Title: Correlated evolution of parental care with dichromatism, colour, and patterns in anurans

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Abstract

Parental care is remarkably widespread among vertebrates because of its clear fitness benefits. Caring however incurs energetic and ecological costs including increasing predation risk. Anurans have diverse forms of parental care, and we test whether the evolution of care is associated with morphology that minimizes predation risk. Specifically, we determine whether dichromatism, specific colours gradients, and patterns that enhance crypticity are associated with anurans that also evolve parental care. From our phylogenetic comparative analyses of 988 anurans distributed globally, we find that parental care is less likely to evolve in species with dichromatism. Contrary to our expectation, specific colours (Green-Brown, Red-Blue-Black, Yellow) and patterns (Plain, Spots, Mottled-Patches) were not associated with the evolution of caregiving behaviours. Only among species with male-only care did we find a positive association with the presence of Bars-Bands. The lack of strong associations between dorsal morphology and caregiving behavior suggest that these colours and patterns may serve other functions and that predation risk during parental care is mediated in other ways. As a strongly sexually selected trait, dichromatism is an effective solution to attract mates, but we find here that its evolution appears to preclude the evolution of parental care behaviour in anurans.

Keywords

Colour; sexual selection; parental care; phylogenetics; evolutionary ecology; amphibians

Introduction

Understanding the patterns and processes underlying the evolution of parental care is central to evolutionary biology. Parental care in animals is an incredibly diverse trait, varying widely across taxa in both complexity and duration [1, 2]. Typically defined to include any post-zygotic investment by either parent [3], parental care includes both behavioural and non-behavioural traits that enhance offspring survivorship [1, 4, 5]. Currently, 11 forms of parental care are recognized across the animal kingdom and these range in complexity from provisioning of gametes and viviparity to protecting and feeding mature offspring [4]. Inevitably, parental care is costly to the parent and theory predicts that caregiving behaviours evolve under circumstances when the benefits outweigh the costs [1, 6-8]. Among the various costs, caregiving parents incur greater energetic expenditure and may undergo physiological stress [9]. Parents also experience reduced resource acquisition opportunities, which can further reduce their allocation to other fitness-enhancing traits, including additional mating opportunities [1, 6]. Because parental care can be a conspicuous activity, caregiving adults must overcome the risk of mortality from predation on themselves as well as their offspring [10]. Depending on whether parents or offspring are at greater risk, caregiving parents can offset predation risk by avoiding detection or by actively engaging in antipredator strategies or both [11].

One strategy to avoid detection and evade predation risk is through camouflage [12]. Effective camouflage can be achieved in multiple ways, from the expression of colours and patterns that closely match the environment, thereby achieving crypsis, to the expression of markings that create the appearance of false edges and boundaries, disrupting the outline and shape of the individual. From the development of body forms for masquerade to the integration of movement strategies to achieve the effects of motion dazzle or motion camouflage, the evolution of body colours and patterns that minimise predation risk is widespread in animals [Reviewed in 13]. Camouflage, however, is ineffective when an

63 organism requires conspicuous body colour or patterns to communicate. Body colour patterns are often
64 under strong sexual selection [14, 15] and several vertebrates use visually striking colours as signals for
65 both inter- and intraspecific communication [16]. A notable exception is aposematic colouration that is
66 intended to be detectable by predators [11, 17]. Conspicuous colours and patterns increase detection
67 probabilities for predators, resulting in a trade-off between being prominent to attract mates, and being
68 camouflaged to avoid predation [18]. Many species mediate this trade-off between sexual and natural
69 selection by delaying the expression of conspicuous colours, restricting the duration of visual displays,
70 dynamically exposing signals only to conspecifics, engaging in dynamic conspicuous colouration, or by
71 evolving sexual dichromatism [19]. Of these, sexual dichromatism is the most widely found evolutionary
72 solution to the trade-off, wherein the sex that experiences greater sexual selection is typically conspicuous
73 [20]. The aforementioned strategies can be an effective solution when employed singly or in combination,
74 enabling a species to benefit from being conspicuous while still engaging in risky behaviours, such as
75 parental care.

76 Amphibians are an ideal model system to examine the evolutionary trade-offs and associations
77 between parental care and conspicuousness. Amphibians are a species-rich group [21] that are colourful
78 [22], dichromatic [19], and show some of the most diverse forms of caregiving behaviours [23]. Parental
79 care behaviour has been documented in approximately 20% of the extant 8200 species in amphibians [24-
80 27] and is an integral component in the classification of the reproductive modes in this group [23, 28].
81 Despite the diversity and complexity of reproductive modes (~40 distinct reproductive modes;[27]), our
82 understanding of parental care evolution in amphibians is still lagging compared to that of other
83 vertebrate groups [24, 29]. What is clear is that caregiving behaviours among anurans are phylogenetically
84 widespread and converge between distantly related lineages [25]. Uniparental care, with males or females
85 alone caring is evolutionarily stable compared to biparental care [26]. Across anuran species, care-giving
86 behaviours vary in duration and intensity [23, 25, 30, 31] as well as form and complexity [26]. Among the

87 nine classified categories of parental care in anurans [See: 24], egg attendance, wherein adults defend,
88 clean, or hydrate eggs is the simplest and most frequently observed form [23, 24, 26] whereas viviparity
89 is complex, requiring specialised anatomical and physiological adaptations that are infrequently observed
90 [24, 26]. Studies have found that parental care behaviour in anurans is correlated with multiple ecological
91 factors, including breeding pool size and terrestrial reproduction [25, 32, 33] that are strong indicators of
92 the risks to adults and young by predators in both the aquatic and terrestrial habitats.

93 Adult anurans are prey to visually hunting predators such as birds, snakes, mammals, and
94 invertebrates [See: 23, 34, 35] and avoiding predation risk by being camouflaged may explain the
95 prevalence of green, brown, and grey dorsal colours that effectively match natural substrates [22, 23].
96 Increasing crypticity of these dorsal colours is further aided by patterns, such as mottling, stripes, bars, or
97 spots [36-38] and even metachrosis [28]. Several anuran families also effectively use aposematism to
98 advertise unpalatability and avoid predation [22, 23]. The adaptive significance of background matching
99 by camouflage as well as aposematism to overcome predation is well supported at multiple scales [e.g.,
100 36, 39, 40-44]. Dichromatism, which has so far been observed in ~2% of extant anurans [45], is also an
101 effective strategy to achieve crypticity, however the frequency of dichromatism is likely to be an
102 underestimate, owing to the ephemeral nature of dynamic dichromatism [22] and the general lack of
103 studies on anurans [21, 22]. Although evidence of the adaptive value of colours and patterns in shaping
104 life-history traits is emerging, none, to the best of our knowledge, examine if costly life-history traits such
105 as parental care are associated with dichromatism as well as specific dorsal colours, and patterns. Such a
106 comparison is particularly relevant to understand how anurans ameliorate the trade-offs between natural
107 and sexual selection.

108 Here, we compare whether the occurrence and type of parental care are evolutionarily correlated
109 with the presence of dichromatism, dorsal colours, and patterns in anurans. Given the relative risks of

110 conspicuous colouration, we hypothesized that caregiving adults are likely to be cryptically coloured and
111 that specific patterns that enhance camouflage, are more likely to be associated with caregiving
112 behaviour. Specifically, we test for the correlated evolution of parental care with the presence of
113 dichromatism, three dorsal colour and four pattern gradients. Further, we examine the co-occurrence
114 pattern with the three types of parental care *viz*., male-only care, female-only care, and biparental care.
115 Using a large-scale phylogenetic comparison that links parental care to dichromatism, dorsal colour and
116 pattern, we bring together seemingly independent traits to better understand the evolution of patterns
117 and potential trade-offs.

118 **Materials and Methods**

119 Information on parental care in anurans was first extracted from data available in Vági, Végvári
120 [25], where we retained the following information: whether parental care is present or absent in each
121 species and the type of care as one of 5 possible categories (no care, male-only care, female-only care,
122 either parent and biparental care). Because 'care by either parent' was rare (seven species only), we
123 merged this category with 'biparental care' for analysis. The presence and form of dichromatism were
124 first classified as per Bell and Zamudio [46] and Bell, Webster [19]. We augmented this list with
125 information from the primary literature, field guides, and online databases (see electronic supplementary
126 material, table S1). A species was classified as dichromatic if any part of the body was differently coloured
127 compared to the other sex. We also recorded the specific body part that was dichromatic (e.g., vocal sac)
128 if such information were available. We retained the classification of dichromatism made by Bell and
129 Zamudio [46], wherein 'ontogenetic dichromatism' between sexes is considered when males and females
130 develop different colours at sexual maturity, and 'dynamic dichromatism' is when the male or female
131 actively changes colour for a short duration at or after sexual maturity.

For dorsal colour and pattern information, one of us (SKS) examined colour photographs, illustrations, and referred to detailed descriptions on public repositories (see electronic supplementary material, table S1) of adult anurans. Because photos are taken under different lighting conditions, hues can vary and thus, photographs were used only to validate the description. The species description in the literature was our primary source for scoring colour categories. We classified dorsal colour of males and females separately according to the following gradients: 'Green-Brown' which included hues of green or brown; 'Red-Blue-Black' which included hues of red or black or blue, and 'Yellow' which included any hue of yellow (figure 1). We combined the hues of red, blue and black into a single category because independent occurrence of these colours was rare and were often found in combination. We scored the pattern type into four categories *viz*., plain: where the dorsum is lacking any pattern; bars or bands: dorsum having thin bars or wide bands; spots: dorsum is interspersed with distinct speckles or larger spots and, mottled or patches: where dorsum has blotches or indistinct shaped patches (figure 1). The colour and pattern of polymorphic species (< 1 % of all species in our database) were classified from the type specimen, described in the original species descriptions. These colour gradients enabled us to categorize species into broad colour schemes that were not directly quantifiable from specimens or photographs or illustrations as others have done [e.g., 47]. The four pattern categories are reliably distinguishable by observers and have been used successfully to address similar questions in reptiles [see 48]. After removing species for which reliable information on dichromatism, colour, and pattern was unavailable, our final dataset comprised 988 species belonging to 45 families. Species names follow Frost [49].

Comparative analyses

To examine the evolutionary association of parental care and body colouration, we modified the consensus tree provided by Jetz and Pyron [50] to only include the 988 species in our database. Data on dichromatism and parental care were plotted on a phylogenetic tree with branch lengths transformed by

155 Graphen's 'ρ' (rho) for illustrations [51]. Data on parental care, type of care, dichromatism, colour, and
156 pattern were binary, and therefore we used a phylogenetic generalized linear mixed model for binary data
157 using the function BinaryPGLMM [52]. We ran six phylogenetically corrected comparative models to test
158 for correlations. The models returned estimated regression coefficients, standard errors, and strength of
159 the phylogenetic signal (s^2) based on a variance-covariance matrix [53]. The occurrence of parental care
160 (care or no care) and Type of care (no care, male only, female only, and biparental care) were treated as
161 dependent variables. Dichromatism (present or absent), Dorsal colour (Green-Brown or Red-Blue-Black or
162 Yellow) and, Pattern (Plain, Bars-Bands, Spots, Mottled-Patches) with the latter two variables for males
163 and females separately, were treated as independent variables. For dichromatic species, we only included
164 the colour and pattern of the caregiving sex. All analyses were performed using RStudio v 1.3 [54] using
165 the following packages 'caper'[55], 'ape'[52], 'geiger'[56], 'phytools'[57], 'ggtree'[58].

166 **Results**

167 *Overview of Parental care, Dichromatism, Body Colour, and Pattern in anurans.*

168 Parental care was present in 375 species (out of 988 species) wherein male-only care was most frequent
169 (n = 204) followed by female only (n = 106), and bi-parental care (n = 65). Dichromatism was observed in
170 221 species and the ontogenetic form (n = 131) was more frequent than dynamic dichromatism (n = 90).
171 Of these 221 species, all males (n = 221) and only females were dichromatic. Dichromatism was most
172 common in Green-Brown coloured males (n = 172), followed by Yellow males (n =31) and, Red-Blue-Black
173 males (n = 18). Furthermore, dichromatism was most common in males lacking any dorsal pattern (n =
174 77), followed by those with mottled-patches (n = 70), bars-bands (n = 44), and spots (n = 30). Overall,
175 Green-Brown was the predominant dorsal colour gradient (male = 720, female = 720) followed by Red-
176 Blue-Black (male = 146, female = 150), and Yellow (male = 122, female = 118). Mottled-patches was the

177 predominant pattern (male = 303, female = 303) followed by Spots (male = 243, female = 250), Bars-Bands
178 (male = 225, female = 218), and Plain (male = 217, female = 217).

179 *Comparative analysis*

180 1. The association of parental care with dichromatism

181 Dichromatism was widespread across the phylogeny (figure 2a, electronic supplementary material, figure
182 S1) with a strong phylogenetic signal ($s^2 = 20.62$, $p < 0.005$). The association between the presence of
183 parental care was stronger with non-dichromatic species than dichromatic species (figure 2b, table 1,
184 model 1). Types of care were distributed across the phylogeny (figure 1c) with a moderately strong
185 phylogenetic signal ($s^2 = 3.3$, $p < 0.005$). All three types of parental care were negatively associated with
186 the presence of dichromatism, but the association was statistically significant with male-only and female-
187 only care (figure 1d, table 1, model 2).

188 2. The association between type of care with dorsal colours and patterns

189 The proportion of caregiving species and the type of care varied between the colour (figure 2a, b) and
190 pattern (figure 2c, d) gradients. Male-only care had a strong phylogenetic signal with colours as well as
191 patterns but was not significantly correlated with any of the three colour gradients (table 1, model 3).
192 Male-only care was, however, significantly correlated with the presence of Bars-Bands. In contrast,
193 female-only care was not significantly correlated with any of the three colours or four patterns (table 1,
194 model 4).

195 **Discussion**

196 Our understanding of the evolution of anuran parental care has largely been focussed on determining
197 costs and benefits [6] or the macro-evolutionary comparisons with other ecological factors, such as
198 terrestriality [25]. Here, we aimed to test if parental care behaviours were correlated with morphological

199 traits under both natural and sexual selection. Our large-scale phylogenetic analysis revealed that
200 dichromatism is extremely variable among anurans but overall, a greater number of non-dichromatic
201 species care for their offspring than dichromatic species. We also found that species with male-only care
202 were positively correlated with the presence of bars and bands on the dorsum, irrespective of dorsal
203 colour. No correlations between female-only care and biparental care with dorsal colour and pattern were
204 found. Differences in the associated evolution of some morphological traits with parental care by males
205 and females suggests interesting sex-specific differences in the trade-offs between natural and sexual
206 selection. Taken together, these findings suggest that the evolution of parental care among anurans is
207 more strongly associated with non-dichromatic species, but the colours and patterns of care-giving
208 species is not tightly linked to the evolution of care overall.

209 **Parental care and Dichromatism**

210 Our results show that dichromatic species are less likely to care for the offspring compared to
211 non-dichromatic species, and the pattern is consistent irrespective of the caregiving sex. Because
212 dichromatism is a sexually selected trait, anurans that evolve dichromatism appear to deprioritize
213 parental care, potentially over mate selection. Typically, dichromatism involves a change to a bright,
214 conspicuous colour on the body either with age or sexual maturity or during the breeding season.
215 Dichromatism among anurans is known to be evolutionarily labile and has been lost and gained multiple
216 times over their evolutionary history [19]. However, only two studies have so far examined the
217 macroevolutionary patterns of dichromatism in anurans: one highlights the presence of dichromatism
218 among anuran lineages and contextualizes existing knowledge [46], while the other finds that the
219 evolution of dynamic dichromatism and explosive breeding are correlated [19, 59]. Evolution of
220 dichromatism appears to have been preceded by breeding in aggregations[19], therefore enabling male-
221 male recognition [60, 61] as well as female assessment of male quality [62]. Anurans that form

222 aggregations may not engage in parental care behaviours such as egg attendance or froglet transport that
223 inherently require prolonged association with immobile offspring [23]. It is also unlikely that anurans
224 would aggregate to find mates and go elsewhere to deposit eggs because fertilization is largely external
225 [28]. Some dichromatic anurans may be capable of prioritizing both sexual and natural selection using an
226 ingenious solution of restricting the conspicuousness to a small portion of the body (see electronic
227 supplementary material, table S1 for references) such as feet (Forelimbs turn orange in males of
228 *Pyxicephalus adspersus*), throat (Males of *Phrynoidis asper* have black throat), or the ventral surface
229 (Males of *Hyloxalus delatorreae* have a spotted underside). We suspect that this strategy of restricted
230 dichromatism may reduce the risk of predation further because the conspicuous signal is directed
231 specifically to a receiver, presumably females or other males and may only be exposed in close
232 encounters, thus avoiding the attention of unintended recipients.
233
234 **Parental care, colour, and pattern**
235 The presence of Green-Brown colours is thought to render advantages for camouflage to anurans
236 [40, 59]. Contrary to our expectation, we did not find caregiving species to be those that are also green or
237 brown. In fact, none of the three colour gradients were significantly associated with the occurrence of
238 care, irrespective of the caregiving sex. The absence of an association between dorsal colour and parental
239 care may reflect the many other functions of body colouration. Red colour, for instance, is a ubiquitous
240 warning colour across different taxonomic groups [17] and is an effective deterrent of predation as in the
241 case of the Strawberry poison dart frog, *Oophaga pumilo,* where the green morph is more likely to be
242 attacked than the red morph [42]. Although bright or high-contrast colours have generally been associated
243 with aposematism, some anurans such as *Dendrobates tinctorius* use yellow and black patterns in a dual-
244 role as disruptive camouflage as well as aposematism [63]. Furthermore, several palatable species use
245 aposematic colouration to mimic unpalatability [e.g. Uropeltid snakes 64]. What is particularly informative

246 of our results is that neither the cryptically coloured nor the conspicuously-coloured species were more
247 likely to evolve parental care. Because the effectiveness of colours in reducing predation risk depends on
248 the visual acuity of predators and the visual complexity of habitats, our evolutionary hypotheses about
249 patterns of these morphological traits and parental care may be better understood by including current
250 ecological conditions.

251 Of the four pattern categories we classified in anurans, only the presence of Bars-Bands had a
252 significant positive association with male-only care. In contrast, the association of this pattern with
253 female-only care was weak and negative. None of the other three pattern types, *viz*., Plain, Mottled-
254 Patches, or Spots had a significant association with the sex of the caregiver. We suspect that the
255 differences in the association between male-only and female-only care may be an artefact of fewer
256 species having female-only care compared to male-only care. However, the fact that at least in males,
257 bars and bands could be an added advantage for the care-giving parent, seems to suggest some sex-
258 specific trade-offs between natural and sexual selection. In allied taxa such as geckos and snakes, bars-
259 bands or zig-zag patterns on the dorsum are known to enhance survival, irrespective of body colour [65,
260 66]. The presence of bars and bands on the dorsum in anurans may enable background matching,
261 especially for males that occupy linear habitats such as grass or tree bark [48]. Mottled patterns and spots
262 would likely match backgrounds such as mud or leaf litter [22], but the effectiveness of different patterns
263 for background matching in anurans across habitats remain to be quantified. It also remains to be seen if
264 males and females occupy different oviposition sites or microhabitats depending on their specific dorsal
265 pattern. While we know that colours in amphibians are regulated *via.* chromatophores, the mechanism
266 underlying the temporary, rapid colour change process of dynamic dichromatism has not been fully
267 understood [19, 28, 67]. Our categorisation of colour and patterns into three and four categories
268 respectively may not necessarily reflect the true extent of camouflage or conspicuousness as perceived
269 by predators, especially since thermal conditions also modulate colour patterns [23]. We also recognise

270 that our findings are based on colour and patterns perceived in the visible spectrum but there is mounting
271 evidence of some anurans using the ultra-violet spectrum (UV) and being fluorescent [68].

272 **Predation risk and behavioural responses**

273 Predation is a key driver for the evolution of parental care in amphibians [23]. There is strong
274 evidence showing that parental care behaviours increase offspring survivorship [e.g., 24, 30, 69, 70-74].
275 However, little is known about the magnitude of predation risk on caregiving parents themselves. Many
276 caregiving anuran species, such as *Feihyla hansenae,* actively defend their eggs from predators such as
277 Katydids [75]. If the predation risk reducing strategy is to be cryptic against the background, this is only
278 effective until the organism moves. Once detected by a predator, anurans will have to engage in
279 behavioural responses such as attacking the predator, startling predators by displaying flashy colours, or
280 actively escaping [76]. Documenting the suite of predators and predation rates on different colours and
281 patterns of caregiving adult anurans, as well as a careful evaluation of life-history traits such as the
282 presence of toxicity and aposematism, may reveal further insights on combinations of anti-predator
283 strategies that anurans can utilise. Experiments that evaluate the risk of predation across the three colours
284 and four dorsal patterns among anurans will be particularly useful to understand if specific combinations
285 of colour and pattern indeed enhance camouflage. From our phylogenetic analysis, the lack of strong
286 correlations between the expression of parental care and specific dorsal colours (Green-Brown, Red-Blue-
287 Black and, Yellow) and patterns (Plain, Spots, and Mottled-Patches) reflects the fact that these
288 morphological traits do not appear to preclude the evolution of care-giving behaviour.

289 Because of the general lack of data, what is noticeably missing is information about the diurnal or
290 nocturnal habit of anurans. Several conspicuously coloured anurans are diurnal but nocturnality may
291 inherently enhance crypsis and reduce detection by diurnal predators. The adaptive values of colours and
292 patterns will be influenced by whether these anurans are conspicuous and at risk to their predators when

they are active and expressing parental care. The paucity of natural history information continues to limit our understanding of amphibian ecology and evolution. With amphibians being the most threatened vertebrate [21], documenting detailed information on key aspects such as reproductive behaviour, parental care duration, egg development duration, and the suite of predators is critical. Such information will not only provide insights into their evolutionary ecology but also enable efforts to conserve the wide and multifaceted phenotypic variation we see among amphibians.

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References

[1] Clutton-Brock, T.H. 1991 *The Evolution of Parental Care*. Princeton, Princeton University Press.
[2] Balshine, S. 2012 Patterns of parental care in vertebrates. In *The evolution of parental care* (eds. N.J. Royle, P.T. Smiseth & M. Kölliker), pp. 62-80. Oxford, Oxford University Press.
[3] Trivers, R.L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man.* (ed. Campbell B), pp. 136–179. Aldine, Chicago.
[4] Smiseth, P.T., Kölliker, M. & Royle, N.J. 2012 What is parental care? In *The Evolution of Parental Care* (eds. N.J. Royle, P.T. Smiseth & M. Kölliker), pp. 1-17. Oxford, Oxford University Press.
[5] Lindstedt, C., Boncoraglio, G., Cotter, S.C., Gilbert, J.D.J. & Kilner, R.M. 2019 Parental care shapes evolution of aposematism and provides lifelong protection against predators. (doi:10.1101/644864).
[6] Alonso-Alvarez, C. & Velando, A. 2012 Benefits and costs of parental care. (eds. N.J. Royle, P.T. Smiseth & M. Kölliker), pp. 40-61. Oxford, Oxford University Press.
[7] Klug, H. & Bonsall, M.B. 2014 What are the benefits of parental care? The importance of parental effects on developmental rate. *Ecol Evol* **4**, 2330-2351. (doi:10.1002/ece3.1083).
[8] Royle, N.J., Smiseth, P.T. & Kölliker, M. 2012 *The evolution of parental care*, Oxford University Press.

[9] Fowler, M.A. & Williams, T.D. 2017 A Physiological Signature of the Cost of Reproduction Associated with Parental Care. *Am Nat* **190**, 762-773. (doi:10.1086/694123).
[10] Owens, I.P.F. & Bennett, P.M. 1994 Mortality costs of parental care and sexual dimorphism in birds. *Proc R Soc London B* **257**, 1-8. (doi:10.1098/rspb.1994.0086).
[11] Caro, T. & Allen, W.L. 2017 Interspecific visual signalling in animals and plants: a functional classification. *Philos Trans R Soc Lond B Biol Sci* **372**. (doi:10.1098/rstb.2016.0344).
[12] Stevens, M. & Merilaita, S. 2011 Animal Camouflage. In *Animal camouflage: mechanisms and function* (eds. M. Stevens & S. Merilaita), p. 357. United Kingdom, Cambridge University Press.
[13] Stevens, M. & Merilaita, S. 2009 Defining disruptive coloration and distinguishing its functions. *Philos Trans R Soc Lond B Biol Sci* **364**, 481-488. (doi:10.1098/rstb.2008.0216).
[14] Darwin, C. 1871 *The Descent of man, and Selection in Relation to sex*. Murray, London.
[15] Endler, J.A. & Mappes, J. 2017 The current and future state of animal coloration research. *Philos Trans R Soc Lond B Biol Sci* **372**. (doi:10.1098/rstb.2016.0352).
[16] Bradbury, J.W. & Vehrencamp, S.L. 1998 *Principles of Animal Communication*. Sunderland, MA., Sinauer Associates.
[17] Mappes, J., Marples, N. & Endler, J.A. 2005 The complex business of survival by aposematism. *Trends Ecol Evol* **20**, 598-603. (doi:10.1016/j.tree.2005.07.011).
[18] Endler, J.A. 1980 Natural selection on color patterns in *Poecilia reticulata*. *Evolution* **34**, 76–91.
[19] Bell, R.C., Webster, G.N. & Whiting, M.J. 2017 Breeding biology and the evolution of dynamic sexual dichromatism in frogs. *J Evol Biol* **30**, 2104-2115. (doi:10.1111/jeb.13170).
[20] Andersson, M.B. 1994 *Sexual Selection*. Princeton, USA., Princeton University Press.
[21] Wake, D.B. & Koo, M.S. 2018 Amphibians. *Curr Biol* **28**, R1237-R1241. (doi:10.1016/j.cub.2018.09.028).
[22] Rojas, B. 2017 Behavioural, ecological, and evolutionary aspects of diversity in frog colour patterns. *Biol. Rev. Camb. Philos. Soc.* **92**, 1059-1080. (doi:10.1111/brv.12269).
[23] Wells, K.D. 2007 *The ecology and behavior of amphibians*. Chicago, IL. , Univ Chicago Press.
[24] Schulte, L.M., Ringler, E., Rojas, B. & Stynoski, J.L. 2020 Developments in Amphibian Parental Care Research: History, Present Advances, and Future Perspectives. *Herpetol Monogr* **34**, 71. (doi:10.1655/herpmonographs-d-19-00002.1).
[25] Vági, B., Végvári, Z., Liker, A., Freckleton, R.P. & Szekely, T. 2019 Parental care and the evolution of terrestriality in frogs. *Proc Biol Sci* **286**, 20182737. (doi:10.1098/rspb.2018.2737).
[26] Furness, A.I. & Capellini, I. 2019 The evolution of parental care diversity in amphibians. *Nat Commun* **10**, 4709. (doi:10.1038/s41467-019-12608-5).
[27] Crump, M.L. 2015 Anuran reproductive modes: evolving perspectives. *J Herpetol* **49**, 1-16. (doi:10.1670/14-097).
[28] Duellman, W.E. & Trueb, L. 1994 *Biology of amphibians*. Baltimore, Johns Hopkins University Press.
[29] Stahlschmidt, Z.R. 2011 Taxonomic chauvinism revisited: insight from parental care research. *PLoS ONE* **6**, e24192. (doi:10.1371/journal.pone.0024192).
[30] Delia, J.R.J., Bravo-Valencia, L. & Warkentin, K.M. 2017 Patterns of parental care in Neotropical glassfrogs: fieldwork alters hypotheses of sex-role evolution. *J Evol Biol* **30**, 898-914. (doi:10.1111/jeb.13059).
[31] Crump, M.L. 1995 Parental care. In *Amphib Biol* (eds. H. Heatwole & B.K. Sullivan), pp. 518–567. Chipping Norton, UK, Surrey Beatty and Sons
[32] Brown, J.L., Morales, V. & Summers, K. 2010 A key ecological trait drove the evolution of biparental care and monogamy in an amphibian. *Am Nat.* **175**, 436-446. (doi:10.1086/650727).
[33] Brown, J.L., Twomey, E., Summers, K. & Morales, V. 2008 Phytotelm size in relation to parental care and mating strategies in two species of Peruvian poison frogs. *Behaviour* **145**, 1139-1165. (doi:10.1163/156853908785387647).

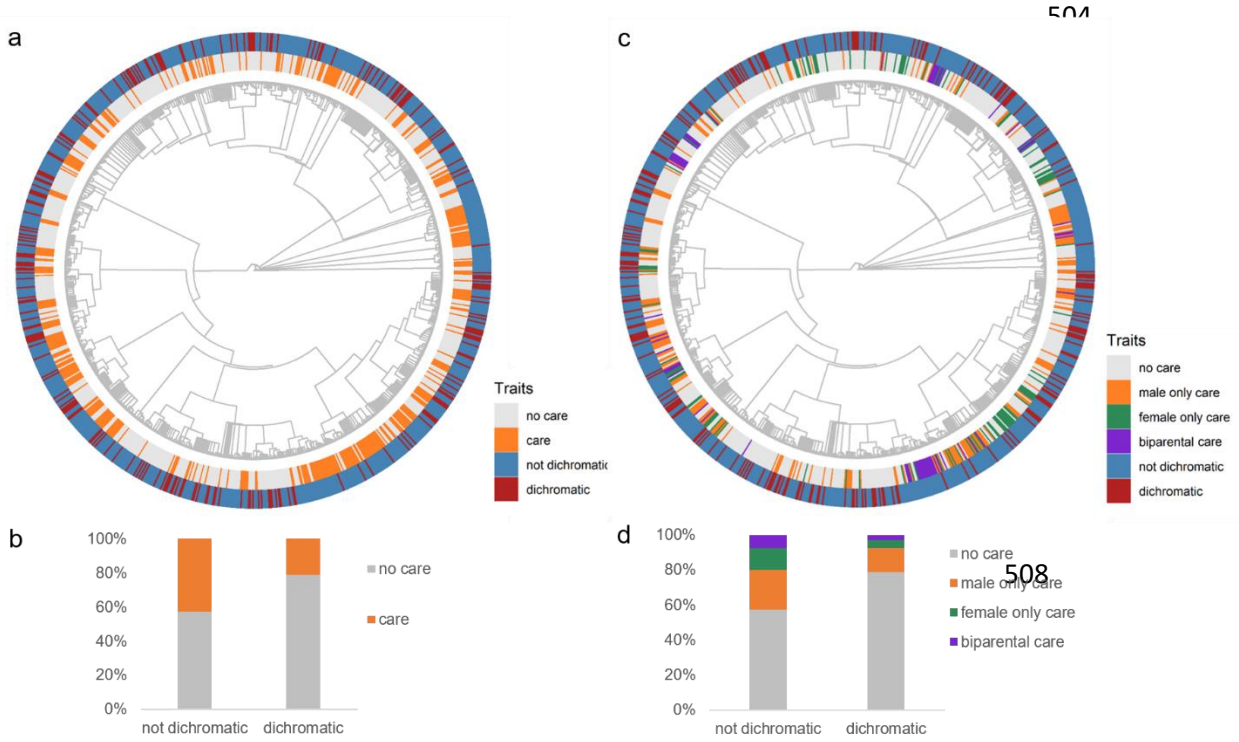
[34] Toledo, L.F. 2005 Predation of juvenile and adult anurans by invertebrates: current knowledge and perspectives. . *Herpetol Rev* **36**, 395-400.
[35] Toledo, L.F., Ribeiro, R.S. & Haddad, C.F.B. 2007 Anurans as prey: an exploratory analysis and size relationships between predators and their prey. *J. Zool.* **271**, 170-177. (doi:10.1111/j.1469-7998.2006.00195.x).
[36] Choi, N. & Jang, Y. 2004 Background matching by means of dorsal color change in treefrog populations (*Hyla japonica*). *Journal of Experimental Zoology A: Ecological Genetics and Physiology* **321**, 108–118.
[37] Kang, C., Kim, Y.E. & Jang, Y. 2016 Colour and pattern change against visually heterogeneous backgrounds in the tree frog Hyla japonica. *Sci Rep* **6**, 22601. (doi:10.1038/srep22601).
[38] Nilsson Skold, H., Aspengren, S. & Wallin, M. 2013 Rapid color change in fish and amphibians - function, regulation, and emerging applications. *Pigment Cell Melanoma Res* **26**, 29-38. (doi:10.1111/pcmr.12040).
[39] Cooper, W.E.J., Caldwell, J.P. & Vitt, L.J. 2008 Effective crypsis and its maintenance by immobility in *Craugastor* frogs. *Copeia*, 527–532.
[40] Taboada, C., Brunetti, A.E., Lyra, M.L., Fitak, R.R., Faigón Soverna, A., Ron, S.R., Lagorio, M.G., Haddad, C.F.B., Lopes, N.P., Johnsen, S., et al. 2020 Multiple origins of green coloration in frogs mediated by a novel biliverdin-binding serpin. *Proceedings of the National Academy of Sciences*, 202006771. (doi:10.1073/pnas.2006771117).
[41] Chiari, Y., Vences, M., Vieites, D.R., Rabemananjara, F., Bora, P., Ramilijaona Ravoahangimalala, O. & Meyer, A. 2004 New evidence for parallel evolution of colour patterns in Malagasy poison frogs (Mantella). *Mol Ecol* **13**, 3763-3774. (doi:10.1111/j.1365-294X.2004.02367.x).
[42] Hegna, R.H., Saporito, R.A. & Donnelly, M.A. 2012 Not all colors are equal: predation and color polytypism in the aposematic poison frog Oophaga pumilio. *Evol. Ecol.* **27**, 831-845. (doi:10.1007/s10682-012-9605-z).
[43] Rojas, B., Rautiala, P. & Mappes, J. 2014 Differential detectability of polymorphic warning signals under varying light environments. *Behav Processes* **109 Pt B**, 164-172. (doi:10.1016/j.beproc.2014.08.014).
[44] Summers, K. & Clough, M.E. 2001 The evolution of coloration and toxicity in the poison frog family (Dendrobatidae). *Proc Natl Acad Sci U S A* **98**, 6227-6232. (doi:10.1073/pnas.101134898).
[45] Portik, D.M., Bell, R.C., Blackburn, D.C., Bauer, A.M., Barratt, C.D., Branch, W.R., Burger, M., Channing, A., Colston, T.J., Conradie, W., et al. 2019 Sexual Dichromatism Drives Diversification within a Major Radiation of African Amphibians. *Syst Biol* **68**, 859-875. (doi:10.1093/sysbio/syz023).
[46] Bell, R.C. & Zamudio, K.R. 2012 Sexual dichromatism in frogs: natural selection, sexual selection and unexpected diversity. *Proc Biol Sci* **279**, 4687-4693. (doi:10.1098/rspb.2012.1609).
[47] Dale, J., Dey, C.J., Delhey, K., Kempenaers, B. & Valcu, M. 2015 The effects of life history and sexual selection on male and female plumage colouration. *Nature* **527**, 367-370. (doi:10.1038/nature15509).
[48] Allen, W.L., Moreno, N., Gamble, T. & Chiari, Y. 2020 Ecological, behavioral, and phylogenetic influences on the evolution of dorsal color pattern in geckos. *Evolution* **74**, 1033-1047. (doi:10.1111/evo.13915).
[49] Frost, D.R. 2020 Amphibian Species of the World: an Online Reference. Version 6.1 (December 1st). Electronic Database accessible at https://amphibiansoftheworld.amnh.org/index.php. American Museum of Natural History, New York, USA. doi.org/10.5531/db.vz.0001
[50] Jetz, W. & Pyron, R.A. 2018 The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nat Ecol Evol* **2**, 850-858. (doi:10.1038/s41559-018-0515-5).
[51] Grafen, A. 1989 The phylogenetic regression. *Philosophical Transactions of the Royal Society B* **326**, 119-157.

[52] Paradis, E., Claude, J. & Strimmer, K. 2004 APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, 289–290.
[53] Ives, A.R. & Helmus, M.R. 2011 Generalized linear mixed models for phylogenetic analyses of community structure. *Ecol. Monogr.* **81**, 511–525.
[54] RStudio Team. 2020 RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/. (
[55] Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S. & Isaac, N.J.R.p.v. 2013 The caper package: comparative analysis of phylogenetics and evolution in R. **5**, 1-36.
[56] Pennell, M.W., Eastman, J.M., Slater, G.J., Brown, J.W., Uyeda, J.C., FitzJohn, R.G., Alfaro, M.E. & Harmon, L.J.J.B. 2014 geiger v2. 0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. **30**, 2216-2218.
[57] Revell, L.J. 2012 phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**, 217-223.
[58] Yu, G., Smith, D.K., Zhu, H., Guan, Y., Lam, T.T.Y.J.M.i.E. & Evolution. 2017 ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. **8**, 28-36.
[59] Wells, K.D. 1977 The social behaviour of anuran amphibians. *Anim. Behav.* **25**, 666-693.
[60] Kindermann, C. & Hero, J.-M. 2016 Rapid dynamic colour change is an intrasexual signal in a lek breeding frog (Litoria wilcoxii). *Behav. Ecol. Sociobiol.* **70**, 1995-2003. (doi:10.1007/s00265-016-2220-1).
[61] Sztatecsny, M., Preininger, D., Freudmann, A., Loretto, M.-C., Maier, F. & Hödl, W. 2012 Don't get the blues: conspicuous nuptial colouration of male moor frogs (Rana arvalis) supports visual mate recognition during scramble competition in large breeding aggregations. *Behav. Ecol. Sociobiol.* **66**, 1587-1593. (doi:10.1007/s00265-012-1412-6).
[62] Gomez, D., Richardson, C., Lengagne, T., Plenet, S., Joly, P., Lena, J.P. & Thery, M. 2009 The role of nocturnal vision in mate choice: females prefer conspicuous males in the European tree frog (Hyla arborea). *Proc Biol Sci* **276**, 2351-2358. (doi:10.1098/rspb.2009.0168).
[63] Barnett, J.B., Michalis, C., Scott-Samuel, N.E. & Cuthill, I.C. 2018 Distance-dependent defensive coloration in the poison frog Dendrobates tinctorius, Dendrobatidae. *Proc Natl Acad Sci U S A* **115**, 6416-6421. (doi:10.1073/pnas.1800826115).
[64] Cyriac, V.P. & Kodandaramaiah, U. 2019 Conspicuous colours reduce predation rates in fossorial uropeltid snakes. *PeerJ* **7**, e7508. (doi:10.7717/peerj.7508).
[65] Niskanen, M. & Mappes, J. 2005 Significance of the dorsal zigzag pattern of Vipera latastei gaditana against avian predators. *J Anim Ecol* **74**, 1091-1101. (doi:10.1111/j.1365-2656.2005.01008.x).
[66] Wuster, W., Allum, C.S., Bjargardottir, I.B., Bailey, K.L., Dawson, K.J., Guenioui, J., Lewis, J., McGurk, J., Moore, A.G., Niskanen, M., et al. 2004 Do aposematism and Batesian mimicry require bright colours? A test, using European viper markings. *Proc Biol Sci* **271**, 2495-2499. (doi:10.1098/rspb.2004.2894).
[67] Doucet, S.M. & Mennill, D.J. 2010 Dynamic sexual dichromatism in an explosively breeding Neotropical toad. *Biol Lett* **6**, 63-66. (doi:10.1098/rsbl.2009.0604).
[68] Taboada, C., Brunetti, A.E., Pedron, F.N., Carnevale Neto, F., Estrin, D.A., Bari, S.E., Chemes, L.B., Peporine Lopes, N., Lagorio, M.G. & Faivovich, J. 2017 Naturally occurring fluorescence in frogs. *Proc Natl Acad Sci U S A* **114**, 3672-3677. (doi:10.1073/pnas.1701053114).
[69] Townsend, D.S. 1986 The costs of male parental care and its evolution in a neotropical frog. *Behav Ecol Sociobiol* **19**, 187-195.
[70] Bickford, D. 2002 Male parenting of New Guinea froglets. *Nature* **428**, 601-602.
[71] Bickford, D. 2004 Differential parental care behaviors of arboreal and terrestrial microhylid frogs from Papua New Guinea. *Behav. Ecol. Sociobiol.* **55**, 402-409. (doi:10.1007/s00265-003-0717-x).

[72] Delia, J., Bravo-Valencia, L. & Warkentin, K.M. 2020 The evolution of extended parental care in glassfrogs: Do egg-clutch phenotypes mediate coevolution between the sexes? *Ecol. Monogr.* (doi:10.1002/ecm.1411).
[73] Seshadri, K.S. & Bickford, D.P. 2018 Faithful fathers and crooked cannibals: the adaptive significance of parental care in the bush frog *Raorchestes chalazodes*, Western Ghats, India. *Behav. Ecol. Sociobiol.* **72**. (doi:10.1007/s00265-017-2420-3).
[74] Poo, S. & Bickford, D.P. 2013 The Adaptive Significance of Egg Attendance in a South-East Asian Tree Frog. *Ethology* **119**, 671-679. (doi:10.1111/eth.12108).
[75] Poo, S., Evans, T.A., Tan, M.K. & Bickford, D.P. 2016 Dynamic switching in predator attack and maternal defence of prey. *Biol. J. Linn. Soc.* **118**, 901-910. (doi:10.1111/bij.12786).
[76] Toledo, L.F., Sazima, I. & Haddad, C.F.B. 2011 Behavioural defences of anurans: an overview. *Ethol. Ecol. Evol.* **23**, 1-25. (doi:10.1080/03949370.2010.534321).

Figure 1. Combinations of the three colours (rows), and four dorsal patterns (columns) categorised for anurans in our dataset: a. Green-Brown with plain dorsum in *Agalychnis annae* (Adam W. Bland); b. Green Brown with Bars-Bands in *Craugastor fitzingeri* (Brian Kubicki); c. Green-Brown with Spots in *Lithobates vibicarius* (David A. Rodríguez); d. Green-Brown with Mottled-Patches in *Scaphiophryne marmorata* (Peter Janzen); e. Red-Blue-Black with Plain dorsum in *Andinobates opisthomelas* (Daniel Vásquez-Restrepo); f. Red-Blue-Black with Bars-Bands in *Oophaga lehmanni* (Arachnokulture); g. Red-Blue-Black with Spots in *Nyxtixalus pictus* (Seshadri KS); h. Red-Blue-Black with Mottled-Patches in *Dendrobates auratus* (Peter Janzen); i. Yellow with Plain dorsum in *Mantella laevigata* (Miguel Vences); j. Yellow with Bars and Bands in *Kassina senegalensis* (Alberto Sanchez-Vialas); k. Yellow with Spots in *Dendropsophus sanborni* (Raul Maneyro) and; l. Yellow with Mottled-Patches in *Uperodon systoma* (Seshadri KS). All images except g & l are sourced from CalPhotos with permission from respective owners (credits in parentheses).

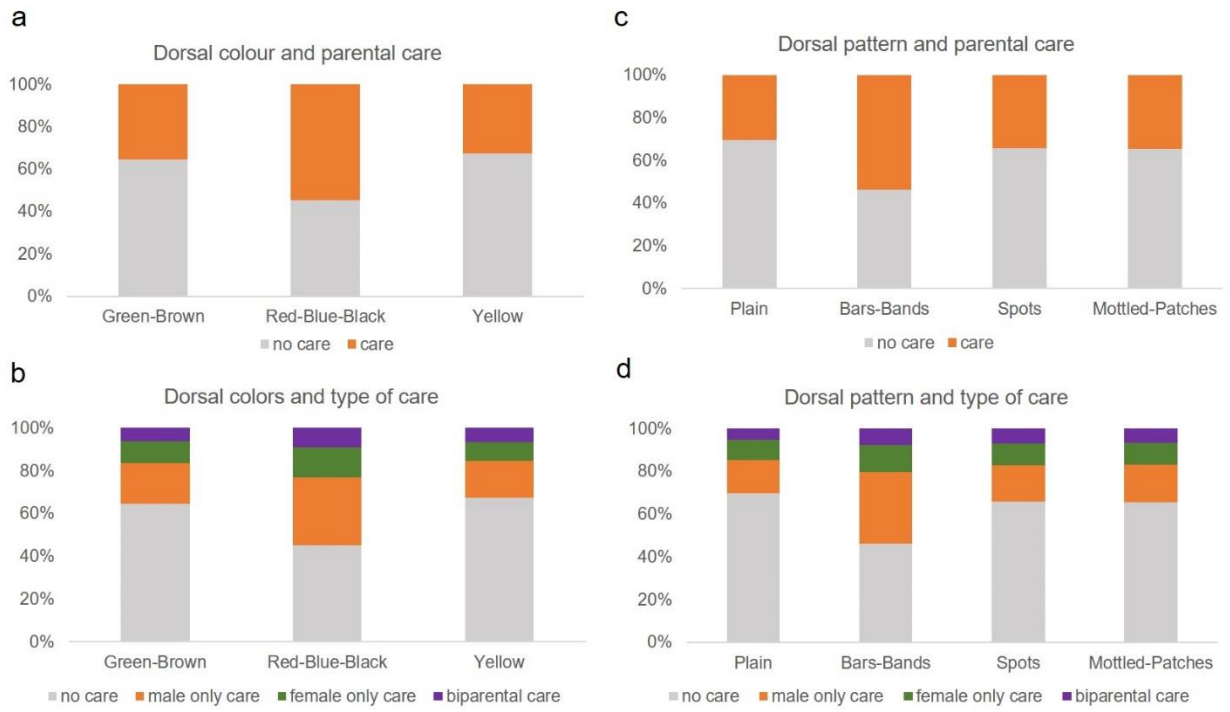
Figure 2. The association between dichromatism and parental care in anurans (N = 988 species). (a) Phylogenetic distribution and (b) co-occurrence of dichromatism (presence or absence) with parental care (care or no care). (c) Phylogenetic distribution and (d) co-occurrence of dichromatism (presence or absence) with different types of parental care (no care, male-only care, female-only care, biparental care).



521 **Figure 3.** Parental care (no care, care) and type of parental care (no care, male- only care, female- only

522 care, and biparental care) are weakly correlated with (a, b) dorsal colour and (c, d) dorsal pattern except

523 male only care and bars-bands. Data from males of 988 species are presented.



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531 **Table 1**. Evolutionary associations between life-history traits (occurrence and type of parental care) and the presence of dichromatism, and
532 gradients of dorsal colour and pattern. Shown are outputs of binaryPGLMM regressions with the dependent and explanatory variables listed
533 according to the models tested. P < 0.05 are indicated by an '*'. All models tested data from 988 species. N is the number of species having the
534 condition listed as a dependent variable, e.g., parental care was present in 375 species.

Model no	Dependent	Explanatory	Estimate ± SE	Z	P	Phylogenetic signal	Pr	N
1	Parental care	Not dichromatic (Intercept)	-0.5 ± 1.6	-0.30	0.76	20.62	1.00E-41	375
		Dichromatic	-0.71 ± 0.3	-2.15	0.03*			
2	Dichromatism	No care (Intercept)	-1.68 ± 0.7	-2.29	0.02*	3.319	2.30E-38	221
		Male only care	-0.83 ± 0.3	-2.51	0.01*			
		Female only care	-0.96 ± 0.4	-2.29	0.02*			
		Biparental care	-0.98 ± 0.5	-1.86	0.06.			
3	Male only care	Plain (Intercept)	-2.2 ± 1.6	-1.39	0.16	1.85E+01	5.25E-57	204
		Bars-Bands	0.9 ± 0.4	2.33	0.02*			
		Spots	0 ± 0.4	0.1	0.92			
		Mottled-Patches	0.4 ± 0.4	1.19	0.24			
4	Male only care	Green-Brown (Intercept)	-1.8 ± 1.5	-1.13	0.26	18.63	2.94E-60	204

		Red-Blue-Black	-0.3 ± 0.3	-0.87	0.39			
		Yellow	-0.2 ± 0.3	-0.54	0.59			
5	Female only care	Plain (Intercept)	-0.3 ± 1.5	-1.94	0.05	15.01	1.35E-67	106
		Bars-Bands	-0.4 ± 0.5	-0.96	0.34			
		Spots	-0.2 ± 0.4	-0.35	0.73			
		Mottled-Patches	-0.3 ± 0.4	-0.71	0.48			
6	Female only care	Green-Brown (Intercept)	-3.3 ± 1.5	-2.14	0.03*	15.19	2.42E-67	106
		Red-Blue-Black	0.2 ± 0.4	0.5	0.62			
		Yellow	0.2 ± 0.5	0.4	0.69			