

1 **The global diversity and distribution of lizard clutch sizes**

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7 **Research paper**

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45

### 46 Biosketch

47 Shai Meiri is interested in the evolution of traits, and its relationship with geography

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9 **Title: The global diversity and distribution of lizard clutch sizes**10 **running title:** global distribution of lizard clutch sizes

11

12 **Abstract**

13 Aim. Clutch size is a key life-history trait. In lizards, it ranges over two orders of magnitude. The  
14 global drivers of spatial and phylogenetic variation in clutch have been extensively studied in  
15 birds, but such tests in other organisms are lacking. To test the generality of latitudinal gradients  
16 in clutch size, and their putative drivers, we present the first global-scale analysis of clutch sizes  
17 across of lizard taxa.

18 Location, Global

19 Time period. Recent

20 Major taxa studied. Lizards (Reptilia, Squamata, Sauria)

21 Methods. We analysed clutch-size data for over 3900 lizard species, using phylogenetic  
22 generalized least-square regression to study the relationships between clutch sizes and  
23 environmental (temperature, precipitation, seasonality, primary productivity, insularity) and  
24 ecological factors (body mass, insularity, activity times, and microhabitat use).

25 Results. Larger clutches are laid at higher latitudes and in more productive and seasonal  
26 environments. Insular taxa lay smaller clutches on average. Temperature and precipitation per se  
27 are unrelated to clutch sizes. In Africa, patterns differ from those on other continents. Lineages  
28 laying small fixed clutches are restricted to low latitudes.

29 Main conclusions. We suggest that the constraint imposed by a short activity season coupled  
30 with abundant resources is the main driver of large-clutch evolution at high latitudes and highly  
31 seasonal regions. We hypothesize that such conditions—which are unsuitable for species  
32 constrained to laying multiple small clutches—may limit the distribution of fixed-clutch taxa.

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34

35 Key words

36 Ashmole's hypothesis, fecundity, fixed clutch size, geographic variation, Lack's rule, latitude,  
37 reproductive strategy, seasonality

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39

## 40 **Introduction**

41 Reproductive effort is a critical component of animal life histories. How reproductive effort  
42 is allocated through a single reproductive event, over a breeding season, and over an entire  
43 lifespan, has major fitness consequences. Clutch size, laying frequency, length of the  
44 reproductive season, and reproductive lifespan can vary dramatically between and within taxa  
45 (Roff, 2002; Pincheira-Donoso and Hunt, 2017). Of these components, the number of offspring  
46 within a single clutch ('clutch size') probably varies most: from one to many millions of eggs in  
47 some invertebrates and anamniote vertebrates laying oligolecithal eggs (e.g., the brown crab,  
48 *Cancer pagurus*; Ungfors 2007; the sea hare, *Aplysia californica*; MacGinitie 1934; the cod,  
49 *Gadus moruha*; May, 1967; Lambert; 2008; see also Sadovy, 2001). In amniotes (birds,  
50 mammals, and reptiles) laying large, yolk-laden macrolecithal eggs, clutch (and litter) size  
51 variation is narrower but clutches still range from one to ~160 eggs (Vitt and Caldwell, 2013).

52 Among squamates (lizards and snakes), clutch sizes vary across two orders of magnitude,  
53 from one to over 100 eggs in some large snakes (Reed and Rodda, 2009; Vitt and Caldwell,  
54 2013) and to over 90 eggs in some chameleons (Tilbury, 2010; Zug, 2013; Meiri 2018). The  
55 causes underlying this enormous variation have inspired decades of research. Thus, clutch size  
56 and was found to be correlated with traits such as body size, growth rates, and longevity,  
57 supporting the notion of a fast-slow continuum (Tinkle et al., 1970; Dunham et al., 1988; Clobert  
58 et al., 1998; Pincheira-Donoso and Tregenza, 2011; Scharf et al. 2015). Clutch size was found to  
59 be negatively correlated with egg size and clutch frequency across multiple studies (e.g., In den  
60 Bosch and Bout, 1998; King, 2000; Amat, 2008; Meiri et al., 2012). In lizards, as in most  
61 ectotherms (Shine, 1988), clutch size has been repeatedly found to increase with increasing  
62 maternal body size (e.g., Tinkle et al., 1970; Dunham et al., 1988; Scharf and Meiri, 2013) —  
63 both within and between species. An exception is lineages where females only lay one or two  
64 eggs. The evolutionary correlates of such fixed clutch sizes (e.g., small body size, but large  
65 variation in egg sizes: Shine and Greer, 1991; Kratochvil and Kubicka, 2007; Meiri et al., 2015;  
66 Schwarz and Meiri, 2017) have been widely studied. The consequences of the transition to  
67 viviparity (reviewed in Shine, 2005; Murphy and Thompson, 2011; Sites et al., 2011; Pincheira-  
68 Donoso et al., 2013) for the number of offspring per reproductive event were widely studied  
69 (Huang, 2010; Meiri et al., 2020), generally finding no relationship between reproductive mode  
70 and brood size.

71 Compared to the multitude of studies exploring various biological drivers of clutch size  
72 variation, studies of geographic signals underlying clutch-size variation in most organisms,  
73 including squamates, remain scarce. In reptiles, some studies focused on reduction of clutch sizes  
74 with insularity (e.g., Huang, 2007; Siliceo and Diaz, 2010; Pafilis et al., 2011; Novosolov et al.,  
75 2013; Brandley et al., 2014; Slavenko et al., 2015), forested habitats (e.g., Werneck et al., 2009),  
76 and saxicolous and arboreal habits (Vitt, 1981; Schall, 1983; Mesquita et al. 2016).

77 Few studies have addressed adaptive responses in reptile clutch size to global variation in  
78 climate. This is somewhat surprising as such climatic gradients in clutch size have been  
79 intensively studied in avian reptiles for well over a century. In fact, 75 years ago, Moreau (1944)  
80 wrote: “It is over a hundred years ago since the view was first put forward that, on the whole,  
81 tropical birds tend to lay fewer eggs than birds of the temperate zones”. Birds lay larger clutches  
82 at higher latitudes and in colder, more seasonal environments (Rensch, 1938; Ricklefs, 1980).

83 This has been shown repeatedly both within (e.g., Rensch, 1938; Moreau, 1944; Lack, 1947;  
84 Cody, 1966; Vaugoyeau et al., 2016) and among (e.g., Ricklefs, 1980; Jetz et al., 2008; Boyer et  
85 al., 2010; cf. Yom-Tov et al., 1994) species and clades.

86 In comparison, studies of geographic gradients in clutch size (excluding island effects) of  
87 other tetrapod taxa are few and far between, never quite achieving the paradigmatic status they  
88 have for birds (Pincheira-Donoso & Hunt, 2017). Morrison and Hero (2003) found that  
89 amphibian clutches are smaller at higher latitudes once maternal body sizes were accounted for.  
90 Studies of geographic trends in mammalian litter sizes are also uncommon (but see Virgos et al.,  
91 2006; Bywater et al., 2010). When large-scale comparative studies of squamate life histories  
92 have been carried out, geographic variation in clutch size was rarely the focus (e.g., Andrews and  
93 Rand 1974; Dunham et al., 1988; Clobert et al., 1998; Mesquita et al., 2016). Fitch (1985) found  
94 that clutch size increased with latitude within the six turtle species he studied, a result later  
95 corroborated by Iverson et al. (1993) based on a much larger sample. Fitch (1985) nonetheless  
96 claimed that snakes, and especially lizards, show much weaker trends. Clutch size was higher at  
97 higher latitudes in half (8 of 16) the lizard species he studied, seven species showed a reverse  
98 trend, and one showed none (Fitch 1985). The mean difference in clutch size between the high  
99 and low latitude populations was just 1%. Interspecifically, Tinkle et al. (1970) found no  
100 differences between clutch sizes of tropical and temperate lizards, but Meiri et al. (2013), and  
101 Mesquita et al. (2016), identified significant, albeit weak, negative associations between clutch  
102 size and environmental temperatures.

103 Mechanisms responsible for observed geographic variation in clutch size have likewise  
104 mostly been studied in birds. Moreau (1944) hypothesized that increased winter mortality selects  
105 for large clutch sizes at high latitudes. Lack (1947) suggested that high-latitude birds benefit  
106 from longer days during the breeding seasons, enabling them to obtain more food. If valid, this  
107 mechanism is likely to hold for birds, a mostly diurnal clade, but for taxa with a more varied diel  
108 activity cycle it may mean that only clutches of diurnal species will increase with latitude. If true,  
109 clutch sizes may well decrease with latitude in nocturnal taxa, because nights during the summer  
110 activity season are short at high latitudes. Ashmole (1963), and Ricklefs (1980), hypothesized  
111 that high mortality rates, caused by increased seasonality, reduce population density at the  
112 beginning of each breeding season. They reasoned that this, coupled with abundant resources in  
113 the short breeding season, increases per-individual resource availability that can be channelled

114 towards offspring production (“Ashmole’s hypothesis”). Jetz et al. (2008) and Griebeler et al.  
115 (2010) likewise stressed the importance of juvenile and adult mortality, respectively, in selecting  
116 for a positive clutch-size/seasonality association in birds. Griebeler et al. (2010) suggested that  
117 increased predation pressure on chicks and adults at high latitudes could result in the observed  
118 pattern (but see Ricklefs 1980, Pincheira-Donoso & Hunt 2017). Cooper et al. (2005) theorized  
119 that temperature may directly cause the observed patterns through its effect on incubation costs  
120 and survival.

121 Importantly, nearly all the mechanisms suggested to account for the observed geographic  
122 variation in bird clutch sizes are likely to apply more generally across other organisms. Andrews  
123 and Rand (1974) further suggested that lizards in seasonal environments lay larger clutches than  
124 in aseasonal tropical regions. In the tropics, they suggested that short-term fluctuations in rainfall  
125 will favour frequent laying of small clutches. They claimed that arboreal lizards (especially those  
126 using adhesive toe pads) are constrained to lay small clutches because a large clutch of eggs  
127 would severely limit the climbing agility of the mother. Following a similar logic, Vitt (1981, see  
128 also Schwarzkopf et al. 2010), and Ashton (2005), suggested that saxicolous and fossorial  
129 species, respectively, will lay smaller clutches than terrestrial species – to better allow the  
130 pregnant mother to use rock fissures and narrow burrows.

131 Because there are no large-scale studies of geographic variation in clutch size of non-avian  
132 vertebrates, a global test of the environmental correlates of lizard clutch size could be insightful  
133 as well as timely. Using a global dataset of clutch sizes, we test a range of predictions regarding  
134 the evolutionary mechanisms influencing this important reproductive trait. We predict that lizard  
135 clutch sizes will be (1) positively correlated with latitude, and (2) positively correlated with  
136 temperature and precipitation seasonality. These three variables are probably good proxies for  
137 the length of the reproductive and activity seasons of lizards (see below), and—because  
138 predation is likely to be weakened when animals hibernate below grounds—perhaps also of  
139 mortality rates (Stark et al. 2018). If day length during the reproductive season (i.e., spring and  
140 summer for non-tropical lizards) affects clutch size (Lack 1947), we predict that (3) latitude will  
141 be positively correlated with clutch size in diurnal species but negatively associated with it in  
142 nocturnal species. We further predict (4) that in regions where resources are abundant, females  
143 will lay larger clutches because they can bear the energetic costs of doing so. We further  
144 examine the distribution of lizard lineages laying small, fixed clutches of one or two eggs

145 relative to the distribution of lizards laying variable, usually larger, clutches. We attempt to infer  
146 (5) whether differences in their geographic distribution conform to the general relationship  
147 between clutch size and geographic distribution. Incidentally, we thus also test (6) whether  
148 clutch sizes increase with body mass (e.g., Dunham et al., 1988), (7) decrease with insularity  
149 (Novosolov et al., 2013), or (8) are lower in arboreal (Andrews and Rand 1974), fossorial  
150 (Ashton 2005) and saxicolous species than in terrestrial ones (Vitt 1981).

151

## 152 **Methods**

### 153 Lizard clutch-size data

154 We obtained data on lizard (Squamata exclusive of Serpentes) clutch size, body size,  
155 diurnal/nocturnal habits, and microhabitat preferences from the literature (e.g., Slavenko et al.,  
156 2016; Meiri, 2018, see Appendix 1 for a list of sources) and our personal observations in the  
157 field, laboratory, and natural-history collections. Some of the species in our database are  
158 viviparous, but Meiri et al. (2020) found no systematic differences between clutch sizes of  
159 oviparous squamates and litter sizes of viviparous ones. Hence we use the term ‘clutch size’  
160 throughout, for simplicity, although live-bearing species are included. We used data on mean  
161 clutch sizes, and, when lacking means, we averaged the smallest and largest clutch sizes reported  
162 for a species. If multiple means were available we averaged the smallest and largest values  
163 (rather than average all means, because often a single mean is reported multiple times among  
164 studies, without proper acknowledgement).

165 Body sizes (for testing Hypothesis 6) are mean snout-vent lengths (SVL’s, in mm) of  
166 females, which we converted to masses using clade-specific allometric equations (from Feldman  
167 et al., 2016). Although within-taxon masses are highly variable (e.g., according to the time from  
168 and size of the last meal, body condition and whether a female is distended with eggs), in  
169 squamates, across squamate taxa masses better reflect size than lengths—as animals of identical  
170 length can easily vary by two orders of magnitude in mass (Meiri, 2010). Our clade-specific  
171 equations for legged, leg-reduced, and legless lizards separately take this shape variation into  
172 account and allow us to compare similar-sized taxa across the diversity in shape from long, thin  
173 pygopodids to chubby phrynosomatids (Feldman et al., 2016). As for clutch sizes, when multiple



174 body size means were available, we averaged the smallest and largest values (Meiri, 2018). We  
175 classified lizards as either diurnal, nocturnal, or cathemeral (active during both day and night,  
176 including primarily nocturnal and primarily diurnal species) to test Hypothesis 3, and as  
177 terrestrial, fossorial, or scansorial (i.e., arboreal or saxicolous; Meiri 2018) to test Hypothesis 8.  
178 Species that frequently occur both on trees or rocks (as adults) and on the ground were also  
179 classified as scansorial because we assume the agility of a gravid female would be most greatly  
180 constrained by any climbing activity or when trying to lodge itself in rock crevices (Vitt, 1981,  
181 Schwarzkopf et al. 2010). Semi-aquatic species (n = 75) were classified as scansorial if they are  
182 also semi-arboreal or semi-saxicolous (Grinham & Norman, 2020), or as terrestrial otherwise. A  
183 preliminary analysis showed semi-aquatic species were not significantly different than either  
184 scansorial or terrestrial ones (not shown).

185 Species geographic ranges were obtained from Roll et al. (2017) with some subsequent  
186 updates (e.g., for newly described species). We used these distributional data to find species'  
187 latitudinal centroids in ESRI ArcGIS v.10.6 (ESRI, Redlands, California, USA; to test  
188 Hypotheses 1 & 3) and measures of mean annual temperature (BIO1), temperature seasonality  
189 (BIO4) and precipitation seasonality (BIO15; to test Hypothesis 2). Climatic data are from  
190 CHELSA (Karger et al., 2017), and net primary productivity (=NPP) data are from Imhoff et al.  
191 (2004; Hypothesis 4). We calculated a single value per species for each climatic/environmental  
192 measure by averaging the climatic data across species' distributional ranges. Insular taxa were  
193 defined as those inhabiting only landmasses equal to or smaller than New Guinea, used to test  
194 Hypothesis 7. Taxonomy follows the December 2019 version of the Reptile Database (Uetz,  
195 2019).

196

## 197 Analyses

198 To examine the relationship between clutch size and the climatic and other predictors we  
199 used species-level phylogenetic analyses. We log<sub>10</sub>-transformed clutch sizes and body masses,  
200 NPP, and temperature seasonality data to linearize relationships, improve residual normality, and  
201 reduce heteroscedasticity. We used the absolute value of the latitudinal centroid of each species.  
202 Multi-collinearity was minimal (the maximum VIF was 2.4, for temperature seasonality).  
203 Because latitude is a proxy for several climatic variables (and day length), however, we analysed

204 latitude and climatic factors in separate models. To test whether diurnal and nocturnal species  
205 respond differently to climate (Hypothesis 3) we used two-way interactions between activity  
206 time and latitude. We then conducted a phylogenetic generalized-least squares ANCOVA (PGLS  
207 version of a Brownian-motion model of evolution; see Mesquita et al. 2016) using the caper R  
208 package (Orme et al., 2014), whereby the strength of the phylogenetic signal (using the  $\lambda$   
209 parameter) is assessed using maximum likelihood, and phylogenetic distances are multiplied by  
210  $\lambda$  before independent contrasts are calculated (Freckleton et al., 2002).

211 We used the phylogenetic tree of squamates from Tonini et al. (2016) to calculate contrasts  
212 and distances. This tree is partially based on genetic data and partially inferred from taxonomy –  
213 some of which has become obsolete due to more recent genetic findings (SM, pers. obs.). We  
214 then ran two sets of PGLS models: one with mean female mass, insularity, microhabitat, activity  
215 time, mean annual temperature and its seasonality, mean annual precipitation and its seasonality  
216 and NPP as predictors; and another with mean female mass, insularity, microhabitat, activity  
217 time, latitude and the activity time/latitude interaction, as predictors of clutch size. Over 250 of  
218 the species in our dataset were not found in the tree of Tonini et al. (2016). Therefore, we added  
219 non-phylogenetic sensitivity analyses using an ANCOVA with the same predictors as in the  
220 PGLS. This could further allow us to assess if observed patterns result from evolutionary  
221 responses within taxa or from taxon turnover (Meiri and Thomas 2007, Novosolov and Meiri  
222 2013).

223 We added two additional sensitivity analyses. First, our measure of body size was mean  
224 female body mass in the analyses described above. For 776 species, however, we had no data on  
225 mean female mass whereas we had data on maximum mass of all 3,916 species. To ensure that  
226 such a loss of 20% of the data did not bias our results we repeated the analyses with data on  
227 maximum body mass of all species (taken from either sex).

228 Within most lizard species, clutch sizes can be highly variable (e.g., 1-41 eggs in *Elgaria*  
229 *multicarinata*, 1-33 eggs in *Cyclodomorphus gerrardii* and *Calotes versicolor*, 2-77 eggs in  
230 *Chamaeleo dilepis*). In the Gekkota (geckos and flap-footed lizards), Gymnophthalmidae, and  
231 Dactyloidae (anoles), however, clutches are ‘fixed’, nearly always comprising just one or two  
232 eggs. Because species with fixed clutch sizes cannot, by definition, increase their clutch size in  
233 response to climate, we conducted analyses only for species that have variable clutch sizes, and

234 again for all species (regardless of whether their clutch sizes are variable or fixed). We defined  
235 laying strategy based on phylogenetic affinities rather than basing it on observed clutch sizes.  
236 We designate all members of the Gekkota, Dactyloidae and Gymnophthalmidae as having fixed  
237 clutches even though clutch sizes of three or more eggs have been reported for a few of them.  
238 For example, the gecko, *Mediodactylus kotschyi* sometimes lays three eggs, although clutches of  
239 one or two eggs are much more common (Goldberg, 2012; Slavenko et al., 2015); nonetheless,  
240 we treated it as a fixed-clutch species. Species belonging to all other taxa were treated as having  
241 variable clutch sizes. This includes species that only lay one or two eggs. For example the  
242 agamid *Draco bimaculatus*, the amphisbaenian *Cynisca leonina*, and the lacertid *Holaspis laevis*,  
243 all have a maximum reported clutch size of two. They were treated as having variable clutch  
244 sizes because they belong to families in which most species lay larger clutches. We did this  
245 because we assume that 1–2 egg clutches in variable-clutch-sized lineages reflect ecologically  
246 induced selection pressures of the type we aim to identify here, whereas in fixed-clutched  
247 lineages such clutch sizes reflect constraints.

248

## 249 **Results**

250 We obtained clutch-size data for 3,916 lizard species. Mean clutch size per species varied  
251 between one (in 434 species) to 52 (in *Chamaeleo senegalensis*,  $n = 5$  individuals; Cisse and  
252 Karns 1978), with a mode of two eggs (1191 species; 1273 with mean clutch sizes of 1.9-2.1  
253 eggs). All 44 lizard families are represented in our dataset, which covers 56% of global lizard  
254 diversity (3916 of 6950 recognized species; Appendix 1, Figure 1).

255 The results of the four types of global phylogenetic models (with either all species or just  
256 lizards with variable clutch sizes, and using either average female or maximum body mass) are  
257 highly congruent (Tables 1, 2, Appendix 2). Body mass is positively correlated with clutch size  
258 (Figure 2), which supports Hypothesis 6. Insular taxa lay fewer eggs, supporting Hypothesis 7;  
259 and fossorial (perhaps also scansorial) species have smaller clutch sizes than terrestrial species,  
260 supporting Hypothesis 8. Under more stringent criteria for assessing statistical significance (e.g.,  
261  $p = 0.005$ , see Johnson, 2013, Benjamin et al., 2018), differences in clutch size among  
262 microhabitats are often not significant (Tables 1 and 2). Clutch sizes increase with latitude  
263 (supporting Hypothesis 1) and, in climatic models, increase with net temperature seasonality

264 (Hypothesis 2) and primary productivity (Hypothesis 4), under any threshold for statistical  
265 significance and across all global tests. Clutch sizes increase with increased precipitation  
266 seasonality (Hypothesis 2) in taxa with variable clutch sizes, but patterns for precipitation  
267 seasonality are inconsistent across analyses (Appendix 2). Mean annual precipitation and mean  
268 annual temperature, however, are not related to clutch sizes (Table 1, Appendix 2). Activity time  
269 was generally unrelated to clutch size (see, e.g., ANOVA tables in Appendix 2), but it had a  
270 significant interaction with latitude in several models. Near the equator, nocturnal species have  
271 larger clutches than diurnal species, but clutch sizes of nocturnal taxa do not increase with  
272 latitude (or seasonality), whereas those of diurnal taxa do increase poleward (Figure 3; see  
273 Hypothesis 3, above). Because of the high similarity across models we discuss below the models  
274 using maximum body mass and only taxa with variable clutch sizes, highlighting other models  
275 only when they show different patterns.

276 Although in global analyses clutch sizes increase with latitude, in Africa they are larger at  
277 low latitudes (Figure 3, Appendix 2). We thus explored models for different biogeographic  
278 realms individually (Appendix 2). In the Afrotropical realm (which excludes the Sahara and  
279 Madagascar, but includes the southern parts of the Arabian Peninsula) clutch sizes do not  
280 respond to latitude (tested in taxa with variable clutch sizes, with maximum body mass as an  
281 additional predictor. Slope =  $0.0020 \pm 0.0016$ ,  $p = 0.23$ ,  $n = 284$ ). Even in the Afrotropics,  
282 however, clutch sizes increase with temperature seasonality (Hypothesis 2; slope =  $0.296 \pm$   
283  $0.074$ ,  $p < 0.0001$ ; but not with precipitation seasonality, slope =  $0.0008 \pm 0.0005$ ,  $p = 0.16$ ;  
284 Appendix 2). We suspected that the high clutch sizes in equatorial Africa were a result of the  
285 inclusion of chameleons. Chameleons are almost exclusively confined to Africa and Madagascar  
286 and have by far the largest clutches among all lizard families (13.4 eggs on average, not many  
287 more than the New World Iguanidae with 12.0, but chameleons are much smaller animals, and  
288 include many more species: 135 vs. 24 in our analyses; the family with the third-largest clutches,  
289 the Neotropical Polychrotidae, has an average clutch size of 9.0,  $n=7$ ). However, omitting  
290 chameleons does not change the overall conclusion that lizard clutch sizes in Africa are large  
291 compared to other equatorial regions (Appendix 3).

292 Results of the non-phylogenetic models are very similar to those of the phylogenetic models  
293 except that, in the non-phylogenetic models for taxa with variable clutch sizes, scansorial species  
294 have similar values to terrestrial species (Appendix 2e). The important factors remain body mass

295 (positive, Hypothesis 6), insularity (negative, Hypothesis 7), latitude (positive in diurnal species;  
296 hypotheses 1 & 3), seasonality (positive; especially for temperature seasonality; Hypothesis 2),  
297 and NPP (positive; Hypothesis 4 Appendix 2e).

298

## 299 **Discussion**

300 Our global-scale evidence reveals that lizard clutch sizes are larger at higher latitudes  
301 (Hypothesis 1) and in more seasonal environments. Lizard clutch sizes thus show similar  
302 geographic patterns to those seen in birds. Africa, however, emerges as a strong anomaly in  
303 lizards (Figure 3) but not in birds (see Figure 4a in Jetz et al., 2008). Lizard clutch sizes could  
304 thus be explained by similar mechanisms as those operating on birds (Jetz et al., 2008),  
305 suggesting the generality of these mechanisms beyond endotherms.

306 We are unaware of large-scale data on predation intensities that would allow us to assess  
307 whether predation too is higher in seasonal environments and higher latitudes (as hypothesized  
308 for birds by, e.g., Griebeler et al., 2010). The lack of temperature effects, however, leads us to  
309 conclude that seasonality (Hypothesis 2) is a stronger force than cold weather per se  
310 ('harshness', Morrongiello et al., 2012), at least in lizards. In highly seasonal environments, the  
311 window of opportunity for reproduction is short. Although temperature seasonality and latitude  
312 are but proxies for the length of the activity season of lizards (and also vary with other relevant  
313 factors), we think they are good proxies (see Appendix 4). High latitudes are often characterized  
314 by a high seasonal peak in environmental productivity (Geist, 1987; Huston and Wolverton,  
315 2011), enabling lizards to produce large clutches. We posit that in such environments animals  
316 can both find sufficient resources, and are under strong selection pressure, to be as fecund as  
317 possible (Hypothesis 4).

318 There is another angle from which such results need to be viewed: What are the reasons that  
319 many species in stable, less-seasonal environments do not lay large clutches? The logical  
320 converse of our proposed explanation for high clutch sizes is that lizards in less-seasonal  
321 environments do not lay large clutches because environmental productivity lacks a seasonal  
322 peak. Under these circumstances it may take more time to accrue sufficient energetic resources  
323 to produce even one or two eggs. We hypothesize that laying few eggs in a single clutch may be

324 advantageous as long as the female can compensate for the reduced number of eggs by laying  
325 more frequently (Meiri et al., 2013) — a requirement that stable environments allow for. Laying  
326 small, frequent clutches may be a safer bet if egg (or adult) predation pressure is high.  
327 Furthermore, there may be a high physiological strain on mothers laying large clutches (e.g.,  
328 Blazquez et al., 2000; Pincheira-Donoso & Hunt, 2017): carrying many eggs in the abdominal  
329 cavity may reduce locomotory performance and thereby increase predation risk, reduce foraging  
330 success, or convey additional energetic costs associated with carrying a heavy clutch of eggs  
331 (Vitt and Congdon, 1978). In some lizard taxa, the clutch may approach the weight of the mother  
332 (e.g., Diaz-Paniagua et al., 2002; Roitberg et al., 2013; Foster et al., 2019). Although this  
333 obviously also holds where seasons are short, in such regions the advantage of producing more  
334 eggs may outweigh the penalty paid for lower performance because producing multiple clutches  
335 each season is not a viable option.

336 The tendency of clutch sizes to be larger at higher latitudes (Hypothesis 1) and in more  
337 seasonal environments has been known for a long time, but only in birds has it received broad  
338 attention and the status of an ecological rule (sensu Mayr, 1956). The mechanisms suggested to  
339 explain this pattern, however, are hardly bird specific, as the evidence we present here shows. Of  
340 the suggested mechanisms we are aware of only the supposed additional costs of nesting and  
341 nestling mortality in cold regions (Cooper et al., 2005) may be specific to birds and probably  
342 irrelevant for lizards. We note that cold temperatures per se emerged in our models as unrelated  
343 to clutch size; thus, this mechanism really does not apply to lizards. Another hypothesis—that  
344 latitude is important as it relates to day length (Lack 1947) —suggests a difference between  
345 nocturnal and diurnal taxa. Perhaps most mammals, snakes, and owls, would show the reverse  
346 trends, though data are scant. Murray (1976) found that clutch sizes mostly increased northwards  
347 in seven species of North American owls, whereas Donázar (1990) did not find a pattern in the  
348 European Eagle owl. Interestingly, Evans et al. (2009) found that clutch size increased with day  
349 length in seven diurnal bird species in Britain, but decreased with day length (i.e., increased with  
350 night length) in the single owl in their study (*Strix aluco*). Consistent with this, we found that  
351 nocturnal and diurnal lizards differ in the relationship they show between clutch size and  
352 latitude. Diurnal lizard clutch sizes increase with latitude, whereas those of nocturnal lizards do  
353 not, as predicted by our Hypothesis 3. Thus, at high latitudes during the spring and summer  
354 reproductive seasons, longer days may enable diurnal lizards to acquire more food or shuttle

355 more efficiently between basking and foraging activities. Nocturnal lizards do not reach the  
356 highest latitudes that some diurnal species inhabit (Vidan et al., 2017), presumably because the  
357 short summer nights at high latitudes do not allow enough time to balance energetic requirements  
358 and/or the cold night-time temperatures do not allow for activity in most lizard lineages. Thus,  
359 variation in night length is lower for them at the low latitudes they inhabit, and they can  
360 reproduce year round. Furthermore, there are few nocturnal lizards with variable clutch sizes (93  
361 species in our dataset), and, thus, the lack of a latitudinal effect on their reproduction may reflect  
362 low statistical power.

363 Africa emerges as a strong anomaly for the latitudinal clines we identify. Australia likewise  
364 seems to have lizards with relatively small clutch sizes for its latitudinal range and seasonality,  
365 and little within-continent variation (Fig. 3, but see Fig. S1). We cannot readily explain these  
366 unexpected anomalies – although the presence of many fossorial species in deserts of both  
367 continents could explain some of these patterns. We hypothesized that the mostly tropical,  
368 African-endemic, radiation of chameleons, with their huge clutches, could explain the large  
369 clutch sizes of tropical African lizards. We further reasoned that much of the pattern will  
370 disappear once body mass is accounted for, because variation in clutch size seemed to mirror  
371 body-mass variation in Africa (compare Figure 3 with Figure 1c in Slavenko et al., 2019).  
372 Removing chameleons from the analyses and accounting for body mass, however, still leaves us  
373 with an anomaly in Africa (Appendix 2, supplementary Figure S2). More research is needed to  
374 identify why this is so, and we note that our models still leave much unexplained variation (as do  
375 many models in ecology and evolution; Møller and Jennions 2002; Peek et al. 2003). For  
376 Australia, it may be that poor soils and low primary productivity (Hypothesis 4) constrain lizards  
377 to lay relatively small clutches. We note that, although clutch sizes in African lizards do increase  
378 with temperature seasonality, no factor except body mass (Hypothesis 6) emerged as related to  
379 lizard clutch size within Australia (Appendix 2). It may be that clutch size data for a larger  
380 proportion of African lizards are missing than for other regions (see also Tolley et al. 2016,  
381 Tingley et al. 2016). The lack of data is always a worry, though we have little reason to think  
382 these missing data would create systematic biases.

383 Birds and mammals are much better studied than reptiles generally (Bonnet et al., 2002;  
384 Donaldson et al., 2016; Meiri and Chapple, 2016; Troudet et al., 2017). It is therefore  
385 unsurprising that latitudinal variation in bird clutch sizes has been much more intensively studied

386 than in reptiles. Interestingly, studies of geographic variation in litter sizes of mammals are few  
387 (but see Virgos et al., 2006; Bywater et al., 2010). Thus, words written over 80 years ago – “A  
388 corresponding rule of the litter-size of mammals is not yet sufficiently founded” (Rensch, 1938)  
389 – still ring true. Nonetheless, our study demonstrates that insights from the study of reptiles are  
390 not just interesting in their own right, but could inform more pervasive patterns. That patterns  
391 shown by birds and lizards are broadly similar suggests a wider generality across more taxa and  
392 perhaps similar mechanisms.

### 393 Additional factors potentially affecting clutch sizes

394 Our results support key predictions regarding other factors that affect clutch sizes. Clutch  
395 size increases with body mass (supporting Hypothesis 6) – most steeply when average female  
396 mass of taxa with variable clutch sizes is considered (Table B; the only analysis where the 95%  
397 CI of the slope includes the canonical 0.25 slope). Clutches are smaller on islands (Hypothesis  
398 7), as expected under the predictions of the island syndrome (Adler and Levins, 1994; Covas,  
399 2012; Pafilis et al., 2011; Novosolov et al., 2013), whereby life history is assumed to ‘slow  
400 down’ on islands. This pattern is consistent across phylogenetic and non-phylogenetic models  
401 and remains true when fixed-clutched taxa are excluded. Thus, we posit that this reflects, at least  
402 in part, an evolutionary response of insular lizards to the ecological settings they encounter  
403 (Hypothesis 7) rather than simply a matter of taxon turnover related to the greater propensity of  
404 geckos and anoles to colonize islands (Novosolov and Meiri, 2013). Strong intraspecific  
405 competition on islands (Judd and Ross, 1978; Melton, 1982; Adler and Levins, 1994; Novosolov  
406 et al., 2016; Itescu et al., 2017), in the face of lower predation and interspecific competition  
407 pressures, has been suggested to drive this. Interestingly, however, within insular taxa there does  
408 not seem to be an association between clutch size and island area (examining the largest island  
409 inhabited by a species; results not shown).

410 Microhabitat preferences were related to clutch size in many models (though not always  
411 significantly so, especially at  $\alpha < 0.005$ ; see Appendix 2). Scansorial species seem to lay smaller  
412 clutches than terrestrial species of similar sizes that inhabit similar regions. This agrees with  
413 Hypothesis 8 that carrying a large clutch of eggs can be a disadvantage to arboreal species,  
414 limiting the female’s ability to climb (Andrews and Rand, 1974; Shine et al., 1998; Kratochvil  
415 and Kubicka, 2007). It also agrees with Vitt (1981), who found that some crevice-living species



416 have small clutches, and who hypothesized that evolving large clutch sizes may prevent females  
417 from entering their retreats. Schwarzkopf et al. (2010) have shown experimentally that gravid  
418 females with larger clutch sizes had wider mid-bodies and required larger crevices.

419 We note, however, that most chameleons are arboreal, yet have the largest clutches of all  
420 lizards. Distinguishing between arboreal taxa, that respond to predators by fleeing (as most  
421 lizards do), rather than by camouflage (as most chameleons do), may prove illuminating. The  
422 prehensile tail of chameleons may also facilitate their ability to climb while gravid with large  
423 clutches. In our main analyses we designated all lizards that often climb rocks or vegetation as  
424 scansorial. We did not distinguish between strictly arboreal, strictly saxicolous, arboreal and  
425 saxicolous or even arboreal and terrestrial or terrestrial and saxicolous species, reasoning that  
426 climbing constrain the clutch sizes of all such species. In further analyses we found no  
427 significant differences between strictly terrestrial and strictly arboreal species, whereas species  
428 classified as both arboreal and saxicolous had slightly larger clutches than strictly arboreal ones  
429 (Appendix 5; see also Table 5 Mesquita et al. 2016, showing that semi-arboreal species have  
430 larger clutches than either saxicolous or arboreal ones).

431 Fossorial taxa emerged as having smaller clutches than terrestrial species in some models  
432 (Table 2, Appendix 2). Overall, our results add some evidence to support Ashton's (2005) claim  
433 that because the fossorial *Plestiodon reynoldsi* lays small clutches it is "similar to those of other  
434 fossorial lizards". We further note that within skinks (the only lizard clade with variable clutch  
435 sizes and multiple transitions to a fossorial lifestyle) fossoriality is indeed associated with small  
436 clutches (see Appendix 2 for within-clade models). We suspect this may be caused by increased  
437 energetic demand on burrowing for gravid females. Overall our results generally support the  
438 hypothesis that scansorial and fossorial lizards have smaller clutches than terrestrial ones, but  
439 effect sizes are generally small, and support varied across models.

#### 440 The Geographic distribution of lizards with fixed and variable clutches

441 We have found that lizard clutches are generally larger in higher latitudes and in seasonal  
442 regions even when only taxa with variable clutch sizes are considered and when phylogenetic  
443 non-independence is accounted for (Figure 3). We note that the distribution of lizards with fixed  
444 clutch sizes would only serve to strengthen the generality of these patterns. Although taxa in  
445 which females lay only one or two eggs are, of course, not expected to show geographic

446 variation in this parameter, they can nonetheless inform us about the relationship between clutch  
447 size and the environment. With the exception of a few gecko taxa (e.g., the New Zealand  
448 radiation, Nielsen et al., 2011; Cree and Hare, 2016; the South American *Homonota darwini*;  
449 *Ibarguengoytia* & Casalins, 2007; Weeks and Espinoza, 2013), the distribution of fixed-clutch  
450 lizards is mostly limited to tropical, subtropical, and desert regions (geckos) or tropical and  
451 subtropical regions alone (anoles, gymnophthalmids; Roll et al., 2017). One could easily come  
452 up with hypotheses relating to the distribution of each of these three taxa. Gymnophthalmids,  
453 being mostly leaf-litter inhabitants, and anoles, being predominately scansorial (mostly arboreal,  
454 but with many leaf-litter species; e.g., Losos, 2009; Vitt and Caldwell, 2013), could perhaps not  
455 penetrate temperate desert belts and migrate further north. This, however, would not necessarily  
456 explain their absence from more temperate, higher latitudes south of the Equator in South  
457 America. Geckos, being predominately nocturnal (Bauer, 2013; Gamble et al., 2015), may be  
458 restricted largely to low latitudes by their inability to tolerate the cold nights prevailing at higher  
459 latitudes. Indeed Vidan et al. (2017) identified a sharp distinction between the distributions of  
460 Eurasian diurnal lizards, which could range above the Arctic Circle, and nocturnal taxa (mostly  
461 geckos), which do not reach anywhere near this far north. However, geckos have another trick up  
462 their sleeve: some of them evolved diurnal activity at colder regions, or bask during the day and  
463 forage at night (e.g., New Zealand *Naultinus*, *Tarentola mauritanica* in S. Europe, *Ptyodactylus*  
464 *puiseuxi* in northern Israel, and *Quedenfeldtia* in the Atlas Mountains; see, e.g., Gamble et al.,  
465 2015; Hare and Cree, 2016).

466 In the light of our findings, we tentatively suggest an alternative mechanism (Hypothesis 5):  
467 it may be that such taxa are restricted to low latitudes because their reproductive strategy – laying  
468 few eggs frequently – is simply not viable at higher latitudes (Figure 4). At high latitudes and  
469 other highly seasonal environments the reproductive season is short, and laying multiple clutches  
470 is thus not viable. It could be that fixed-clutch species are excluded from high latitudes and  
471 highly seasonal regions not because of cold climates but because the short activity seasons in  
472 those regions do not allow them to produce enough offspring to ensure population replacement.  
473 If this hypothesis is true it would suggest that evolving a fixed clutch size has implications  
474 beyond its immediate effects on reproduction. What are the proximal mechanisms constraining  
475 species to this strategy, and which ultimate mechanisms allow fixed-clutched lizards to thrive,  
476 are fascinating questions for future research.

477 In summary, lizard clutches are highly attuned to geographic cues, whether in the form of  
478 insularity or as climatic clines. It seems though, that rather than climate per se, lizard clutch sizes  
479 respond to the degree of seasonality through its effect on the number of opportunities for  
480 reproduction within a year and perhaps through seasonal effects on food abundance, mortality  
481 rates, and foraging opportunities.

482

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487

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764

765 **Data Accessibility Statement:**

766 All data used in the analyses are available as Appendix 1.

767

768

769 **Tables**

770 Table 1. ANOVA results and parameter estimates of clutch sizes as a function of ecological  
771 and geographical predictors. For full results see Appendix 2.

772

773 A. ANOVA tables, all taxa, maximum body mass; a model with NPP and precipitation  
774 followed by model with latitude

775 B. Parameter estimates, all taxa, maximum body mass

776 C. ANOVA table, taxa with variable clutch sizes, maximum body mass

777 D. Parameter estimates, taxa with variable clutch sizes, maximum body mass

778

779 A.

780 1. ANOVA table, climatic model

	Df	sum of squares	mean squares	F	p
Body Mass	1	0.271	0.271	774.512	<0.0001
Insularity	1	0.033	0.033	93.108	<0.0001

Microhabitat	2	0.004	0.002	5.411	0.005
Precipitation seasonality	1	0.003	0.003	7.469	0.006
Temperature seasonality	1	0.025	0.025	71.423	<0.0001
NPP	1	0.013	0.013	38.149	<0.0001
Residuals	3425	1.198	0.0004		

781

782

783

784 2. ANOVA table, latitude model

Factor	Df	sum of squares	mean squares	F	p
Body Mass	1	0.252	0.252	693.800	<0.0001
Insularity	1	0.029	0.029	78.450	<0.0001
Microhabitat	2	0.005	0.002	6.318	0.002
Activity time	2	0.0009	0.0004	1.177	0.308
Latitude	1	0.015	0.015	40.794	<0.0001
Activity time: Latitude interaction	2	0.004	0.002	5.500	0.004
Residuals	3228	1.17365	0.00036		

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787

788 B. Parameter estimates, all taxa, maximum body mass

789 1. Parameter estimates, climate and NPP model

Factor	Estimate	SE	t	p
Terrestrial	0.420	0.146	-5.651	<0.0001
Fossorial	0.392	0.147	-2.131	0.0331
Scansorial	0.405	0.147	-2.152	0.0314

Mainland	0.420	0.010	-3.337	0.0009
Insular	0.389	0.144	-5.974	<0.0001
Mass	0.176	0.006	27.943	<0.0001
Precipitation seasonality	0.0003	0.0001	2.716	0.0066
Temperature seasonality	0.119	0.012	10.041	<0.0001
NPP	0.057	0.009	6.177	<0.0001

790

791

792 All species, maximum body mass,  $\lambda = 0.776$ , model  $R^2 = 0.225$ . Mass, seasonality and  
793 NPP estimates are slopes (log 10 transformed except precipitation seasonality). Values  
794 (clutch sizes, log 10 transformed) of the categorical variables are for the means of the  
795 continuous predictors: a mass of 12.3 g (back transformed from logarithm), log NPP = 11.37  
796 ( $\text{g C m}^{-2}, \text{yr}^{-1}$ , log 10 transformed), Temperature seasonality = 3.3 (standard deviation,  
797  $^{\circ}\text{C} \times 100$ , log 10 transformed), precipitation seasonality = 66.3 (coefficient of variation of  
798 monthly values). Values for microhabitats are shown for mainland species. Values for  
799 insularity/mainland are shown for terrestrial species. Estimates are presented with their  
800 standard errors. t and p values are for differences from zero (with the continuous variables set  
801 to zero) for terrestrial and mainland species, from terrestrial species for fossorial and  
802 scansorial ones, and from insular species from mainland species. Terrestrial species have  
803 smaller clutches than both scansorial and fossorial species. There are no significant  
804 differences between scansorial and fossorial species ( $t = 0.923$ ,  $p = 0.356$ ).

805

806 2. Parameter estimates, latitude and activity time model

Factor	Estimate	se	t	p
Terrestrial	0.475	0.083	2.737	0.006
Fossorial	0.433	0.084	2.721	0.0065
Scansorial	0.456	0.083	2.581	0.0099
Mainland	0.475	0.083	2.737	0.006
Insular	0.408	0.083	1.926	0.054



Latitude (diurnal species)	0.0031	0.0004	7.179	<0.0001
Latitude (nocturnal species)	0.001	0.001	0.671	0.502
Mass	0.170	0.007	26.142	<0.0001

807

808 All species, maximum body mass,  $\lambda = 0.794$ , model  $R^2 = 0.206$ . Mass (log 10  
809 transformed) and latitude estimates are slopes. Values (clutch sizes, log 10 transformed) of  
810 the categorical variables are for the means of the continuous predictors: a mass of 12.3 g  
811 (back transformed from logarithm), latitude (absolute value):  $19.55^\circ$  (decimal). Values for  
812 microhabitats are shown for diurnal mainland species. Values for insularity/mainland are  
813 shown for diurnal terrestrial species. Estimates are presented with their standard errors; t and  
814 p values are for differences from zero (with mass and latitude set to zero) for terrestrial and  
815 mainland species, from terrestrial species for fossorial and scansorial ones, and from insular  
816 species from mainland species. Terrestrial species have smaller clutches than both scansorial  
817 and fossorial species but there are no significant differences between scansorial and fossorial  
818 species ( $t = 1.383$ ,  $p = 0.167$ ). Latitudinal slope for cathemeral species not shown.

819 C. taxa with variable clutch sizes, maximum body mass

820 1. ANOVA table, climatic model

Factor	Df	sum of squares	mean squares	F	p
Body Mass	1	0.324	0.324	654.103	<0.0001
Insularity	1	0.047	0.047	94.249	<0.0001
Microhabitat	2	0.004	0.002	3.811	0.022
Precipitation seasonality	1	0.006	0.006	11.588	0.001
Temperature seasonality	1	0.029	0.029	58.862	<0.0001
NPP	1	0.025	0.025	51.457	<0.0001
Residuals	2196	1.086	0.000		

821

822 2. ANOVA table, latitude model

Factor	Df	sum of	mean	F	p
--------	----	--------	------	---	---

		squares	squares		
Body Mass	1	0.310	0.310	568.559	<0.0001
Insularity	1	0.045	0.045	82.018	<0.0001
Microhabitat	2	0.004	0.002	4.055	0.017
Activity time	2	0.002	0.001	1.557	0.211
Latitude	1	0.016	0.016	29.321	<0.0001
Activity time: Latitude interaction	2	0.002	0.001	1.444	0.236
Residuals	2013	1.097	0.001		

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829 D. taxa with variable clutch sizes, maximum body mass

830 1. Parameter estimates, climate and NPP model

Factor	Estimate	SE	t	p
Terrestrial	0.499	0.211	-6.967	<0.0001
Fossorial	0.471	0.210	1.0645	0.100
Scansorial	0.483	0.211	1.0673	0.094
Mainland	0.499	0.211	-6.967	<0.0001
Insular	0.464	0.206	-7.319	<0.0001
Mass	0.216	0.008	25.585	<0.0001
Precipitation seasonality	0.0006	0.0001	3.846	0.0001
Temperature seasonality	0.169	0.017	9.896	<0.0001
NPP	0.096	0.013	7.173	<0.0001

831

832 Only species with variable clutch sizes, maximum body mass,  $\lambda = 0.801$ , model  $R^2 =$   
 833 0.286. Mass, seasonality and NPP estimates are slopes (log 10 transformed except  
 834 precipitation seasonality). Values (clutch sizes, log 10 transformed) of the categorical  
 835 variables are for the means of the continuous predictors: a mass of 18.8 g (back transformed  
 836 from logarithm),  $\log NPP = 11.36$  ( $\text{g C m}^{-2}, \text{yr}^{-1}$ , log 10 transformed), temperature  
 837 seasonality = 3.35 (standard deviation,  $^{\circ}\text{C} * 100$ , log 10 transformed), and precipitation  
 838 seasonality = 65.9 (coefficient of variation of monthly values). Values for microhabitats are  
 839 shown for mainland species. Values for insularity/mainland are shown for terrestrial species.  
 840 Estimates are presented with their standard errors. t and p values are for differences from  
 841 zero (i.e., with mass, seasonality and NPP set to zero) for terrestrial and mainland species,  
 842 from terrestrial species for fossorial and scansorial ones, and from insular species from  
 843 mainland species. Terrestrial species have similar clutch sizes to both scansorial and fossorial  
 844 species and there are no significant differences between scansorial and fossorial species ( $t =$   
 845 0.677,  $p = 0.498$ ). The latitudinal slope for cathemeral species is not shown.

846

## 847 2. Parameter estimates, latitude and activity time model

Factor	Estimate	SE	t	p
Terrestrial	0.572	0.114	2.074	0.038
Fossorial	0.526	0.116	2.260	0.024
Scansorial	0.553	0.115	1.902	0.057
Mainland	0.572	0.114	2.074	0.038
Insular	0.472	0.115	1.180	0.238
Latitude (diurnal species)	0.003	0.001	5.595	<0.0001
Latitude (nocturnal species)	0.0005	0.0008	0.648	0.517
Mass	0.212	0.009	23.565	<0.0001

848

849 Only species with variable clutch sizes, maximum body mass,  $\lambda = 0.825$ , model  $R^2 =$   
 850 0.256. Mass (log 10 transformed) and latitude estimates are slopes. Values (clutch sizes, log  
 851 10 transformed) of the categorical variables are for the means of the continuous predictors: a  
 852 mass of 18.8 g (back transformed from logarithm), latitude (absolute value):  $20.92^{\circ}$

853 (decimal). Values for microhabitats are shown for diurnal mainland species. Values for  
 854 insularity/mainland are shown for diurnal terrestrial species. Estimates are presented with  
 855 their standard errors t and p values are for differences from zero (with mass and latitude set  
 856 to zero) for terrestrial and mainland species, from terrestrial species for fossorial and  
 857 scansorial ones, and from insular species from mainland species. Terrestrial species have  
 858 smaller clutches than fossorial – but not scansorial species. There are no significant  
 859 differences between scansorial and fossorial species ( $t = 1.251$ ,  $p = 0.211$ ). The latitudinal  
 860 slope for cathemeral species is not shown.

861 For full results see Appendix 2.

862

863 **Table 2.** Summary of statistical significance of different models ( $\alpha = 0.05$ ). +: significant,  
 864 positively associated with clutch size, -: significant, negatively associated with clutch size, ns:  
 865 non-significantly associated with clutch size. Fossorial, scansorial, and semi-aquatic species are  
 866 compared to terrestrial ones. Nocturnal and cathemeral species are compared to diurnal ones (see  
 867 ANOVA tables in Table 1 for overall significant of multilevel factors). Nocturnal:latitude and  
 868 Cathemeral:latitude are interaction terms and depict whether, and in which direction, the  
 869 latitudinal slope differs from the slope for diurnal species. VCS: variable clutch size. n (all -  
 870 deleted): number of species used in the analysis after deletion of species with missing data. n  
 871 (deleted): species deleted from the analysis because of missing data. See Table 1 and Appendix 2  
 872 for parameter estimates (contrasts and slopes).

873 A. Models with climatic and environmental predictors (seasonality and NPP)

Model	all taxa	all taxa	VCS taxa	VCS taxa
	average female size	maximum size	average female size	maximum size
lambda	0.818	0.794	0.849	0.817
n	2617	3163	1723	1995
Mass	+	+	+	+
Insularity	-	-	-	-
Fossorial	-	-	ns	-
Scansorial	-	-	ns	ns
Nocturnal	ns	ns	ns	ns
Cathemeral	ns	ns	+	+

Seasonality (precipitation)	ns	+	+	+
Seasonality (temperature)	+	+	+	+
NPP	+	+	+	+
R <sup>2</sup>	0.239	0.225	0.302	0.288

874

875

## 876 B. Models with latitude and activity times

Model	all taxa	all taxa	VCS taxa	VCS taxa
	average female size	maximum size	average female size	maximum size
lambda	0.818	0.794	0.854	0.825
n	2566	3238	1743	2023
Mass	+	+	+	+
Insularity	-	-	-	-
Fossorial	-	-	-	-
Scansorial	-	-	ns	ns
Nocturnal	ns	+	ns	ns
Cathemeral	+	+	ns	+
Latitude	+	+	+	+
Nocturnal:latitude	-	-	ns	ns
Cathemeral:latitude	-	-	ns	ns
R <sup>2</sup>	0.216	0.206	0.265	0.256

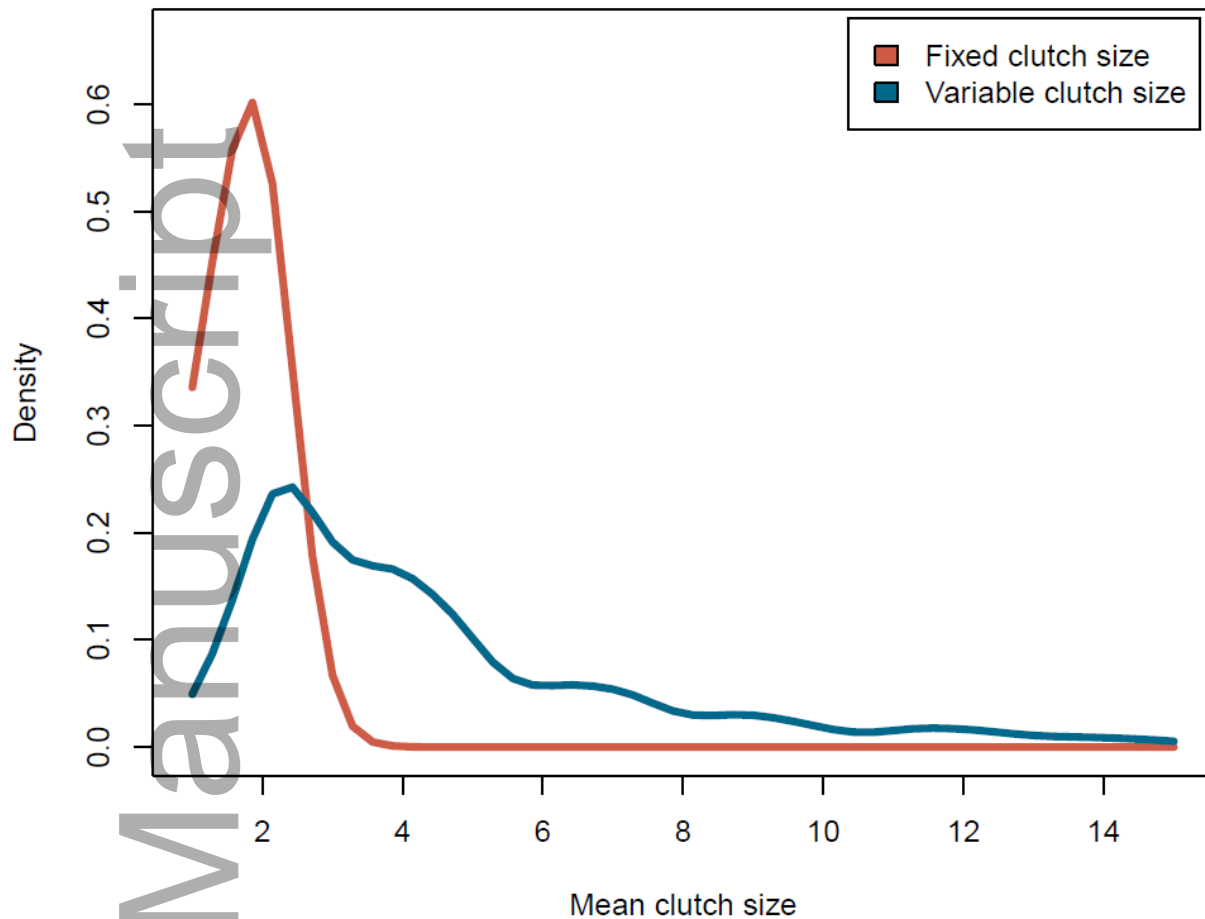
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879 **Figure legends and embedded figures**

880

881 **Figure 1.** Density plot of mean clutch sizes for the 3916 species analysed, separated between  
 882 species with fixed (red) and variable (blue) clutch sizes.



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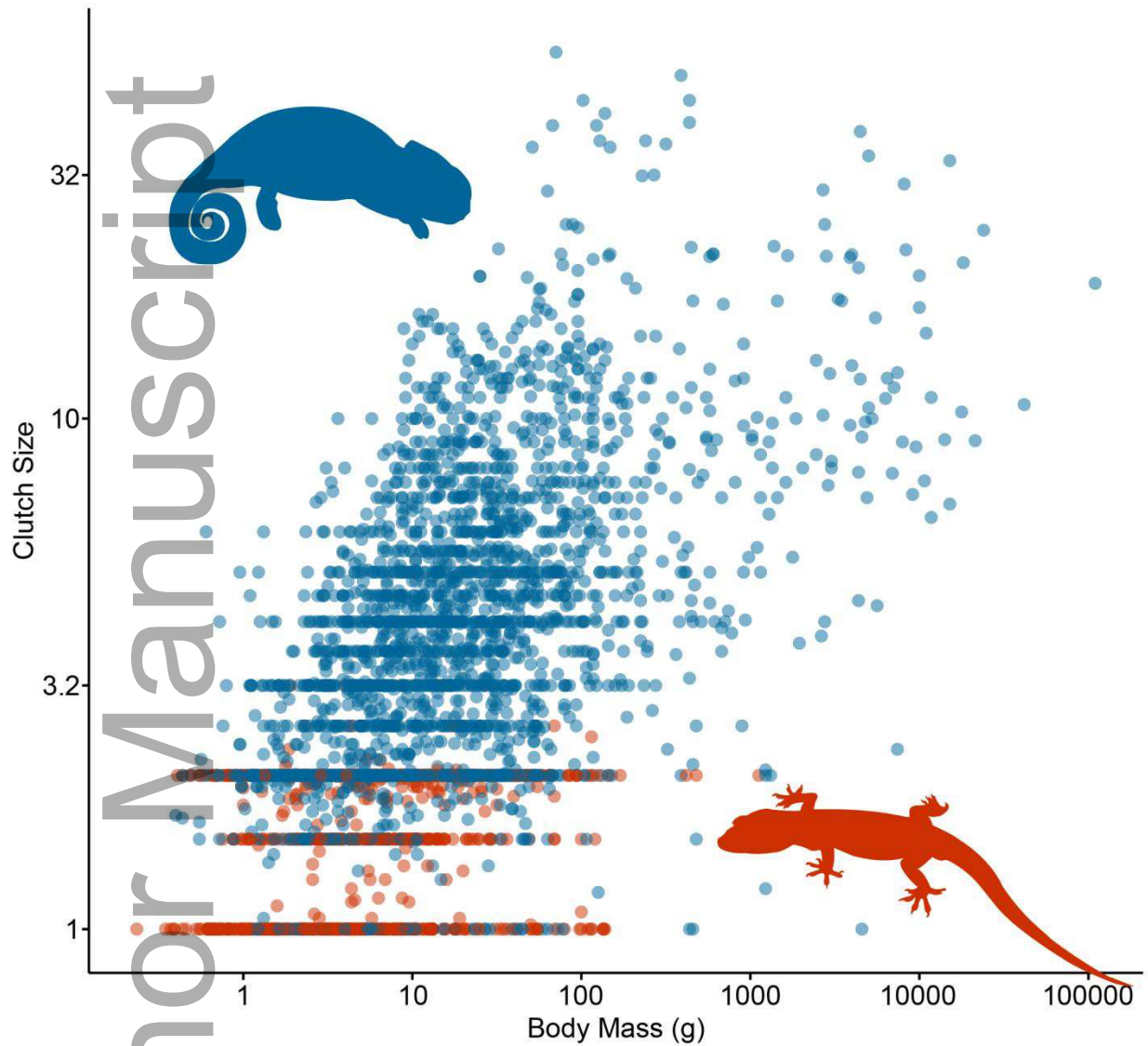
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888 **Figure 2.** The relationship between clutch size (log<sub>10</sub> transformed) and maximum body mass (in  
 889 grams, log<sub>10</sub> transformed) in the 3916 species in our dataset. The OLS slope is  $0.241 \pm 0.005$ .  $R^2$   
 890 = 0.334. Taxa with variable clutch sizes shown in blue, those with fixed clutch sizes in red.



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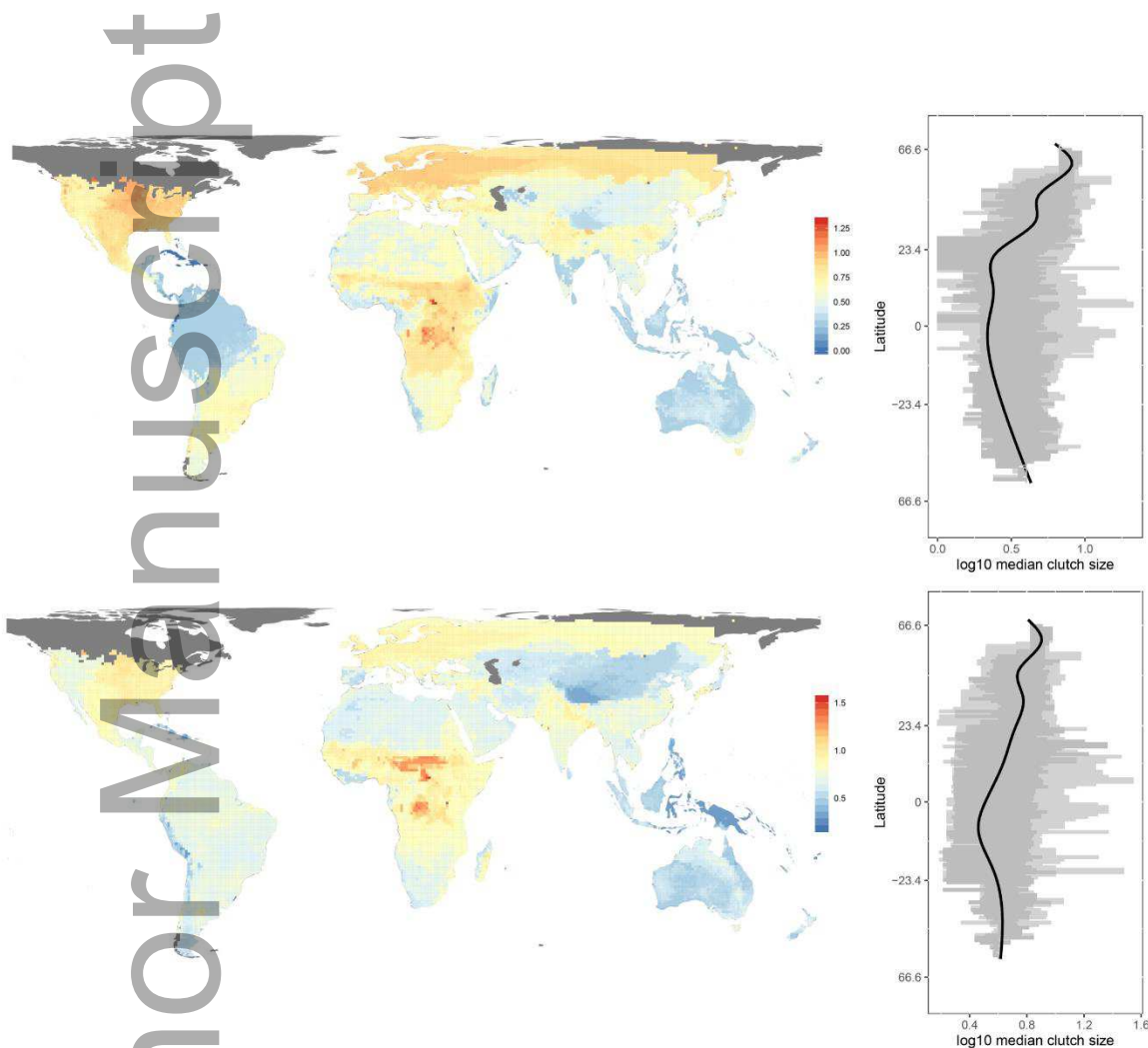
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894 **Figure 3.** Median log-transformed clutch size in 96\*96 km grid cells globally. Top: all lizards;  
 895 Bottom: only lizards with variable clutch sizes. Note that the colour scale differs between the  
 896 maps. To the right of each map is a curve showing a generalized additive model of the mapped  
 897 variable (in black), the 95% confidence intervals of the mapped variable per 96km latitudinal  
 898 band (shaded dark grey), and the range of values of the mapped variable per 96 km latitudinal

899 band (shaded light grey). For similar maps where residuals from a phylogenetic clutch-size on  
 900 body-size analysis are portrayed see Supplementary Figures S1-S2. Equal area Behrmann  
 901 projection, 96\*96 km resolution.

902



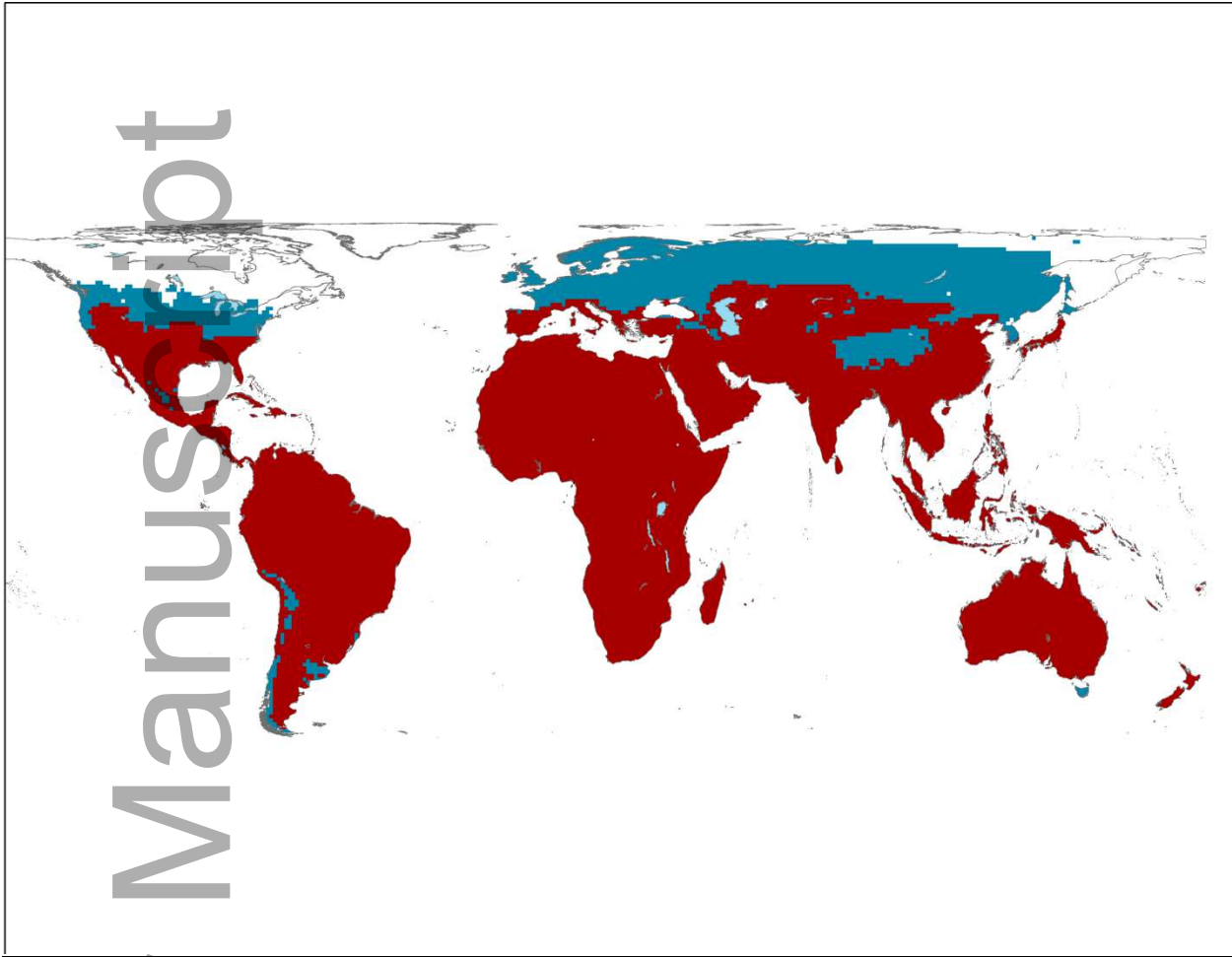
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904

905 **Figure 4.** Distribution of lizards with fixed clutch sizes (red). Note that in the northernmost (N.  
 906 America, N. Eurasia) and southernmost distribution of lizards (S. America; Australia, Tasmania,  
 907 and New Zealand), and cold regions (e.g., C. Asia, the Caucasus and the Andes), fixed clutched  
 908 taxa are generally absent. Lizards with variable clutch sizes inhabit all regions (both red and  
 909 blue) that lizards occur in. White regions have no lizards. Equal area Behrmann projection,  
 910 96\*96 km resolution.



911



912

### 913 Supplementary Material

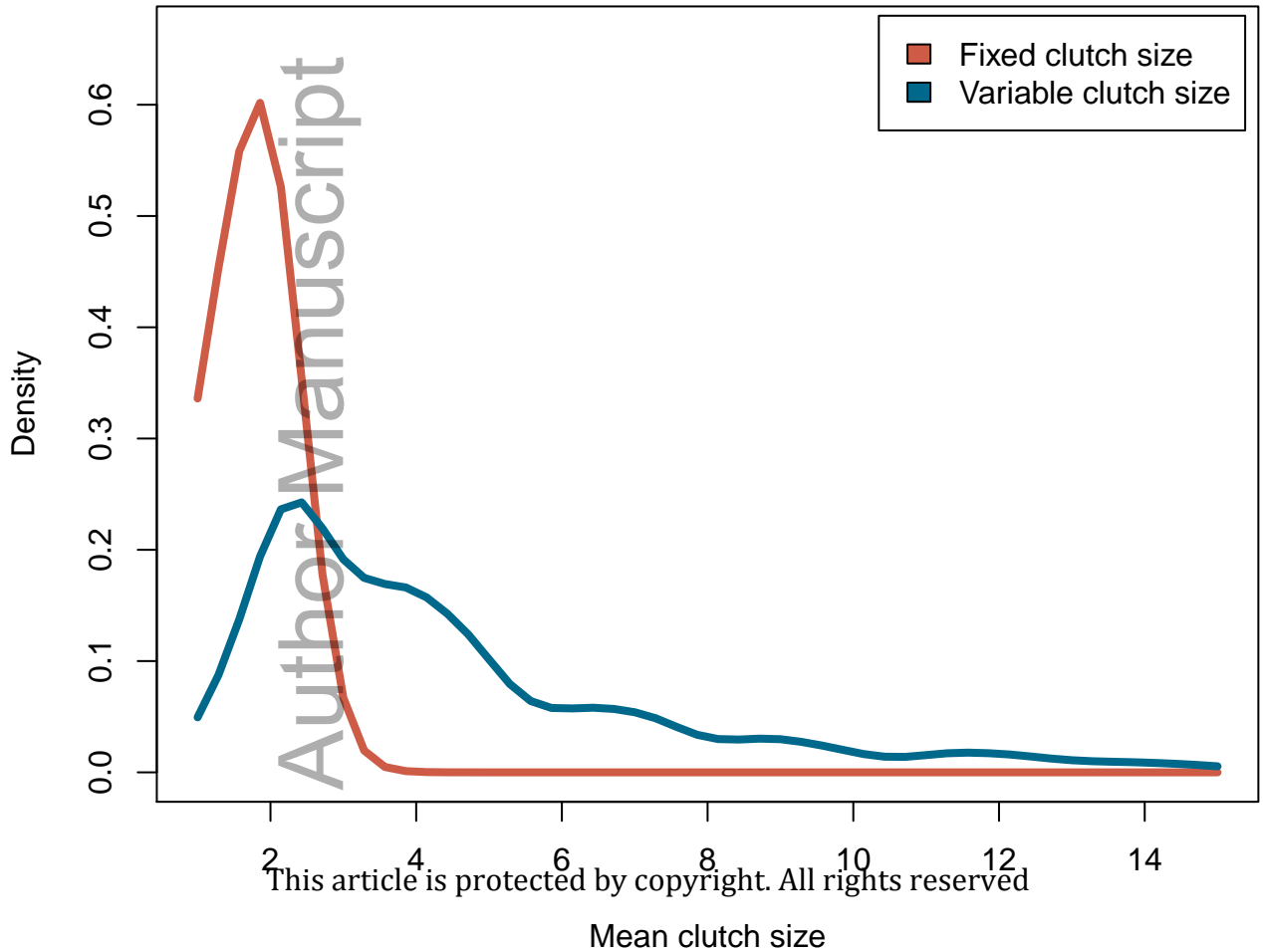
914 Appendix 1 – The dataset and the metadata used to assemble it

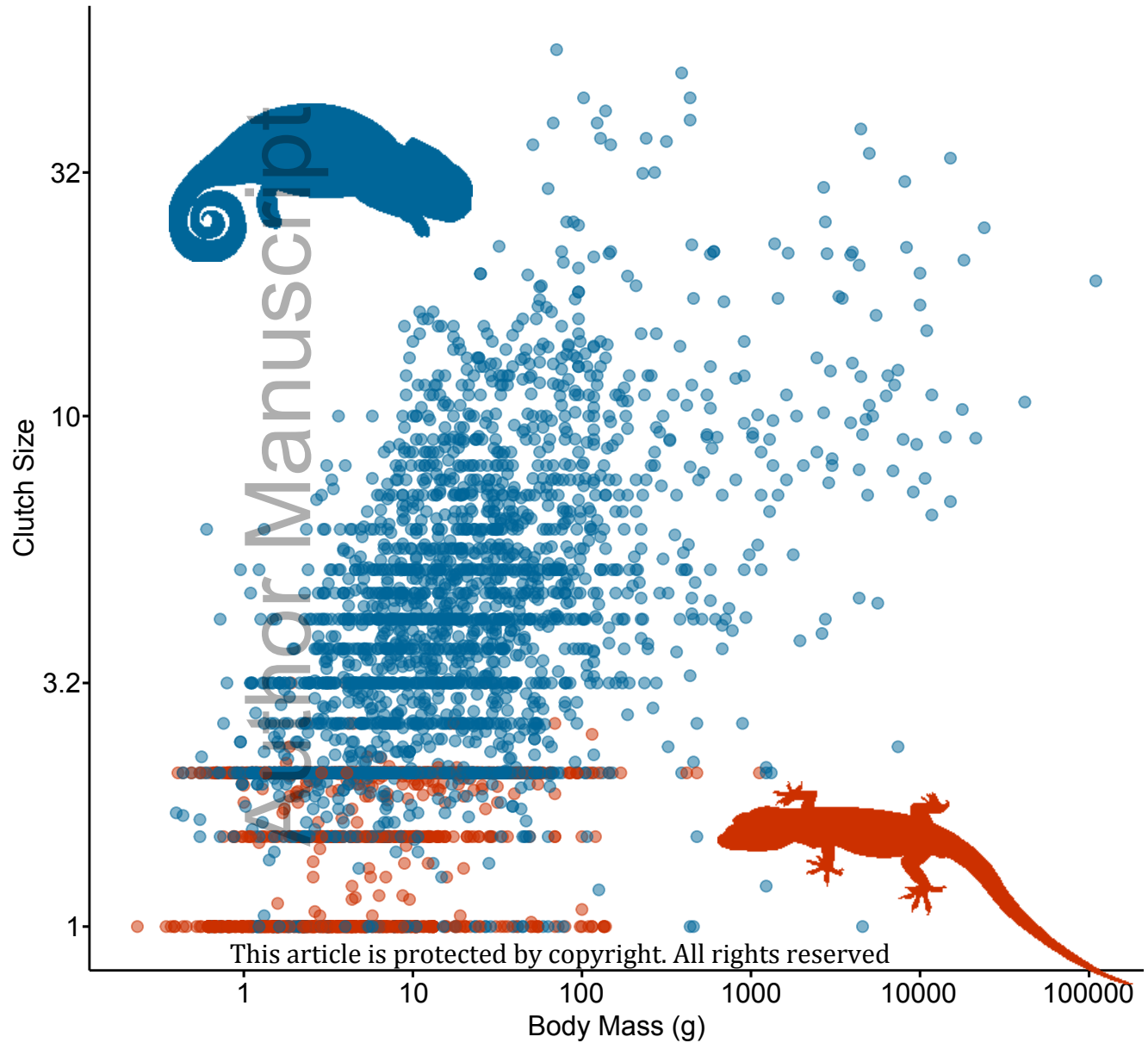
915 Appendix 2 – Results for all models and sensitivity analyses

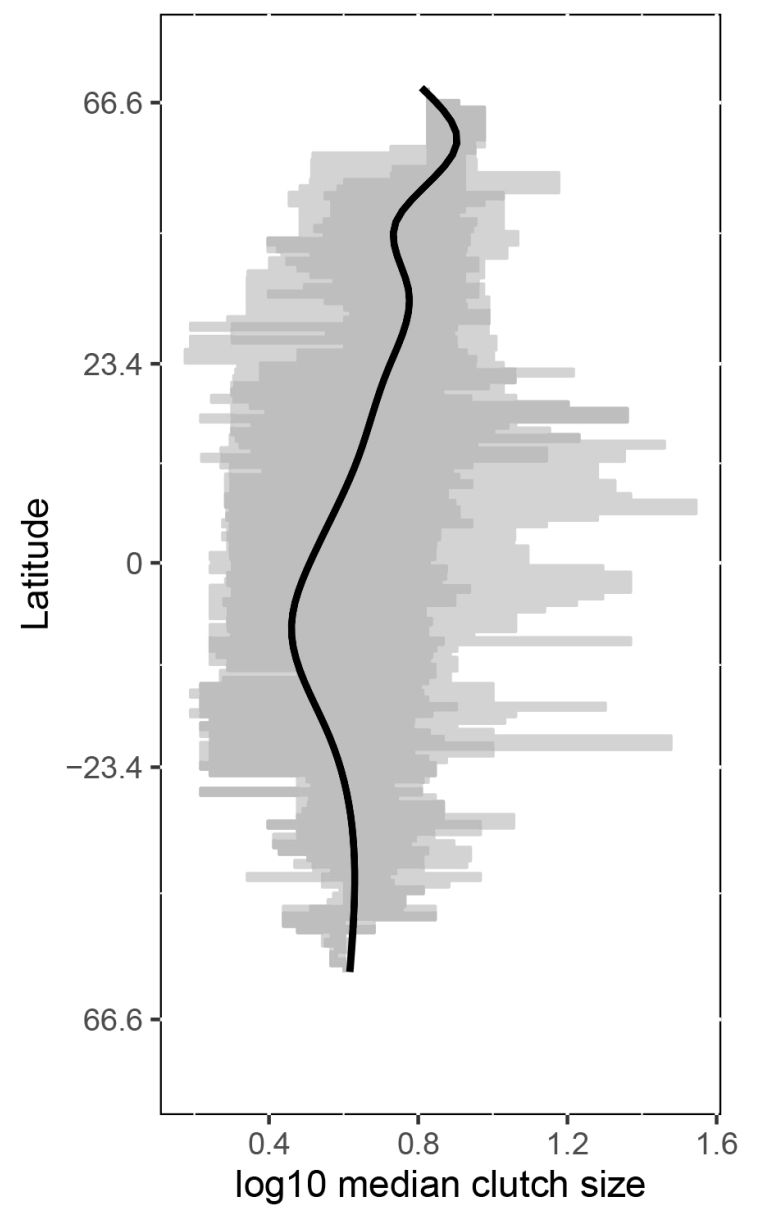
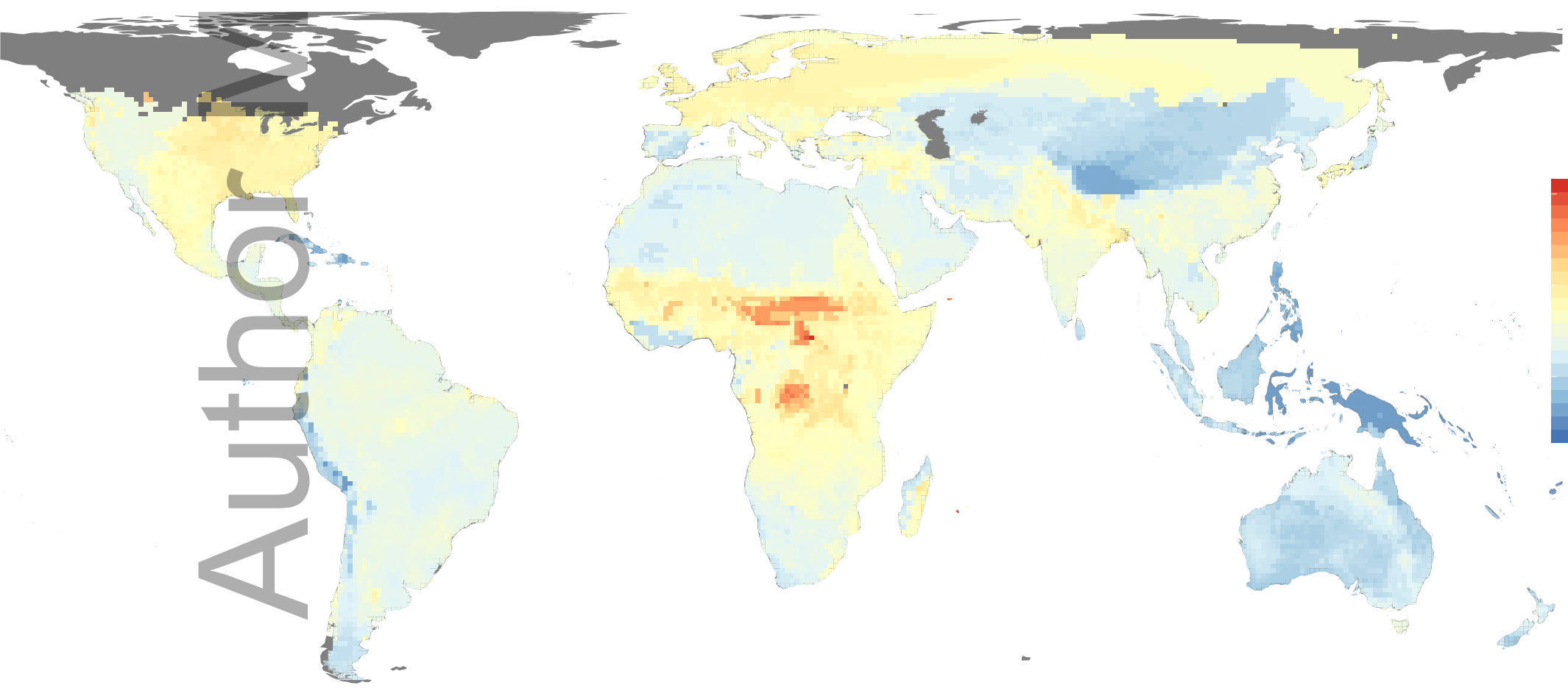
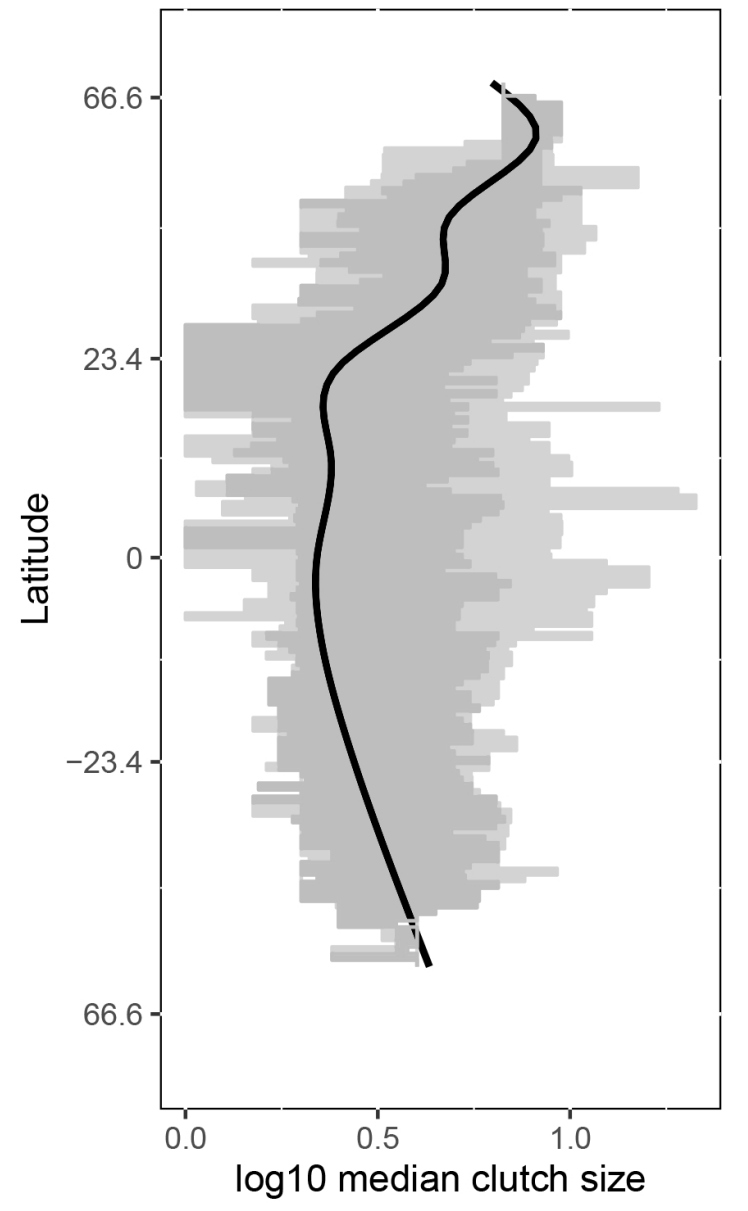
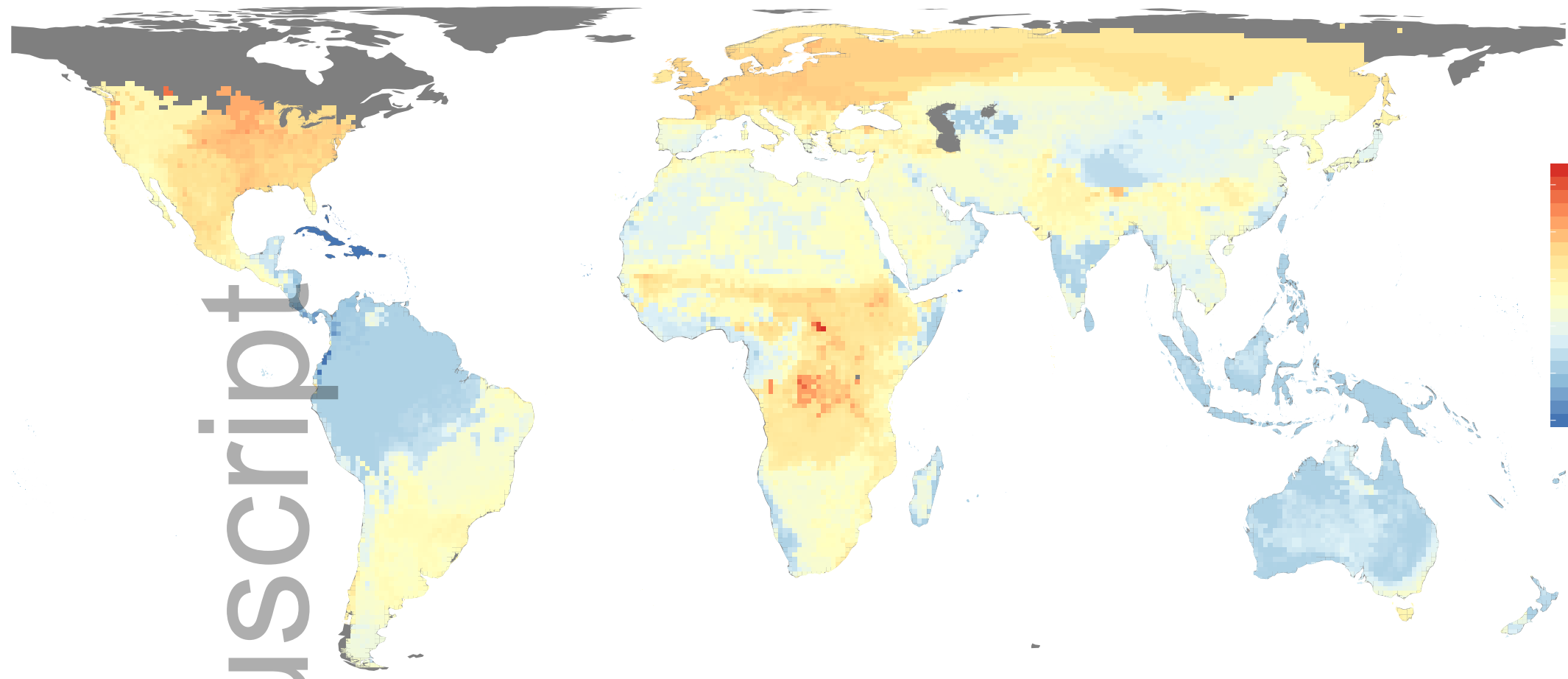
916 Appendix 3 – Supplementary figures

917 Appendix 4 – Relationships between the activity season of lizards and latitude, temperature  
918 seasonality, and precipitation seasonality of their ranges

919 Appendix 5 – Comparisons of clutch sizes of saxicolous and arboreal lizards







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