

1 Reproductive and ecological adaptations to climate
2 underpin the evolution of sociality in lizards

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15 **Abstract**

16

17 Identifying the environmental factors associated with group living is important
18 for understanding how social systems originate, persist and diversify. In endothermic
19 birds and mammals, living in social groups is associated with habitat constraints and
20 harsh climatic conditions. We use phylogenetic comparative analyses to test whether
21 climate and habitat have played similar roles in the evolution of social grouping in a
22 globally distributed clade of ectothermic vertebrates, lizards ($N_{\text{species}} = 1696$). Social
23 grouping was strongly associated with cool, dry climates across the lizard phylogeny.
24 However, this climatic signature arose indirectly, by association with live birth
25 (common in cool climates) and a reliance on rock crevices (common in dry climates),
26 traits which increase parent-offspring associations and reduce offspring dispersal. In
27 contrast, direct effects of cool temperature on the evolution of social grouping were
28 marginal and restricted to live bearing species. Our results demonstrate that
29 relationships between climate and sociality may result from climatic adaptations that
30 go on to promote the emergence of grouping behaviour.

31

32 **Key words:** Social Grouping, Lizards, Climate, Viviparity, Habitat Constraints, Family

33 Introduction

34 Evolutionary transitions from solitary to group living are strongly shaped by the
35 environment. Climatic factors mediate the availability of resources, affecting the
36 frequency, costs, and benefits of interactions among individuals (Wynne-Edwards,
37 1998; AlRashidi et al., 2010, 2011; Vincze et al., 2017; Lejeune et al., 2019). Other
38 aspects of the environment, such as habitat structure and availability, can restrict
39 dispersal and breeding opportunities, generating selection for increased social
40 tolerance and cooperation (Emlen 1982; 1995; Komdeur 1992; Hatchwell & Komdeur
41 2000; Halliwell et al. 2017b). This has resulted in strong associations between
42 environmental conditions and sociality in diverse clades across the tree of life (Jetz &
43 Rubenstein 2011; Lukas & Clutton-Brock 2017; Cornwallis et al. 2017; Firman et al.
44 2020; Qi et al. 2023).

45 Most evidence that climate and habitat explain variation in social systems
46 comes from complex forms of sociality, such as cooperative breeding (Rubenstein &
47 Abbot 2017). Studies tend to focus on how the environment mediates the costs and
48 benefits of independent breeding versus helping relatives to breed. For example, in
49 birds and mammals, cooperative breeding is associated with climates where
50 independent breeding is difficult, and the benefits of helping are high (Firman et al.
51 2020; Cornwallis et al. 2017; Lukas & Clutton-Brock 2017; Jetz & Rubenstein 2011).
52 However, our understanding of the environmental drivers of sociality in vertebrates is
53 potentially biased by a strong focus on endothermic species. We know comparatively
54 little about the role of environment in ectothermic vertebrates, despite even greater
55 potential for climate to mediate social behaviour (Moss & While 2021).

56 We use a global dataset of lizards to test how environmental factors have
57 shaped the evolution of social grouping in this diverse clade of ectotherms.
58 Environmental factors may have a more direct effect on social grouping in lizards
59 compared to endotherms for several reasons. First, cool climates impose constraints
60 on activity (Vidan et al. 2017), affecting dispersal and opportunities for social
61 interactions (Price-Rees et al. 2014; Rat et al. 2020; Moss et al. 2023). Second, cool
62 climates may alter kin structure by reducing polyandry (Olsson et al., 2011), and
63 intraspecific aggression (Baird & May, 2003), with consequences for inclusive fitness.

64 Finally, climatic conditions may select for adaptations that affect opportunities for
65 interacting with relatives. In particular, the evolution of live birth (viviparity) is
66 associated with cool climates in lizards (Zimin et al. 2022) and appears to have
67 facilitated transitions to social grouping, in part, by promoting parent-offspring
68 associations (Halliwell et al. 2017).

69 Conversely, some aspects of environmental variation may have more general
70 effects that promote sociality in both endotherms and ectotherms. Like birds and
71 mammals, lizards require specific habitat features that can be limited or clustered
72 across the landscape, often dependent on local climatic conditions. Such clustering
73 can favour the evolution of social tolerance, especially if constraints on dispersal
74 promote interactions between kin (Halliwell et al. 2017b; Le Galliard et al. 2003; Massot
75 et al. 2002). However, whether such general environmental conditions can explain the
76 evolution of sociality across diverse taxa remains unclear.

77 We integrated data on social grouping (Halliwell et al. 2017), breeding climates
78 (Caetano et al. 2022; Harris et al. 2020), habitat preferences (Meiri 2024) and
79 reproductive mode (Zimin et al. 2022) across 1696 lizard species. Sociality in lizards
80 ranges from transient associations to stable transgenerational aggregations (Whiting &
81 While 2017; While et al. 2019), but commonly occurs as family units based on delayed
82 dispersal and prolonged parent-offspring associations (Whiting & While 2017). These
83 simple social groups have evolved multiple times independently (Halliwell et al. 2017),
84 making it possible to estimate how social grouping, climate and habitat preferences
85 coevolve. We used phylogenetic comparative methods to 1) test if social grouping is
86 explained by climate and habitat after accounting for viviparity; 2) evaluate alternative
87 causal models for the relationships between these traits and; 3) test for differences in
88 reconstructed trait values between nodes estimated to represent different stages in the
89 evolution of social grouping.

90

91 **Methods**

92 **Data Collection**

93 *Social grouping and reproductive mode*

94 We used data on lizard social grouping from Halliwell et al. (2017) updated with
95 reports of social grouping published between 2017 and 2024. Social grouping was
96 assigned based on reports of social aggregations containing both adults and juveniles.
97 One key challenge to such studies is assigning the absence of a trait. Species were
98 classified as non-social if they met any of the following four criteria (see Halliwell et al.
99 2017 for details): (1) Other forms of parental care (e.g. nest construction, egg guarding)
100 have been reported for the species with no mention of associations between adults and
101 juveniles in any of the literature accessed; (2) Studies of life history, reproductive
102 biology, or ecology involving active field sampling are available for the species, but do
103 not report associations between adults and juveniles; (3) The species is well studied
104 (citation count of ≥ 100 peer-reviewed publications according to Web of Science), but
105 no reports of associations between adults and juveniles were found during the
106 literature search; (4) complete absence of reports of social grouping for that taxonomic
107 family.

108 Data on reproductive mode were extracted from Zimin et al., (2022). The final
109 data set used for analyses contained 1696 species.

110

111 *Climatic niche*

112 The climatic niche of each species was estimated using data from the CRU TS v.
113 4.07 climate grids. This contains monthly temperature and precipitation estimates for
114 0.5° grid cells across all global land areas (excluding Antarctica) for the period between
115 1901 and 2022 (Harris et al. 2020). Species distribution maps from Caetano et al. (2022;
116 also see Roll et al. 2017) were intersected with the CRU database to calculate the
117 median value of mean monthly temperature (degrees Celsius) and precipitation rate
118 (mm/month) across grid cells for each species. This resulted in a median value for each
119 climatic variable for each species for each month of every year. From this, we only used
120 data for the 6 months of the year that are most relevant to embryo development and
121 early post-natal life in lizards, i.e., breeding season (April – September for N
122 hemisphere; October – March for S hemisphere). From these data, we calculated a
123 mean for each species for each climatic variable. These temperature and precipitation
124 values (henceforth temperature and precipitation) represent averages over each
125 species geographic range during the breeding season. Predictability in temperature

126 and precipitation were measured via Colwell's P (Colwell et al. 1974), an index that
127 captures among-year variation in onset, intensity and duration of periodic phenomena
128 ranging from 0 (completely unpredictable) to 1 (completely predictable). We chose
129 Colwell's P over measures of variability such as standard deviations because these
130 metrics were less strongly correlated to temperature and precipitation in our data
131 (Figure S1), and facilitate comparisons with other studies (Cornwallis et al. 2017;
132 Fristoe et al. 2017; Griesser et al. 2017; Firman et al. 2020; Martin et al. 2020; Diamant
133 et al. 2021). However, it is worth noting that the interpretation of predictability should
134 be guided by an assessment of the relative contribution of constancy and periodicity to
135 predictability estimates (Liu et al. 2024). These supporting analyses are provided as
136 supplementary information (Figure S2). Temperature (after conversion to K) and
137 precipitation values were log-transformed before calculating species means and
138 Colwell's P values.

139

140 *Habitat associations*

141 We extracted data on habitat associations from SquamBase (Meiri 2024).
142 Habitat associations included 4 broad non-exclusive habitat types: arboreal (living and
143 foraging on vegetation – 766 spp.), fossorial (henceforth “burrowing”, digging or foraging
144 underground or under objects – 127 spp.), saxicolous (henceforth “rock dwelling”, living
145 and foraging in and on rocks – 334 spp.) and terrestrial (moving and foraging on the
146 ground and leaf litter – 990 spp.) coded as binary variables (i.e., is the species found in
147 this habitat type? yes/no).

148

149 **Statistical Analyses**

150 We used three complementary approaches to investigate coevolution between
151 climate, habitat, reproductive mode and social grouping in lizards. First, we used
152 phylogenetic mixed models to: 1) estimate regression coefficients between
153 environmental predictors and social grouping while accounting for phylogenetic
154 dependence; 2) explore interactions between environmental variables and viviparity on
155 the probability of social grouping; 3) estimate phylogenetic correlations between
156 environmental variables and social grouping using multi-response models. Second, we
157 used phylogenetic path analyses to gain insight into the causal network underlying trait

158 correlations. Third, we performed ancestral state reconstructions to test for differences
159 in climatic niche and habitat associations among ancestral species (internal nodes)
160 that did, and did not, give rise to sociality in descendant lineages. The R code necessary
161 to replicate all analyses is included as supplementary information.

162

163 *Testing for trait relationships while controlling for phylogeny*

164 We used Bayesian phylogenetic mixed models (PMM) (MCMCglmm package;
165 Hadfield 2010) to fit phylogenetic regressions that tested for associations between
166 social grouping, reproductive mode, climatic niche and habitat associations while
167 controlling for phylogenetic relatedness among species. In PMMs, phylogenetic
168 random effects are modelled via (co)variance matrices that assume a Brownian motion
169 model of evolution (Hadfield and Nakagawa 2010). We modelled social grouping as a
170 binary trait (yes vs no) on the probit link scale using a “threshold” error distribution and
171 each climate variable and habitat association as a fixed effect predictor. To test
172 whether the effects of climate and habitat were independent of reproductive mode, we
173 re-fit the model with viviparity (yes vs no) as an additional predictor and checked for
174 changes in the significance of fixed effects.

175 Based on initial analyses identifying viviparity and rock dwelling as key
176 predictors of social grouping (see results; Table S2) we fitted a series of PMMs to test
177 whether these traits interact with climate variables (or each other) to influence the
178 probability of social grouping. Specifically, a series of candidate models specifying all
179 possible two-way interactions between both viviparity and rock dwelling, and each
180 climate variable, as well as all three-way interactions between viviparity, rock dwelling,
181 and each climate variable (Table S3). We then compared these models to a null model
182 including only the main effects of viviparity and rock dwelling using deviance
183 information criterion (DIC) as a measure of predictive performance that accounts for
184 the effective degrees of freedom (EDF) in models including both fixed and
185 (phylogenetic) random effects (Hadfield 2010). Although model scores such as WAIC or
186 LOO may be preferable to DIC due to their asymptotic properties (Gelman et al. 2014),
187 these options are not available for phylogenetically structured data in the Gibbs
188 sampling framework of MCMCglmm.

189

190 *Testing for phylogenetic correlations*

191 Phylogenetic regressions model dependence in the residual error structure
192 attributable to phylogeny, and therefore ‘control for phylogeny’ when estimating
193 regression coefficients. However, when predictor variables also contain phylogenetic
194 signal, multi-response (MR) PMMs offer a more informative decomposition of trait
195 covariances (Westoby et al. 2023; Halliwell et al. 2022). We used MR-PMM to examine
196 phylogenetic correlations between social grouping, viviparity, rock dwelling, burrowing,
197 and each of the 4 climate variables (8 response variables in total). We excluded
198 terrestrial and arboreal habitat associations as response variables in MR-PMM to
199 minimise the number of estimated model parameters, as these habitat associations
200 showed a weaker relationship with social grouping (social grouping occurs in only 4% of
201 terrestrial species and 2.3% of arboreal species) compared with rock dwelling (11.3%)
202 and burrowing (9.4%) (Table S4). We modelled the binary traits of social grouping,
203 viviparity, rock dwelling and burrowing on the probit link scale using “threshold” error
204 distributions. We modelled the continuous traits of (log) temperature, (log)
205 precipitation, temperature predictability and precipitation predictability using a
206 Gaussian error distribution. All continuous traits were z-transformed prior to analyses.

207 For the MR-PMM, we removed the global intercept to allow separate intercepts
208 for each trait and specified an 8x8 unstructured phylogenetic covariance matrix for the
209 random effects. The variance partitioning achieved with MR-PMM also allows
210 covariances between traits on the residual level (i.e., covariances independent of
211 phylogeny) to be estimated. However, for binary traits, the residual variance is not
212 identifiable and is fixed in the prior specification of the model (Hadfield 2010). We
213 therefore specified structured (diagonal) residual covariance matrices for the residual
214 errors in MR-PMM and relied on phylogenetic regression to estimate trait relationships
215 residual to phylogeny. For both PMMs and MR-PMMs, we incorporated phylogenetic
216 uncertainty by fitting models over a sample of 100 candidate topologies from Tonini et
217 al. (2016) and concatenated MCMC chains of parameters across fits for inference.
218 Each tree was pruned to contain only those species for which data on reproductive
219 mode, environmental variables and social grouping was available (n = 1696).

220

221 *Testing for phylogenetic correlations separately for oviparous and viviparous species*

222 We investigated whether correlations between social grouping, rock dwelling
223 and temperature differed between oviparous and viviparous species by fitting a MR-
224 PMM that estimated separate phylogenetic correlations between these traits for the
225 two reproductive modes using at.level coding in MCMCglmm (see code in
226 supplementary information). This approach doubles the number of estimated model
227 parameters, asking more of the data (especially for viviparous species, $n = 197$).
228 Therefore, we did not attempt it for the full MR-PMM including 8 response traits.

229

230 *Model settings, diagnostics and parameter estimation*

231 The prior settings used for each analysis are specified in the R code in the
232 supplementary information. Following de Villemereuil (2018), we used parameter
233 expanded priors for random effects in binary response models. The residual variance of
234 binary traits was fixed to 1. Otherwise, an inverse-Wishart prior was specified for
235 residual variances. Model parameter estimates are reported as posterior modes and
236 95% credible intervals.

237 We examined the convergence of MR-PMMs by fitting two separate MCMC
238 chains and: 1) visually inspecting traces of the MCMC posterior estimates and their
239 overlap; and 2) calculating potential scale reduction factors (\hat{r}), a convergence
240 diagnostic test that compares within- and between-chain variance (Vehtari et al. 2019).
241 \hat{r} values greater than 1.1 indicate chains with poor convergence properties. We
242 confirmed \hat{r} values were less than 1.1 for all parameters, though for most parameters \hat{r}
243 was considerably lower ($\hat{r} \leq 1.01$).

244 For Gaussian traits, we estimated the proportion of variance explained by
245 phylogenetic dependence (sometimes referred to as phylogenetic signal, λ) from the
246 MR-PMM as, $\lambda = \frac{\sigma_{phy}^2}{\sigma_{phy}^2 + \sigma_{res}^2}$, where σ_{phy}^2 and σ_{res}^2 are the phylogenetic and residual
247 variances for a given trait from the fitted model, respectively. For binary traits, the
248 residual variance was fixed (see above) and therefore we used the intraclass correlation
249 coefficient to estimate phylogenetic signal. This is calculated as, $\lambda = \frac{\sigma_{phy}^2}{\sigma_{phy}^2 + V + D}$, where
250 V is the level of residual variance (additive over-dispersion) fixed in the prior

251 specification (here, $V = 1$) and $D = 1$ is the distribution specific variance term for the
252 binomial distribution with a probit link (Nakagawa & Schielzeth 2013).

253 We calculated the phylogenetic correlation between two traits, as:

$$254 \quad \rho_{ij}^{phy} = \frac{\Sigma_{ij}^{phy}}{\sqrt{\Sigma_{ii}^{phy} \Sigma_{jj}^{phy}}} \quad 1.$$

255 Where ρ_{ij}^{phy} is the phylogenetic correlation between traits i and j , Σ_{ij}^{phy} is the
256 phylogenetic covariance between traits i and j , and Σ_{ii}^{phy} is the phylogenetic variance in
257 trait i . To evaluate evidence for conditional dependencies between traits, (i.e.,
258 relationships after controlling for covariances with other response traits) we also
259 calculated partial phylogenetic correlations. To compute partial correlations, we
260 substituted elements of the inverse trait-level phylogenetic covariance matrix, Σ^{phy-1} ,
261 into equation 1 following Halliwell et al. (2022) (also see Popovic et al. 2019). To
262 evaluate the significance of correlation estimates, we checked whether the 95% HPD of
263 the posterior distribution of parameter estimates crossed zero.

264

265 *Phylogenetic Path Analysis*

266 To evaluate different hypotheses of the causal network underpinning trait
267 relationships, we conducted phylogenetic path analyses in the ‘phylopath’ package
268 (van der Bijl 2018). We utilised frequentist approaches for these analyses due to the
269 computational constraints on fitting many alternative causal models across a posterior
270 sample of trees in a fully Bayesian framework. Specifically, based on results from
271 phylogenetic mixed models (Figure 3a; Table S2), we defined 27 candidate models for
272 the network of relationships between social grouping, viviparity, rock dwelling,
273 precipitation, and temperature (Figure S3). We then fit this set of candidate models via
274 maximum likelihood to each of 100 candidate topologies and summarised the
275 distribution of point estimates generated for each path coefficient. We also examined
276 the distribution of model weights (Figure S4) to assess the influence of phylogenetic
277 uncertainty on model selection, and the distribution of standardized regression
278 coefficients to assess the significance of trait relationships. Inferences were drawn by
279 averaging over all candidate models, weighted by their relative evidence, with

280 confidence intervals for regression coefficients calculated using 100 bootstrap
281 replicates.

282

283 *Ancestral State Reconstruction*

284 We reconstructed ancestral states for reproductive mode and social grouping
285 using hidden Markov models (HMM) in the R package corHMM (Beaulieu et al 2013;
286 Beaulieu & O’Meara 2014). This modelling framework uses “hidden” states to
287 parametrize multiple rate matrices, allowing transition rates in a discrete character to
288 vary across the phylogeny (i.e., allowing transition rates to vary between clades). We
289 chose this approach based on recent research indicating that the likelihood of evolving
290 viviparity varies considerably across squamates, which has important effects on
291 ancestral state reconstructions (Pettersen 2023; also see King & Lee 2015; Wright et al.
292 2015).

293 For each trait (e.g. reproductive mode), we fit HMM that allowed between 1 and 3
294 different rate categories from one state (oviparity) to the other (viviparity) across the
295 tree. Reversals from viviparity to oviparity were prohibited because such events are
296 thought to have been rare in the squamates (Blackburn 2015; Shine 2015; Griffith et al.
297 2015). We used AICc to compare models and identify the most likely number of rate
298 categories (1-3) across a sample of 100 candidate topologies. A model with 2 rate
299 categories was preferred for social grouping (lowest AICc for 92/100 trees) and a model
300 with 3 rate categories was preferred for reproductive mode (lowest AICc for 74/100
301 trees). The preferred model for each trait was used in all subsequent analyses.

302 Joint estimates of ancestral states at internal nodes from HMMs were then used
303 to identify transitions in social grouping for oviparous and viviparous species
304 separately, by classifying internal nodes according to their estimated state and that of
305 their descendants, e.g., oviparous non-social with at least one social descendant
306 (O.NSG_O.SG). Nodes inferred to have undergone simultaneous transitions in
307 reproductive mode and social grouping (e.g., O.NSG_V.SG) were treated as NA. These
308 unresolved nodes mean we are likely to underestimate the number of transitions to
309 social grouping within our sample, especially for viviparous species (Table S5), which
310 may influence our results. Therefore, we conducted sensitivity analyses in which these
311 nodes were included, and confirmed equivalent results whether simultaneous

312 transitions were treated as reproductive mode or social grouping (Figure S5) changing
313 first in the sequence (e.g., O.NSG_V.SG treated as V.NSG_V.SG or O.SG_V.SG).

314 Following Cornwallis et al. (2017), we used these node classifications to test for
315 differences in reconstructed trait values between nodes representing different stages in
316 the evolutionary history of social grouping. For temperature, we used a PMM with
317 temperature as the only response trait, node transition classification (e.g.,
318 O.NSG_O.SG) as a fixed effect, and a phylogenetic random effect linked to internal
319 nodes. This model uses observed temperature values from species at the tips to
320 reconstruct values at internal nodes and estimate fixed effects for each node
321 classification category. Using the posterior distribution of fixed effects estimated for
322 each node classification category, we constructed contrasts that test different
323 hypotheses about the sequence of evolutionary events. Specifically, to test if
324 temperature values differed between the ancestors of social and non-social lineages
325 (i.e., to test for differences in temperature at the origin of social grouping), we
326 compared reconstructed values for non-social ancestors that gave rise to only non-
327 social descendants with those of non-social ancestors that gave rise to at least one
328 social descendants (e.g., O.NSG_O.NSG - O.NSG_O.SG). To test for changes in
329 temperature values following the emergence of social grouping, we compared non-
330 social ancestors that gave rise to at least one social descendant with social ancestors
331 that gave rise only to social descendants (e.g., O.NSG_O.SG - O.SG_O.SG). To test for
332 differences in temperature values associated with the maintenance of social grouping,
333 we compared non-social ancestors that gave rise only to non-social descendants with
334 social ancestors that gave rise only to social descendants (e.g., O.NSG_O.NSG -
335 O.SG_O.SG). The same procedure was repeated for ancestral state reconstructions of
336 rock dwelling.

337 For each comparison, we evaluated significance by subtracting the vector of
338 posterior samples for the fixed effect of the first node category from those for the
339 second node category (e.g., $\hat{\beta}_{\text{O.NSG_O.NSG}} - \hat{\beta}_{\text{O.NSG_O.SG}}$) and checking whether the 95%
340 credible interval of the resulting distribution overlapped zero (coloured bars in Figure 4).
341 Finally, to test for differences between reproductive modes in the results of these
342 contrasts, we subtracted relevant contrast distributions for viviparous species from
343 those for oviparous species for each comparison (black bars in Figure 4).

344

345 **Results**

346 The species included in our analysis occupied a wide range of climates (Figure
347 1), representing almost the entire global range of environments occupied by lizards (Pie
348 et al. 2017; Roll et al. 2017). Social grouping occurred in 71 species (out of 1696, 4.2%)
349 across 14 families, including 53 viviparous species (out of 197; 26.9%) and 18
350 oviparous species (out of 1499; 1.2%). Reconstructions from a hidden Markov model
351 indicate that social grouping has arisen approximately 15 times in this sample of
352 species (mean number of transitions (\pm 95% CI): oviparous lineages = 8.5 (5, 12);
353 viviparous lineages = 6.1 (4, 11.5)) (Figure 2), though exclusion of uncertain nodes
354 means the true number of independent origins is likely to be higher for viviparous
355 species (see methods; Table S5). Based on the proportion of branch time spent in a
356 state of oviparity (93.3%) versus viviparity (6.7%) from stochastic character mapping
357 (Figure 2), these reconstructions indicate the transition rate to social grouping is at
358 least 10 times faster from a background of viviparity.

359 Social grouping was more likely to occur in species that occupied cool climates
360 and rocky substrates (P_{MCMC} values from phylogenetic regression <0.001 ; Table S1).
361 Despite trends in the data suggesting social species occur in drier climates with more
362 predictable temperature and less predictable precipitation (Figure 1), main effects of all
363 other climate and habitat predictors were non-significant (Table S1). One explanation
364 for the relationship between temperature and social grouping is that species occupying
365 cooler climates are more likely to be viviparous (Zimin et al. 2022), which in turn
366 promotes sociality (Halliwell et al. 2017). In support of this hypothesis, the effect of
367 cool climate disappeared when viviparity was included as a predictor in the model,
368 while the positive effect of rock dwelling remained unchanged (Table S2).

369 There was a positive phylogenetic correlation between social grouping and rock
370 dwelling, and a negative phylogenetic correlation between social grouping and
371 temperature (Figure 3a; Table S7), indicating conserved relationships between these
372 traits across the lizard phylogeny. However, consistent with our phylogenetic
373 regression analyses, there was no evidence for a partial phylogenetic correlation
374 between social grouping and temperature (i.e., when controlling for viviparity). In

375 contrast, there were partial phylogenetic correlations between social grouping and
376 both viviparity and rock dwelling (Figure 3a; Table S7). These results indicate
377 independent coevolutionary relationships between each of these traits and social
378 grouping that go beyond correlated responses to climate. Furthermore, a negative
379 partial phylogenetic correlation between rock dwelling and precipitation (Figure S6;
380 Table S7) suggests that, in addition to promoting transitions in reproductive mode,
381 climate may also have indirect effects on the evolution of social grouping by influencing
382 the probability that species occur on rocky substrates.

383 There was limited evidence for social grouping being influenced by interactions
384 between climate, viviparity and rock-dwelling (Table S3). The preferred model (lowest
385 DIC for 87/100 trees) contained an interaction between viviparity and rock-dwelling,
386 indicating that live-bearing species in rocky habitats were more likely to be social, but
387 this effect was weak ($P_{\text{MCMC}} = 0.07$; Figure S7). Furthermore, this model was significantly
388 preferred ($\delta\text{DIC} > 2$) over a null model containing just the main effects of viviparity and
389 rock dwelling for only 23/100 trees (mean $\delta\text{DIC} = 1.47$; Table S3).

390 Phylogenetic path analyses indicated a strong positive influence of viviparity and
391 rock dwelling, and a weak negative influence of temperature, on social grouping (Figure
392 3b,c). The model obtained by averaging over all candidate models, weighted by their
393 relative evidence, also indicated a negative influence of temperature on both viviparity
394 and rock dwelling, and a negative influence of precipitation on rock dwelling (Figure 3b).
395 Each of these effects were significant based on the distribution of standardized
396 regression coefficients across trees in the weighted model (Figure 3c).

397 Based on strong phylogenetic signal in all traits and environmental variables
398 (Table S6), we performed ancestral state reconstructions to assess the effects of cool
399 climates and rock dwelling across three key evolutionary stages: the origin, following
400 the emergence, and during the maintenance of social grouping. There was a higher
401 probability of rock dwelling at the origin of social grouping in both oviparous (marginal)
402 and viviparous species, consistent with a general causative role of rock dwelling in the
403 initial emergence of social grouping behaviour (Figure 4). Marginally cooler
404 temperatures were also found at the origin of social grouping, but only for viviparous
405 species. Consistent with these findings, rock dwelling and social grouping showed
406 partial phylogenetic correlations across both oviparous and viviparous species, where-

407 as temperature was only marginally negatively correlated to social grouping across
408 viviparous species (Figure S8; Table S8).

409

410 **Discussion**

411 Climate has been repeatedly implicated as a causal factor mediating the
412 evolution of vertebrate social behaviour (Jetz & Rubenstein 2011; Lukas & Clutton-
413 Brock 2017; Firman et al. 2020). We show that social grouping in lizards also exhibits a
414 strong climatic signature, typically occurring in species that occupy cool, dry climates.
415 However, closer examination reveals that these effects are largely explained by
416 association with viviparity and rock dwelling, both of which promote social grouping.
417 Viviparity is an adaptation to cool climates in reptiles (Zimin et al. 2022; Ma et al. 2018)
418 and is thought to promote group living by increasing the opportunity for interactions
419 between parents and offspring following birth (Halliwell et al. 2017). Rock dwelling is
420 strongly associated with dry climates but may also increase opportunities for social
421 interaction among kin by promoting territoriality and ecological constraints on offspring
422 dispersal (see below). Thus, associations between viviparity, rock dwelling and climate
423 create a strong, yet largely indirect, climatic signature of social grouping.

424 Our finding that direct effects of climate on social grouping in lizards are weak
425 contrasts with those from endothermic vertebrates (i.e., birds and mammals) where
426 family life and cooperative breeding are often strongly associated with climate (Jetz &
427 Rubenstein 2011; Cornwallis et al. 2017; Griesser et al. 2017; Firman et al. 2020; Qi et
428 al. 2023), and harsh environments are thought to increase the relative benefits of social
429 behaviour (Hatchwell 2000; Covas et al. 2008; Rubenstein et al. 2011). These
430 differences can be understood by considering two important points.

431 First, associations between climate and complex social behaviour in birds and
432 mammals are largely related to offspring provisioning (Qi et al. 2023; Cornwallis et al.
433 2017; Jetz & Rubenstein 2011). In this context, climate influences resource availability
434 and thus the costs and benefits of prolonged investment in parental and alloparental
435 care (Hatchwell 2009; Hatchwell & Komdeur 2000). This is likely tied to higher energy
436 demands of endotherms which, all else being equal, make feeding offspring more
437 important compared to ectotherms (Beekman et al. 2019; 2019b). There is no evidence

438 that lizards provision their offspring and no evidence of alloparental care (While et al.
439 2014), potentially decoupling the functional links between climate, resource availability
440 and social behaviour that underpin climatic signatures of social evolution in
441 endothermic vertebrates. Conversely, climate may have distinct effects on the
442 evolution of social behaviour in ectotherms due to inherent differences in thermal
443 physiology (see introduction). In particular, thermal constraints on activity may
444 promote kin sociality in lizards by stabilising social networks and reducing rates of
445 extra-pair paternity (Moss & While 2021; Olsson et al 2011). We find some support for
446 cooler temperatures promoting the emergence of social grouping, but only in viviparous
447 species. This result suggests that direct effects of cooler temperatures may operate
448 only when other conditions supporting the emergence of social grouping (i.e., viviparity)
449 are already present. Living in generally cool climates may also mean that, for viviparous
450 species, further reductions in temperature represent a direct metabolic constraint on
451 activity, where-as in warmer regions (where oviparous species predominate) breeding-
452 season temperatures rarely impose constraints on activity.

453 Second, our results indicate that climatic adaptations, more than climate per
454 se, have mechanistic links to the evolution of social grouping in lizards. Climate often
455 results in selection on a suite of adaptations which in turn select for social grouping.
456 For example, climatic adaptation often involves morphological and life history traits
457 (e.g., longevity, late maturation, and large body sizes), that can also mediate both the
458 opportunity for kin groups to form, and the costs and benefits of grouping behaviour
459 (e.g., Hatchwell & Komdeur 2000; Covas & Griesser 2007; Downing et al. 2015; 2020;
460 Scharf et al. 2015; Griesser et al. 2017; Firman et al. 2020). Our analyses support this
461 indirect association between climate and social grouping. Indeed, both reproductive
462 (viviparity) and ecological (rock dwelling) traits were associated with climate adaptation
463 and were shown to promote social grouping in lizards. Furthermore, we find marginal
464 support for a positive interaction between viviparity and rock dwelling, suggesting these
465 traits may act in concert to expedite the evolution of social grouping. This supports the
466 observation that social grouping occurs most commonly in viviparous, rock dwelling
467 clades (e.g., among the Australasian Scincidae, American Liolaemidae and African
468 Cordylidae; Figure 2).

469 An additional novel finding of this study is that social grouping in lizards is
470 associated with rocky habitats, and that occurrence in rocky habitats itself is
471 associated with drier climates (Figure S6; Table S7). As ectotherms, lizards rely on
472 refuge sites that offer specific microclimates and access to basking areas. Suitable
473 refugia are often limiting, and habitat structure is particularly important in determining
474 population dispersion and opportunities for offspring dispersal (e.g., Halliwell et al.
475 2017b; Botterill-James et al. 2016; Gardner et al 2016). As rock dwelling promotes
476 social grouping in both oviparous and viviparous species, it follows that rocky habitats
477 may have important effects on offspring dispersal regardless of reproductive mode.
478 Reliance on persistent, defensible or manipulable home sites is consistent with the
479 evolution of group living in other systems, such as transitions to eusociality in
480 invertebrates (Howard & Thorne 2011; Nowak et al. 2010; Crespi 2001) and group living
481 in rodents (Epsenberger 2001; Ebsenberger & Hayes 2016). In contrast, we did not find
482 an association between social grouping and fossoriality (burrow dwelling) as might be
483 expected if general benefits related to shared refuge sites are an important driver of
484 social grouping (e.g., Shah et al. 2003; Rabosky et al. 2012; also see Leu et al. 2011).
485 However, the possibility to extend or excavate new borrow systems may mean that
486 burrows are not limiting in the same sense as rock crevices.

487 In summary, we find the strong climatic signature of social grouping in lizards
488 can be explained by association with viviparity and rock dwelling; reproductive and
489 ecological adaptations to cool, dry climates that ultimately drive the emergence of
490 grouping behaviour. Direct effects of climate are weak but suggest that cool
491 temperatures may further promote the emergence of social grouping in viviparous
492 lineages. Our results indicate that relationships between the environment and sociality
493 are a product of interactions between past adaptations and current ecological
494 challenges. Disentangling such effects can be difficult, requiring large datasets and
495 sophisticated comparative methods. However, we show that such an approach is
496 sometimes necessary to understand how and why social organisation varies across the
497 tree of life.

498

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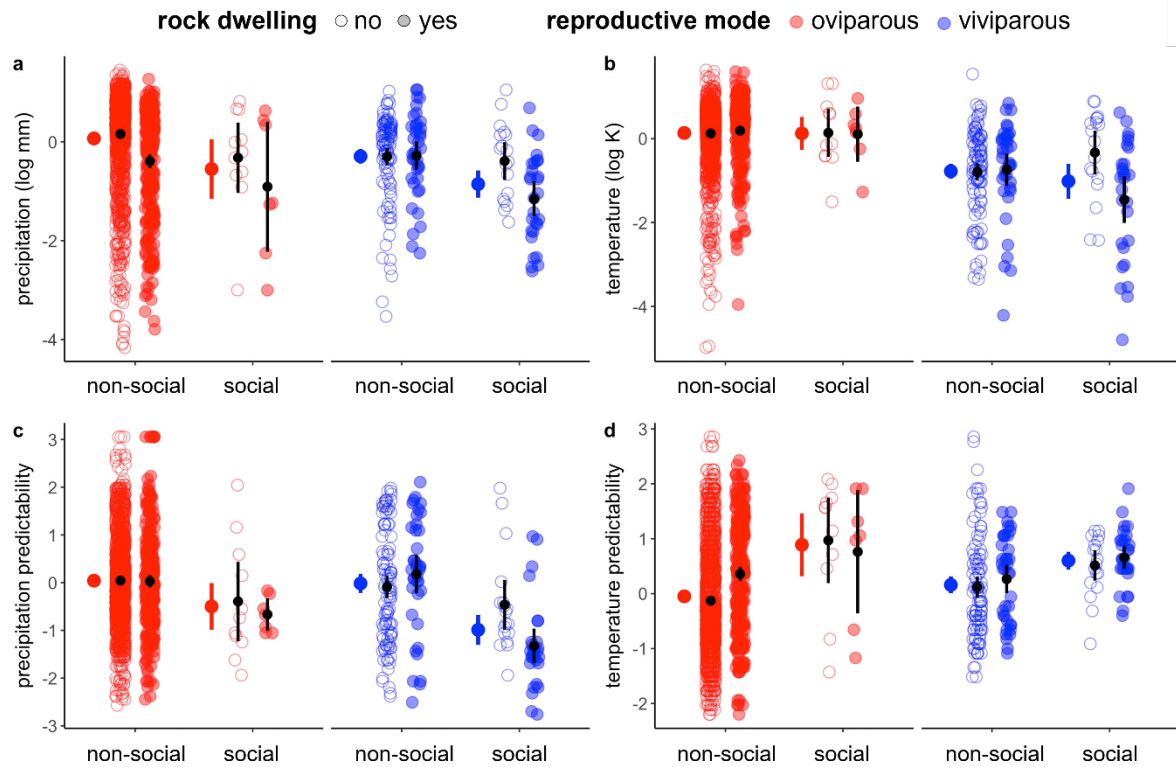


Figure 1. Reproductive (viviparity) and ecological (rock dwelling) adaptations to climate create a strong climatic signature of social grouping in lizards. Climate niche variables (z-scale) for lizard species ($n = 1687$) grouped by reproductive mode, rock dwelling and presence of social grouping. Means and 95% confidence intervals for each group are shown in black. Means and 95% confidence intervals for each combination of reproductive mode and social grouping (i.e., pooling across presence/absence of rock dwelling) shown to the left of each group combination. **a** log mean monthly precipitation during the breeding season. **b** log mean temperature during the breeding season. **c** inter-annual autocorrelation of mean monthly precipitation during the breeding season. **d** inter-annual autocorrelation of temperature during the breeding season. Outliers ($n = 9$) excluded for plotting.

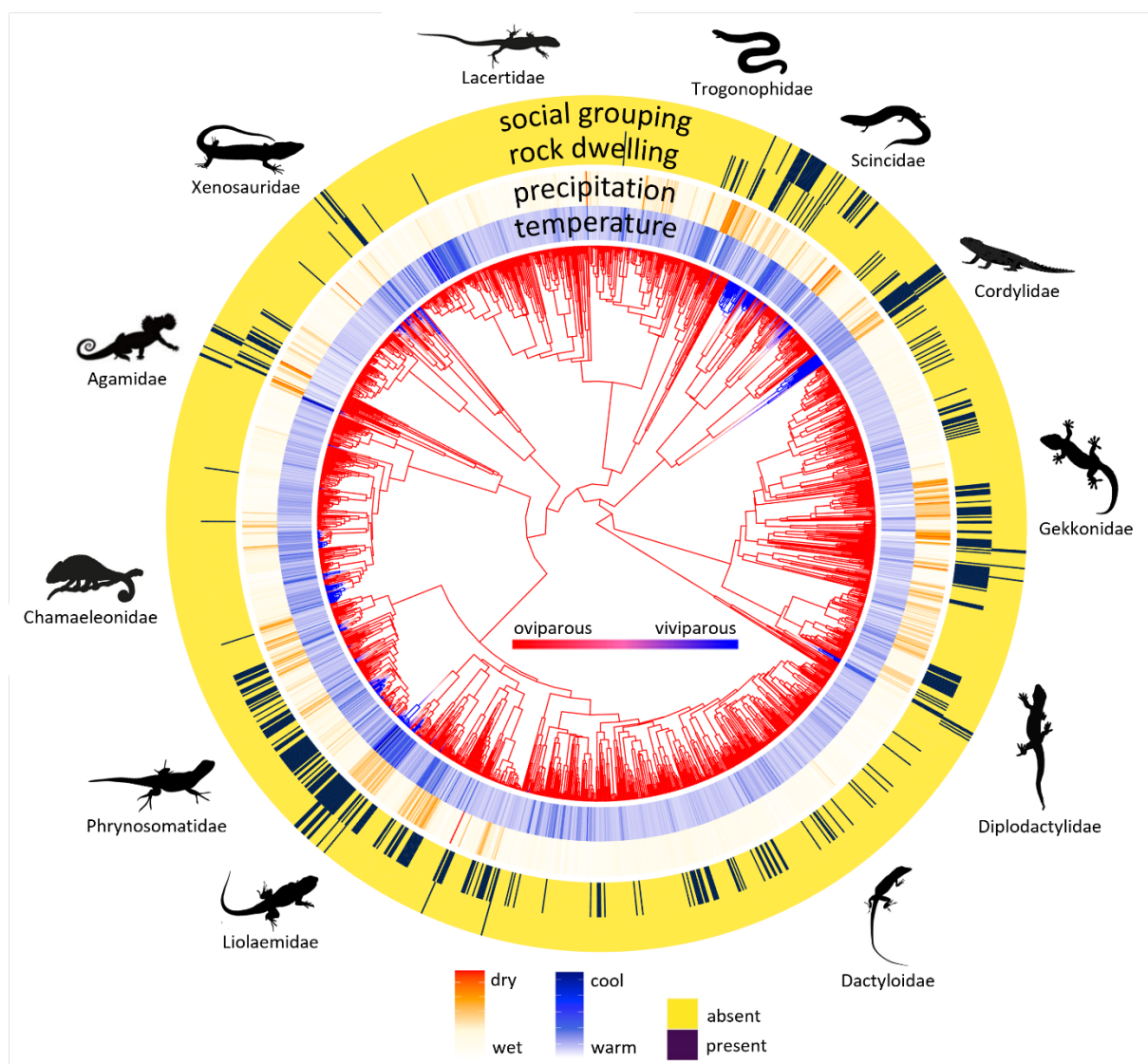


Figure 2. The phylogenetic distribution of viviparity, rock dwelling and climatic niche in lizards indicates that social grouping is a product of past adaptations and current ecological challenges. Branch colour represents the probability of oviparity (red) and viviparity (blue) based on 100 stochastic character histories simulated from a hidden Markov model with three rate classes (see Methods). Mean breeding-season temperature and precipitation (inner), as well as presence/absence of rock dwelling and social grouping (outer) among extant taxa (n = 1696) is indicated.

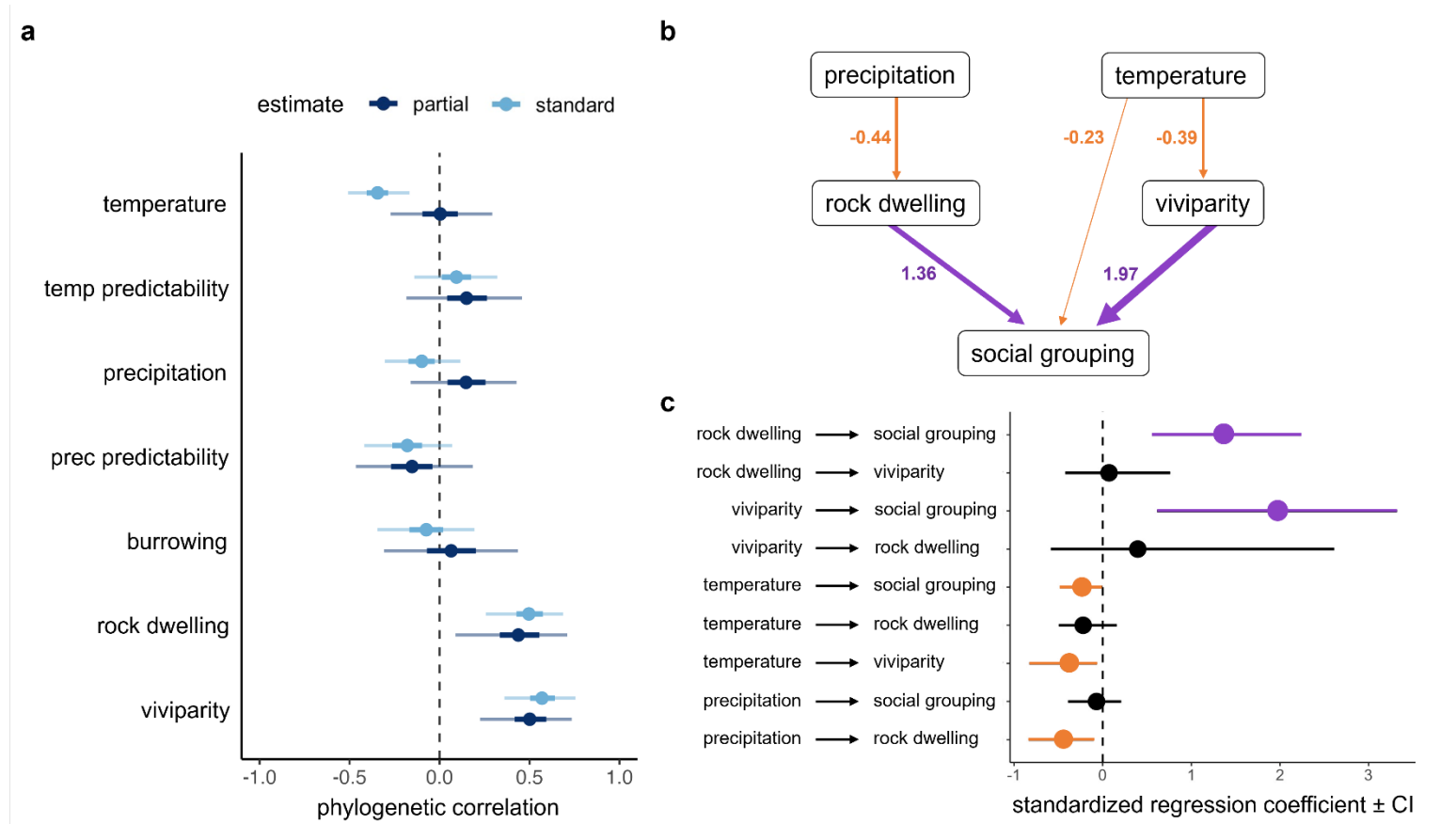


Figure 3. Viviparity and rock dwelling independently promote the evolution of social grouping across the lizard phylogeny, with limited evidence for direct climatic effects. **a** Phylogenetic correlations between species traits and social grouping from a MR-PMM fit over 100 candidate topologies. Estimates in light and dark blue represent standard and partial correlation coefficients. Partial correlations represent the relationship between two response variables after controlling for variation explained by other response variables. Points represent the posterior means, with heavy and light whiskers indicating the 0.5 and 0.95 credible intervals for each estimate. All pairwise correlations shown in Table S7. **b** Weighted average model from phylogenetic path analysis. Significant positive and negative paths shown in purple and orange, respectively. Coefficients associated with paths represent the mean standardized regression coefficient for each path across 100 candidate topologies. **c** Summaries of standardized regression coefficient estimates from weighted average model. Points and confidence intervals represent means and 95% confidence intervals for each coefficient estimate based on 100 bootstrap replicates across each of 100 candidate topologies.

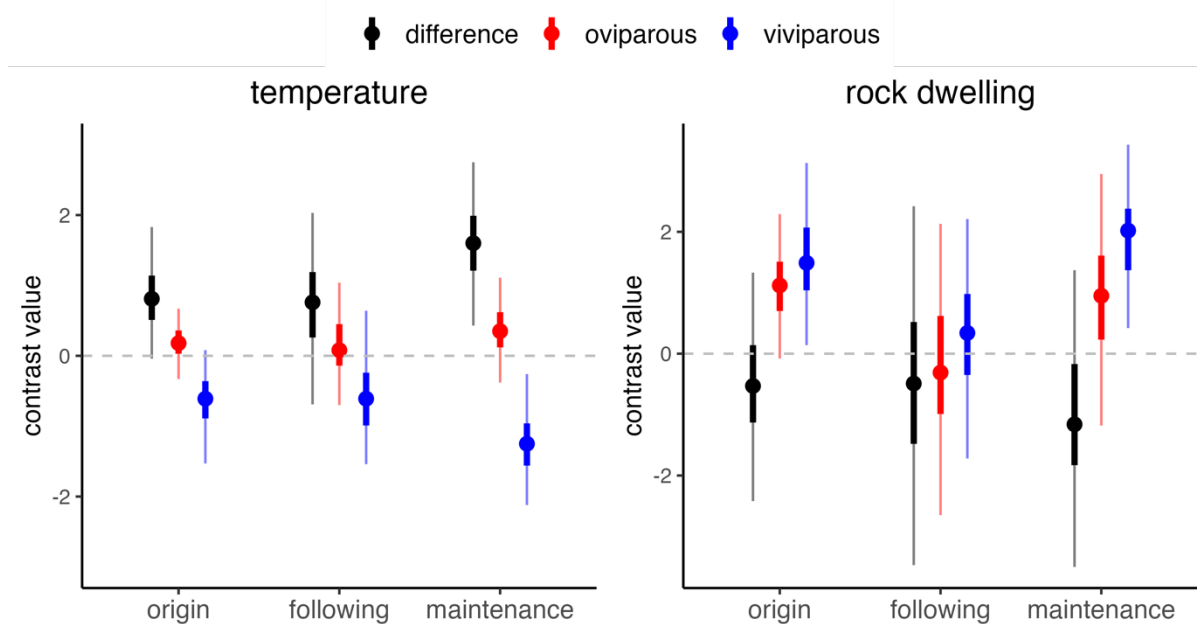


Figure 4. Rock dwelling promotes the emergence of social grouping regardless of reproductive mode, while effects of cool temperature are restricted to viviparous species. Contrasts between node transition categories representing different stages in the evolution of social grouping (see methods) for temperature (left) and rock dwelling (right). Values shown are posterior means (points) with 50% (heavy wicks) and 95% (light wicks) credible intervals calculated from phylogenetic mixed models fit across 100 candidate topologies. Contrasts for oviparous and viviparous lineages are displayed in red and blue, respectively. The difference between contrasts for oviparous and viviparous species are shown in black.

References

- AlRashidi, M., Kosztolányi, A., Küpper, C., Cuthill, I. C., Javed, S., & Székely, T. (2010). The influence of a hot environment on parental cooperation of a ground-nesting shorebird, the Kentish plover *Charadrius alexandrinus*. *Frontiers in Zoology*, 7(1), 1-10.
- AlRashidi, M., Kosztolányi, A., Shobrak, M., Küpper, C., & Szekely, T. (2011). Parental cooperation in an extreme hot environment: natural behaviour and experimental evidence. *Animal Behaviour*, 82(2), 235-243.
- Baird, J. M., & May, M. L. (2003). Fights at the dinner table: agonistic behavior in *Pachydiplax longipennis* (Odonata: Libellulidae) at feeding sites. *Journal of Insect Behavior*, 16, 189-216.
- Beaulieu, J. M., O'Meara, B. C., & Donoghue, M. J. (2013). Identifying hidden rate changes in the evolution of a binary morphological character: the evolution of plant habit in campanulid angiosperms. *Systematic biology*, 62(5), 725-737.
- Beaulieu, J. M., & O'Meara, B. C. (2014). Hidden Markov models for studying the evolution of binary morphological characters. *Modern phylogenetic comparative methods and their application in evolutionary biology: Concepts and practice*, 395-408.
- Blackburn, D. G. (2015). Evolution of viviparity in squamate reptiles: reversibility reconsidered. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 324(6), 473-486.
- Botterill-James, T., Halliwell, B., Cooper-Scott, E., Uller, T., Wapstra, E., & White, G. M. (2016). Habitat structure influences parent-offspring association in a social lizard. *Frontiers in Ecology and Evolution*, 4, 96.
- Caetano, G. H. D. O., Chapple, D. G., Grenyer, R., Raz, T., Rosenblatt, J., Tingley, R., ... & Roll, U. (2022). Automated assessment reveals that the extinction risk of reptiles is widely underestimated across space and phylogeny. *PLoS Biology*, 20(5), e3001544.
- Colwell, R. K., Ecology, S., Summer, N. L. & Colwell, R. K. (1974) Predictability, constancy, and contingency of periodic phenomena. *Ecology* 55, 1148–1153.
- Cornwallis, C. K., Botero, C. A., Rubenstein, D. R., Downing, P. A., West, S. A., & Griffin, A. S. (2017). Cooperation facilitates the colonization of harsh environments. *Nature Ecology & Evolution*, 1(3), 0057.
- Covas, R., & Griesser, M. (2007). Life history and the evolution of family living in birds. *Proceedings of the Royal Society B: Biological Sciences*, 274(1616), 1349-1357.
- Covas, R., Du Plessis, M. A. & Doutrelant, C. (2008) Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. *Behavioural Ecology and Sociobiology*, 63, 103–112.

Crespi, B. J. (2001). The evolution of social behavior in microorganisms. *Trends in Ecology & Evolution*, 16(4), 178-183.

Diamant, E.S., Falk, J.J. & Rubenstein, D.R. (2021). Male-like female morphs in hummingbirds: the evolution of a widespread sex-limited plumage polymorphism. *Proc. R. Soc., Ser. B*, 288, 20203004.

de Villemereuil, P. (2018). Quantitative genetic methods depending on the nature of the phenotypic trait. *Annals of the New York Academy of Sciences*, 1422(1), 29-47.

Downing, P. A., Cornwallis, C. K., & Griffin, A. S. (2015). Sex, long life and the evolutionary transition to cooperative breeding in birds. *Proceedings of the Royal Society B: Biological Sciences*, 282(1816), 20151663.

Downing, P. A., Griffin, A. S., & Cornwallis, C. K. (2020). Group formation and the evolutionary pathway to complex sociality in birds. *Nature Ecology & Evolution*, 4(3), 479-486.

Ebensperger, L. A. (2001). A review of the evolutionary causes of rodent group-living. *Acta Theriologica*, 46, 115-144.

Ebensperger, L. A., & Hayes, L. D. (2016). Causes and evolution of group-living. *Sociobiology of caviomorph rodents: an integrative approach*, 173-200.

Emlen, S. T. (1982). The evolution of helping. I. An ecological constraints model. *The American Naturalist*, 119(1), 29-39.

Emlen, S. T. (1995). An evolutionary theory of the family. *Proceedings of the National Academy of Sciences*, 92(18), 8092-8099.

Firman, R. C., Rubenstein, D. R., Moran, J. M., Rowe, K. C., & Buzatto, B. A. (2020). Extreme and variable climatic conditions drive the evolution of sociality in Australian rodents. *Current Biology*, 30(4), 691-697.

Fristoe, T. S., Iwaniuk, A. N., & Botero, C. A. (2017). Big brains stabilize populations and facilitate colonization of variable habitats in birds. *Nature ecology & evolution*, 1(11), 1706-1715.

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2014). *Bayesian Data Analysis*. Chapman and Hall/CRC.

Griesser, M., Drobniak, S. M., Nakagawa, S., & Botero, C. A. (2017). Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLoS biology*, 15(6), e2000483.

Griffith, O. W., Blackburn, D. G., Brandley, M. C., Van Dyke, J. U., Whittington, C. M., & Thompson, M. B. (2015). Ancestral state reconstructions require biological evidence to test evolutionary hypotheses: a case study examining the evolution of reproductive

mode in squamate reptiles. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 324(6), 493-503.

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of statistical software*, 33, 1-22.

Hadfield, J. D., & Nakagawa, S. (2010). General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of evolutionary biology*, 23(3), 494-508.

Halliwell, B., Uller, T., Holland, B. R., & While, G. M. (2017). Live bearing promotes the evolution of sociality in reptiles. *Nature communications*, 8(1), 2030.

Halliwell, B., Uller, T., Chapple, D. G., Gardner, M. G., Wapstra, E., & While, G. M. (2017b). Habitat saturation promotes delayed dispersal in a social reptile. *Behavioral Ecology*, 28(2), 515-522.

Halliwell, B., Yates, L. A., & Holland, B. R. (2022). Multi-response phylogenetic mixed models: Concepts and application. *BioRxiv*, 2022-12.

Hatchwell, B. J., & Komdeur, J. (2000). Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal behaviour*, 59(6), 1079-1086.

Hatchwell, B. J. (2009). The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1533), 3217-3227.

Harris, I., Osborn, T. J., Jones, P., & Lister, D. (2020). Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific data*, 7(1), 109.

Howard, K. J., & Thorne, B. L. (2011). Eusocial evolution in termites and Hymenoptera. *Biology of termites: a modern synthesis*, 97-132.

Jetz, W., & Rubenstein, D. R. (2011). Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology*, 21(1), 72-78.

King, B., & Lee, M. S. (2015). Ancestral state reconstruction, rate heterogeneity, and the evolution of reptile viviparity. *Systematic Biology*, 64(3), 532-544.

Komdeur, J. (1992). Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature*, 358(6386), 493-495.

Le Galliard, J.-F., Ferrière, R., & Clobert, J. (2003). Mother-Offspring Interactions Affect Natal Dispersal in a Lizard. *Proceedings: Biological Sciences*, 270(1520), 1163-1169. <http://www.jstor.org/stable/3558843>

Leu, S. T., Kappeler, P. M., & Bull, C. M. (2011). The influence of refuge sharing on social behaviour in the lizard *Tiliqua rugosa*. *Behavioral ecology and sociobiology*, 65, 837-847.

Lejeune, L., Savage, J. L., Bründl, A. C., Thiney, A., Russell, A. F., & Chaine, A. S. (2019). Environmental effects on parental care visitation patterns in blue tits *Cyanistes caeruleus*. *Frontiers in Ecology and Evolution*, 7, 356.

Liu, M., Bell-Roberts, L., Botero, C. A., Cornwallis, C. K., West, S. W. (in review). Capturing the influence of climatic variation and predictability on trait evolution. *Methods in Ecology and Evolution*.

Lukas, D., & Clutton-Brock, T. (2017). Climate and the distribution of cooperative breeding in mammals. *Royal Society open science*, 4(1), 160897.

Ma, L., Buckley, L. B., Huey, R. B., & Du, W. G. (2018). A global test of the cold-climate hypothesis for the evolution of viviparity of squamate reptiles. *Global Ecology and Biogeography*, 27(6), 679-689.

Martín, J., Rodríguez-Ruiz, G., & Cuervo, J. J. (2023). Coping with drought? The hidden microhabitat selection and underground movements of amphisbaenians under summer drought conditions. *Current Zoology*, zoad034.

Martin, J., Ringen, E., Duda, P. & Jaeggi, A. (2020). Harsh environments promote alloparental care across human societies. *Proc. R. Soc., Ser. B*, 287, 20200758.

Massot, M., Clobert, J., Lorenzon, P., & Rossi, J. M. (2002). Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. *Journal of Animal Ecology*, 71(2), 253-261.

Meiri, S. (2024). SquamBase—A database of squamate (Reptilia: Squamata) traits. *Global Ecology and Biogeography*.

Moss, J. B., & White, G. M. (2021). The thermal environment as a moderator of social evolution. *Biological Reviews*, 96(6), 2890-2910.

Moss, J. B., Borthwick, Z., Wapstra, E., & White, G. M. (2023). Thermal Plasticity in Behavioral Traits Mediates Mating and Reproductive Dynamics in an Ectotherm. *The American Naturalist*, 201(6), 851-863.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in ecology and evolution*, 4(2), 133-142.

Nowak, M. A., Tarnita, C. E., & Wilson, E. O. (2010). The evolution of eusociality. *Nature*, 466(7310), 1057-1062.

Olsson, M., Wapstra, E., Schwartz, T., Madsen, T., Ujvari, B., & Uller, T. (2011). In hot pursuit: fluctuating mating system and sexual selection in sand lizards. *Evolution*, 65(2), 574-583.

Pettersen, A. K., Feiner, N., Noble, D. W., While, G. M., Uller, T., & Cornwallis, C. K. (2023). Maternal behavioral thermoregulation facilitated evolutionary transitions from egg laying to live birth. *Evolution Letters*, 7(5), 351-360.

Popovic, G. C., Warton, D. I., Thomson, F. J., Hui, F. K., & Moles, A. T. (2019). Untangling direct species associations from indirect mediator species effects with graphical models. *Methods in Ecology and Evolution*, 10(9), 1571-1583.

Price-Rees, S. J., Lindström, T., Brown, G. P., & Shine, R. (2014). The effects of weather conditions on dispersal behaviour of free-ranging lizards (*Tiliqua*, Scincidae) in tropical Australia. *Functional ecology*, 28(2), 440-449.

Qi, X. G., Wu, J., Zhao, L., Wang, L., Guang, X., Garber, P. A., ... & Li, B. (2023). Adaptations to a cold climate promoted social evolution in Asian colobine primates. *Science*, 380(6648), eabl8621.

Rabosky, A. R. D., Corl, A., Liwanag, H. E., Surget-Groba, Y., & Sinervo, B. (2012). Direct fitness correlates and thermal consequences of facultative aggregation in a desert lizard. *PLoS One*, 7(7), e40866.

Rat, M., Mathe-Hubert, H., McKechnie, A. E., Sueur, C., & Cunningham, S. J. (2020). Extreme and variable environmental temperatures are linked to reduction of social network cohesiveness in a highly social passerine. *Oikos*, 129(11), 1597-1610.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., ... & Meiri, S. (2017). The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature ecology & evolution*, 1(11), 1677-1682.

Rubenstein, D. R. (2011). Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proceedings of the National Academy of Sciences*, 108(supplement_2), 10816-10822.

Rubenstein, D. R., & Abbot, P. (Eds.). (2017). *Comparative social evolution*. Cambridge University Press.

Scharf, I., Feldman, A., Novosolov, M., Pincheira-Donoso, D., Das, I., Böhm, M., ... & Meiri, S. (2015). Late bloomers and baby boomers: ecological drivers of longevity in squamates and the tuatara. *Global Ecology and Biogeography*, 24(4), 396-405.

Shah, B., Shine, R., Hudson, S., & Kearney, M. (2003). Sociality in lizards: why do thick-tailed geckos (*Nephurus milii*) aggregate?. *Behaviour*, 1039-1052.

Shine, R. (2014). Evolution of an evolutionary hypothesis: a history of changing ideas about the adaptive significance of viviparity in reptiles. *Journal of Herpetology*, 48(2), 147-161.

Shine, R. (2015). The evolution of oviparity in squamate reptiles: an adaptationist perspective. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 324(6), 487-492.

van der Bijl, W. (2018). phylopath: Easy phylogenetic path analysis in R. *PeerJ*, 6, e4718.

Vehtari, A., Gelman, A., Simpson, D., Carpenter, B. and Bürkner, P. (2019). Rank-normalization, folding, and localization: An improved R-hat for assessing convergence of MCMC. arXiv preprint arXiv:1903.08008.

Vidan, E., Roll, U., Bauer, A., Grismer, L., Guo, P., Maza, E., ... & Meiri, S. (2017). The Eurasian hot nightlife: environmental forces associated with nocturnality in lizards. *Global Ecology and Biogeography*, 26(11), 1316-1325.

Vincze, O., Kosztolányi, A., Barta, Z., Küpper, C., Alrashidi, M., Amat, J. A., ... & Székely, T. (2017). Parental cooperation in a changing climate: fluctuating environments predict shifts in care division. *Global Ecology and Biogeography*, 26(3), 347-358.

Westoby, M., Yates, L., Holland, B., & Halliwell, B. (2023). Phylogenetically conservative trait correlation: quantification and interpretation. *Journal of Ecology*, 111(10), 2105-2117. Whiting, M. J., & While, G. M. (2017). Sociality in Lizards. *Comparative social evolution*, 390.

While, G. M., Halliwell, B., & Uller, T. (2014). The evolutionary ecology of parental care in lizards. *Reproductive Biology and Phylogeny of Lizards and Tuatara* (JL Rheubert, DS Siegel, and SE Trauth, eds.). CRC Press, USA, 588-619.

While, G. M., Gardner, M. G., Chapple, D. G., & Whiting, M. J. (2019). 10 Stable Social Grouping in Lizards. *Behavior of lizards: Evolutionary and mechanistic perspectives*, 321.

Whiting, M. J., & While, G. M. (2017). 13 Sociality in Lizards. *Comparative social evolution*, 390.

Wright, A. M., Lyons, K. M., Brandley, M. C., & Hillis, D. M. (2015). Which came first: the lizard or the egg? Robustness in phylogenetic reconstruction of ancestral states. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 324(6), 504-516.

Wynne-Edwards, K. E. (1998). Evolution of parental care in *Phodopus*: conflict between adaptations for survival and adaptations for rapid reproduction. *American Zoologist*, 38(1), 238-250.

Zimin, A., Zimin, S. V., Shine, R., Avila, L., Bauer, A., Böhm, M., ... & Meiri, S. (2022). A global analysis of viviparity in squamates highlights its prevalence in cold climates. *Global Ecology and Biogeography*, 31(12), 2437-2452.