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1 **Reduction of baseline corticosterone secretion correlates with**  
2 **climate warming and drying across wild lizard populations**

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18

19 **Abstract**

- 20 1. Climate change should lead to massive loss of biodiversity in most taxa but the detailed  
21 physiological mechanisms underlying population extinction remain largely elusive so far.  
22 In vertebrates, baseline levels of hormones such as glucocorticoids (GCs) may be  
23 indicators of population state since their secretion to chronic stress can impair survival  
24 and reproduction. However, the relationship between GC secretion, climate change and  
25 population extinction risk remains unclear.
- 26 2. In this study we investigated whether levels of baseline corticosterone (the main GCs in  
27 reptiles) correlate with environmental conditions and associated extinction risk across  
28 wild populations of the common lizard *Zootoca vivipara*.
- 29 3. First, we performed a cross-sectional comparison of baseline corticosterone levels along  
30 an altitudinal gradient among 14 populations. Then, we used a longitudinal study in 8  
31 populations to examine the changes in corticosterone levels following the exposure to a  
32 heat wave period.
- 33 4. Unexpectedly, baseline corticosterone decreased with increasing thermal conditions at  
34 rest in females, and was not correlated with extinction risk. In addition, baseline  
35 corticosterone levels decreased after exposure to an extreme heat wave period. This  
36 seasonal corticosterone decrease was more pronounced in populations without access to  
37 standing water.
- 38 5. We suggest that low basal secretion of corticosterone may entail down-regulating activity  
39 levels and limit exposure to adverse climatic conditions, especially to reduce water loss.  
40 These new insights suggest that rapid population decline might be preceded by a down-  
41 regulation of the corticosterone secretion.

42 **Keywords.** Altitude, corticosterone, ectotherm, population decline, temperature, water  
43 availability.

#### 44 **Introduction**

45 An increasing number of living organisms are on the verge of extinction, mostly due to  
46 human-related factors such as land use, exploitation or climate change (Pereira et al., 2010;  
47 Thomas et al., 2004). For instance, nearly half of all plant and animal species have already  
48 faced population extinctions over the last 50 years (Wiens, 2016), and the pace of extinction is  
49 greater than expected in vertebrates (Ceballos, Ehrlich, & Dirzo, 2017). This Earth "sixth  
50 mass extinction crisis" has led to an intense effort to understand the liabilities of global  
51 change on biodiversity loss, and the search of reliable physiological mechanisms underlying  
52 population declines and of physiological determinants of extinction risk (Cooke et al., 2013;  
53 Wikelski & Cooke, 2006). Indeed, physiological studies are useful because they could unravel  
54 individual-level mechanisms underlying population declines and the identification of relevant  
55 biomarkers of the extinction risk could ease conservation status assessment and prioritization  
56 of management actions.

57 In vertebrates, hormones such as glucocorticoids (GCs) modulate daily and seasonal  
58 routines, such as reproductive cycles, as well as behavioural and life history responses to cope  
59 with both predictable and unpredictable events (Angelier & Wingfield, 2013; Landys,  
60 Ramenofsky, & Wingfield, 2006; Wingfield et al., 1998). The baseline secretion of GCs by  
61 the hypothalamic–pituitary–adrenal axis help individuals to mobilise energy associated with  
62 the demands of specific homeostatic states, where homeostasis refers to the tendency of the  
63 individual organism to maintain a state of physiological equilibrium on the long run (Landys  
64 et al., 2006; Romero, Dickens, & Cyr, 2009). However, individuals chronically exposed to  
65 stressors may show increased levels of baseline GCs, changes in the magnitude of the GCs  
66 response to an acute stress, and/or a reduction in the capacity to recover from perturbations,  
67 all of which may impair survival and/or reproduction on the long term (Angelier, Wingfield,  
68 Weimerskirch, & Chastel, 2010; Breuner, Patterson, & Hahn, 2008; Meylan, Miles, &

69 Clobert, 2012; Romero & Wikelski, 2010; Wingfield, 2013). Therefore, the regulation of GCs  
70 secretion may trigger adaptive responses to environmental changes, although empirical  
71 studies have shown that the fitness outcomes of the stress response are often complex and  
72 species-specific (Angelier et al., 2010; Bonier, Martin, Moore, & Wingfield, 2009; Bonier,  
73 Moore, & Robertson, 2011).

74 In wild populations, a range of chronic stressors from anthropogenic disturbance,  
75 including exposure of animals to unregulated ecotourism (Ellenberg, Setiawan, Cree,  
76 Houston, & Seddon, 2007; French, DeNardo, Greives, Strand, & Demas, 2010), habitat  
77 pollution (Crino, Klassen Van Oorschot, Johnson, Malisch, & Breuner, 2011; Meillère et al.,  
78 2016; Wikelski, Romero, & Snell, 2001), or landscape fragmentation (Janin, Léna, & Joly,  
79 2011; Martínez-Mota, Valdespino, Sánchez-Ramos, & Serio-Silva, 2007) may result in  
80 chronic elevation of baseline GC level, population declines and increased risks of rapid  
81 population extinction. There is also some direct evidence that lower corticosterone level may  
82 improve fitness of individuals exposed to desiccation and thermal stress in terrestrial  
83 ectotherms (Jessop, Letnic, Webb, & Dempster, 2013). And yet, a demonstration that  
84 secretion of GCs consistently correlate with the status and future fate of populations exposed  
85 to climate warming has not emerged yet, because of a wide variation in the sensitivity of GCs  
86 to anthropogenic disturbances across individuals and variable pathways between patterns of  
87 GCs secretion and individual fitness (Dantzer, Fletcher, Boonstra, & Sheriff, 2014; Dickens &  
88 Romero, 2013). These results thus question the GCs as a pertinent bio-marker of population  
89 extinction status.

90 Climate change represents an ubiquitous environmental challenge for living organisms  
91 that may interact with other environmental stressors and accelerate population declines  
92 (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Cahill et al., 2012; Flesch,  
93 Rosen, & Holm, 2017). Ectothermic vertebrates are expected to be particularly vulnerable due

94 to their behavioural and physiological sensitivity to environmental temperature (Deutsch et  
95 al., 2008; Frishkoff, Hadly, & Daily, 2015; Kingsolver, Diamond, & Buckley, 2013; Le  
96 Galliard, Massot, Baron, & Clobert, 2012; Telemeco et al., 2017). In these species, flexible  
97 secretion GCs may therefore determine the ability of individuals and populations to cope with  
98 acute or chronic changes in thermal conditions (Jessop et al., 2016). For instance, the baseline  
99 secretion of GCs may be up-regulated to help individuals adjust their physiology (e.g.,  
100 metabolic rate) and/or behaviour (e.g., flight response, behavioural thermoregulation) when  
101 they are exposed to non-optimal environmental temperatures (Dupoué, Brischoux, Lourdais,  
102 & Angelier, 2013; Telemeco & Addis, 2014). Still, although body and environmental  
103 temperatures generally correlate with secretion of GCs across and within species in  
104 ectothermic vertebrates (Jessop et al., 2016), the relationships between baseline levels of GCs,  
105 climate change and extinction risk in wild populations have not been investigated.

106 In this study, we examined the variation of baseline plasma corticosterone (the  
107 primary GCs in birds and reptiles) across 14 populations of the European common lizard  
108 (*Zootoca vivipara*) distributed across an altitudinal gradient. Our study populations occupy  
109 habitats that differ in thermal microclimates and access to free standing water (Dupoué,  
110 Rutschmann, Le Galliard, Miles, et al., 2017; Rutschmann et al., 2016), and are distributed  
111 along an extinction risk gradient including rapidly declining populations at the lowest  
112 altitudes and steady populations at mountaintops (Chamaillé-Jammes, Massot, Aragon, &  
113 Clobert, 2006; Sinervo et al., 2010). So far, population extinction has been directly related to  
114 warmer conditions in lowland populations although the proximate mechanisms remain  
115 unknown (Bestion, Teyssier, Richard, Clobert, & Cote, 2015). It is noteworthy that natural  
116 populations also differ in other parameters including vegetation cover (Lorenzon, Clobert,  
117 Oppliger, & John-Alder, 1999; Rutschmann et al., 2016), or slope orientation and local wind  
118 speed conditions (pers. obs.), which may influence corticosterone levels. However, we

119 focused here on the environmental covariates that are associated with population decline  
120 (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017). In each population, we sampled the  
121 representative demographic structure by capturing females and males from two age classes,  
122 including reproductive adults and non-reproductive yearlings. In Summer 2015, we combined  
123 two complementary studies to compare and clarify the factors responsible for variation in  
124 baseline corticosterone levels along the altitudinal gradient. First, we designed a cross-  
125 sectional study in which we compared baseline corticosterone levels across the 14 populations  
126 at a single time point in the early summer, which corresponds to the mid-gestation period in  
127 females. We then used a longitudinal study on lizards from 8 out of these 14 populations to  
128 investigate seasonal changes in corticosterone after three weeks in the middle of summer.  
129 During this specific time period, all populations experienced an extreme heat wave which  
130 ranked 6<sup>th</sup> in severity of European heat waves since 1950 according to meteorological reports  
131 (Russo, Sillmann, & Fischer, 2015). Our general hypothesis is that baseline corticosterone  
132 levels should be higher in populations where lizards are chronically exposed to extreme  
133 environmental conditions, such as consistently higher temperatures at the lower altitudes or  
134 extended periods of high temperatures (e.g., heat waves), ultimately leading to population  
135 collapse.

## 136 **Material and methods**

### 137 *Studied species and populations*

138 The European common lizard, *Zootoca vivipara*, is a small (adult size ~ 50 - 75 mm),  
139 widespread species (Family: Lacertidae) that inhabits peat bogs and heathlands across  
140 northern Eurasia. In 2015, we studied 14 populations found in the Massif Central Mountains  
141 in south-central France, which corresponds to the southern range limits for the viviparous  
142 form of the species in France (Rutschmann et al., 2016). In our focal populations, males  
143 emerge in mid-April while females emerge in early May. Males copulate with females shortly



144 after their emergence with fertilization occurring in mid to late May (Bleu et al., 2013).  
145 Gestation has a duration of 2 to 3 months, with parturition occurring between late-June and  
146 early August.

147 In each population, we characterized local environmental conditions, including  
148 altitude, permanent or periodic access to free standing water, and thermal microclimate (Table  
149 S1) (Dupoué, Rutschmann, Le Galliard, Miles, et al., 2017). We also calculated the relative  
150 changes in lizard abundance observed during the past decade and the extinction status  
151 according to IUCN indexes (IUCN, 2017). We distinguished the populations with permanent  
152 access to water in peat bogs or humid meadow habitats from those with periodic access in dry  
153 meadows with no water during summer except precipitations and morning dew. This  
154 objective score correlates with physiological regulation of the water balance in these  
155 populations such that lizards from populations without permanent access to water down-  
156 regulate their water loss rates to remain normosmotic (Dupoué, Rutschmann, Le Galliard,  
157 Miles, et al., 2017). We used two to three temperature data loggers (iButtons, Maxim  
158 Integrated Products, Sunnyvale, CA, USA,  $\pm 0.0625^{\circ}\text{C}$ ) per population. Loggers were placed  
159 within vegetation in the shade and protected in a polyvinyl cylinder pipe (diameter=5 cm,  
160 length=15 cm) to measure microclimatic temperature every hour from 29 June to 17 July  
161 between our two sampling sessions. This three weeks sampling period was chosen to reflect  
162 accurately the differences in microclimatic conditions during the active season among  
163 populations. We extracted the mean daily minimum and mean daily maximum temperatures  
164 ( $T_{\min}$ , and  $T_{\max}$ , respectively) to assess the thermal microclimate of each population.  
165 Population indices calculated with this method were correlated between years (2015-2017)  
166 either for  $T_{\min}$  (Pearson's  $r = 0.75$ ) or  $T_{\max}$  ( $r = 0.42$ ).

167 These populations have been monitored since 2005, so we could estimate relative  
168 changes in lizard abundance over a decade. Lizards are captured during days in active seasons

169 when the weather conditions and external temperature are optimal. During the searches,  
170 people randomly scan the populations to find lizards that are then captured by hand. Lizard  
171 abundance was calculated in summers 2005, 2015 and 2017 based on the number of lizards  
172 captured divided by the total time spent searching, the number of people capturing and the  
173 area of the study site (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017). We used the  
174 relative changes in abundance to determine the IUCN status of each population, and we  
175 identified two populations extremely at risk, one population at risk and 11 non-threatened  
176 populations (Table S1). This classification is consistent with the predictive model of climate  
177 change effect on population trends derived from a previous field experiment (Bestion et al.,  
178 2015). We managed to sample 135 individuals from those populations in a critical state, and it  
179 is worth noting that studies including as much individuals and replicates of collapsing  
180 populations are rare and urgently needed. Besides, many populations from this Mountain  
181 range have been extirpated during the 2-3 last decades following higher exposure to warm  
182 spells and summer droughts (Sinervo et al., under review) suggesting that population decline  
183 precedes inevitable extinction.

#### 184 *Sampling procedures*

##### 185 Cross-sectional study

186 Between the 19 and 26 of June 2015 (early summer session), we caught a total of 312 adult  
187 pregnant females (mean  $\pm$  SE, body mass (BM) =  $4.77 \pm 0.07$  g, snout-vent length (SVL) =  
188  $61.24 \pm 0.25$  mm), 132 adult males (BM =  $3.54 \pm 0.06$  g, SVL =  $54.75 \pm 0.30$  mm), 87  
189 yearling females (BM =  $1.85 \pm 0.06$  g, SVL =  $47.02 \pm 0.49$  mm), and 131 yearling males (BM  
190 =  $2.01 \pm 0.05$  g, SVL =  $46.10 \pm 0.32$  mm) from the 14 populations. Within 5 min of capture,  
191 we bled all individuals using a standard protocol (Meylan, Dufty, & Clobert, 2003). Blood  
192 samples (40-60  $\mu$ l whole blood) were collected from the post-orbital sinus using 2-3 20  $\mu$ l  
193 microcapillary tubes. Samples were kept fresh in a cooler on ice and brought back to a field

194 laboratory the same day. In the laboratory, blood samples were centrifuged for 5 min at  
195 11,000 rpm, plasma and blood cells were separated and kept frozen in airtight tubes until  
196 subsequent analyses.

197 Adult females and males were transferred to the laboratory and housed in individual  
198 terraria (18 x 12 x 12 cm) with sterilized soil, a shelter, and basking opportunities to record  
199 parturition date and measurement of reproductive effort (litter size and mass) (Rutschmann et  
200 al., 2016). We calculated the reproductive timing (i.e., the embryonic stage at the sampling) as  
201 the difference between parturition and sampling dates. Each lizard was provided a 20-30°C  
202 thermal gradient for 6 hours per day (09:00-12:00 and 14:00-17:00) using a 25 W  
203 incandescent light bulb placed over one end of each terrarium. We also provided water 3  
204 times per day and fed lizards with 2 crickets (*Acheta domesticus*) every two days. In 2017, we  
205 measured the critical maximal temperature limits (CT<sub>max</sub>) in a subsample of 57 individuals  
206 from the monitored populations, using a standard protocol (Gilbert & Miles, 2017).  
207 Individuals were continuously heated (~1°C per minute) under a 60 W incandescent light  
208 bulb, and flipped on the back every minute. Once they stop responding to this stimuli by  
209 righting themselves within 5s, we measured their cloacal temperature with a digital  
210 thermometer, considering as the individual CT<sub>max</sub>. We released each male and female  
211 together with its offspring at its exact capture location within three days after parturition.

### 212 Longitudinal study

213 In 8 out of the 14 populations, we repeated the sampling procedures as described above  
214 between 19 and 23 July (mid-summer session). We focused on yearlings to avoid  
215 confounding effects of seasonal changes in reproductive state with those of seasonal changes  
216 in environmental conditions during a heat wave period. We sampled 76 yearling females (BM  
217 = 2.50 ± 0.06 g, SVL = 53.36 ± 0.42 mm) and 77 males (BM = 2.81 ± 0.06 g, SVL = 51.29 ±  
218 0.30 mm). Although we repeated sampling from the same populations than the cross-sectional

219 study, the probability to recapture the very same individuals was pretty low relative to the  
220 sample size (Meylan, Clobert, & Sinervo, 2007), so all measurements were considered as  
221 independent.

#### 222 *Plasma corticosterone levels*

223 Plasma corticosterone assays were performed with a competitive enzyme-immunoassay  
224 method (IDS Corticosterone EIA kit, ref AC-14F1, Immunodiagnostic Systems Ltd, France)  
225 after 1:10 dilution of all samples. This method quantifies total plasmatic corticosterone using  
226 a polyclonal corticosterone antibody and is based on a highly repeatable colorimetric assay of  
227 absorbance at 450 nm. The reported sensitivity of the kit is  $0.55 \text{ ng mL}^{-1}$ , and our estimates of  
228 corticosterone levels were indeed highly repeatable [12 plates with 4 repeats of a standard per  
229 plate: intra-plate repeatability:  $r = 0.98$ ,  $F_{1,34} = 168.7$ ,  $p < 0.001$ ; inter-plate repeatability:  $r =$   
230  $0.81$ ,  $F_{11,34} = 9.6$ ,  $p < 0.001$  (Lessells & Boag, 1987)]. Such repeatability, the coefficient of  
231 variation we obtained (intra-plate: 14%; inter-plate: 23%) and the similar levels of  
232 corticosterone assessed either by ELISA or by RIA methods (Meylan et al., 2003) suggest  
233 reliable results of corticosterone assays.

#### 234 *Statistical analyses*

235 Plasma corticosterone were  $\log_{10}$  transformed to achieve normal distribution and analysed  
236 with linear models in the R software (R Development Core Team, version 3.2.0, [http://cran.r-](http://cran.r-project.org/)  
237 [project.org/](http://cran.r-project.org/)). In the cross-sectional study, the initial model included the quadratic effect of  
238 time of day to test for non-linear daily variation in corticosterone (Dauphin-Villemant &  
239 Xavier, 1987), and the fixed effects of population, sex, age class, and first- and second order  
240 interaction terms. In the longitudinal study, the initial model included the quadratic effect of  
241 time of day, fixed effects of population, sex, and sampling session, and first- and second order  
242 interaction terms. In the studied populations, lizard morphology strongly varies among and  
243 between populations, sex and age class as previously demonstrated (e.g., Chamailé-Jammes

244 et al., 2006; Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017; Massot, Clobert, Pilorge,  
245 Lecomte, & Barbault, 1992). Therefore to avoid multicollinearity, lizard morphological  
246 indexes were not included in the model selection since we aimed to specifically test the  
247 influence of environmental conditions on baseline corticosterone levels independently from  
248 variation in morphology. We compared all models to a null model including the intercept only  
249 (cross-sectional study: Table S2; longitudinal study: Table S3).

250 We found significant variation in corticosterone levels among populations in the final  
251 model of each study, and therefore tested the influence of environmental covariates on  
252 corticosterone levels in a second step. To do so, we used an approach using the Akaike  
253 information criterion corrected for small sample size (AICc, package AICcmodavg, Mazerolle  
254 2016). We compared mixed-effect linear models [package nlme, (Pinheiro, Bates, DebRoy,  
255 Sarkar, & R, 2016)] in which population identity was included as a random factor to account  
256 for non-independence within the same population. In all selected models, the random effects  
257 of populations had significant contribution to explain variation in baseline corticosterone (all  
258  $p < 0.001$ ). Environmental covariates were treated one by one. Water access was treated as a  
259 categorical factor while the relative changes in abundance, temperature metrics (i.e.,  $T_{\min}$  and  
260  $T_{\max}$ ), and altitude, were treated as linear covariates. Given that several variables were highly  
261 correlated and related to population collapse, we computed the relative changes in abundance,  
262  $T_{\min}$  and the altitude together in a principal component analysis [package ade4, (Dray &  
263 Dufour, 2007)]. We used the first axis (PC<sub>1</sub>) as a composite score of extinction risk since it  
264 was mainly determined by the relative changes in lizard abundance (Table S4), since this  
265 integrative score of population decline has been demonstrated to correlate with molecular  
266 markers of physiological stress (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017). We  
267 compared all models, including additive effects of each environmental covariate or the PC<sub>1</sub>  
268 score (6 variables), as well as two-way interactions with age and sex (cross-sectional study,

269 Table S5) and two-way interactions with sex and sampling session (longitudinal study, Table  
270 S6).

271 In adult pregnant females, we also investigated the relationships between baseline  
272 corticosterone levels and reproduction. We compared mixed effects models (population as  
273 random factor), with reproductive timing and reproductive effort as linear covariates and  
274 compared to a null model with the intercept only (Table S7). It is indeed predicted that GC  
275 secretion may increase during gestation and be higher in females with a higher reproductive  
276 effort (Dauphin-Villemant & Xavier, 1986; Lorient, Angelier, & Lourdais, 2016). For all  
277 model comparisons, the best model was then chosen as the one with the lowest AICc and  
278 models that have a difference of AICc lower than 2 comparably support the data (see Tables  
279 S2, S3, S5, S6 & S7 for model comparisons).

## 280 **Results**

### 281 *Cross-sectional study*

282 Baseline corticosterone levels differed across the 14 populations ( $F_{13,619} = 3.86$ ,  $p < 0.001$ ),  
283 between sexes ( $F_{1,619} = 38.42$ ,  $p < 0.001$ ), but did not show daily variation (time of day:  $F_{13,617}$   
284  $= 1.48$ ,  $p = 0.225$ , time of day<sup>2</sup>:  $F_{13,617} = 0.92$ ,  $p = 0.338$ ). Baseline corticosterone levels were  
285 significantly impacted by the two-way interactions between age and sex ( $F_{1,619} = 31.46$ ,  $p <$   
286  $0.001$ ), so that corticosterone levels differed between age classes in females but not in males  
287 (mean  $\pm$  SE; pregnant females:  $36.35 \pm 1.34$  ng.ml<sup>-1</sup>, yearling females:  $23.44 \pm 1.83$  ng.ml<sup>-1</sup>,  
288 adult males:  $17.07 \pm 1.33$  ng.ml<sup>-1</sup>, and yearling males:  $17.26 \pm 1.18$  ng.ml<sup>-1</sup>).

289 Baseline corticosterone levels were also significantly impacted by the two-way  
290 interactions between age and population ( $F_{13,619} = 2.33$ ,  $p = 0.005$ ) and between sex and  
291 population ( $F_{13,619} = 3.53$ ,  $p < 0.001$ ). According to our model selection procedure, most of  
292 the inter-population variation in baseline corticosterone levels was explained by  $T_{\min}$  and the  
293 two-way interactions between  $T_{\min}$  and age class and between  $T_{\min}$  and sex (model likelihood

294  $w_i = 0.74$ , see Table S5). Specifically, baseline corticosterone levels decreased with  $T_{\min}$  in  
295 females (adults:  $t_{1,12} = -2.31$ ,  $p = 0.039$ , Fig. 1a; yearlings:  $t_{1,12} = -4.01$ ,  $p = 0.002$ , Fig. 1b) but  
296 not in males (adults:  $t_{1,12} = 0.98$ ,  $p = 0.347$ , Fig. 1c; yearlings:  $t_{1,12} = -1.33$ ,  $p = 0.209$ , Fig. 1d).  
297 Other models had very low relative statistical support ( $w_i \leq 0.09$ ) indicating that the  
298 relationships with other covariates were negligible (Table S5). In addition, in adult pregnant  
299 females, we did not find any significant relationship between baseline corticosterone and  
300 reproductive timing or reproductive effort (Table S7).

### 301 *Longitudinal study*

302 During the heat wave period in 2015, temperatures were higher and overpassed the lizard  
303 CTmax 42.5% of time during normal activity period (10:00 to 19:00), while remaining lower  
304 and non-constraining (0% of CTmax overpassing) in 2017 (Fig. 2). Overall, baseline  
305 corticosterone levels were lower after the heat wave period than before (early summer  
306 session:  $20.29 \pm 1.40 \text{ ng.ml}^{-1}$ , mid-summer session:  $13.68 \pm 0.83 \text{ ng.ml}^{-1}$ ;  $F_{1,244} = 9.82$ ,  $p =$   
307  $0.002$ ), and this seasonal variation between sampling sessions differed among populations  
308 (population x sampling session:  $F_{7,244} = 3.45$ ,  $p = 0.002$ ). In addition, corticosterone levels  
309 showed non-linear daily variation (time of day:  $F_{1,244} = 4.51$ ,  $p = 0.035$ , time of day<sup>2</sup>:  $F_{1,244} =$   
310  $4.09$ ,  $p = 0.044$ , Fig. 3a), and were overall higher in yearling females compared to males  
311 ( $F_{1,244} = 7.66$ ,  $p = 0.006$ ).

312 Differences among populations in their seasonal changes in baseline corticosterone  
313 levels were best explained by the access to free standing water since the two best models for  
314 baseline corticosterone levels included a two-way interaction between this covariate and the  
315 measurement session (combined likelihood  $w_i = 0.35$ , see Table S6). Specifically, according  
316 to the top ranking model, baseline corticosterone levels decreased during the heat wave in  
317 yearlings from populations characterized by periodic access to water ( $t_{1,257} = -4.05$ ,  $p < 0.001$ ,  
318 Fig. 3b), while corticosterone levels remained similar in populations with permanent access to

319 water ( $t_{1,257} = -0.81$ ,  $p = 0.417$ , Fig. 3b). Other models had lower degree of relative support ( $w_i$   
320  $\leq 0.08$ ) suggesting that the relationships with other covariates were not important (Table S6).

## 321 **Discussion**

322 We designed two complementary field studies to examine geographic variation in baseline  
323 corticosterone levels among wild populations of lizards across a gradient of environmental  
324 conditions and extinction risk. We found strong geographic variation in baseline  
325 corticosterone levels, interactively or additively with lizard sex and age class. Contrary to our  
326 expectations, these differences were poorly related with extinction risks as indicated by an  
327 integrative score (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017) and IUCN  
328 conservation status. Instead, baseline corticosterone levels of females were lower in local  
329 populations with higher minimum daily temperature, and decreased on average in yearlings  
330 after a heat wave, suggesting that chronic heat stress was correlated with a lower  
331 corticosterone secretion. Importantly, our results also revealed that access to free standing  
332 water in each population may determine the sensitivity of corticosterone secretion during the  
333 exposure to an intense heat wave.

334 In this study, we found greater plasma corticosterone levels in adult females compared  
335 to males or yearling which is consistent with previous findings showing temporal increase in  
336 corticosterone over pregnancy in squamate reptiles (Dauphin-Villemant & Xavier, 1987;  
337 Lorigoux et al., 2016; Taylor, DeNardo, & Jennings, 2004). Surprisingly in pregnant females,  
338 the higher baseline corticosterone levels was not correlated with any index of reproductive  
339 performance, thus questioning the proximate causes of variations in hormonal profile during  
340 gestation. Besides these predictable variations in baseline corticosterone across life stages, we  
341 found sex-specific relationships between baseline corticosterone levels and local thermal  
342 conditions during the night (i.e., minimum daily temperatures), which describe local climate  
343 conditions when individuals are at rest. Baseline corticosterone levels decreased with  $T_{\min}$  in



344 females but not in males. This sex-specific pattern may result from a differential sensitivity to  
345 temperature, which is likely related to sex-specific life history strategies in this species  
346 (Massot et al., 1992). In support of this, it is noteworthy that baseline corticosterone  
347 concentration strongly depends on body temperature in ectotherms (Dupoué et al., 2013;  
348 Jessop et al., 2016). Further studies would help to clarify if thermoregulation differs within  
349 (sex and age specific response) and between populations, and whether differences across  
350 populations are a direct consequence of changes in body temperature or due to functional  
351 plasticity or local adaptations.

352         These relationships could mirror the negative correlation between baseline GCs and  
353 environmental temperatures observed across species in reptiles (Jessop et al., 2016). One  
354 explanation for the higher baseline corticosterone levels in reptile species inhabiting colder  
355 habitats is that a high baseline GCs level helps in supporting the faster energy demand and  
356 mobilisation needed during activity periods when thermoregulatory opportunities are fewer  
357 (Dupoué et al., 2013; Jessop et al., 2016; Telemeco & Addis, 2014). If this hypothesis holds  
358 true, we would expect a stronger correlation between baseline GCs levels and thermal  
359 conditions during the activity period of the day than during the resting period. However, we  
360 did not find any influence of daily maximal temperature ( $T_{max}$ ), suggesting that geographic  
361 differences in thermoregulation opportunities during the day did not explain the changes in  
362 corticosterone levels. Alternatively, lower minimum temperatures may trigger higher level of  
363 circulating corticosterone to compensate and/or maintain a level of physiological  
364 performances that are classical decreased at lower body temperature (Angilletta, 2009; Qualls  
365 & Andrews, 1999). Experiments where lizards are exposed to separate changes in nocturnal  
366 and daily minimum and maximum environmental temperatures are needed to test if low  
367 minimum daily temperatures can indeed induce higher GC secretion and therefore represent  
368 "more stressful" conditions than high temperatures.

369 We suggest instead that individuals responded to abnormally high thermal conditions at  
370 rest (i.e., during night-time) because lowering plasma corticosterone may help down regulate  
371 maintenance costs at rest and energy expenditure during activity (e.g., locomotion or the  
372 proportion of time basking). Low secretion of GC in the warmest populations may thus be an  
373 adaptive physiological response in order to save energy and water (Cote, Clobert, Meylan, &  
374 Fitze, 2006; Cote, Clobert, Poloni, Haussy, & Meylan, 2010; Preest & Cree, 2008). Indeed,  
375 high metabolism at rest and strong behavioural activity in warmer environments could induce  
376 diverse physiological costs such as higher energy expenditure, higher risk of dehydration, and  
377 eventually negative impacts on survival and reproduction (Bestion et al., 2015; Dillon, Wang,  
378 & Huey, 2010; Huey et al., 2012; Kearney, Shine, & Porter, 2009; McKechnie & Wolf,  
379 2010). Alternatively, the studied populations can associate micro-adaptations (e.g., significant  
380 genetic differentiation among populations), different trajectory in life history strategies  
381 (Chamaillé-Jammes et al., 2006; Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017;  
382 Rutschmann et al., 2016), which might explain some variations in corticosterone levels  
383 between populations. Besides, we must acknowledge that baseline corticosterone alone may  
384 not always correlate with individual stress and animal welfare (Otovic & Hutchinson, 2015).  
385 Instead, the acute GC response to a stressor following a standard capture-restrain process or  
386 the capacity to recover from such stress response represent complementary indicators of GC  
387 secretion that might better predict reproduction and/or survival rate than baseline levels (Blas,  
388 Bortolotti, Tella, Baos, & Marchant, 2007; Romero & Wikelski, 2010). However, analyses of  
389 the GC secretion in response to acute stressors would require repeated blood sampling, which  
390 could not be done for ethical reasons and logistic in this large scale study with small bodied  
391 lizards (adult body mass ~3 - 5g) involving many populations. Other physiological indicators  
392 of stress could also provide crucial insights on the responses to abnormally high temperatures  
393 and desiccation. For instance, the heat shock proteins represent particularly promising

394 components of the stress response that are likely impacted by global warming and should  
395 correlate with population extinction status (Sørensen, 2010). Besides, we recently documented  
396 in these populations that telomere length, another integrative indicator of aging and thermal  
397 stresses has been recently shown to non-linearly shorten in populations facing high risk of  
398 extinction when compared to non-threatened ones (Dupoué, Rutschmann, Le Galliard,  
399 Clobert, et al., 2017). Therefore, further comparative studies are required to depict the specific  
400 causes of variation in baseline GC level, GC stress response, GC recovery, or other pertinent  
401 physiological indexes of stress and the further effects on individual fitness.

402       Following a similar tendency, we found that baseline corticosterone decreases  
403 seasonally during an intense heat wave period, especially in the driest (i.e., with no access to  
404 free standing water) populations. The heat wave was particularly pronounced in 2015 since it  
405 ranked 6th in severity in Europe since 1950 (Russo et al., 2015) with abnormally high  
406 temperatures and no precipitation (Dong, Sutton, Shaffrey, & Wilcox, 2016). Instead,  
407 according to our initial hypothesis, a seasonal increase in baseline corticosterone was  
408 expected as individuals were most likely exposed to chronic heat stress and summer droughts,  
409 especially in the populations without access to water (Wingfield, 2013). Seasonal differences  
410 in mean corticosterone levels could come from intra-individual changes (i.e., physiological  
411 flexibility) but also from inter-individual viability selection (i.e., selective removal of  
412 individuals with different initial baseline levels) or from a combination of both processes. We  
413 cannot exclude that individuals with higher corticosterone levels at the beginning of the  
414 summer were selected against through lower survival rate during the heat wave period, which  
415 could have been determined with a repeating sampling all over the exposure to the heat  
416 waves. However, this hypothesis would involve a strong selection and a high repeatability of  
417 corticosterone levels over time, which is very unlikely according to current estimates of inter-  
418 individual repeatability of GC levels (Holtmann, Lagisz, & Nakagawa, 2017). Our results thus

419 alternatively suggest that individual down regulated corticosterone secretion and decreased  
420 their resting metabolism and behavioural activity to limit the costs associated with warm and  
421 dry environments (see above). Since this seasonal decrease was restricted to populations  
422 without access to free standing water, regulation of the water balance may be an important  
423 target in the behavioural regulation of activity level in wild lizards (Lorenzon et al., 1999).  
424 Water balance is the sum of water entrance (i.e., drinking behaviour) and water exit (i.e.,  
425 faeces, evaporative water losses through ventilation and transpiration). The rate of evaporative  
426 water loss and eventually the rate of dehydration will depend on temperature, humidity and  
427 activity levels. When facing extreme heat waves, the behavioural regulation of the water  
428 balance through lower corticosterone secretion could represent an adaptive response to avoid  
429 overheating, dehydration and premature death (Jessop et al., 2013). Further investigations  
430 should now clarify the role of corticosterone in sheltering, microhabitat selection, and the  
431 following outcomes on the regulation of water balance, and on individual fitness and general  
432 demographic trends in the context of climate change.

433 Heat wave frequency, intensity and duration will considerably increase in the next  
434 decades (Easterling et al., 2000; Meehl & Tebaldi, 2004). Although the responses to extreme  
435 temperatures are complex and various among taxa (Buckley & Huey, 2016), the exposure to  
436 such climatic events is predicted to lead to massive changes in demographic trends  
437 (McKechnie & Wolf, 2010). Within individuals, the allostasis concept posits that hormones  
438 such as corticosterone constitute the crucial interfaces between the energy demands associated  
439 with predictable life-history stages and unpredictable environmental changes, such as heat  
440 waves and dry episodes (McEwen & Wingfield, 2010; Romero et al., 2009). To avoid the  
441 exposure to abnormally high temperature and water deprivation, lowering activity and  
442 sheltering may thus be crucial to ensure immediate survival in many ectothermic species, and  
443 our results suggest that baseline corticosterone may contribute to mediate this adaptive

444 response in the common lizard. Yet, even if baseline corticosterone might be essential to  
445 mitigate the immediate costs of being active in harmful conditions, it was uncorrelated with  
446 population decline, thus questioning the pertinence of using high baseline corticosterone as a  
447 relevant biomarker of population extinction risk. In the long run, lower activity may even alter  
448 foraging or reproductive opportunities and eventually lead to population extinction in our  
449 study populations (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017; Sinervo et al.,  
450 2010). Together, our results therefore suggest that climate change is associated with a down-  
451 regulation of corticosterone GC secretion preceding the population decline.

452

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### 462 **Authors' Contributions**

463 AD, AR, JFLG, JC, and SM conceived the ideas and design methodology, and all authors  
464 contributed to data collection; AD analysed the data and led the writing of the manuscript. All  
465 authors contributed critically to the drafts and gave final approval for publication.

### 466 **Ethics of Experiment**

467 All methods were performed in accordance with laws relative to capture, transport and  
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#### 471 **Conflicts of interest**

472 We declare no competing financial interest.

473

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721 **Figure captions**

722 **Figure 1.** Relationships between baseline corticosterone levels and minimal daily ambient  
723 temperature ( $T_{\min}$ ) across 14 populations of common lizards. Baseline corticosterone  
724 decreases slightly with  $T_{\min}$  in a) adult females ( $n = 312$ ), b) yearling females ( $n = 87$ ), but not  
725 in c) adult males ( $n = 132$ ), and d) yearling males ( $n = 131$ ). For significant relationships, the  
726 predictions of the best model from Table S3 were fitted on the data (solid line) together with  
727 the 95% confidence interval (dashed lines). Note the logarithmic scale of corticosterone levels  
728 and wide range of variation within each population.

729

730 **Figure 2.** Thermal profile of the 8 populations from the longitudinal study during the heat  
731 waves (2015) and during the same period of a year with normal climatic conditions (2017).  
732 During the heat wave period, air temperatures measured in shade within vegetation  
733 approached or overpassed the maximal critical thermal limit (CT<sub>max</sub>) ranging from 37.7 to  
734 42.6°C, thus highlighting a strong constraint for activity to avoid overhear (Sinervo et al.,  
735 2010).

736

737 **Figure 3.** Daily and seasonal variation in baseline corticosterone during a summer heat wave  
738 in yearling common lizards inside eight populations with periodic (closed circles) or  
739 permanent (filled circles) access to water. Baseline corticosterone levels a) non-linearly  
740 decreased within the day (time of day:  $F_{1,244} = 4.51$ ,  $p = 0.035$ , time of day<sup>2</sup>:  $F_{1,244} = 4.09$ ,  $p =$   
741 0.044) and b) decreased during the heat wave in yearlings from populations with periodic  
742 access to water ( $t_{1,257} = -4.05$ ,  $p < 0.001$ ), while remaining similar in populations with  
743 permanent access to water ( $t_{1,257} = -0.81$ ,  $p = 0.417$ ).

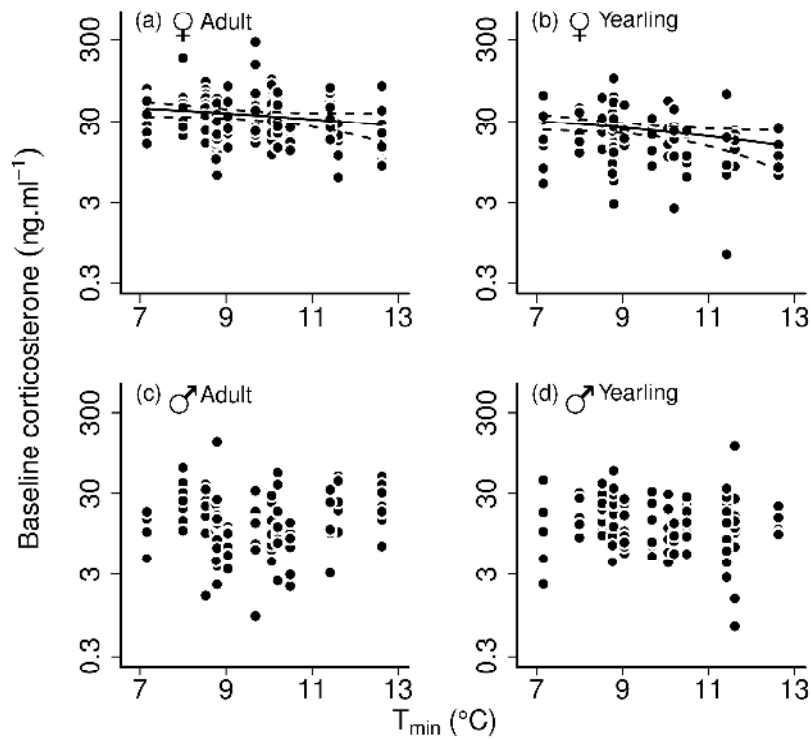


Figure 1. Relationships between baseline corticosterone levels and minimal daily ambient temperature ( $T_{min}$ ) across 14 populations of common lizards. Baseline corticosterone decreases slightly with  $T_{min}$  in a) adult females ( $n = 312$ ), b) yearling females ( $n = 87$ ), but not in c) adult males ( $n = 132$ ), and d) yearling males ( $n = 131$ ). For significant relationships, the predictions of the best model from Table S3 were fitted on the data (solid line) together with the 95% confidence interval (dashed lines). Note the logarithmic scale of corticosterone levels and wide range of variation within each population.

279x361mm (300 x 300 DPI)

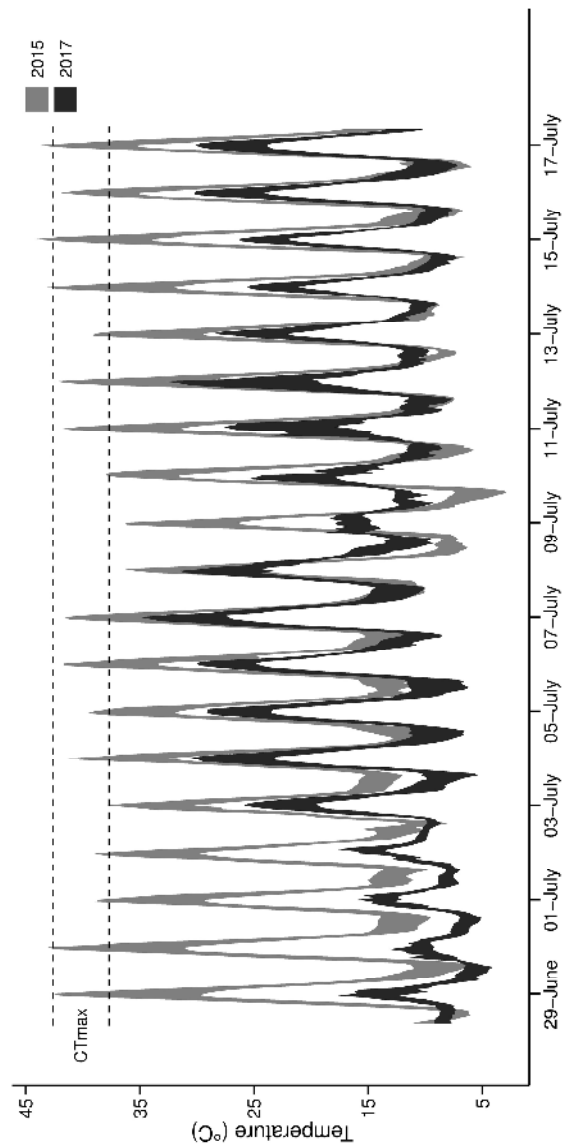


Figure 2. Thermal profile of the 8 populations from the longitudinal study during the heat waves (2015) and during the same period of a year with normal climatic conditions (2017). During the heat wave period, air temperatures measured in shade within vegetation approached or overpassed the maximal critical thermal limit (CTmax) ranging from 37.7 to 42.6°C, thus highlighting a strong constraint for activity to avoid overheating (Sinervo et al., 2010).

279x361mm (300 x 300 DPI)

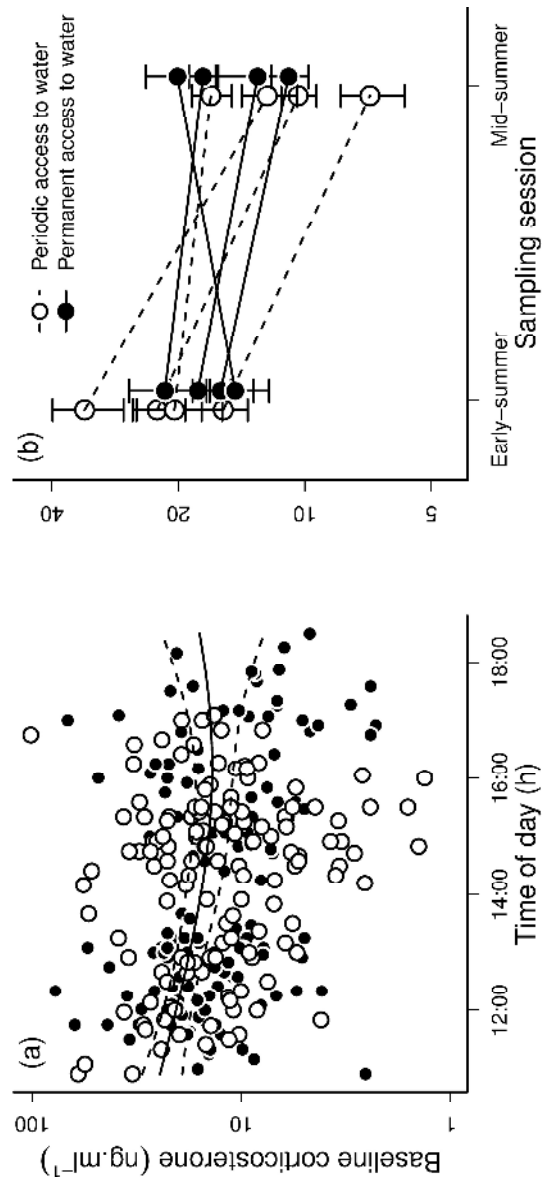


Figure 3. Daily and seasonal variation in baseline corticosterone during a summer heat wave in yearling common lizards inside eight populations with periodic (closed circles) or permanent (filled circles) access to water. Baseline corticosterone levels a) non-linearly decreased within the day (time of day:  $F_{1,244} = 4.51$ ,  $p = 0.035$ , time of day2:  $F_{1,244} = 4.09$ ,  $p = 0.044$ ) and b) decreased during the heat wave in yearlings from populations with periodic access to water ( $t_{1,257} = -4.05$ ,  $p < 0.001$ ), while remaining similar in populations with permanent access to water ( $t_{1,257} = -0.81$ ,  $p = 0.417$ ).

279x361mm (300 x 300 DPI)

**Table S1.** Localisation (GPS coordinates), elevation, climatic conditions and water access in the focal populations of the common lizard (*Z. vivipara*). Values of environmental temperature (minimal:  $T_{\min}$  and maximal:  $T_{\max}$ ) are the mean  $\pm$  SE, which were recorded between June 29 and July 17, 2015. We used the relative change in abundance ( $r$ ) to assess the index of IUCN conservation status of each population [ $r = (\text{Abundance}^{2015} - \text{Abundance}^{2005}) / \text{Abundance}^{2005}$ ]<sup>1</sup>. See text for details.

<sup>1</sup> *IUCN Red List Categories and Criteria and Guidelines for Using the IUCN Red List Categories and Criteria. Scenario A2.* Endangered (EN): very high risk of extinction in the wild; Vulnerable (VU): high risk of extinction in the wild; Least Concern (LC): non-threatened populations.

Population		Coordinates	Altitude (m)	$T_{\min}$ (°C)	$T_{\max}$ (°C)	Water access	Abundance <sup>2005</sup>	Abundance <sup>2015</sup>	$r$	IUCN status
Barnesac	(BAS)	44°25'59.48"N 3°45'20.07"E	1515	9.04 ± 0.62	38.50 ± 0.62	Permanent	1,30	2,53	1,0	LC
Belair	(BEL)	44°40'20.79"N 4° 1'29.84"E	1418	8.80 ± 0.56	33.96 ± 0.49	Periodic	1,09	1,55	0,4	LC
M <sup>t</sup> Caroux	(CAR)	43°36'08.75"N 2°58'54.25"E	1047	11.39 ± 0.43	27.31 ± 0.50	Permanent	0,17	0,06	-0,6	EN
Carmantran	(CARM)	45°09'22.05"N 2°50'16.30"E	1267	9.68 ± 0.92	32.97 ± 0.79	Permanent	3,13	3,18	0,0	LC
Chalet du M <sup>t</sup> Lozère	(CHA)	44°26'56.72"N 3°44'51.79"E	1429	10.49 ± 0.77	35.63 ± 0.68	Periodic	0,38	0,39	0,0	LC
Col du cheval mort	(COM)	44°40'1.29"N 3°31'57.98"E	1405	10.20 ± 0.61	29.93 ± 0.68	Permanent	0,42	0,41	0,0	LC
Col du pendu	(COP)	44°39'18.38"N 4°01'49.79"E	1421	7.16 ± 0.43	44.74 ± 0.77	Permanent	0,53	0,75	0,4	LC
Source de la Loire	(JOC)	44°50'6.66"N 4°12'39.65"E	1296	8.77 ± 0.53	35.78 ± 0.61	Permanent	0,68	1,81	1,6	LC
Gerbier de jonc	(JON)	44°50'30.31"N 4°12'54.30"E	1398	10.06 ± 0.43	33.73 ± 0.68	Periodic	0,60	0,74	0,2	LC
Lajo	(LAJ)	44°50'41.10"N 3°25'51.01"E	1330	8.79 ± 0.46	39.04 ± 0.66	Periodic	1,55	1,64	0,1	LC
Montselgues	(MON)	44°30'40.26"N 4°00'29.36"E	1049	11.42 ± 0.42	33.13 ± 0.32	Permanent	0,27	0,09	-0,7	EN
Pejouzou	(PEJ)	45°09'52.24"N 2°50'37.52"E	1254	8.00 ± 0.95	39.19 ± 1.04	Permanent	0,92	1,02	0,1	LC
Puy Mary	(PUY)	45°6'25.77"N 2°41'6.10"E	1434	12.63 ± 0.60	32.55 ± 0.84	Permanent	0,07	0,05	-0,3	VU
Viala	(VIA)	44°20'17.43"N 3°46'04.76"E	1191	8.53 ± 0.52	35.45 ± 0.58	Permanent	0,50	0,66	0,3	LC

**Table S2.** Initial AICc based model selection comparing the effect of age, sex, population and their interactions on the plasma corticosterone levels in common lizards (n = 662). Models are compared to a null model (model 12) including the intercept only.

Model number	Specification of fixed effects	k	AICc	$\Delta$ AICc	$w_i$	Log likelihood	$r^2_m$
1	Age + Sex + Population + Age : Sex + Age : Population + Sex : Population	44	168.01	0.00	0.93	-36.80	39.48
2	Age + Sex + Population + Age : Sex + Age : Population + Sex : Population + Age : Sex : Population	57	173.18	5.17	0.07	-24.12	41.15
3	Age + Sex + Population + Age : Sex	18	184.23	16.22	0.00	-73.58	33.58
4	Age + Sex + Population + Sex : Population	30	203.93	35.92	0.00	-70.49	33.77
5	Age + Sex + Age : Sex	5	212.40	44.38	0.00	-101.15	28.31
6	Sex + Age + Population + Age : Population	30	214.57	46.56	0.00	-75.81	32.72
7	Sex + Population + Sex : Population	29	220.19	52.17	0.00	-79.72	31.98
8	Sex	3	257.85	89.84	0.00	-125.91	22.82
9	Age + Population + Age : Population	29	357.43	189.41	0.00	-148.34	16.85
10	Age	3	373.01	204.99	0.00	-183.49	8.18
11	Population	15	398.98	230.97	0.00	-184.12	7.87
12	<i>Null</i>	2	427.54	259.53	0.00	-211.76	0.00

k : number of parameters,  $\Delta$ AICc: difference with AICc of the best model,  $w_i$ : model likelihood,  $r^2_m$  : marginal R-squared

**Table S3.** Initial AICc based model selection comparing the effects of sampling session, sex, population and their interaction in yearling common lizards (n = 371). Models are compared to a null model (model 12) including the intercept only.

Model number	Specification of fixed effects	k	AICc	$\Delta$ AICc	$w_i$	Log likelihood	$r^2_m$
1	Sex + Session + Session:Population	20	106.62	0.00	0.70	-31.63	25.80
2	Session + Sex + Population + Session:Sex + Session:Population + Sex:Population	28	108.40	1.78	0.29	-22.85	29.56
3	Session + Sex + Population + Sex:Population	20	115.46	8.84	0.01	-36.05	23.46
4	Session + Population + Session:Population	19	116.08	9.46	0.01	-37.53	22.74
5	Session + Sex + Population + Session:Sex + Session:Population + Sex:Population + Session:Sex:Population	35	119.52	12.90	0.00	-19.40	30.59
6	Session + Sex + Population + Session:Sex	14	119.63	13.01	0.00	-44.99	18.88
7	Sex + Population + Sex:Population	19	123.95	17.33	0.00	-41.46	20.57
8	Session + Sex + Session:Sex	7	128.09	21.47	0.00	-56.83	12.05
9	Session	5	132.09	25.47	0.00	-60.93	9.45
10	Population	11	132.76	26.15	0.00	-54.87	13.11
11	Sex	5	134.54	27.92	0.00	-62.16	8.64
12	Null	4	139.02	32.40	0.00	-65.43	6.45

k : number of parameters,  $\Delta$ AICc: difference with AICc of the best model,  $w_i$ : model likelihood,  $r^2_m$  : marginal R-squared



**Table S4. Principal component analysis (PCA) including the main determinants of population collapse.** Variables included in the PCA are the relative change in abundance ( $\Delta$ abundance), the minimal temperatures ( $T_{\min}$ ), and the altitude. Table shows the eigenvalue of the 3 axes (PC<sub>1</sub> to PC<sub>3</sub>), percentage of variance explained, and the inertia of each variables on the first two axes.

		PCA Axes		
		PC <sub>1</sub>	PC <sub>2</sub>	PC <sub>3</sub>
Eigenvalue		1.89	0.78	0.33
Variance		63.01	25.94	11.04
Inertia	$\Delta$ abundance	4273	54	-
	$T_{\min}$	3219	3733	-
	Altitude	2508	6213	-

**Table S5.** AICc based model selection comparing the effect of environmental conditions in early summer session on the plasma corticosterone levels in adult or yearling and female or male common lizards ( $n = 662$ ). Each environmental covariate was treated one by one (5 models per covariate). Environmental covariates were also computed in a principal component analysis to extract an integrative index of population extinction risk ( $PC_1$  – first axis of a principal component analysis including relative change in abundance,  $T_{min}$ , and altitude, see Table S2). Population was treated as a random factor to account for non-independence.

Model number	Specification of fixed effects	k	AICc	$\Delta AICc$	$w_i$	Log likelihood	$r^2_m$	$r^2_c$
1	Age + Sex + $T_{min}$ + Age : Sex + Age : $T_{min}$ + Sex : $T_{min}$	9	180.87	0.00	0.74	-81.30	30.79	33.77
2	Age + Sex + $PC_1$ + Age : Sex + Age : $PC_1$ + Sex : $PC_1$	9	185.02	4.16	0.09	-83.37	29.29	33.30
3	Age + Sex + $T_{min}$ + Age : Sex + Sex : $T_{min}$	8	185.14	4.27	0.09	-84.46	30.10	33.20
4	Age + Sex + water access + Age : Sex + Age : water access + Sex : water access	9	188.13	7.26	0.02	-84.93	28.68	33.01
5	Age + Sex + water access + Age : Sex + Age : water access	8	188.18	7.31	0.02	-85.98	28.44	32.83
6	Age + Sex + $T_{min}$ + Age : Sex + Age : $T_{min}$	8	189.72	8.85	0.01	-86.75	29.76	32.54
7	Age + Sex + $T_{min}$ + Age : Sex	7	190.73	9.86	0.01	-88.28	29.39	32.28
8	Age + Sex + $PC_1$ + Age : Sex + Age : $PC_1$	8	191.24	10.37	0.00	-87.51	28.43	32.42
9	Age + Sex + $\Delta$ abundance + Age : Sex + Age : $\Delta$ abundance + Sex : $\Delta$ abundance	9	191.94	11.07	0.00	-86.83	28.35	32.42
10	Age + Sex + $T_{max}$ + Age : Sex + Age : $T_{max}$ + Sex : $T_{max}$	9	191.94	11.08	0.00	-86.83	28.82	32.61
11	Age + Sex + Age : Sex	6	192.84	11.97	0.00	-90.35	27.53	31.90
12	Age + Sex + $\Delta$ abundance + Age : Sex + Age : $\Delta$ abundance	8	192.95	12.08	0.00	-88.37	28.05	32.06
13	Age + Sex + altitude + Age : Sex + Age : altitude	8	193.02	12.15	0.00	-88.40	28.04	32.06
14	Age + Sex + $T_{max}$ + Age : Sex + Sex : $T_{max}$	8	193.11	12.25	0.00	-88.45	28.49	32.26

15	Age + Sex + PC <sub>1</sub> + Age : Sex + Sex : PC <sub>1</sub>	8	193.19	12.33	0.00	-88.49	28.13	32.47
16	Age + Sex + T <sub>max</sub> + Age : Sex + Age : T <sub>max</sub>	8	193.21	12.35	0.00	-88.50	28.50	32.25
17	Age + Sex + T <sub>max</sub> + Age : Sex	7	193.28	12.41	0.00	-89.55	28.27	32.02
18	Age + Sex + altitude + Age : Sex + Age : altitude + Sex : altitude	9	193.37	12.50	0.00	-87.55	28.24	32.21
19	Age + Sex + PC <sub>1</sub> + Age : Sex	7	194.55	13.69	0.00	-90.19	27.79	32.04
20	Age + Sex + altitude + Age : Sex	7	194.80	13.93	0.00	-90.31	27.53	31.85
21	Age + Sex + Δabundance + Age : Sex	7	194.83	13.96	0.00	-90.33	27.51	31.84
22	Age + Sex + water access + Age : Sex	7	194.87	14.00	0.00	-90.35	27.52	32.88
23	Age + Sex + Δabundance + Age : Sex + Sex : Δabundance	8	196.01	15.14	0.00	-89.90	27.57	32.00
24	Age + Sex + altitude + Age : Sex + Sex : altitude	8	196.59	15.73	0.00	-90.19	27.56	31.88
25	Age + Sex + water access + Age : Sex + Sex : water access	8	196.60	15.74	0.00	-90.19	27.56	31.90
26	Age + Sex	5	221.76	40.89	0.00	-105.83	24.36	28.59
27	Sex	4	238.51	57.65	0.00	-115.23	22.08	26.74
28	Age	4	357.56	176.70	0.00	-174.75	7.46	12.38
29	T <sub>min</sub>	4	405.79	224.92	0.00	-198.86	2.19	6.17
30	<i>Null</i>	3	408.20	227.33	0.00	-201.08	0.00	6.18
31	T <sub>max</sub>	4	408.41	227.54	0.00	-200.17	0.87	6.07
32	PC <sub>1</sub>	4	409.35	228.48	0.00	-200.64	0.47	6.18
33	Δabundance	4	410.17	229.30	0.00	-201.05	0.03	6.19
34	water access	4	410.17	229.31	0.00	-201.06	0.03	6.18

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35	altitude	4	410.22	229.35	0.00	-201.08	0.00	6.18
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k : number of parameters,  $\Delta\text{AICc}$ : difference with AICc of the best model,  $w_i$ : model likelihood,  
 $r^2_m$  : marginal R-squared,  $r^2_c$  : conditional R-squared

**Table S6.** AICc based model selection comparing the effects of environmental conditions during the heat wave period on plasma corticosterone levels in yearling common lizards ( $n = 371$ ). Each environmental covariate was treated one by one (5 models per covariate). Environmental covariates were also computed in a principal component analysis to extract an integrative index of population extinction risk ( $PC_1$  – first axis of a principal component analysis including relative change in abundance,  $T_{\min}$ , and altitude, see Table S2). Population was treated as a random factor to account for non-independence.

Model number	Specification of fixed effects	k	AICc	$\Delta AICc$	$w_i$	Log likelihood	$r^2_m$	$r^2_c$
1	Session + Sex + water access + Session : water access + Sex : water access	10	117.95	0.00	0.24	-48.55	16.43	21.82
2	Session + Sex + water access + Session : water access	9	119.55	1.61	0.11	-50.43	15.31	20.57
3	Session + Sex + $T_{\min}$	8	120.26	2.31	0.08	-51.85	15.94	17.89
4	Session + Sex + $\Delta$ abundance + Sex : $\Delta$ abundance	9	120.45	2.50	0.07	-50.88	15.62	19.68
5	Session + Sex + $PC_1$ + Sex : $PC_1$	9	120.91	2.96	0.06	-51.11	15.71	18.82
6	Session + Sex + $\Delta$ abundance + Session : $\Delta$ abundance + Sex : $\Delta$ abundance	10	121.03	3.08	0.05	-50.09	15.86	19.90
7	Session + Sex + $PC_1$ + Session : $PC_1$ + Sex : $PC_1$	10	121.07	3.12	0.05	-50.11	16.12	19.19
8	Session + Sex + $T_{\min}$ + Sex : $T_{\min}$	9	121.47	3.52	0.04	-51.39	16.20	18.13
9	Session + Sex + $T_{\min}$ + Session : $T_{\min}$	9	121.65	3.70	0.04	-51.48	16.07	17.96
10	Session + Sex + $PC_1$ + Session : $PC_1$	9	121.97	4.02	0.03	-51.64	15.18	18.41
11	Session + Sex + $PC_1$	8	122.17	4.22	0.03	-52.81	14.69	17.98
12	Session + Sex + $T_{\max}$	8	122.27	4.32	0.03	-52.86	14.74	18.05
13	Session + Sex	7	122.29	4.34	0.03	-53.93	13.55	18.68
14	Session + Sex + water access + Sex : water access	9	122.51	4.56	0.02	-51.91	14.82	20.08
15	Session + Sex + $T_{\min}$ + Session : $T_{\min}$ + Sex : $T_{\min}$	10	122.66	4.71	0.02	-50.90	16.39	18.26
16	Session + Sex + $\Delta$ abundance + Session : $\Delta$ abundance	9	123.14	5.19	0.02	-52.22	14.52	18.72

17	Session + Sex + $\Delta$ abundance	8	123.36	5.42	0.02	-53.41	14.08	18.32
18	Session + Sex + altitude	8	123.70	5.75	0.01	-53.57	14.44	18.74
19	Session + Sex + $T_{\max}$ + Session : $T_{\max}$	9	124.35	6.40	0.01	-52.83	14.79	18.12
20	Session + Sex + water access	8	124.39	6.44	0.01	-53.92	13.58	18.70
21	Session + Sex + $T_{\max}$ + Sex : $T_{\max}$	9	124.41	6.46	0.01	-52.86	14.74	18.05
22	Session + Sex + altitude + Sex :	9	124.63	6.68	0.01	-52.97	14.81	19.12
23	altitude + Session :	9	125.75	7.80	0.00	-53.53	14.39	18.57
24	altitude	9	125.75	7.80	0.00	-53.53	14.39	18.57
24	Session + Sex + $T_{\max}$ + Session : $T_{\max}$ + Sex : $T_{\max}$	10	126.50	8.56	0.00	-52.83	14.79	18.11
25	Session + Sex + altitude + Session :	10	126.77	8.83	0.00	-52.96	14.79	19.04
25	altitude + Sex :	10	126.77	8.83	0.00	-52.96	14.79	19.04
25	altitude	10	126.77	8.83	0.00	-52.96	14.79	19.04
26	Session	6	129.21	11.26	0.00	-58.45	10.46	14.91
27	Sex	6	130.54	12.59	0.00	-59.11	11.09	16.32
28	$T_{\min}$	6	135.22	17.27	0.00	-61.45	10.00	11.85
29	<i>Null</i>	5	136.48	18.53	0.00	-63.13	8.06	12.51
30	PC <sub>1</sub>	6	136.75	18.80	0.00	-62.22	9.02	12.04
31	$T_{\max}$	6	136.91	18.97	0.00	-62.30	9.05	12.12
32	$\Delta$ abundance	6	137.79	19.84	0.00	-62.74	8.52	12.34
33	altitude	6	138.12	20.18	0.00	-62.90	8.74	12.63
34	water access	6	138.57	20.62	0.00	-63.12	8.04	12.48

k : number of parameters,  $\Delta$ AICc: difference with AICc of the best model,  $w_i$ : model likelihood,  $r^2_m$ : marginal R-squared,  $r^2_c$ : conditional R-squared