_{1,1005}$ = 54.58; p < 0.0001).

202   Terrestrial reproduction was a key factor associated with parental care (figure 1). All forms of care

203 were more common in terrestrial taxa than in aquatic ones (figure 2) including protection by males (5.5%

204 and 46.5% of aquatic and terrestrial taxa, respectively), protection by females (1% and 39.0%), and

205 nourishment (5.0% and 34.5%). Terrestrial reproduction was associated with increased levels of care by

206 both males and females (figure 2 and electronic supplementary material, table S3). Consequently, the

207 number of caring parents was significantly higher in terrestrial frogs than in aquatic ones (PGLS; $F_{1,591}$ =

208 80.47; p < 0.0001).

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

210 sexes, and provisioning by the female (figure 3 and electronic supplementary material, table S4).

211 However, since egg size and clutch volume often depend on body size, we also investigated the

212   relationship between egg size, clutch volume and care by including body size as an explanatory variable

213   in phylogenetically corrected models (table S5). When body size was statistically controlled for, neither

214   egg size nor clutch volume remained correlated with care with the exception of nourishment, and small

215   clutch volume remained associated with male care (electronic supplementary material, table S5).

216   Sexual size dimorphism was associated with male care but not female care (electronic

217   supplementary material, table S4 and figure S3). However, male care was associated with increased

218   male size relative to female size (table S4). The latter relationship remained significant when absolute

219   body size was controlled for in the analysis (table S5). The latter relationship between size dimorphism

220   and body size suggests that Anura exhibit an allometric relationship between sizes of males and

221   females known as Rensch's rule [44,61] (PGLS; $F_{1,430} = 7.39$; $p = 0.007$).

222   Terrestrial reproduction remained the main predictor of both care duration and offspring

223   protection in multipredictor analyses, but not for nourishment (table 1). These results suggest that the

224   relationships between life history and care we uncovered using bivariate analyses (electronic

225   supplementary material, table S4) may be mediated by terrestrial reproduction. Nevertheless, in multi-

226   predictor models male-biased size dimorphism remained associated with male care (table 1), and

227   nourishment remained associated with clutch size and body size.

228   Trophic egg feeding (i.e, exotrophic tadpoles feed on external food sources versus tadpoles fed

229   by trophic eggs or skin secretion) was associated with sexual dimorphism and clutch volume (electronic

230   supplementary material, tables S3–S4), and these relationships remained significant after controlling for

231   body size (table S5, S6).

232

4. Discussion

234   Our comprehensive phylogenetic analyses of the extent of male and female care show that care is

235   extremely variable both within and among major clades of frogs. Not only the presence or absence of

236   care varies – that has been uncovered by previous studies [18,26] – but also the type and duration of

237   care are highly variable. In contrast to reptiles and mammals, in which the females are the main care

238   provider, or to birds in which biparental care is the predominant form of care [9,62], in frogs female-only,

239   male-only and biparental care are all widespread among various lineages, and the involvement of males

240   and females in care is comparable. Because in ~20% of newts and salamanders (urodeles) one of the

241   parents guards the eggs or the offspring [5,9,63,64], and caecilians in which females feed their offspring

242   using an excretion of their skin [65,66], the overall richness of caring is spectacular in amphibians. This

243   suggests that over the course of amniote evolution, the phylogenetically younger tetrapod clades (e.g.,

244   reptiles, birds and mammals) became specialised to a limited set of care patterns [62].

245   Consistently with previous studies [11–13], we found that the transition towards terrestrial

246 reproduction facilitated parental care. Moreover, our work advances the understanding of evolutionary

247 relationships by showing that terrestrial reproduction is related to all forms of both male and female

248 care, except nourishment. Thus, when early tetrapods invaded terrestrial niches, both males and

249 females may have been under the effects of selection forces to improve the survival of their offspring, so

250 that both males and females evolved various forms of care provisioning in response to terrestrial

251 reproduction. Therefore, the subsequent canalization of parental care largely towards females (e.g., in

252 reptiles and mammals) and cooperation by both sexes (in birds) may have been the result of additional

253 selective pressures that the ancestors of these clades faced during their radiation into various ecological

254 niches. This implies that the predominance of maternal care coevolved with internal fertilization [67, but

255 see 68]. In urodeles, where internal fertilization is more frequent, only phylogenetically basal external

256 fertilizers with aquatic reproduction appear to provide paternal care [5,63], although clutch attending by

257 females is widespread especially in those with terrestrial reproduction [63].

258   We also found that egg size and clutch volume are related to parental care, although these

259 associations became non-significant by including terrestriality in the models. On the one hand, terrestrial

260 egg-layers have larger eggs and smaller clutches than aquatically reproducing frogs [8,13,26], which

261 may be predicted by other factors besides parental care, such as selection on offspring size [69] or

262 protection against the hostile environment [11]. However, egg size and clutch size were no longer

263 associated with care duration and protection when body size was statistically controlled. Therefore, the

264 associations between egg size, clutch size and parenting showed by previous studies [8,13,26] may

265 have been mediated by other factors, e.g. body size and/or terrestrial reproduction. On the other hand,

266 increased nutrient transfer to the offspring is associated with reduced clutch size, which seems to be the

267 result of an increased investment to individual offspring [3] traded off against fecundity. Moreover,

268 trophic egg feeding is also associated with reduced egg size [table S6], implying that mothers may

269 reduce the cost egg production using this type of nourishment.

270   Finally, the evolutionary relationship between male care and size dimorphism has been debated

271 [32-34], and our results using fine-scaled care variables, multi-predictor models and more extensive

272 taxonomic coverage than previous studies, confirm that male care is associated with sexual size

273 dimorphism [44]. We suggest two mutually non-exclusive explanations for the increased male size

274 (relative to female size) with the extent of male care. On the one hand, sexual selection may favour

275 larger males in male caring species if females prefer large males and/or large males are more

276 successful in coercive mating [38,39], provided that these males are more successful in nursing the

277 offspring. On the other hand, male care may reduce the fecundity selection pressure on females, so that

278   female size decreases in those species in which the males provide care [44,61]. To distinguish between

279   these scenarios, further experimental and phylogenetic analyses are warranted [9,17].

280   Here we treat parental care as an invariable trait for a given species, although this assumption

281   suits some species better than others. For example, *Allobates femoralis* exhibits variation in parenting

282   since females transport tadpoles but this behaviour is only provoked by the absence of the father that is

283   normally the care-providing parent [41]. Therefore, future phylogenetic analyses should pay attention to

284   the flexibility of care provisioning [41,70]. Care provision can be further tuned by variation in the

285   ecological [25,71,72] or social environment [41], and this plasticity not only enables better adaptation to

286   seasonal and unpredictable changes of the environment, but it may also act as the origin of evolutionary

287   changes in the extent of care [41,45] or in parental roles [41,43,45]. Field-based and laboratory-based

288   studies will likely add more examples for this plasticity and would help in identifying environmental

289   factors which provokes shifts.

290   In summary, parental care is predicted by ecological and life history variables in frogs. Care is a

291   complex social trait and specific aspects of care have different predictors in males and females. Further

292   analyses are needed to investigate the impacts of climate, reproductive modes and mating systems on

293   care strategies. Since new forms of parental care are cropping up [71,72], field-based studies of yet

294   unstudied species are needed to explore breeding systems (including parenting) in frogs that live in

295   remote areas and/or inhabit extreme environments. Taken together, studies of anuran parental care

296   provide important contributions to the understanding of reproduction, evolution and diversification in the

297   most threatened vertebrate class of the Anthropocene.

298

309

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Figure legends

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 guard 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. 0 refers to no care in a particular trait, whereas 3, 5 and 2 refer to the most advanced stage in offspring development in care duration, protection (for males and females separately) and nourishment (for females), respectively.

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 + SD; on the right). Red shades represent female care, blue shades represent male care.

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 electronic supplementary material, table S4–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.

518

519 **Figure 1**
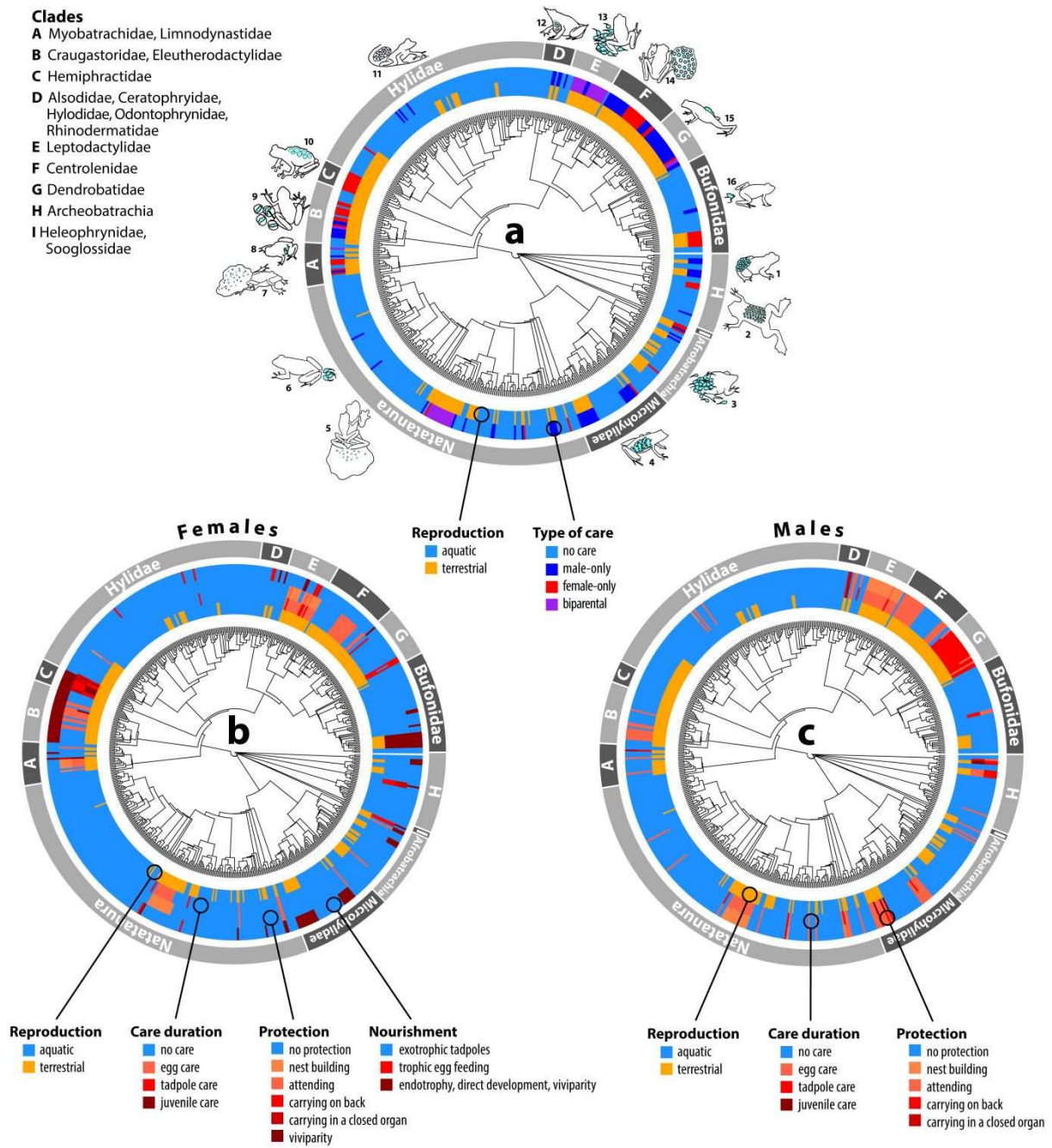
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524 **Figure 2**

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528   **Figure 3**

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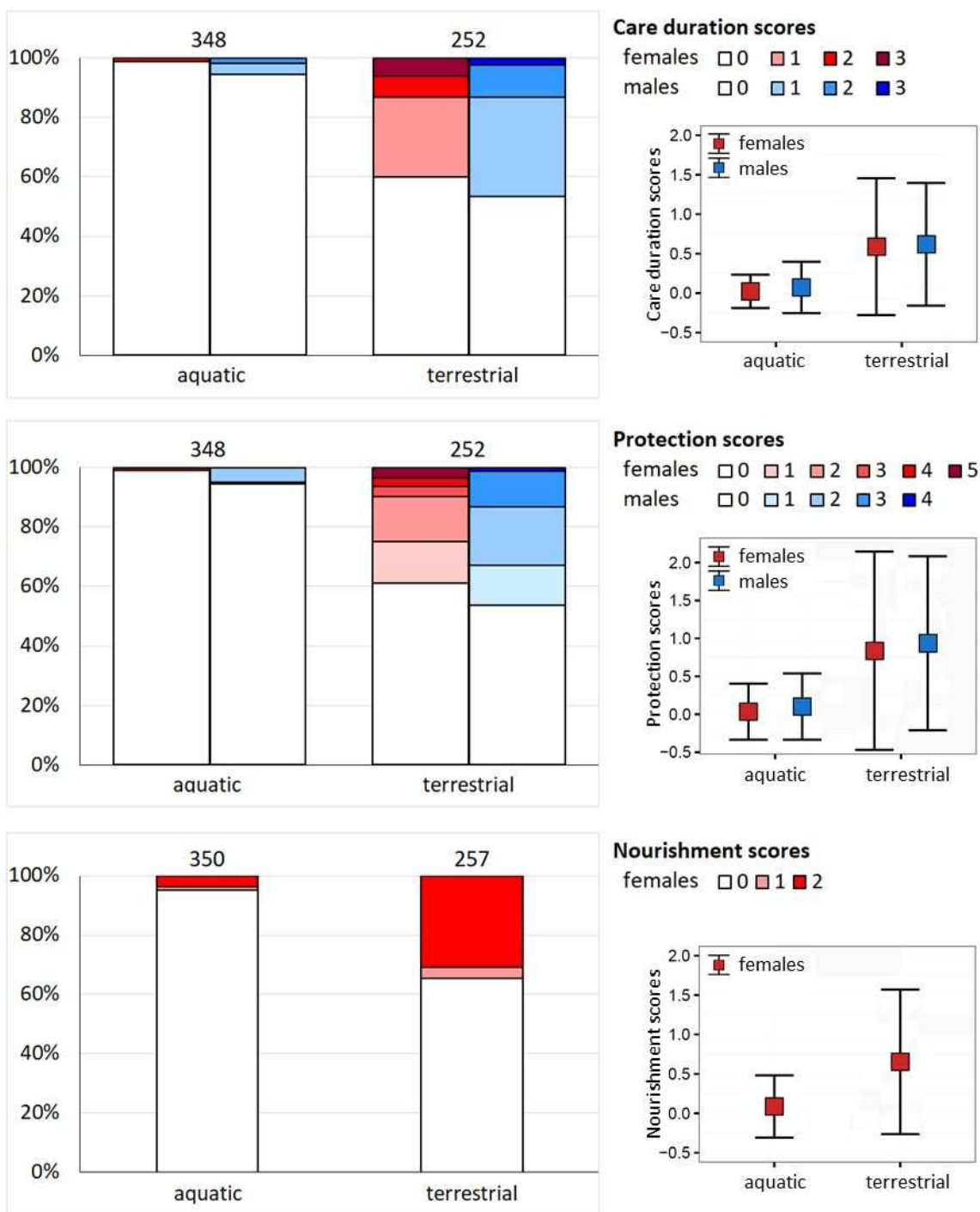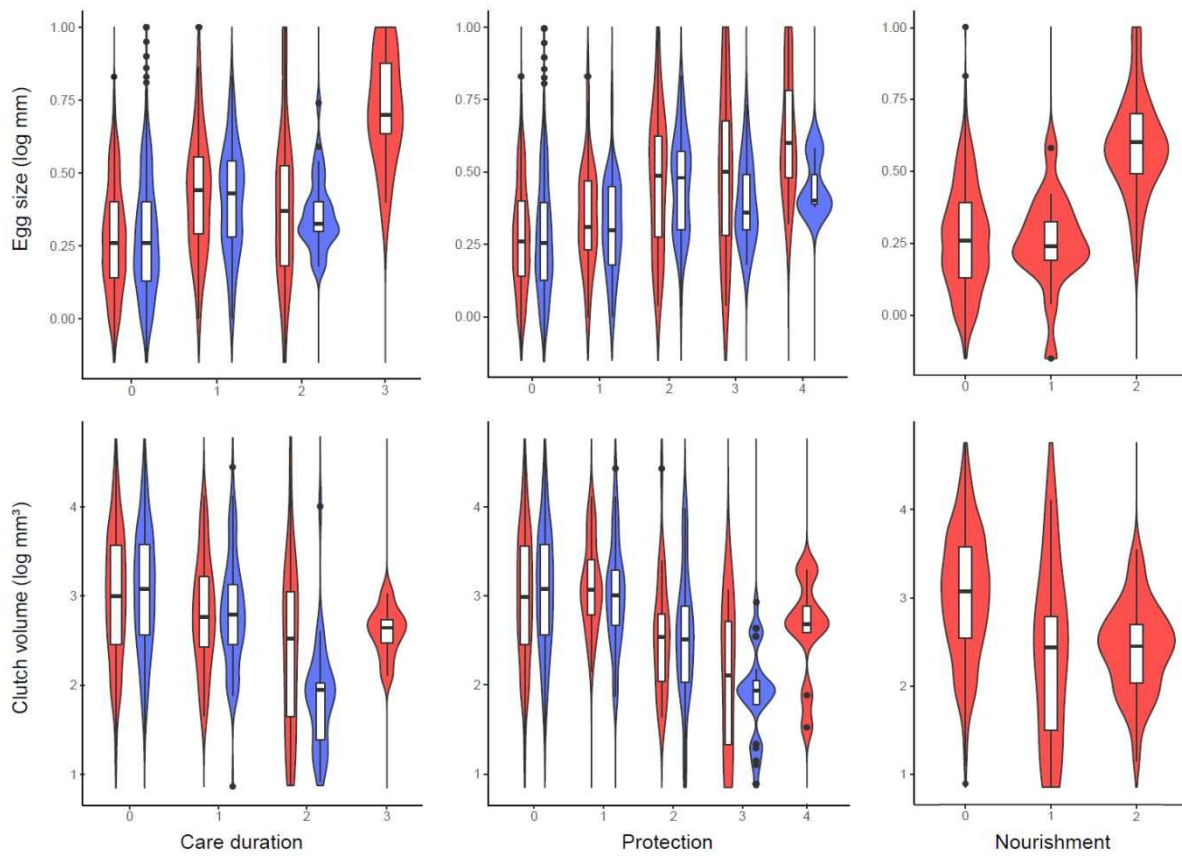
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533   **Table 1.** Parental care in relation to ecology, life-history and sexual dimorphism in Anura using

534   phylogenetically corrected generalized linear squares (PGLS) models. Multipredictor PGLS models for

535   each care variable are provided separately for males and females; note that only females provide

536   nourishment. Higher node was included in the models except for nourishment (see Methods). Italics

537   indicate significant predictors. Egg size is provided as diameter in mm. Clutch volume is calculated as

538   egg volume × clutch size and provided as mm^3. Clutch volume and egg size were log-transformed prior

539   to the analyses. Body size refers to the average snout-vent length (SVL) in mm. Sexual size dimorphism

540   was calculated as $\log_{10}(SVL_{male}/SVL_{female})$. We provide parameter estimates with standard error ($\beta \pm$

541   *SE),* the corresponding *t* and *P* values, and the adjusted R^2 for the model including $F(df_{effect}, df_{error})$ and

542   *P* values, respectively.

Care duration	by females			by males		
	β ± SE	T	P	β ± SE	t	P
Terrestrial reproduction	0.227 ± 0.103	2.209	0.028	0.278 ± 0.093	3.000	0.003
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	1.070 ± 0.376	2.842	0.005
Model	0.155	2.961 (18, 175)	0.0001	0.175	3.254 (18, 174)	< 0.0001

Protection	by females			by males		
	β ± SE	T	P	β ± SE	t	P
Terrestrial reproduction	0.426 ± 0.137	3.113	0.002	0.414 ± 0.158	2.626	0.009
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	2.156 ± 0.701	3.075	0.002
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		
	β ± SE	T	P	β ± SE	t	P
Terrestrial reproduction	0.018 ± 0.098	0.186	0.853	0.014 ± 0.055	0.265	0.792
Clutch size	-0.180 ± 0.053	3.389	< 0.001	-0.066 ± 0.030	2.162	0.032
Egg size	0.119 ± 0.169	0.706	0.481	-0.195 ± 0.097	2.010	0.046

Body size	*0.003 ± 0.001*	*2.043*	*0.042*	*0.003 ± 0.001*	*3.513*	*0.001*
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

Research

Parental care and the evolution of terrestriality in frogs

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Subject Category

Evolution

Subject Areas

behaviour, evolution

1   Frogs and toads (Anura) exhibit some of the most diverse parental strategies in vertebrates. Identifying

2   the evolutionary origins of parenting is fundamental to understanding the relationships between sexual

3   selection, social evolution and parental care systems of contemporary Anura. Moreover, parenting has

4   been hypothesized to allow the invasion of terrestrial habitats by the ancestors of terrestrial vertebrates.

5   Using comprehensive phylogenetic analyses of frogs and toads based on data from over 1000 species that

6   represent 46 out of 55 Anura families, we test whether parental care is associated with terrestrial

7   reproduction and several life history traits. Here we show that both the duration of care and offspring

8   protection by males and females have co-evolved with terrestrial reproduction. Sexual size dimorphism is

9   also related to care, since large male size relative to female size is associated with increased paternal care.

10   Furthermore, increased egg size and reduced clutch volume are associated with increased care in bivariate

11   but not in multivariate analyses, suggesting that the relationships between care, egg size and clutch volume

12   are mediated by terrestrial reproduction. Taken together, our results suggest that parenting by males and

13   females has co-evolved, and complex parenting traits have evolved several times independently in Anura in

14   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 caregiving 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 has been extensively investigated in experimental and game-theoretic analyses of social interactions [14–16]. Since 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 ~~class~~ 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

48   addition, several frogs show extensive post-hatch care by carrying the tadpoles (or froglets) on their

49   backs or in specialized brooding organs [21,23]. Terrestrially reproducing frogs may have endotrophic

50   larvae that develop in a protected chamber, or directly developing embryos which skip larval phase and

51   hatch as fully-developed froglets [5,13]. These offspring rely upon parental provisions until they reach

52   the next stage of their development (e.g., metamorphosis, hatching or birth). Consequently, anurans

53   may enhance offspring care by extending the duration of care, by providing more protection for the

54   offspring and/or by increasing nutrient provisioning in nutrient-scarce environments. These behaviours

55   enable the offspring to spend a longer period of their development in a safe place [18,24,25].

56   Here we investigate three hypothesized drivers of parental care. We focus on the evolution of

57   care by scoring aspects of care on a finer scale and, to our knowledge, we present the most detailed

58   phylogenetic analyses of parenting in any taxa. First, we test whether terrestrial vs aquatic reproduction

59   relates to different care types, since caring is expected to provide protection against hostile

60   environments [5,10,13]. Second, we investigate whether life history variables including egg size and

61   clutch size correlate with the duration of care, protection and nourishment provided by any of the

62   parents. Specifically, we hypothesize that large eggs are associated with longer care and more

63   protection than small eggs [1,5,26]. Third, sexual selection has been linked to parental care since

64   Trivers' [27] seminal idea (reviewed by [1,9,28]), therefore we also investigate whether intense sexual

65   selection is associated with reduced care provisioning [29–31]. We use sexual size dimorphism (SSD)

66   as a proxy for the intensity of sexual selection [30,31]. Note that SSD as an indicator of sexual selection

67   has been debated in frogs, since SSD may reflect selections acting on females, e.g. to increase

68   fecundity [32–34]. Nonetheless, large size in males is associated with high reproductive success in

69   several species of frogs (reviewed by [5,35]) due to competition for mates or female choice [36–39], with

70   the latter processes being clearly linked to sexual selection.

71   To address these objectives, we use a comprehensive dataset that represents 46 out of 55 extant

72   anuran families. We analyse three main components of care: duration of care, protection of eggs and

73   young, and nutrient transfer to offspring. We consider these separately, because complex social traits

74   such as caring may have multiple components that evolve independently, or traded off against each

75   other and thus respond to different selection pressures [40–43]. Second, instead of combining male-only

76   care, female-only care and biparental care into a single variable (for instance, presence or absence of

77   care by either parent), we treat care by males and females separately, since ecological and life-history

78   variables may exert stronger effects on one sex than on the other. For instance, reproductive effort such

79   as egg size and clutch volume may be an important constraint of female care, whereas the intensity of

80   sexual competition may be an important constraint of male care [8,42,43]. Our work demonstrates that

81   these distinctions are important, since some of the relationships between care components and

82   ecological and life history variables differ between males and females.

83

2. Methods

(a) Data collection

86   We compiled the initial dataset from comprehensive phylogenetic comparative publications which

87   contain information on parental care in frogs [8,13,18,26,42,44,45]. Next, we augmented this dataset

88   with data from primary research publications (see Supporting Information), online databases [46,47],

89   and peer-reviewed books [5,48,49]. Our final database holds information from 1044 species; 399 of

90   these species exhibit some form of care. 46 of 55 Anura families are represented in our database that

91   hold approximately 95% of extant species (electronic supplementary material, table S1).

92

(b) Parental care variables

94   We used 4 variables for coding parental care. First, type of care was scored on a five point scale: 0–no

95   care; 1–male-only care; 2–female-only care; 3–biparental care; 4–care either by the male or the female.

96   Because the latter (i.e, uniparental care either by male or female) was reported only from seven

97   species, we excluded these species from the analyses. We considered biparental care if both parents

98   participate in offspring care. In the analysis of the number of care-providing parents, male-only care and

99   female-only care (scores 1 and 2) were combined as uniparental care, whereas score 3 was kept as

100   biparental care.

101   Second, we scored the duration of care based on discrete ontogenetic stages of the offspring

102   (egg, tadpole and juvenile care), and recorded the most advanced stage when a particular caring

103   behaviour has been reported. Care duration was defined as 0–no care; 1–egg care; 2–tadpole care; 3–

104   juvenile care. Care duration was scored separately for males and females.

105   Third, we scored offspring protection as a separate variable on a 6 point scale: 0–no protection;

106   1–offspring protected in a nest but not attended by parent(s); 2–parental attendance; 3–carrying on the

107   back of parent(s); 4–carrying in a closed organ (brooding pouch, dermal invagination, stomach or vocal

108   sack) of parent(s); 5–viviparity. This scoring was based on the logic that protection is more effective

109   when eggs or offspring are enclosed (e.g., in a brooding pouch, stomach, vocal sack, skin invagination)

110   rather than exposed on the back of the parent(s). The highest level of protection appears to be in

111   viviparous species because in these species the offspring only leave the reproductive tract of the mother

112   in a well-developed stage. Protection was scored separately for males and females.

113   Fourth, nourishment was categorized as follows: 0–exotrophic tadpoles feed mainly on external

114   food sources after depleting their yolk provided in the egg; 1–feeding tadpoles by trophic eggs or skin

115   secretion; 2–endotrophic tadpoles and directly developing species (which complete metamorphosis

116   inside the egg) reach metamorphoses nourishing only upon the egg's yolk. Nourishment was only

117   provided by the female except in two species in which the males provision the offspring (*Ecnomiohyla*

118   *rabborum, Rhinoderma darwini* [5,50]). Consequently the latter two species were excluded from the

119   analyses of nourishment.

120   In order to investigate the consistency of our parental care scores with three published datasets

121   that scored parenting as a binary variable (presence/ absence) [13,26,44], we calculated the

122   correlations between these four datasets. The association between our dataset and the three

123   independent datasets were highly significant (electronic supplementary material, table S2).

124

(c) Life-history variables

126   Egg size was defined as the diameter of the egg (vitelline) in millimetres, excluding the gelatinous

127   capsule. Clutch size was defined as the number of eggs laid during one egg-laying event. We use clutch

128   volume (calculated as egg volume in cm^3 multiplied by clutch size) instead of clutch size in bivariate

129   analyses, because clutch volume appears to be a more appropriate indicator of female reproductive

130   expenditure than clutch size alone. However, to separate the potential effects of egg size and clutch

131   size in multivariate analyses, we included egg size and clutch size in the models. Snout-vent length

132   (SVL) was calculated separately for males and females, computed as mean values across all available

133   data for a given species. Body size (mean SVL) was calculated as the average of male and female

134   SVLs (in mm) for each species, whereas sexual size dimorphism was $\log_{10} (SVL_{male} / SVL_{female})$. Clutch

135   size, clutch volume and egg size were transformed to logarithmic scale to ensure homoscedasticity. If

136   several data points were available for a given species, we calculated their arithmetic mean.

137   Terrestrial reproduction and direct development were treated as binary variables (present or

138   absent), following previous classifications [13,21]. Terrestrial reproduction included floating foam nest on

139   water, as in this case the eggs themselves are ~~in~~ included in an air-filled chamber, and also viviparity

140   and egg-brooding in different organs (pouches, stomach, vocal sac) provided by terrestrial parents. In

141   contrast, members of the genus *Pipa* which lay eggs in water and brood by aquatic parents were

142   considered aquatic breeders. We established these categories because anuran eggs are adapted

143   primarily to aquatic development and placing them outside water exposing them to hostile conditions,

144   and we considered the strategy for this challenge as an important aspect of parental care.~~We scored~~

145   ~~reproduction as aquatic when the eggs are laid in water (including foam nests floating on water surface),~~

146   ~~and terrestrial when eggs are deposited in a terrestrial environment. The latter included species with~~

147   ~~internal brooding and viviparity.~~

148

149   ## (d) Phylogeny

150   We used a comprehensive amphibian phylogenetic tree (the consensus tree from [51]) which included

151   the majority of species in our database. Archaeobatrachians were treated as all anurans outside the

152   Neobatrachia clade, and basal Neobatrachians as all Neobatrachians outside the Hyloidea and

153   Ranoidea clade (figure 1 and electronic supplementary material, figure S1). In figure 1a–c we used

154   Grafen-transformed branch lengths for better visualisation.

155   Anuran phylogenies tend to hold consistent patterns, at least in the topology of deeper nodes

156   [51,52]. Since most variation in care is between genera and families, our results appear to be robust to

157   different phylogenetic hypotheses. Nonetheless, to check the sensitivity of our results to alternative

158   phylogenies, we re-analysed the major models using an alternative tree: a composite tree based on

159   [53]. We augmented the latter tree [53] with 145 additional species inserted next to their closest species

160   (whenever known), based on recent phylogenetic information. Nodes were collapsed to polytomies

161   when no further information was available on the phylogenetic relationships within a genus. The species

162   we added manually are listed in electronic supplementary material, table S7, along with the references

163   for their phylogenetic relationships. We use the branch lengths of the original trees [51,53]. In composite

164   phylogeny we assumed half branch length for the new species we included using 'phytools' package

165   [54] in R 3.1.0 [55]. Importantly, the results using the alternative phylogeny were highly consistent with

166   those of the main phylogeny (see table 1, electronic supplementary material, tables S3–S6).

167

168   ## (e) Comparative analyses

169   We tested associations between parental care and life history variables using Phylogenetic Least

170   Squares (PGLS) [56–58]. This approach controls for the non-independence among species by

171   incorporating a variance–covariance matrix that represents their phylogenetic relationships. All analyses

172   incorporated phylogenetic dependence by estimating Pagel's λ [58]. We built separate multipredictor

173   PGLS models for each parental care variable (i.e., care duration by females, care duration by males;

174   protection by females, protection by males, nourishment by females) in which one of the care variables

175   was the dependent variable, and log clutch size, log egg size, average SVL, sexual dimorphism,

176   terrestrial reproduction and direct development were the predictors.

177   We also included the higher nodes (i.e., superfamily ID, see supporting data s2) as a factor in

178   PGLS models [53,59]. This was to control for the lack of variation in key traits within higher taxa: for

179   traits that do not vary within higher nodes, the effective level of replication and appropriate degrees of

180   freedom can be questioned. Due to the lack of variation within clades, three species-poor lineages

181   ('Crown Hyloidea' that includes Alsodidae, Ceratophryidae, Hylodidae, Odontophrynidae and

182   Rhinodermatidae, 12 species in total; Heleophrynidae, 2 species; and Sooglossoidea, 3 species) were

183   excluded from analyses that included higher node as factor. Higher nodes were not included in analyses

184   on trophic egg feeding (Nourishment excluding species in Nourishment category 2) – in this case, most

185   of the clades showed little variance to the trait.

186   We tested multicollinearity between predictors using variance inflation factor (VIF) analysis: all

187   predictors had VIF values less than 5 (VIF_{max} = 2.02). In multiple regression models, we included six

188   predictor variables (see table 1) except in models of nourishment we did not include developmental

189   mode since nourishment and developmental mode were correlated by definition. All analyses were

190   carried out using R 3.1.0 [55] with 'caper' package [60].

191

3. Results

193   Types of care varied across Anura, with each type of care occuring in several clades (figure 1; electronic

194   supplementary material, table S1). Major clades exhibited substantial variations in sex of care provider,

195   protection and nourishment (figure 1): exceptional diversity was exhibited by five clades that include

196   Eleutherodactylidae, Dendrobatidae, Leptodactylidae and Microhylidae, figure S1).

197   Care duration, protection and nourishment were not different between species with female-only

198   care, male-only care and biparental care (Phylogenetic Generalised Least Squares PGLS, care

199   duration: figure S2, $F_{2,379}$ = 0.716; p = 0.489; protection: $F_{2,375}$ = 0.502; p = 0.610; nourishment: $F_{2,370}$ =

200   0.502; p = 0.426), nor between uniparental and biparental species (PGLS, care duration: $F_{1,387}$ = 0.415;

201   p = 0.520; protection: $F_{1,382}$ = 0.788; p = 0.375; nourishment: $F_{1,378}$ = 1.694; p = 0.194). Thus, males and

202   females provide similar extents of care in anurans. Interestingly, the extent of parental care by males

203   was associated with the extent of female care both in care duration (PGLS; $F_{1,1006}$ = 8.674; p < 0.0001)

204   and protection ($F_{1,1005}$ = 54.58; p < 0.0001).

205   Terrestrial reproduction was a key factor associated with parental care (figure 1). All forms of care

206   were more common in terrestrial taxa than in aquatic ones (figure 2) including protection by males (5.5%

207   and 46.5% of aquatic and terrestrial taxa, respectively), protection by females (1% and 39.0%), and

208   nourishment (5.0% and 34.5%). Terrestrial reproduction was associated with increased levels of care by

209   both males and females (figure 2 and electronic supplementary material, table S3). Consequently, the

210   number of caring parents was significantly higher in terrestrial frogs than in aquatic ones (PGLS; $F_{1,591}$ =

211   80.47; p < 0.0001).

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

213   sexes, and provisioning by the female (figure 3 and electronic supplementary material, table S4).

214   However, since egg size and clutch volume often depend on body size, we also investigated the

215   relationships between egg size, clutch volume and care by including body size as an explanatory

216   variable in phylogenetically corrected models (table S5). When body size was statistically controlled for,

217   neither egg size nor clutch volume remained correlated with care with the exception of nourishment, and

218   small clutch volume remained associated with male care (electronic supplementary material, table S5).

219   Sexual size dimorphism was associated with male care but not female care (electronic

220   supplementary material, table S4 and figure S3). However, male care was associated with increased

221   male size relative to female size (table S4). The latter relationship remained significant when absolute

222   body size was controlled for in the analysis (table S5). The latter relationship between size dimorphism

223   and body size suggests that Anura exhibit an allometric relationship between sizes of males and

224   females known as Rensch's rule [44,61] (PGLS; $F_{1,430}$ = 7.39; p = 0.007).

225   Terrestrial reproduction remained the main predictor of both care duration and offspring

226   protection in multipredictor analyses, but not for nourishment (table 1). These results suggest that the

227   relationships between life history and care we uncovered using bivariate analyses (electronic

228   supplementary material, table S4) may be mediated by terrestrial reproduction. Nevertheless, in multi-

229   predictor models male-biased size dimorphism remained associated with male care (table 1), and

230   nourishment remained associated with clutch size and body size.

231   Trophic egg feeding (i.e, exotrophic tadpoles feed on external food sources versus tadpoles fed

232   by trophic eggs or skin secretion) was associated with sexual dimorphism and clutch volume (electronic

233   supplementary material, tables S3–S4), and these relationships remained significant after controlling for

234   body size (table S5, S6).

235

4. Discussion

237   Our comprehensive phylogenetic analyses of the extent of male and female care show that care is

238   extremely variable both within and among major clades of frogs. Not only the presence or absence of

239   care varies – that has been uncovered by previous studies [18,26] – but also the type and duration of

240   care are highly variable. In contrast to reptiles and mammals, in which the females are the main care

241   provider, or to birds in which biparental care is the predominant form of care [9,62], in frogs female-only,

242   male-only and biparental care are all widespread among various lineages, and the involvement of males

243   and females in care is comparable. Because in ~20% of newts and salamanders (urodeles) one of the

244   parents guards the eggs or the offspring [5,9,63,64], and caecilians in which females feed their offspring

245   using an excretion of their skin [65,66], the overall richness of caring is spectacular in amphibians. This

246   suggests that over the course of amniote evolution, the phylogenetically younger tetrapod clades (e.g.,

247   reptiles, birds and mammals) became specialised to a limited set of care patterns [62].

248   Consistently with previous studies [11–13], we found that the transition towards terrestrial

249   reproduction facilitated parental care. Moreover, our work advances the understanding of evolutionary

250   relationships by showing that terrestrial reproduction is related to all forms of both male and female

251   care, except nourishment. Thus, when early tetrapods invaded terrestrial niches, both males and

252   females may have been under the effects of selection forces to improve the survival of their offspring, so

253   that both males and females evolved various forms of care provisioning in response to terrestrial

254   reproduction. Therefore, the subsequent canalization of parental care largely towards females (e.g., in

255   reptiles and mammals) and cooperation by both sexes (in birds) may have been the result of additional

256   selective pressures that the ancestors of these clades faced during their radiation into various ecological

257   niches. This implies that the predominance of maternal care coevolved with internal fertilization [67, but

258   see 68]. In urodeles, where internal fertilization is more frequent, only phylogenetically basal external

259   fertilizers with aquatic reproduction appear to provide paternal care [5,63], although clutch attending by

260   females is widespread especially in those with terrestrial reproduction [63].

261   We also found that egg size and clutch volume are related to parental care, although these

262   associations became non-significant by including terrestriality in the models. On the one hand, terrestrial

263   egg-layers have larger eggs and smaller clutches than aquatically reproducing frogs [8,13,26], which

264   may be predicted by other factors besides parental care, such as selection on offspring size [69] or

265   protection against the hostile environment [11]. However, egg size and clutch size were no longer

266   associated with care duration and protection when body size was statistically controlled. Therefore, the

267   associations between egg size, clutch size and parenting showed by previous studies [8,13,26] may

268   have been mediated by other factors, e.g. body size and/or terrestrial reproduction. On the other hand,

269   increased nutrient transfer to the offspring is associated with reduced clutch size, which seems to be the

270   result of an increased investment to individual offspring [3] traded off against fecundity. Moreover,

271   trophic egg feeding is also associated with reduced egg size [table S6], implying that mothers may

272   reduce the cost egg production using this type of nourishment.

273   Finally, the evolutionary relationship between male care and size dimorphism has been debated

274   [32-34], and our results using fine-scaled care variables, multi-predictor models and more extensive

275   taxonomic coverage than previous studies, confirm that male care is associated with sexual size

276   dimorphism [44]. We suggest two mutually non-exclusive explanations for the increased male size

277   (relative to female size) with the extent of male care. On the one hand, sexual selection may favour

278   larger males in male caring species if females prefer large males and/or large males are more

279   successful in coercive mating [38,39], provided that these males are more successful in nursing the

280   offspring. On the other hand, male care may reduce the fecundity selection pressure on females, so that

281   female size decreases in those species in which the males provide care [44,61]. To distinguish between

282   these scenarios, further experimental and phylogenetic analyses are warranted [9,17].

283   Here we treat parental care as an invariable trait for a given species, although this assumption

284   suits some species better than others. For example, *Allobates femoralis* exhibits variation in parenting

285   since females transport tadpoles but this behaviour is only provoked by the absence of the father that is

286   normally the care-providing parent [41]. Therefore, future phylogenetic analyses should pay attention to

287   the flexibility of care provisioning [41,70]. Care provision can be further tuned by variation in the

288   ecological [25,71,72] or social environment [41], and this plasticity not only enables better adaptation to

289   seasonal and unpredictable changes of the environment, but it may also act as the origin of evolutionary

290   changes in the extent of care [41,45] or in parental roles [41,43,45]. Field-based and laboratory-based

291   studies will likely add more examples for this plasticity and would help in identifying environmental

292   factors which provokes shifts.

293   In summary, parental care is predicted by ecological and life history variables in frogs. Care is a

294   complex social trait and specific aspects of care have different predictors in males and females. Further

295   analyses are needed to investigate the impacts of climate, reproductive modes and mating systems on

296   care strategies. Since new forms of parental care are cropping up [71,72], field-based studies of yet

297   unstudied species are needed to explore breeding systems (including parenting) in frogs that live in

298   remote areas and/or inhabit extreme environments. Taken together, studies of anuran parental care

299   provide important contributions to the understanding of reproduction, evolution and diversification in the

300   most threatened vertebrate class of the Anthropocene.

301

312

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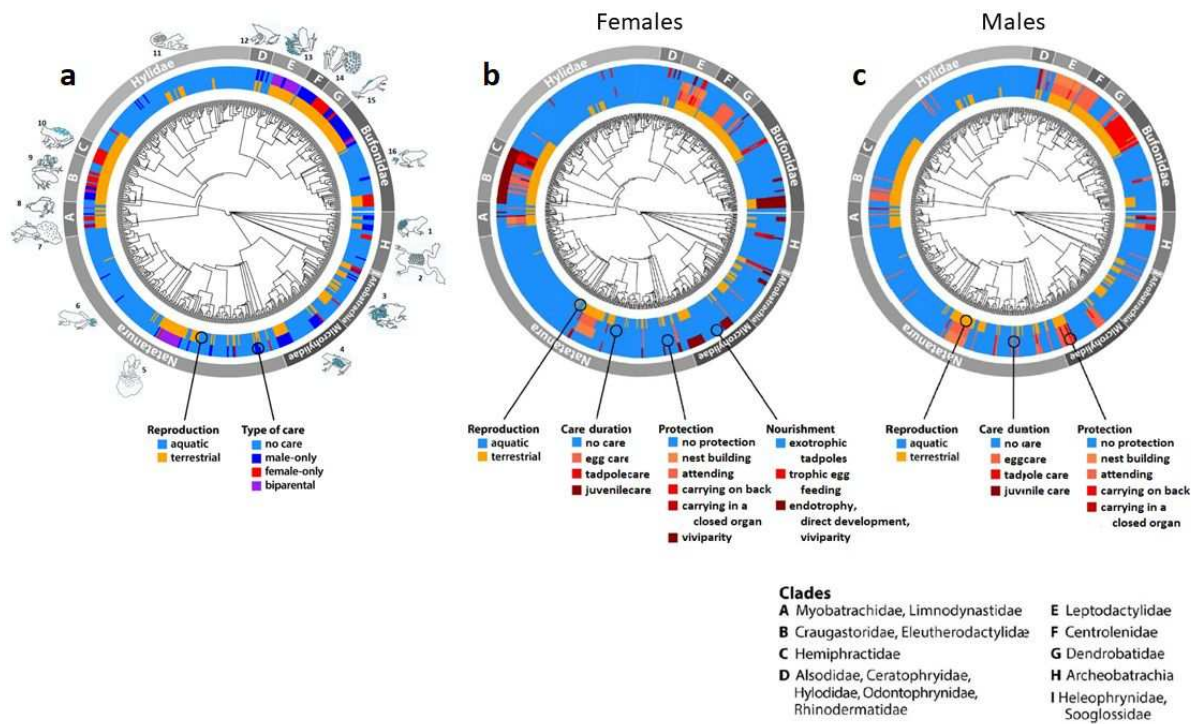486   10.1371/journal.pone.0119988)

Figure legends

Figure 1. Phylogenetic distribution of parental care and breeding habitat in frogs. (aA) 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 guard 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). (bB) Diversity of female care (care duration, protection and nourishment, 594 species). (cC) Diversity of male care (care duration and protection, 593 species). Grafen-transformed branch lengths are shown. 0 refers to no care in a particular trait, whereas 3, 5 and 2 refer to the most advanced stage in offspring development in care duration, protection (for males and females separately) and nourishment (for females), respectively.

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 + SD; on the right). Red shades represent female care, blue shades represent male care.

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 electronic supplementary material, table S4–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.

521
522 **Figure 1**

Females (b)

Males (c)

a

Reproduction
■ aquatic
■ terrestrial

Type of care
■ no care
■ male-only
■ female-only
■ biparental

Reproduction
■ aquatic
■ terrestrial

Care duration
■ no care
■ egg care
■ tadpole care
■ juvenile care

Protection
■ no protection
■ nest building
■ attending
■ carrying on back
■ carrying in a closed organ
■ viviparity

Nourishment
■ exotrophic tadpoles
■ trophic egg feeding
■ endotrophy, direct development, viviparity

Reproduction
■ aquatic
■ terrestrial

Care duration
■ no care
■ egg care
■ tadpole care
■ juvenile care

Protection
■ no protection
■ nest building
■ attending
■ carrying on back
■ carrying in a closed organ

Clades

A Myobatrachidae, Limnodynastidae
B Craugastoridae, Eleutherodactylidae
C Hemiphractidae
D Alsodidae, Ceratophryidae, Hylodidae, Odontophrynidae, Rhinodermatidae

E Leptodactylidae
F Centrolenidae
G Dendrobatidae
H Archeobatrachia
I Heleophrynidae, Sooglossidae

523

Clades
A Myobatrachidae, Limnodynastidae
B Craugastoridae, Eleutherodactylidae
C Hemiphractidae
D Alsodidae, Ceratophryidae, Hylodidae, Odontophrynidae, Rhinodermatidae
E Leptodactylidae
F Centrolenidae
G Dendrobatidae
H Archeobatrachia
I Heleophrynidae, Sooglossidae

Reproduction
■ aquatic
■ terrestrial

Type of care
■ no care
■ male-only
■ female-only
■ biparental

Females

Reproduction
■ aquatic
■ terrestrial

Care duration
■ no care
■ egg care
■ tadpole care
■ juvenile care

Protection
■ no protection
■ nest building
■ attending
■ carrying on back
■ carrying in a closed organ
■ viviparity

Nourishment
■ exotrophic tadpoles
■ trophic egg feeding
■ endotrophy, direct development, viviparity

Males

Reproduction
■ aquatic
■ terrestrial

Care duration
■ no care
■ egg care
■ tadpole care
■ juvenile care

Protection
■ no protection
■ nest building
■ attending
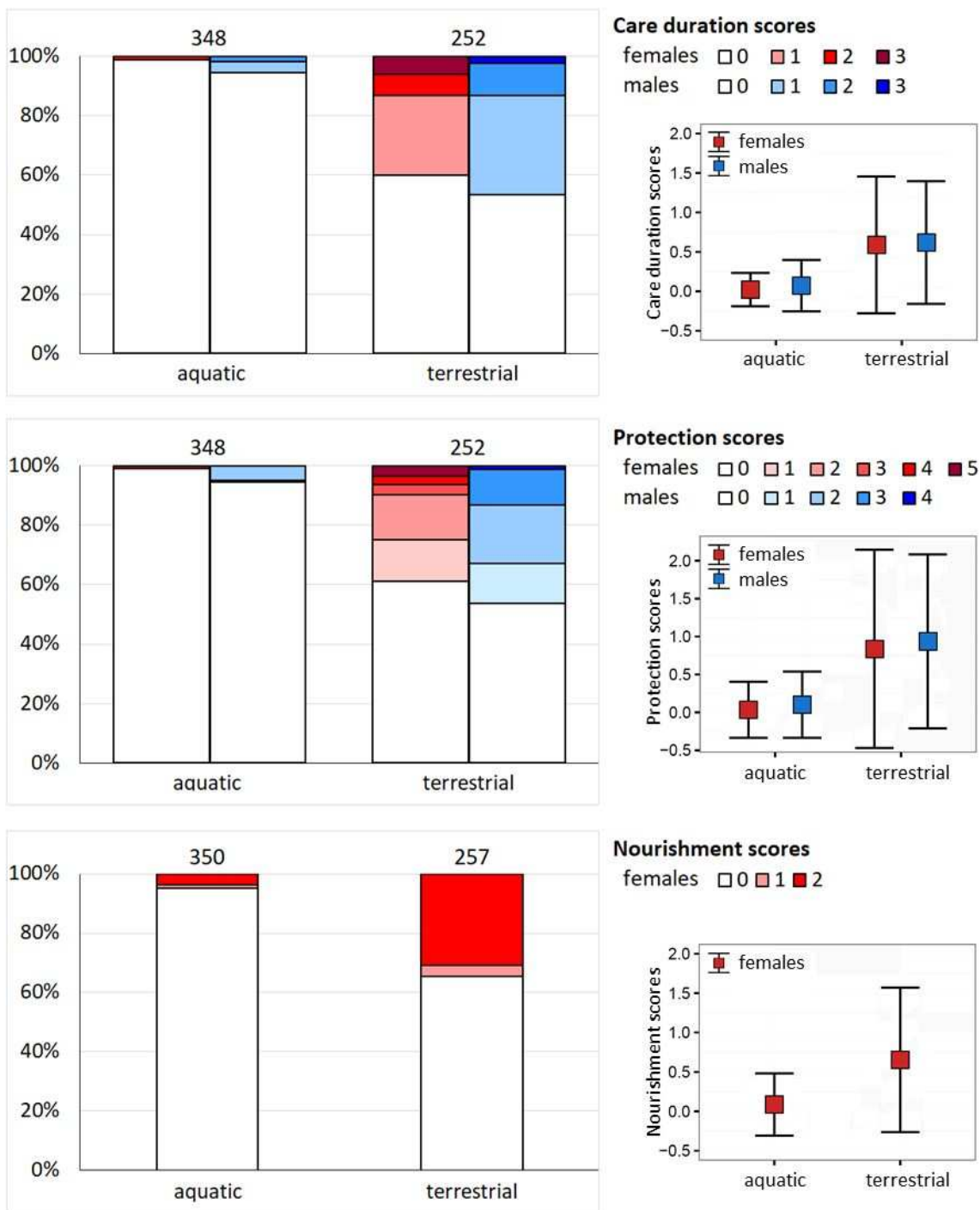■ carrying on back
■ carrying in a closed organ
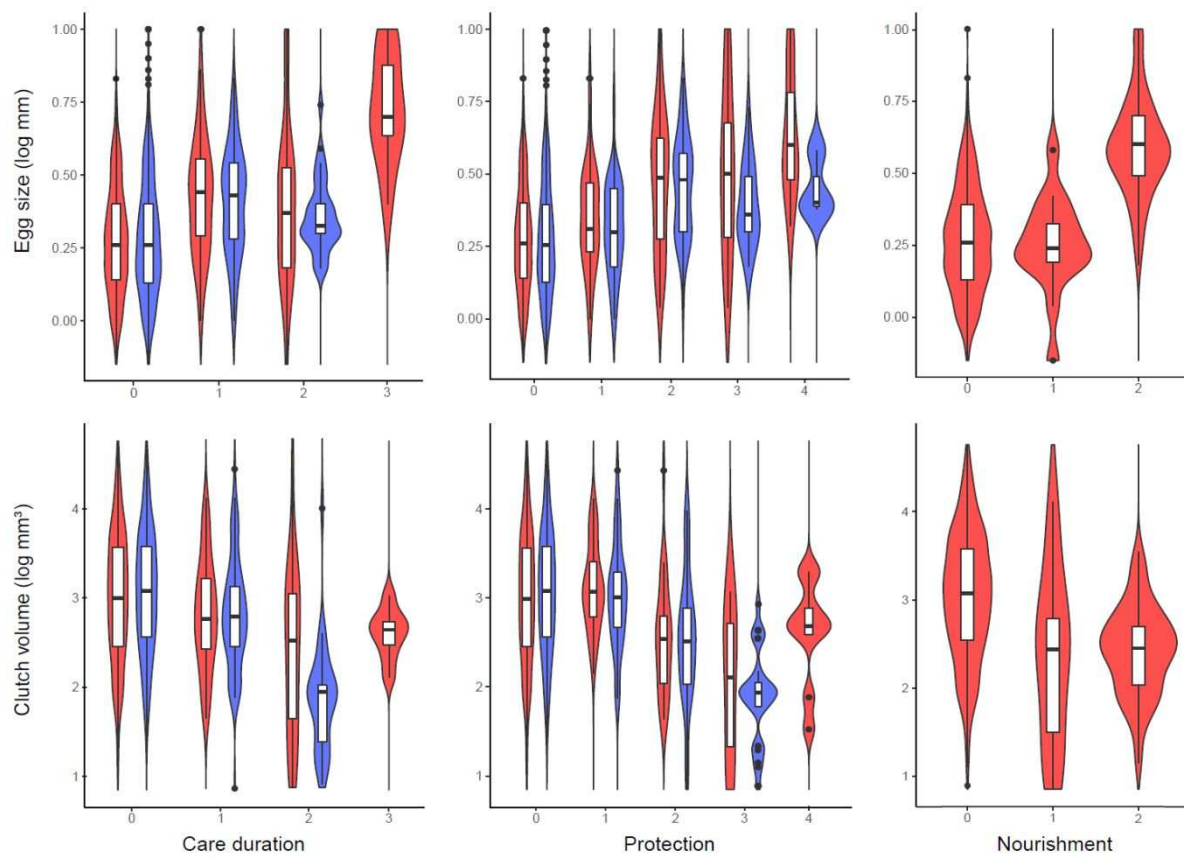
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527
528   **Figure 2**

529

531

Figure 3

533

534

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537   **Table 1.** Parental care in relation to ecology, life-history and sexual dimorphism in Anura using

538   phylogenetically corrected generalized linear squares (PGLS) models. Multipredictor PGLS models for

539   each care variable are provided separately for males and females; note that only females provide

540   nourishment. Higher node was included in the models except for nourishment (see Methods). Italics

541   indicate significant predictors. Egg size is provided as diameter in mm. Clutch volume is calculated as

542   egg volume × clutch size and provided as mm^3. Clutch volume and egg size were log-transformed prior

543   to the analyses. Body size refers to the average snout-vent length (SVL) in mm. Sexual size dimorphism

544   was calculated as log_{10} (SVL_{male} / SVL_{female}). We provide parameter estimates with standard error ($\beta \pm$

545   *SE),* the corresponding *t* and *P* values, and the adjusted R^2 for the model including F(df_{effect}, df_{error}) and

546   *P* values, respectively.

Care duration	by females			by males		
	β ± SE	T	P	β ± SE	t	P
Terrestrial reproduction	0.227 ± 0.103	2.209	0.028	0.278 ± 0.093	3.000	0.003
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	1.070 ± 0.376	2.842	0.005
Model	0.155	2.961 (18, 175)	0.0001	0.175	3.254 (18, 174)	< 0.0001

Protection	by females			by males		
	β ± SE	T	P	β ± SE	t	P
Terrestrial reproduction	0.426 ± 0.137	3.113	0.002	0.414 ± 0.158	2.626	0.009
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	2.156 ± 0.701	3.075	0.002
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		
	β ± SE	T	P	β ± SE	t	P
Terrestrial reproduction	0.018 ± 0.098	0.186	0.853	0.014 ± 0.055	0.265	0.792
Clutch size	-0.180 ± 0.053	3.389	< 0.001	-0.066 ± 0.030	2.162	0.032
Egg size	0.119 ± 0.169	0.706	0.481	-0.195 ± 0.097	2.010	0.046

Body size	*0.003 ± 0.001*	*2.043*	*0.042*	*0.003 ± 0.001*	*3.513*	*0.001*
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

Clades

A Myobatrachidae, Limnodynastidae

B Craugastoridae, Eleutherodactylidae

C Hemiphractidae

D Alsodidae, Ceratophryidae, Hylodidae, Odontophrynidae, Rhinodermatidae

E Leptodactylidae

F Centrolenidae

G Dendrobatidae

H Archeobatrachia

I Heleophrynidae, Sooglossidae

Reproduction
- aquatic
- terrestrial

Type of care
- no care
- male-only
- female-only
- biparental

Females

Males

Reproduction
- aquatic
- terrestrial

Care duration
- no care
- egg care
- tadpole care
- juvenile care

Protection
- no protection
- nest building
- attending
- carrying on back
- carrying in a closed organ
- viviparity

Nourishment
- exotrophic tadpoles
- trophic egg feeding
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