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

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

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Abstract

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

Keywords. Altitude, corticosterone, ectotherm, population decline, temperature, water availability.

Introduction

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

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

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

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

Climate change represents an ubiquitous environmental challenge for living organisms that may interact with other environmental stressors and accelerate population declines (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Cahill et al., 2012; Flesch, Rosen, & Holm, 2017). Ectothermic vertebrates are expected to be particularly vulnerable due to their behavioural and physiological sensitivity to environmental temperature (Deutsch et al., 2008; Frishkoff, Hadly, & Daily, 2015; Kingsolver, Diamond, & Buckley, 2013; Le Galliard, Massot, Baron, & Clobert, 2012; Telemeco et al., 2017). In these species, flexible secretion GCs may therefore determine the ability of individuals and populations to cope with acute or chronic changes in thermal conditions (Jessop et al., 2016). For instance, the baseline secretion of GCs may be up-regulated to help individuals adjust their physiology (e.g., metabolic rate) and/or behaviour (e.g., flight response, behavioural thermoregulation) when they are exposed to non-optimal environmental temperatures (Dupoué, Brischoux, Lourdais, & Angelier, 2013; Telemeco & Addis, 2014). Still, although body and environmental temperatures generally correlate with secretion of GCs across and within species in ectothermic vertebrates (Jessop et al., 2016), the relationships between baseline levels of GCs, climate change and extinction risk in wild populations have not been investigated.

In this study, we examined the variation of baseline plasma corticosterone (the primary GCs in birds and reptiles) across 14 populations of the European common lizard (*Zootoca vivipara*) distributed across an altitudinal gradient. Our study populations occupy habitats that differ in thermal microclimates and access to free standing water (Dupoué, Rutschmann, Le Galliard, Miles, et al., 2017; Rutschmann et al., 2016), and are distributed along an extinction risk gradient including rapidly declining populations at the lowest altitudes and steady populations at mountaintops (Chamaillé-Jammes, Massot, Aragon, & Clobert, 2006; Sinervo et al., 2010). So far, population extinction has been directly related to warmer conditions in lowland populations although the proximate mechanisms remain unknown (Bestion, Teyssier, Richard, Clobert, & Cote, 2015). It is noteworthy that natural populations also differ in other parameters including vegetation cover (Lorenzon, Clobert, Oppliger, & John-Alder, 1999; Rutschmann et al., 2016), or slope orientation and local wind speed conditions (pers. obs.), which may influence corticosterone levels. However, we focused here on the environmental covariates that are associated with population decline (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017). In each population, we sampled the representative demographic structure by capturing females and males from two age classes, including reproductive adults and non-reproductive yearlings. In Summer 2015, we combined two complementary studies to compare and clarify the factors responsible for variation in baseline corticosterone levels along the altitudinal gradient. First, we designed a cross-sectional study in which we compared baseline corticosterone levels across the 14 populations at a single time point in the early summer, which corresponds to the mid-gestation period in females. We then used a longitudinal study on lizards from 8 out of these 14 populations to investigate seasonal changes in corticosterone after three weeks in the middle of summer. During this specific time period, all populations experienced an extreme heat wave which ranked 6th in severity of European heat waves since 1950 according to meteorological reports (Russo, Sillmann, & Fischer, 2015). Our general hypothesis is that baseline corticosterone levels should be higher in populations where lizards are chronically exposed to extreme environmental conditions, such as consistently higher temperatures at the lower altitudes or extended periods of high temperatures (e.g., heat waves), ultimately leading to population collapse.

Material and methods

Studied species and populations

The European common lizard, *Zootoca vivipara,* is a small (adult size ~ 50 - 75 mm), widespread species (Family: Lacertidae) that inhabits peat bogs and heathlands across northern Eurasia. In 2015, we studied 14 populations found in the Massif Central Mountains in south-central France, which corresponds to the southern range limits for the viviparous form of the species in France (Rutschmann et al., 2016). In our focal populations, males emerge in mid-April while females emerge in early May. Males copulate with females shortly after their emergence with fertilization occurring in mid to late May (Bleu et al., 2013). Gestation has a duration of 2 to 3 months, with parturition occurring between late-June and early August.

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

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

Sampling procedures

<u>Cross-sectional study</u>

Between the 19 and 26 of June 2015 (early summer session), we caught a total of 312 adult pregnant females (mean ± SE, body mass (BM) = 4.77 ± 0.07 g, snout-vent length (SVL) = 61.24 ± 0.25 mm), 132 adult males (BM = 3.54 ± 0.06 g, SVL = 54.75 ± 0.30 mm), 87 yearling females (BM = 1.85 ± 0.06 g, SVL = 47.02 ± 0.49 mm), and 131 yearling males (BM = 2.01 ± 0.05 g, SVL = 46.10 ± 0.32 mm) from the 14 populations. Within 5 min of capture, we bled all individuals using a standard protocol (Meylan, Dufty, & Clobert, 2003). Blood samples (40-60 µl whole blood) were collected from the post-orbital sinus using 2-3 20 µl microcapillary tubes. Samples were kept fresh in a cooler on ice and brought back to a field laboratory the same day. In the laboratory, blood samples were centrifuged for 5 min at 11,000 rpm, plasma and blood cells were separated and kept frozen in airtight tubes until subsequent analyses.

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

Longitudinal study

In 8 out of the 14 populations, we repeated the sampling procedures as described above between 19 and 23 July (mid-summer session). We focused on yearlings to avoid confounding effects of seasonal changes in reproductive state with those of seasonal changes in environmental conditions during a heat wave period. We sampled 76 yearling females (BM = 2.50 ± 0.06 g, SVL = 53.36 ± 0.42 mm) and 77 males (BM = 2.81 ± 0.06 g, SVL = 51.29 ± 0.30 mm). Although we repeated sampling from the same populations than the cross-sectional study, the probability to recapture the very same individuals was pretty low relative to the sample size (Meylan, Clobert, & Sinervo, 2007), so all measurements were considered as independent.

Plasma corticosterone levels

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

Statistical analyses

Plasma corticosterone were $\log_{10}$ transformed to achieve normal distribution and analysed with linear models in the R software (R Development Core Team, version 3.2.0, http://cran.r-project.org/). In the cross-sectional study, the initial model included the quadratic effect of time of day to test for non-linear daily variation in corticosterone (Dauphin-Villemant & Xavier, 1987), and the fixed effects of population, sex, age class, and first- and second order interaction terms. In the longitudinal study, the initial model included the quadratic effect of time of day, fixed effects of population, sex, and sampling session, and first- and second order interaction terms. In the studied populations, lizard morphology strongly varies among and between populations, sex and age class as previously demonstrated (e.g., Chamaillé-Jammes et al., 2006; Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017; Massot, Clobert, Pilorge, Lecomte, & Barbault, 1992). Therefore to avoid multicollinearity, lizard morphological indexes were not included in the model selection since we aimed to specifically test the influence of environmental conditions on baseline corticosterone levels independently from variation in morphology. We compared all models to a null model including the intercept only (cross-sectional study: Table S2; longitudinal study: Table S3).

We found significant variation in corticosterone levels among populations in the final model of each study, and therefore tested the influence of environmental covariates on corticosterone levels in a second step. To do so, we used an approach using the Akaike information criterion corrected for small sample size (AICc, package AICcmodavg, Mazerolle 2016). We compared mixed-effect linear models [package nlme, (Pinheiro, Bates, DebRoy, Sarkar, & R, 2016)] in which population identity was included as a random factor to account for non-independence within the same population. In all selected models, the random effects of populations had significant contribution to explain variation in baseline corticosterone (all $p < 0.001$). Environmental covariates were treated one by one. Water access was treated as a categorical factor while the relative changes in abundance, temperature metrics (i.e., T_{min} and T_{max}), and altitude, were treated as linear covariates. Given that several variables were highly correlated and related to population collapse, we computed the relative changes in abundance, T_{min} and the altitude together in a principal component analysis [package ade4, (Dray & Dufour, 2007)]. We used the first axis (PC_1) as a composite score of extinction risk since it was mainly determined by the relative changes in lizard abundance (Table S4), since this integrative score of population decline has been demonstrated to correlate with molecular markers of physiological stress (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017). We compared all models, including additive effects of each environmental covariate or the PC_1 score (6 variables), as well as two-way interactions with age and sex (cross-sectional study,

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

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

Results

Cross-sectional study

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

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

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

Longitudinal study

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

Differences among populations in their seasonal changes in baseline corticosterone levels were best explained by the access to free standing water since the two best models for baseline corticosterone levels included a two-way interaction between this covariate and the measurement session (combined likelihood $w_i = 0.35$, see Table S6). Specifically, according to the top ranking model, baseline corticosterone levels decreased during the heat wave in yearlings from populations characterized by periodic access to water ($t_{1,257} = -4.05$, $p < 0.001$, Fig. 3b), while corticosterone levels remained similar in populations with permanent access to water ($t_{1,257}$ = -0.81, p = 0.417, Fig. 3b). Other models had lower degree of relative support (w_i $\leq$ 0.08) suggesting that the relationships with other covariates were not important (Table S6).

Discussion

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

In this study, we found greater plasma corticosterone levels in adult females compared to males or yearling which is consistent with previous findings showing temporal increase in corticosterone over pregnancy in squamate reptiles (Dauphin-Villemant & Xavier, 1987; Lorioux et al., 2016; Taylor, DeNardo, & Jennings, 2004). Surprisingly in pregnant females, the higher baseline corticosterone levels was not correlated with any index of reproductive performance, thus questioning the proximate causes of variations in hormonal profile during gestation. Besides these predictable variations in baseline corticosterone across life stages, we found sex-specific relationships between baseline corticosterone levels and local thermal conditions during the night (i.e., minimum daily temperatures), which describe local climate conditions when individuals are at rest. Baseline corticosterone levels decreased with T_{min} in females but not in males. This sex-specific pattern may result from a differential sensitivity to temperature, which is likely related to sex-specific life history strategies in this species (Massot et al., 1992). In support of this, it is noteworthy that baseline corticosterone concentration strongly depends on body temperature in ectotherms (Dupoué et al., 2013; Jessop et al., 2016). Further studies would help to clarify if thermoregulation differs within (sex and age specific response) and between populations, and whether differences across populations are a direct consequence of changes in body temperature or due to functional plasticity or local adaptations.

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

We suggest instead that individuals responded to abnormally high thermal conditions at rest (i.e., during night-time) because lowering plasma corticosterone may help down regulate maintenance costs at rest and energy expenditure during activity (e.g., locomotion or the proportion of time basking). Low secretion of GC in the warmest populations may thus be an adaptive physiological response in order to save energy and water (Cote, Clobert, Meylan, & Fitze, 2006; Cote, Clobert, Poloni, Haussy, & Meylan, 2010; Preest & Cree, 2008). Indeed, high metabolism at rest and strong behavioural activity in warmer environments could induce diverse physiological costs such as higher energy expenditure, higher risk of dehydration, and eventually negative impacts on survival and reproduction (Bestion et al., 2015; Dillon, Wang, & Huey, 2010; Huey et al., 2012; Kearney, Shine, & Porter, 2009; McKechnie & Wolf, 2010). Alternatively, the studied populations can associate micro-adaptations (e.g., significant genetic differentiation among populations), different trajectory in life history strategies (Chamaillé-Jammes et al., 2006; Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017; Rutschmann et al., 2016), which might explain some variations in corticosterone levels between populations. Besides, we must acknowledge that baseline corticosterone alone may not always correlate with individual stress and animal welfare (Otovic & Hutchinson, 2015). Instead, the acute GC response to a stressor following a standard capture-restrain process or the capacity to recover from such stress response represent complementary indicators of GC secretion that might better predict reproduction and/or survival rate than baseline levels (Blas, Bortolotti, Tella, Baos, & Marchant, 2007; Romero & Wikelski, 2010). However, analyses of the GC secretion in response to acute stressors would require repeated blood sampling, which could not be done for ethical reasons and logistic in this large scale study with small bodied lizards (adult body mass ~3 - 5g) involving many populations. Other physiological indicators of stress could also provide crucial insights on the responses to abnormally high temperatures and desiccation. For instance, the heat shock proteins represent particularly promising components of the stress response that are likely impacted by global warming and should correlate with population extinction status (Sørensen, 2010). Besides, we recently documented in these populations that telomere length, another integrative indicator of aging and thermal stresses has been recently shown to non-linearly shorten in populations facing high risk of extinction when compared to non-threatened ones (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017). Therefore, further comparative studies are required to depict the specific causes of variation in baseline GC level, GC stress response, GC recovery, or other pertinent physiological indexes of stress and the further effects on individual fitness.

Following a similar tendency, we found that baseline corticosterone decreases seasonally during an intense heat wave period, especially in the driest (i.e., with no access to free standing water) populations. The heat wave was particularly pronounced in 2015 since it ranked 6th in severity in Europe since 1950 (Russo et al., 2015) with abnormally high temperatures and no precipitation (Dong, Sutton, Shaffrey, & Wilcox, 2016). Instead, according to our initial hypothesis, a seasonal increase in baseline corticosterone was expected as individuals were most likely exposed to chronic heat stress and summer droughts, especially in the populations without access to water (Wingfield, 2013). Seasonal differences in mean corticosterone levels could come from intra-individual changes (i.e., physiological flexibility) but also from inter-individual viability selection (i.e., selective removal of individuals with different initial baseline levels) or from a combination of both processes. We cannot exclude that individuals with higher corticosterone levels at the beginning of the summer were selected against through lower survival rate during the heat wave period, which could have been determined with a repeating sampling all over the exposure to the heat waves. However, this hypothesis would involve a strong selection and a high repeatability of corticosterone levels over time, which is very unlikely according to current estimates of inter-individual repeatability of GC levels (Holtmann, Lagisz, & Nakagawa, 2017). Our results thus alternatively suggest that individual down regulated corticosterone secretion and decreased their resting metabolism and behavioural activity to limit the costs associated with warm and dry environments (see above). Since this seasonal decrease was restricted to populations without access to free standing water, regulation of the water balance may be an important target in the behavioural regulation of activity level in wild lizards (Lorenzon et al., 1999). Water balance is the sum of water entrance (i.e., drinking behaviour) and water exit (i.e., faeces, evaporative water losses through ventilation and transpiration). The rate of evaporative water loss and eventually the rate of dehydration will depend on temperature, humidity and activity levels. When facing extreme heat waves, the behavioural regulation of the water balance through lower corticosterone secretion could represent an adaptive response to avoid overheating, dehydration and premature death (Jessop et al., 2013). Further investigations should now clarify the role of corticosterone in sheltering, microhabitat selection, and the following outcomes on the regulation of water balance, and on individual fitness and general demographic trends in the context of climate change.

Heat wave frequency, intensity and duration will considerably increase in the next decades (Easterling et al., 2000; Meehl & Tebaldi, 2004). Although the responses to extreme temperatures are complex and various among taxa (Buckley & Huey, 2016), the exposure to such climatic events is predicted to lead to massive changes in demographic trends (McKechnie & Wolf, 2010). Within individuals, the allostasis concept posits that hormones such as corticosterone constitute the crucial interfaces between the energy demands associated with predictable life-history stages and unpredictable environmental changes, such as heat waves and dry episodes (McEwen & Wingfield, 2010; Romero et al., 2009). To avoid the exposure to abnormally high temperature and water deprivation, lowering activity and sheltering may thus be crucial to ensure immediate survival in many ectothermic species, and our results suggest that baseline corticosterone may contribute to mediate this adaptive response in the common lizard. Yet, even if baseline corticosterone might be essential to mitigate the immediate costs of being active in harmful conditions, it was uncorrelated with population decline, thus questioning the pertinence of using high baseline corticosterone as a relevant biomarker of population extinction risk. In the long run, lower activity may even alter foraging or reproductive opportunities and eventually lead to population extinction in our study populations (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017; Sinervo et al., 2010). Together, our results therefore suggest that climate change is associated with a down-regulation of corticosterone GC secretion preceding the population decline.

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Authors' Contributions

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

Ethics of Experiment

All methods were performed in accordance with laws relative to capture, transport and experiments on *Zootoca vivipara* (DREAL Languedoc Roussillon permit #2013-274-0002, DREAL Midi-Pyrénées permit #81-2013-05, and DREAL Auvergne, permit 2013/DREAL/259).

Conflicts of interest

We declare no competing financial interest.

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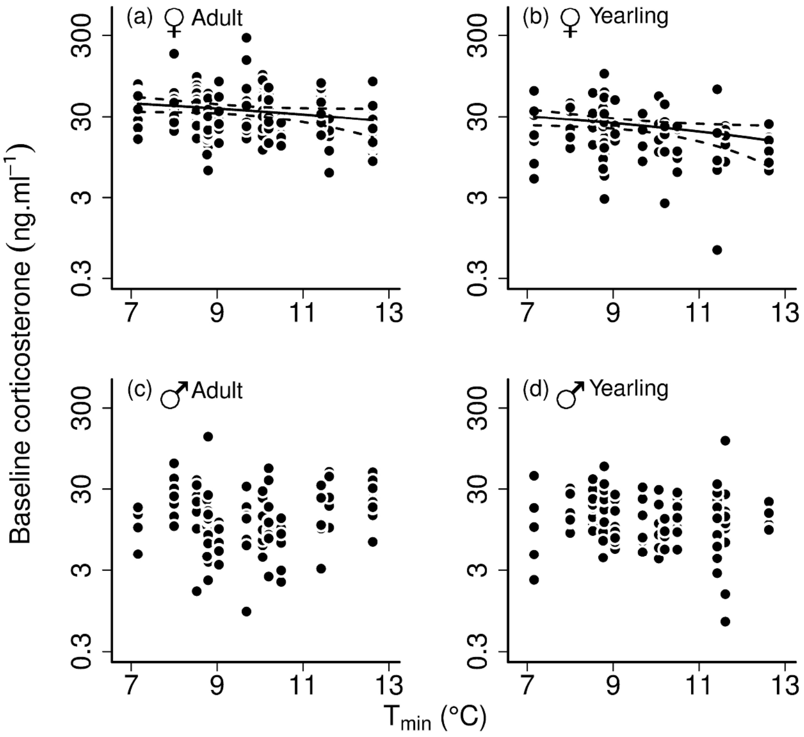
Figure captions

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.

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 overheat (Sinervo et al., 2010).

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 day^2: $F_{1,244} = 4.09$, $p = 0.044$) 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 ($t_{1,257} = -0.81$, $p = 0.417$).



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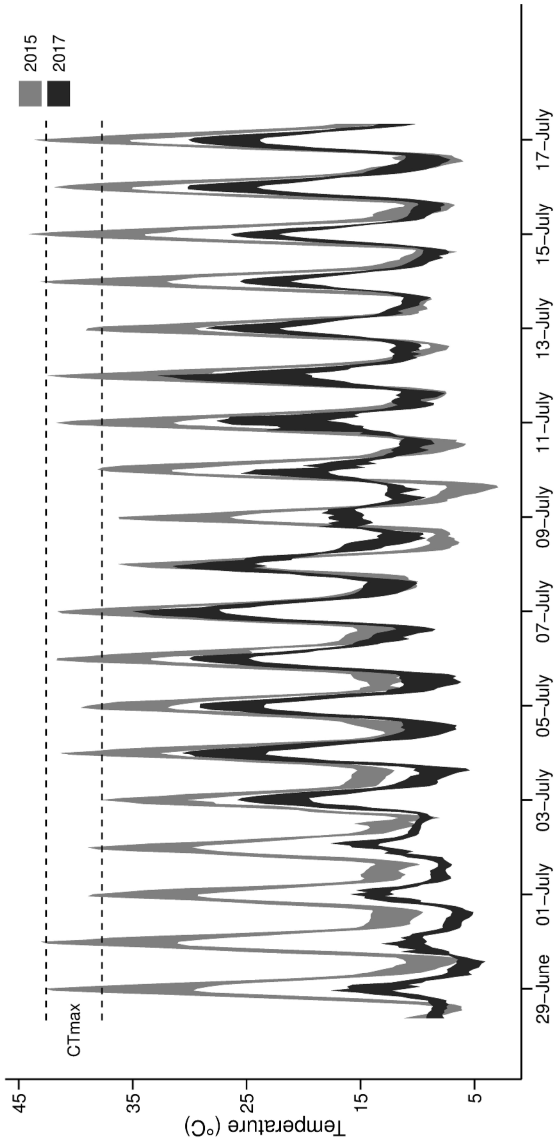

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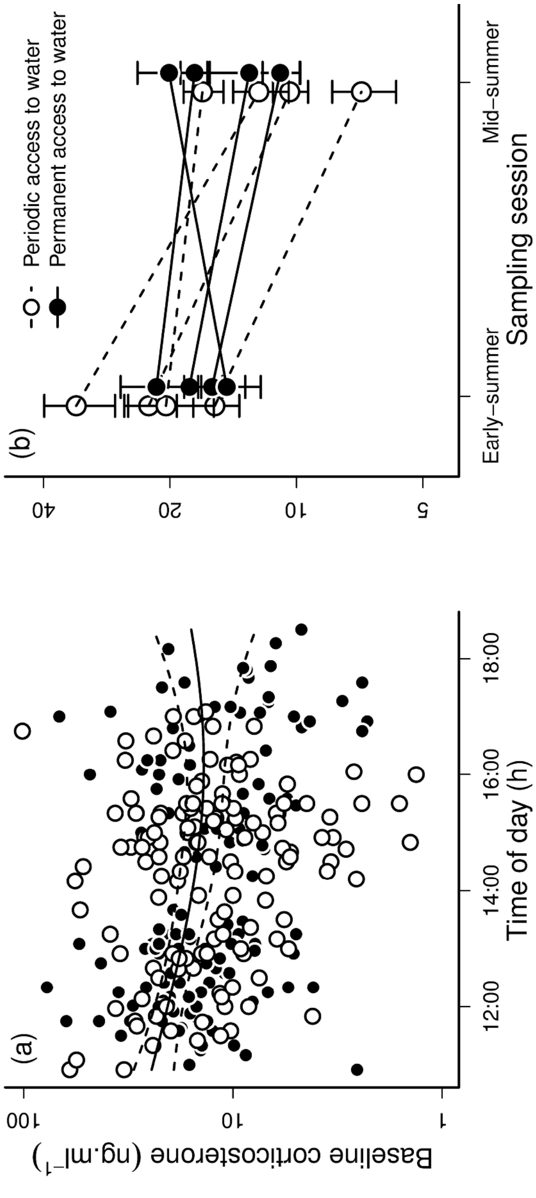

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Table S1. Localisation (GPS coordinates), elevation, climatic conditions and water access in the focal populations of the common lizard (*Z. vivipara*). Values of environmental temperature (minimal: T_{min} and maximal: T_{max}) are the mean ± SE, 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 [$r = (\text{Abundance}^{2015} - \text{Abundance}^{2005}) / \text{Abundance}^{2005}$] [1]. See text for details.

[1] *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^{2005}	Abundance^{2015}	*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^{t} 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^{t} 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	ΔAICc	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	*Null*	2	427.54	259.53	0.00	-211.76	0.00

k : number of parameters, ΔAICc: 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	ΔAICc	w_i	Log likelihood	$r^2{}_\mathrm{m}$
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, ΔAICc: difference with AICc of the best model, w_i: model likelihood, $r^2{}_\mathrm{m}$: 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 (Δabundance**)**, the minimal temperatures (T_{min}), and the altitude. Table shows the eigenvalue of the 3 axes (PC_1 to PC_3), percentage of variance explained, and the inertia of each variables on the first two axes.

		PCA Axes		
		PC_1	PC_2	PC_3
Eigenvalue		1.89	0.78	0.33
Variance		63.01	25.94	11.04
Inertia	Δabundance	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	ΔAICc	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 + Δabundance + Age : Sex + Age : Δabundance + Sex : Δabundance	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 + Δabundance + Age : Sex + Age : Δabundance	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_1 + Age : Sex + Sex : PC_1	8	193.19	12.33	0.00	-88.49	28.13	32.47
16	Age + Sex + T_{max} + Age : Sex + Age : T_{max}	8	193.21	12.35	0.00	-88.50	28.50	32.25
17	Age + Sex + T_{max} + 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_1 + 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_{min}	4	405.79	224.92	0.00	-198.86	2.19	6.17
30	*Null*	3	408.20	227.33	0.00	-201.08	0.00	6.18
31	T_{max}	4	408.41	227.54	0.00	-200.17	0.87	6.07
32	PC_1	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

35	altitude	4	410.22	229.35	0.00	-201.08	0.00	6.18

k : number of parameters, ΔAICc: 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	ΔAICc	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 + Δabundance + Sex : Δabundance	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 + Δabundance + Session : Δabundance + Sex : Δabundance	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 + Δabundance + Session : Δabundance	9	123.14	5.19	0.02	-52.22	14.52	18.72

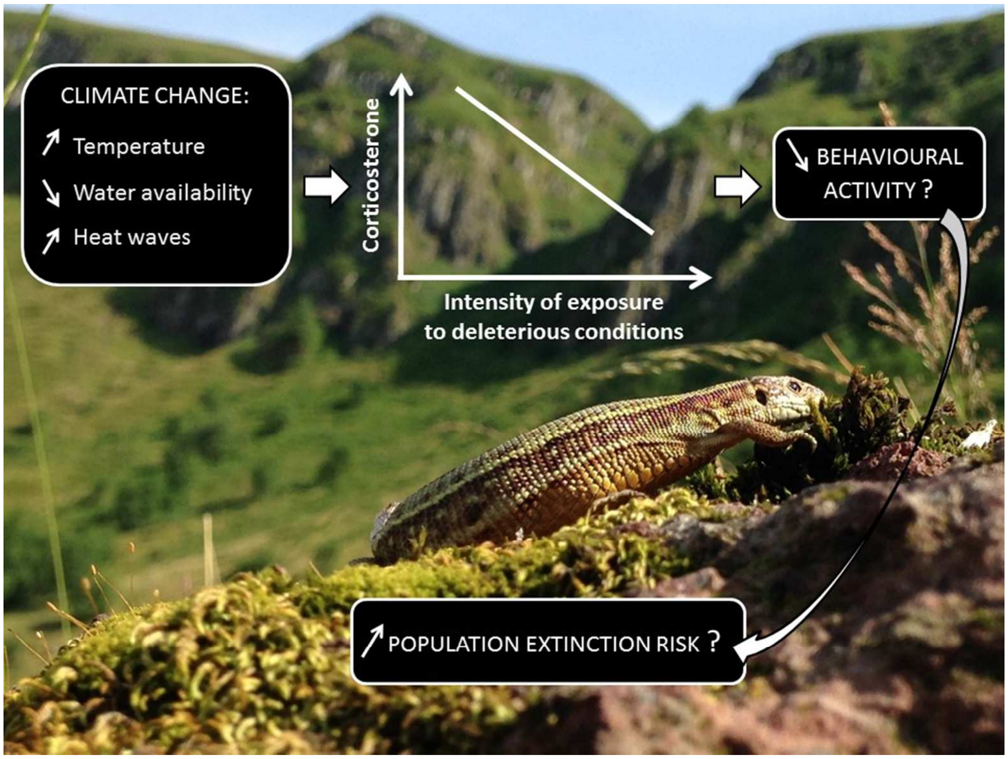
17	Session + Sex + Δabundance	8	123.36	5.42	0.02	-53.41	14.08	18.32
18	Session + Sex + altitude	8	123.70	5.75	0.01	-53.57	14.44	18.74
19	Session + Sex + T_{max} + Session : T_{max}	9	124.35	6.40	0.01	-52.83	14.79	18.12
20	Session + Sex + water access	8	124.39	6.44	0.01	-53.92	13.58	18.70
21	Session + Sex + T_{max} + Sex : T_{max}	9	124.41	6.46	0.01	-52.86	14.74	18.05
22	Session + Sex + altitude + Sex : altitude	9	124.63	6.68	0.01	-52.97	14.81	19.12
23	Session + Sex + altitude + Session : 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 : altitude + Sex : 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	*Null*	5	136.48	18.53	0.00	-63.13	8.06	12.51
30	PC_1	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	Δabundance	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, ΔAICc: difference with AICc of the best model, w_i: model likelihood, r^2_{m} : marginal R-squared, r^2_{c} : conditional R-squared

Table S7. AICc based model selection comparing the effects of reproductive performance on plasma corticosterone levels in pregnant females of common lizards (n = 266). Each index was treated one by one and in addition and compared to a null model with intercept only. Population was treated as a random factor to account for non-independence. We considered the reproductive timing (RT) as the difference between parturition and sampling dates to assess the embryonic developmental stage at the moment of sampling. Litter size and mass included the number and mass of neonate at birth and relative litter size mass (RLS and RLM respectively) were adjusted to female body size (linear relationship).

Model number	Specification of fixed effects	k	AICc	ΔAICc	w_i	Log likelihood	r^2_m	r^2_c
1	RT	4	-114.70	0.00	0.22	61.43	1.77	15.86
2	RT + litter mass	5	-114.21	0.49	0.17	62.22	2.53	17.00
3	RT + litter size	5	-114.01	0.69	0.15	62.12	2.42	17.02
4	*Null*	3	-113.48	1.21	0.12	59.79	0.00	13.94
5	RT + RLM	5	-112.65	2.05	0.08	61.44	1.80	15.80
6	RT + RLS	5	-112.64	2.06	0.08	61.43	1.78	15.96
7	Litter mass	4	-111.85	2.85	0.05	60.00	0.15	14.22
8	Litter size	4	-111.80	2.90	0.05	59.98	0.14	14.29
9	RLM	4	-111.42	3.27	0.04	59.79	0.00	13.97
10	RLS	4	-111.42	3.28	0.04	59.79	0.00	13.96

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



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