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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Habitat degradation increases stress-hormone levels during the breeding season, and decreases survival and reproduction in adult common lizards

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Abstract The allostatic load model describes how individuals maintain homeostasis in challenging environment and posits that costs induced by a chronic perturbation (i.e., allostatic load) are correlated to the secretion of glucocorticoids, such as corticosterone. Habitat perturbations from anthropogenic activities are multiple and functional responses to those are still unclear. Here, we manipulated the habitat quality in 24 semi-natural populations of the common lizard during 1 year. We tested the predictions of the allostatic load model that habitat degradation should increase baseline corticosterone levels, and should induce concomitant physiological changes, such as lipid mobilization and lower immunocompetence, and demographic changes, such as lower body growth, survival and/or reproductive performances. Our results highlight stage-dependent effects of habitat degradation on physiological traits during the breeding season: adult lizards had higher baseline corticosterone levels and yearling lizards had a lower inflammatory response than adults, whereas juveniles had higher circulating lipid levels than yearlings and adults without concomitant change in corticosterone levels. In addition, habitat degradation reduced the performances of adults but not of juveniles: in low habitat quality populations, adult males had a lower survival and females had a smaller fecundity. These results are in accordance with the allostatic load model given that allostatic load was detected only during the season and in life stages of maximal energy expenditure. This underlines the importance to account for individual energy requirements to better understand demographic responses to habitat perturbation.

Keywords Allostasis · Corticosterone · Fitness · Immunocompetence · Triglycerides

Introduction

Anthropogenic global changes increase species exposure to unpredictable environmental changes such as nutritional deficiency, human disturbance, pollution, or climate extremes (e.g., Wingfield 2008; Janin et al. 2010). Such stressors can have dramatic impact on the life history strategies of organisms and ultimately on their population dynamics (Holmgren et al. 2001; Angelier and Wingfield 2013). In vertebrates, one central mechanism mediating these effects is the secretion of glucocorticoids, a class of steroid hormones synthesized in the adrenal cortex (Kuznetsov et al. 2004; Navarro-Castilla et al. 2014; Tarjuelo et al. 2015). For example, more frequent human disturbance and land use conversion due to intensive agriculture both impair nestling quality in barn owls and cause a rise in basal, plasma glucocorticoid levels (Almasi et al. 2015). Similarly, exposure to marine oil pollution increases glucocorticoid secretion and responsiveness, and is associated with higher adult mortality and a significant population

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decline about 1 year after in marine iguanas (Romero and Wikelski 2002; Wikelski et al. 2002). The glucocorticoid response is indeed one major physiological process by which vertebrates deal with chronic and acute perturbations in their environment, and may be an ideal biomarker to assess the population health (Wikelski and Cooke 2006). Yet, whether the regulation of the glucocorticoid response underpins adaptive responses to changing environments, such as changes in behavior, breeding phenology or life history strategies, still remains largely unexplored (Meylan et al. 2002; Angelier and Wingfield 2013).

Corticosterone (dominant in rodents, birds, and reptiles) and cortisol are the main glucocorticoids secreted under chronic perturbation in vertebrates (Nelson 1994). A short-term increase in corticosterone level generates a wide range of physiological and behavioral responses that allow an individual to promote immediate survival by re-allocating energetic resources from storage to activity (reviewed in Sapolsky et al. 2000). In particular, corticosterone facilitates the transfer of energetic resources from storage to the bloodstream by stimulating release of amino acids and mobilization of free fatty acids from muscle, fat tissue and liver, and increasing the generation of glucose substrates from non-carbohydrate sources (i.e., gluconeogenesis, Johnson et al. 1992; Peckett et al. 2011). However, prolonged periods of elevated corticosterone secretion also induce the catabolism of muscle tissue, negative nitrogen balance, and can suppress reproduction and immunocompetence (Sapolsky et al. 2000). These negative effects may impair individual performances and cause demographic decline during a chronic perturbation (Wikelski and Cooke 2006). Still, studies that have tested the relation between physiological and demographic consequences of chronic stress in wild vertebrates have yielded contradictory results (Bonier et al. 2009). Some have shown that prolonged elevation of corticosterone may reduce fitness though infertility or impaired resistance to disease, which is in line with the so-called "corticosterone-fitness" hypothesis (Sapolsky et al. 2000; Bonier et al. 2009; Romero and Wikelski 2010). In contrast, other studies suggested that elevated corticosterone can help compensate for deleterious effects of a chronic perturbation, a scenario known as the "corticosterone adaptation" hypothesis (Bonier et al. 2009; Romero and Wikelski 2010).

The allostatic load model posits that species adjust their physiology and behavior to both predictable and unpredictable events(McEwen and Wingfield 2003, 2010). It provides a conceptual framework to account for these contradictory effects of corticosterone secretion and to predict changes in life history traits and demography in response to chronic environmental stress (e.g., Fefferman and Romero 2013). This model assumes that the energetic demand to ensure physiological homeostasis (i.e., "allostatic load") increases in response to a perturbation, which induces the secretion of corticosterone. The intensity and the duration of allostatic load thus define the cumulative costs to the individual of allostasis and the difference between these energetic costs and the potential rate of energy acquisition, which depends on food resources available in the environment, determines under which conditions a chronic stress may induce deleterious demographic and physiological effects (i.e., allostatic overload, Bonier et al. 2009; Fefferman and Romero 2013). The allostatic load model posits that basal corticosterone levels reflect the cumulative costs of allostasis. It predicts notably that the variable effects of corticosterone release may come from differences in energetic constraints between life history stages and environmental conditions. For example, it has been shown that a chronic increase in plasma corticosterone levels has contrasted effects depending on nutritional state (Cote et al. 2010) or immune status in the common lizard (Meylan et al. 2010). However, the allostatic load model has been criticized because the relationship between basal corticosterone secretion and energy expenditure is often more complex than hypothesized by the model (Bonier et al. 2009). The use of basal corticosterone concentration as a proxy for energy expenditure and cost of allostasis has also been questioned (Romero et al. 2009). A joint quantification of the physiological and demographic responses to a chronic perturbation is thus necessary to assess the validity and the usefulness of the allostatic load model.

Here, we manipulated the habitat quality in semi-natural populations of the common lizard (*Zootoca vivipara*) and evaluated both physiological and demographic responses during a one-year period including a breeding and a non-breeding season and different life stages. We compared three habitat quality levels differing by water access, availability of basking and refuge microhabitat as well as vegetation cover since these are critical determinants of population abundance in the wild (Lorenzon et al. 2001; Penalver-Alcazar et al. 2016). After 1 year of exposure to contrasted field conditions, we further exposed gravid females to different water access conditions in the laboratory (Lorenzon et al. 1999, 2001). This manipulation was done to extend the chronic perturbation during gestation and to assess cumulative effects of habitat quality before and during gestation. The allostatic load model predicts condition-dependent responses to this chronic perturbation because individuals may differ in their energy requirements according to age, sex and time of the year (Wingfield 2013a). We therefore recorded body growth rate, survival and reproductive performances to evaluate the effects of the habitat degradation on fitness of each life stage and population dynamics. At the same time, we quantified plasma concentration of basal corticosterone and lipids as well as the skin-swelling response, a measure of the inflammatory response (e.g., Vinkler et al. 2010). Measuring lipid circulation and skin-swelling response provides us with a rough evaluation of mobilization of stored energetic resources and immunocompetence, respectively. Accumulating evidence in the common lizard suggests a substantial role of corticosterone in modulating behavior and life history strategies. Elevation of corticosterone in the laboratory increases food consumption and behavioral activity (Cote et al. 2010), enhances future survival in males (Cote et al. 2010), and changes reproductive parameters in females (Vercken et al. 2007; Meylan et al. 2010).

In accordance with the allostatic load model, we predicted that habitat degradation increases on average baseline corticosterone concentration. We also expected potential increase in the plasma concentration of circulating lipids, which would last if corticosterone secretion increases food consumption and/or enough food resources are available in low-quality habitats. We further expected that chronic corticosterone secretion would decrease the skin-swelling response and fitness parameters in the case of allostatic overload. Moreover, allostatic load caused by habitat degradation should interact with life stage and physiological state, such that effects on both physiological and fitness traits are higher during the breeding season (Escribano-Avila et al. 2013). Finally, we hypothesized that water deprivation during gestation would have cumulative or non-cumulative effects on allostatic load in adult females. Non-cumulative effects could be due to a suppression or a reduction of the corticosterone stress response to water deprivation in adult females coming from a chronically stressful environment (Homan et al. 2003; Ellenberg et al. 2007).

Materials and methods

Model species

The common lizard *Zootoca vivipara* is a small viviparous species (adult snout-vent length SVL: 53–77 mm) inhabiting humid habitats across northern Eurasia. It is characterized by a 3–4 year life expectancy, continuous growth and plastic life history that is sensitive to food availability (Le Galliard et al. 2005; Mugabo et al. 2010, 2011) and abiotic conditions like habitat humidity and vegetation (Lorenzon et al. 2001; Marquis et al. 2008), or environmental temperature (Sorci et al. 1996; Chamaille-Jammes et al. 2006; Le Galliard et al. 2010). Natural populations are structured in three age classes: juveniles (newborns individuals), yearlings (1–2 years old individuals) and adults (2 years old or more). Before adulthood, lizards have the lowest energy requirements and prioritize energy allocation to growth and sexual maturation. After adulthood, lizards prioritize energy allocation to reproduction: costs of reproduction are strong in adult females and include nutrient allocation to egg and the energetic costs of viviparity (Bleu et al. 2013), whereas reproductive costs are paid essentially during the mating period in adult males. In our study site at the Centre de Recherche en Ecologie Expérimentale et Prédictive (Saint-Pierre-lès-Nemours, France, 48°17′N, 2°41′E), males start to emerge from hibernation around the beginning of March, followed shortly by juveniles and by females few weeks later. Mating period starts upon emergence of females (Bauwens and Verheyen 1985; Bauwens et al. 1989). From June to July, females lay an average clutch of five non-calcified eggs (range 1–13). Offspring hatch shortly after parturition and are immediately autonomous. Lizards enter in hibernation in October.

Capture and rearing condition

Between 18 and 26 May 2014, 203 adult females, 75 adult males, 164 yearling females and 160 yearling males were captured by hand in outdoor enclosures (10 × 10 m). Animals were identified by their unique toe clip code and measured for body size (SVL ±0.5 mm) and body mass (±1 mg). To estimate body condition, we included in a linear mixed model on mass, the size as a fixed effect. Individuals were then maintained in individual terraria (25 × 15 × 16 cm) with a shelter, peat soil as substrate and opportunities for optimal thermoregulation. We used incandescent light bulbs (25 W) for 9 h/d to ensure a thermal gradient from room temperature at 17–23 to 35–38 °C below the bulb during daytime. Room temperature was maintained at 16 °C from 21:00 to 7:30. We provided lizards with water and food ad libitum. Gravid females were maintained in captivity until the parturition. Immediately after parturition, newborns (hereafter called juveniles) were separated from their mother, marked by toe clipping and measured for their SVL and body mass.

Habitat and water deprivation manipulation

Our experimental design combined a field manipulation of habitat quality with a laboratory manipulation of water deprivation in gravid females at the end of the habitat manipulation. We first manipulated the physical environment and vegetation of 24 outdoor enclosures each measuring 10m × 10 m and allowing population-level investigations of the common lizard (Mugabo et al. 2013). We changed simultaneously several habitat features to generate potential multi-factorial changes in habitat quality, and produced three treatment groups with 8 enclosures per treatment. In “control” enclosures, we used our standard microhabitat set-up and maintenance procedures (see Lecomte and Clobert 1996). Each enclosure was equipped with two permanent watering holes (40 L plastic tanks), four piles of stones and logs used as shelters and basking sites by lizards, and a dense and tall vegetation (approximately 40 cm high) was kept throughout the experiment. In the "low quality" enclosures, watering holes, logs and stones were removed, and grass was regularly cut to maintain a maximum vegetation height of 20 cm. In order to avoid direct disturbance or injury of lizards, mowing was done every 2 weeks on average before or after the time of the day when lizards are active or during cloudy and rainy days. Grass is used by lizards during thermoregulation and foraging activities (pers. obs.), and mowing the grass decreases abundance of orthoptera, which are food resources for lizards (Uchida and Ushimaru 2014), and should further reduce soil moisture and shading (Shao et al. 2012). To disentangle effects of vegetation cover from effects of microhabitat diversity and water availability, we further produced "intermediate quality" enclosures where grass was not manipulated but all watering holes, logs and rocks were removed.

At the beginning of the experiment, we released 8–10 adult females, 3–4 adult males, 7–11 yearling females, 6–7 yearling males, 27–30 female and 26–28 male juveniles in each enclosure. Males and non-gravid females were released in a randomly chosen experimental enclosure between June 12 and 14. Gravid females and their offspring were released the day of parturition. Juveniles from the same family were divided into three groups each randomly released in one habitat treatment. At the onset of the experiment, we did not observe differences between habitat quality treatments for SVL (mixed-effects ANOVA, adults and yearlings: Wald $\chi^2 = 2.41$, $df = 2$, $P = 0.299$; juveniles: Wald $\chi^2 = 2.46$, $P = 0.293$) and body condition (adults and yearlings: Wald $\chi^2 = 2.59$, $P = 0.273$; juveniles: Wald $\chi^2 = 2.63$, $P = 0.267$). Populations were then sampled before and after winter according to a protocol described in the next section.

At the end of the experiment, gravid females were returned to the laboratory and water availability was manipulated during the last 2–3 week of the gestation, (i.e., from 1 to 18 June 2015). Each gravid female was assigned randomly to one water restriction treatment. In the control treatment, terraria were sprayed with water three times a day and water was permanently provided with a plastic cup, which corresponds to our standard, ad libitum breeding conditions. In the water deprived treatment, terraria were sprayed only once per day in the morning and no permanent access to water was provided. This water deprivation regime decreases humidity during the day (80 to 40% in the afternoon) and mimics a dry environment where only morning dew is available (Lorenzon et al. 1999).

Demographic measurements

We monitored populations during two successive capture sessions to assess body size and condition, growth, survival and female reproductive performances. In a pre-winter recapture session (15–22 September 2014, between 10:30 pm and 5:00 am), we recaptured 5 adult and yearling lizards and about 9 (8–10) juveniles in each enclosure. In a post-winter recapture session (18–28 May 2015), we recaptured all surviving individuals. Lizards were identified by their unique toe clip code. At each recapture, animals were measured for body size and mass. Body growth rates were calculated as the change in SVL between two captures divided by the time interval. For the post-winter session, we subtracted the number of inactive days spent in hibernation and emergence assumed to be from end of October to beginning of March. We estimated annual survival probabilities between the release and post-winter recapture, assuming that capture probability was very close to 1 (Le Galliard et al. 2005). In June and July 2015, gravid females from the two water restriction treatments (see above) were maintained until parturition in the laboratory to assess their reproductive traits. We counted live newborns, dead newborns and aborted or unfertilized eggs of each clutch. Parturition date, total fecundity (live, dead and aborted newborns), fit fecundity (live newborns) and juvenile characteristics were recorded.

Physiological measurements

We took a blood sample of animals larger than 2 g at each capture session to assess plasma corticosterone and triglyceride concentrations. Blood was sampled in the infra-orbital sinus of the lizards using 2–3 20 µL microhematocrit tubes. Blood was separated in two samples for corticosterone and triglyceride assays. All samples were collected within 3 min of removal of an animal from its home cage (laboratory measurements) or enclosure (field measurements) to avoid the handling-induced stress effects (Dauphin-Villemant and Xavier 1987). Plasma were obtained by centrifugation and stored at −20 °C until assay. Corticosterone levels were measured with a competitive enzyme-immunoassay method using corticosterone EIA (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 (intra-plate repeatability, 17 plates with 4 repeats per plate: coefficient of intraclass correlation, $\rho = 0.89$, $F_{3,60} = 103$, $P < 0.001$; inter-plate repeatability: $\rho = 0.93$, $F_{16,47} = 51.3$, $P < 0.001$, Lessells and Boag 1987).

Levels of circulating triglycerides were measured in plasma by colorimetric assays using 2.5 µl of plasma (Triglyceride Colorimetric Assay kit, ref. 10010303, Cayman Chemical, USA). This method quantifies the total triglycerides using a chain of three enzymatic reactions ending up in hydrogen peroxide production, which is converted into quinoneimine dye quantified by absorbance at 540 nm. The quantification was highly repeatable (intra-plate repeatability: $\rho = 0.96$, $F_{98,194} = 71.2$, $P < 0.001$; inter-plate repeatability: $r = 0.98$, $F_{17,63} = 146$, $P < 0.001$). Body condition was not correlated with triglyceride (summer 2014: Wald $\chi^2 = 1.84$, $df = 1$, $P = 0.175$; pre-winter session: Wald $\chi^2 = 0.03$, $df = 1$, $P = 0.857$, post-winter session: Wald $\chi^2 = 0.33$, $df = 1$, $P = 0.569$) or corticosterone concentration (summer 2014: Wald $\chi^2 = 1.59$, $df = 1$, $P = 0.206$; pre-winter session: Wald $\chi^2 = 1.11$, $df = 1$, $P = 0.292$, post-winter session: Wald $\chi^2 = 2.35$, $df = 1$, $P = 0.125$).

We further assessed immunocompetence at the beginning of the experiment (June 2014) and at each recapture session by measuring secondary skin swelling in response to an injection of a mitogen, the phytohaemagglutinin (PHA). This procedure triggers a local haemagglutination and leukocyte infiltration and involves both adaptive and innate immune components (Martin et al. 2006; Brown et al. 2011). The skin-swelling response is associated with ectoparasite resistance in adults and exposure to ectoparasites in yearlings (Mugabo et al. 2015). In 2014, prior to the first measurement, we injected all animals with a solution of PBS containing 2.5 mg/mL of PHA (PHA-M, Sigma-Aldrich; reference 9008-97-3) in the right posterior leg to elicit a primary response. In 2015, we used the same protocol to stimulate the primary response in juveniles not measured in 2014. We, then, administered a subcutaneous injection of the same PBS-PHA solution in the right posterior leg to measure the secondary skin-swelling response. Time elapsed between the two injection was of a minima of 7 days: previous studies have shown no correlation between measurements of skin swelling after the first and second injection, but an increase in the PHA response during the secondary response (Mugabo et al. 2015). Just before and 12 h after the injection, we measured the thickness of the right posterior leg using a spessimeter (Mitutoyo, ID-C112, Kanagawa, Japan) with an accuracy of 0.01 mm. We spaced the two measurements by 12 h, because this coincided with the greatest swelling response (Mugabo et al. 2015). Swelling response was calculated as the difference in thickness between the post- and pre-injection measurements. At the start of the experiment, we did not find difference between habitat quality treatments for PHA response (adults and yearlings: Wald $\chi^2 = 2.30$, $df = 2$, $P = 0.316$), corticosterone concentration (adults and yearlings: Wald $\chi^2 = 2.95$, $df = 2$, $P = 0.228$) and triglyceride concentration (adults and yearlings: Wald $\chi^2 = 1.76$, $df = 2$, $P = 0.414$).

Statistical analyses

All analyses were performed with R 3.1.0 (R Core Team 2014, https://www.r-project.org/) and statistical procedures available in the *lmer* package (Bates et al. 2015). Data recorded in the summer 2014, the pre-winter and the post-winter capture sessions were analyzed separately in juveniles and in older individuals. Growth rate, morphological (SVL and body condition), and physiological (PHA, corticosterone and triglyceride concentrations) variables were analyzed with linear mixed models with enclosure as random effect. All initial models included fixed effects of habitat manipulation, age class (in older individuals), sex, and their first-order interactions. In the case of swelling response, we added the initial thickness measurement of the injected legs. In the case of body growth, we included also the effect of initial SVL to control for growth deceleration with increasing body size and the effect of the date of release to control for seasonal changes in growth rates. In the case of juveniles, we further included the additive random effect of family identity since similarity among siblings can influence the phenotype of juveniles. To estimate body condition, we included body size as a covariate in a model describing body mass. Concerning the physiological parameters, corticosterone and triglyceride concentrations were log transformed to improve the normality of the residuals.

Annual survival was similarly analyzed with mixed-effect logistic regressions including a logit link and binomial error term. Enclosure was used as random effect and habitat manipulation, age class (in older individuals), and sex were included as fixed effects together with their first-order interactions. Initial SVL was used as covariate to control for size effect on survival.

All yearling and adult females except one bred at the end of the experiment, whereas the proportion of breeding females among released juveniles was less than 50% on average. The proportion of female breeding at the age of 1 year was analyzed with mixed-effect logistic regressions including a logit link and a binomial error term. The logistic regression included enclosure as a random effect and habitat manipulation, growth rate, and initial SVL as fixed effects. We further tested the effects of habitat manipulation, water deprivation, and their interaction on reproductive traits of gravid females with a data set including all age classes. Parturition date and offspring characteristics (SVL and body condition) were analyzed with linear mixed models. Total fecundity and fit fecundity were analyzed with mixed effect log regressions including a log link and a Poisson error term.

Parameters of linear mixed models were estimate with REML (restricted maximum likelihood) procedure, whereas a Laplace approximation of the maximum likelihood was used in the case of logistic and Poisson regressions. Fixed effects were tested with Wald χ^2 statistics from R package “car”. A minimum adequate model was obtained by a backward procedure where we removed non-significant terms one by one. Assumptions of normality and homoscedasticity of linear mixed models were verified and over-dispersion of logistic and Poisson regressions was tested with a Pearson’s goodness-of-fit statistic. When a minimum adequate model was found, we used the Tukey’s procedure to conduct post hoc tests (pairwise comparisons) with the *lsmeans* package (Lenth 2015). Results are presented as mean ± standard error or [lower,upper] at 95% confidential interval unless otherwise stated. All statistical tests are reported with 3 digits accuracy.

Results

Growth and morphology

Juvenile body growth rate was not influenced by habitat manipulation before or after wintering (see Tables 1, 2). Post-wintering growth rate of adult and yearling tended to be higher in intermediate quality comparing to low-quality habitat (Tukey post hoc tests: adjusted $P = 0.08$) but the growth rates in the control habitat fall between those in the two habitats with decreased quality. Juveniles’ pre-winter growth rate was positively correlated with the date of release (slope = 0.002 ± 0.001 mm/day^2). In juveniles, post-winter growth rate was higher in females than in males (contrast = 0.015 ± 0.001 mm/day^2). In older lizards, body growth rate was smaller in adults than in yearlings (Tables 1, 2), higher for females than for males (pre-winter: estimate = 0.04 ± 0.007, adjusted $P < 0.001$; post-winter: estimate = 0.028 ± 0.002 adjusted $P < 0.001$, Table 2) and decreased with initial SVL (pre-winter: slope = −0.005 ± 0.001 day^{-1}; post-winter: slope = −0.002 ± 0.0002 day^{-1}). Not surprisingly given these results, the SVL of lizards at the end of experiment was similar between habitat quality treatments in all age classes (all $P > 0.22$).

Body condition (mass corrected by SVL) was similar between treatments in juveniles as well as in yearling and adult lizards during the pre-winter session (Table 2). Post-winter body condition of adults and yearlings changed among treatments in females but not in males. Females had a higher body condition in the intermediate habitat quality treatment than in control (Tukey post hoc test: estimate = 0.44 ± 0.16, adjusted $P = 0.02$) and low habitat quality treatment (estimate = 0.55 ± 0.16, adjusted $P = 0.003$).

Annual survival

We found no effect of habitat quality manipulation, sex, and SVL at birth on the annual juvenile survival (habitat manipulation: [Wald $\chi^2 = 0.32$, $df = 2$, $P = 0.85$; control = 0.25 (0.18, 0.33), intermediate = 0.28 (0.21, 0.37), low = 0.27 (0.19, 0.35)]). In adults and yearlings, the annual survival of males tended to decrease with habitat degradation, while there was no difference in females (habitat manipulation × sex: Wald $\chi^2 = 8.79$, $df = 2$, $P = 0.012$, Fig. 1).

Reproductive traits

The proportion of females breeding at the age of 1 year was independent of the habitat quality manipulation [Wald $\chi^2 = 3.19$, $df = 2$, $P = 0.203$; control = 0.53 (0.27, 0.78), intermediate = 0.26 (0.1, 0.54), low = 0.18 (0.06, 0.43)]. Juvenile females were more likely to breed at the age of one year if they grew faster earlier in life (Wald $\chi^2 = 18.1$, $df = 1$, $P < 0.001$). Among breeding females, time at parturition was delayed by 3–4 days in the low-quality treatment (Tukey post hoc test: control versus low quality: estimate = −3.5 ± 1.38 days, adjusted $P = 0.05$; intermediate versus low-quality: estimate = −4.37 ± 1.47 days, adjusted $P = 0.02$), but it was not influenced by water deprivation (Table 3). Total fecundity did not differ among habitat quality and water deprivation treatments, and increased with age [adults = 8.58 (8.02, 9.19), yearlings = 7.49 (6.99, 8.03), juveniles = 4.81 (4.31, 5.36), Table 2]. Fit fecundity was not affected by water deprivation but was affected by habitat manipulation. Females from the low-quality treatment had a smaller fit fecundity than females from control (estimate = −0.23 ± 0.09,

Table 1 Growth rate (mm day^{-1}) of adult, yearling, and juvenile common lizards before and after wintering in each habitat quality treatment

	Pre-winter period			Post-winter period		
	Control	Intermediate	Low	Control	Intermediate	Low
Adults	0.044 ± 0.008	0.041 ± 0.008	0.037 ± 0.008	0.007 ± 0.003	0.010 ± 0.003	0.005 ± 0.003
Yearlings	0.078 ± 0.007	0.072 ± 0.007	0.060 ± 0.007	0.029 ± 0.003	0.032 ± 0.003	0.027 ± 0.003
Juveniles	0.318 ± 0.012	0.295 ± 0.011	0.303 ± 0.012	0.154 ± 0.003	0.151 ± 0.003	0.148 ± 0.003

Results shown as mean ± SE

Table 2 Effects of habitat manipulation, sex and and age class on body growth rate (A) and body condition (B) in juveniles and yearlings–adult common lizards

	Factor	Pre-winter session			Post-winter session		
		df	Wald χ^2	*P* value	*df*	Wald χ^2	*P* value
(A) Body growth rate							
Juveniles	Habitat manipulation	2	2.11	0.348	2	2.13	0.345
	Date of release	**2**	**5.11**	**0.024**	1	0.63	0.427
	Sex	1	0.01	0.923	**1**	**135**	**<0.001**
	Initial SVL	1	1.25	0.263	1	0.40	0.525
	Sex × habitat manipulation	2	0.27	0.876	2	3.42	0.181
Yearlings and adults	Habitat manipulation	2	2.83	0.24	2	5.838	0.054
	Date of release	1	0	0.99	**1**	**33.44**	**<0.001**
	Sex	**1**	**32**	**<0.001**	**1**	**152.47**	**<0.001**
	Initial SVL	**1**	**39.32**	**<0.001**	**1**	**88.4**	**<0.001**
	Age class	**1**	**6.63**	**0.01**	**1**	**28.132**	**<0.001**
	Age class × habitat manipulation	2	1.34	0.509	2	1.25	0.535
	Sex × habitat manipulation	2	169	0.429	2	4.27	0.118
	Age class × sex	1	0.14	0.709	1	1.81	0.17
(B) Body condition							
Juveniles	Habitat manipulation	2	0.96	0.62	2	0.13	0.93
	Sex	**1**	**51.58**	**<0.001**	**1**	**43.86**	**<0.001**
	SVL	**1**	**208.96**	**<0.001**	**1**	**223.76**	**<0.001**
	Sex × habitat manipulation	2	0.3	0.863	2	0.87	0.646
Yearlings and adults	Habitat manipulation	2	0.07	0.967	**2**	**13.46**	**0.001**
	Age class	1	0.04	0.842	1	0.004	0.952
	Sex	**1**	**31.02**	**<0.001**	**1**	**8.47**	**0.004**
	SVL	**1**	**31.93**	**<0.001**	**1**	**95.54**	**<0.001**
	Age class × habitat manipulation	1	4.12	0.128	2	1.58	0.453
	Sex × habitat manipulation	2	1.31	0.520	**2**	**6.85**	**0.033**
	Age class × sex	1	2.07	0.151	**1**	**18.08**	**<0.001**

Results are from linear mixed-effects models

Significant tests are bolded (i.e., $P < 0.05$)

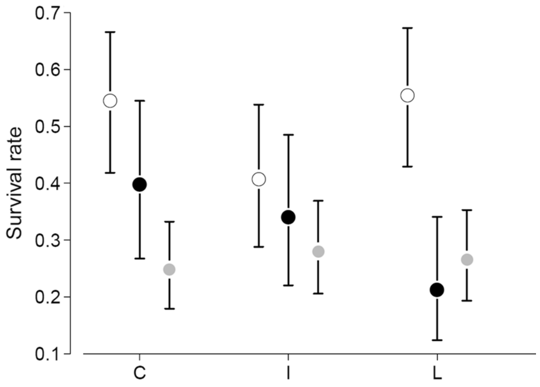

Fig. 1 Annual survival probability of juveniles (*gray circle*), adult, and yearling females (*empty circle*) and males (*black circle*) common lizard in each habitat quality treatment group (*C* control, *I* intermediate, *L* low). Results are shown as means ± 95% confidence intervals

adjusted $P = 0.046$) or intermediate habitat quality treatment (estimate $= -0.30 \pm 0.10$, adjusted $P = 0.002$).

Offspring body condition and SVL were not significantly affected by the habitat quality and water deprivation treatments of their mother (all $P > 0.4$). Mother SVL was a strong positive predictor of offspring body condition (slope $= 0.0018 \pm 0.00002$, Wald $\chi^2 = 67.7$, $df = 1$, $P < 0.001$) and SVL (slope $= 0.07 \pm 0.01$, Wald $\chi^2 = 41.6$, $df = 1$, $P < 0.001$), and female offspring were longer than males on average (Wald $\chi^2 = 394$, $df = 1$, $P < 0.001$).

Physiological traits

During the pre-winter period, habitat manipulation did not influence significantly plasma corticosterone and triglyceride concentrations nor the PHA swelling response (Table 4; Fig. 2a–c). There was a marginal trend towards higher corticosterone concentrations for lizards from intermediate habitat quality populations (Fig. 2a). In contrast,

Table 3 Effects of habitat manipulation, water deprivation during late gestation, and age class on reproductive traits of female common lizards

	Factor	*df*	Wald χ^2	*P* value
(A) Parturition date	Habitat manipulation	**2**	**10.5**	**0.005**
	Water deprivation	1	0.02	0.883
	Age class	**2**	**103**	**<0.001**
	Habitat manipulation × age class	4	3.90	0.419
	Habitat manipulation × water deprivation	2	0.92	0.631
(B) Total fecundity	Habitat manipulation	2	4.22	0.121
	Water deprivation	1	0.16	0.694
	Age class	**2**	**81.7**	**<0.001**
	Habitat manipulation × age class	4	4.02	0.403
	Habitat manipulation × water deprivation	2	0.61	0.738
(C) Fit fecundity	Habitat manipulation	**2**	**11.8**	**0.003**
	Water deprivation	1	0.07	0.79
	Age class	**2**	**27.2**	**<0.001**
	Habitat manipulation × age class	**4**	**10.4**	**0.03**
	Habitat manipulation × water deprivation	2	2.42	0.29

Results are from linear mixed-effects models for parturition date (A) and generalized mixed-effects models for fecundity (B) and fit fecundity (C)

Significant tests are bolded (i.e., $P < 0.05$)

Age = factor with three levels (juveniles, yearlings, and adults)

Table 4 Effects of habitat manipulation on physiological traits, including the plasma corticosterone concentration (A), circulating triglyceride levels (B), and the PHA skin-swelling response (immunocompetence)

	Factor	Pre-winter session			Post-winter session		
		df	Wald χ^2	*P* value	*df*	Wald χ^2	*P* value
(A) Corticosterone	Habitat manipulation	2	4.90	0.085	**2**	**6.78**	**0.034**
	Age class	1	0.42	0.516	2	2.34	0.309
	Sex	1	0.29	0.591	**1**	**43.7**	**<0.001**
	SVL	1	0.94	0.331	1	0.19	0.666
	Age class × habitat manipulation	2	1.47	0.479	**4**	**16.7**	**0.002**
	Sex × habitat manipulation	2	1.32	0.251	2	0.49	0.784
	Age class × sex	1	3.00	0.223	**2**	**6.39**	**0.041**
(B) Triglycerides	Habitat manipulation	2	3.70	0.15	2	2.10	0.350
	Age class	1	0.50	0.477	**2**	**32.2**	**<0.001**
	Sex	1	0.19	0.662	1	3.90	**0.048**
	SVL	1	0.07	0.786	1	0.30	0.585
	Age class × habitat manipulation	2	0.37	0.831	**4**	**18.5**	**<0.001**
	Sex × habitat manipulation	2	2.69	0.260	2	1.23	0.542
	Age class × sex	1	1.37	0.241	2	2.59	0.274
(C) PHA response	Habitat manipulation	2	4.4	0.11	2	1.20	0.549
	Age class	1	1.81	0.178	**2**	**10.14**	**0.006**
	Sex	1	1.92	0.165	**1**	**33.94**	**<0.001**
	SVL	1	1.68	0.195	**1**	**27.02**	**<0.001**
	Value before injection	**1**	**5.60**	**0.018**	**1**	**79.6**	**<0.001**
	Age class × habitat manipulation	2	1.34	0.512	**4**	**9.49**	**0.05**
	Sex × habitat manipulation	2	0.79	0.672	2	0.98	0.612
	Age class × sex	1	0.10	0.751	**2**	**19.52**	**<0.001**

Significant tests are bolded (i.e., $P < 0.05$)

Age class pre-winter session = factor with two levels (yearling and adult lizards). Age class post-winter session = factor with three levels (juveniles, yearlings, and adults)

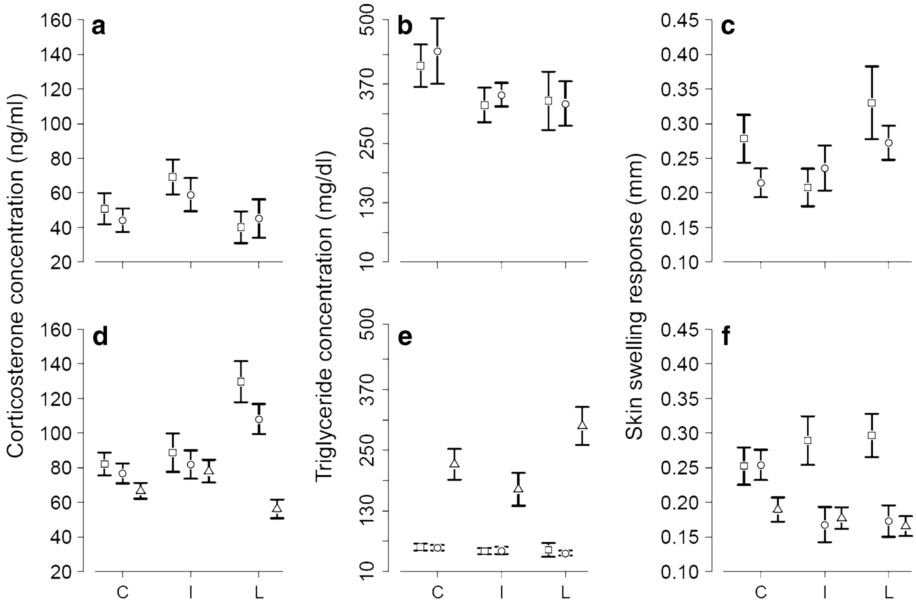

Fig. 2 Plasma corticosterone concentration, circulation triglyceride concentration, and secondary skin-swelling response after PHA injection of adult (*squared*), yearling (*circle*), and juvenile (*triangle*) common lizards per habitat quality treatment group (*C* control, *I* intermediate, *L* low) during the pre-winter (**a**–**c**) and the post-winter capture sessions (**d**–**f**). Results are shown as mean ± SE

physiological traits measured during the post-winter period were all significantly different among treatments (Table 4). First, plasma corticosterone concentrations changed with habitat quality in an age-dependent manner. Corticosterone concentration was higher in adults from low habitat quality populations relative to the two other treatments (Tukey post hoc tests: adjusted $P < 0.06$), but not in yearlings and juveniles (Fig. 2d). In addition females had on average higher plasma corticosterone concentrations than males, especially in adults and yearlings (results not shown). Second, juveniles had higher circulating triglyceride levels than adults and yearlings, and higher levels in low habitat quality than in intermediate quality treatment (adjusted $P = 0.016$, see Fig. 2e). Third, the PHA swelling response of juveniles was not influenced by treatments, but swelling response tended to increase in adults with habitat degradation whereas swelling response of yearling decreased with habitat degradation (Tukey post hoc tests: Intermediate vs Control $P = 0.081$; Low vs Control $P = 0.043$; Fig. 2f).

Discussion

Our experiment reveals condition-dependent effects of habitat degradation on the baseline corticosterone level, lipid concentration and immunocompetence in the common lizard. These effects were dependent upon age class and sex, and were more pronounced after the wintering period than during the pre-winter period. In addition, habitat degradation led to small but significant changes in life history traits suggesting slight, deleterious effects on the fitness of adult males and females undergoing chronic disturbance on the long term but little effects in younger individuals. Water deprivation during gestation had no significant effect on the reproductive performances of adult females independent of the habitat quality manipulation prior to gestation. This last result suggests that reproductive traits were determined prior to gestation, which is in line with our field observations that water availability during vitellogenesis, but not during gestation, influences reproductive effort in this species (Bleu et al. 2013).

During the pre-winter period, food availability is high and thermal conditions are more favorable for basking and feeding, such that lizards can acquire food to grow and restore their body reserves (Bleu et al. 2013). At that time of the year, we did not detect any significant effects of the habitat quality manipulation on physiological traits nor on life history traits. Three potential explanations for the absence of short-term effects of habitat degradation on physiology and demography are (1) that the intensity of the chronic perturbation was too moderate relative to the energetic needs of individuals (McEwen and Wingfield 2003; Wingfield 2013b), (2) that the persistence of chronic perturbation led to acclimatization or selection (reviewed in Wingfield et al. 2011), or (3) that there was more variation among individuals due to predictable differences in life stage (e.g., breeding state, Landyset al. 2006) than between treatments. The last hypothesis is unlikely given that none of the individuals was in a breeding state during the pre-winter period and we found no difference in physiological traits (corticosterone, triglycerides and immunocompetence) between age and sex classes. We can also reject the acclimatization hypothesis because the physiological state of some individuals responded during the post-winter session and the selection hypothesis is also unlikely because survival is usually high during the summer (i.e., close to 70–90% depending on age class). Thus, the most plausible explanation is that allostatic load was not strong enough during the pre-winter period in all age and sex classes. For example, there was no difference in body growth, body size, body condition and circulating lipid concentrations among habitat quality treatments. At that time of the year, baseline corticosterone levels were lower on average than during the post-winter session and lipid concentrations were relatively high and similar to the values recorded under well-fed conditions in the laboratory prior to the experiment. This suggests that food availability and energy allocation to growth were high and not different between treatments (Le Galliard et al. 2005; Mugabo et al. 2010). The summer season was also characterized by frequent rainfall events and relatively short periods of drought (Josserand, pers. obs.), implying that hydric constraints might have been weakly influenced by the habitat manipulation. Additional data on food and microclimatic conditions inside enclosures would be needed to test these hypotheses. Under all these conditions, an increase of allostatic load associated with a higher corticosterone secretion is not expected because no additional energy expenditure is required to cope with stress (e.g., Landys et al. 2006).

Annual survival rate of adult and yearling males decreased in low habitat quality as expected if low habitat quality generates chronic stress, whereas survival rate of adults and yearling females did not change among treatments. Sexual differences in the survival of common lizards have already been reported with lower average survival of males after adulthood and more variable survival in males than in females, especially according to temporal changes in early spring weather condition (e.g., Massot et al. 1992; Le Galliard et al. 2010; Mugabo et al. 2013). This low and more variable survival of breeding males could be due to secretion of testosterone during the mating period (i.e., immune-competence handicap hypothesis, Folstad and Karter 1992). In addition, in low habitat quality enclosures, number of live offspring decreased in the litter of adult females, but not in younger females, and parturition date was delayed from 3 to 4 days in all age classes, whereas offspring characteristics remained unchanged. Meanwhile, adult and yearling males and females increased their corticosterone secretion in low-quality habitats. These results are in agreement with the "corticosterone-fitness" hypothesis (Bonier et al. 2009). Previous studies have shown that increased plasma corticosterone levels during gestation decrease reproductive success, delay the parturition date, and can also influence offspring characteristics in the common lizard (Meylan and Clobert 2005; Meylan et al. 2010).

A higher plasma corticosterone concentration suggests that allostatic load increased in adults and yearlings from low-quality habitats. In support of this and as expected, we also found a decrease of immunocompetence in yearling lizards from low habitat quality populations. However, circulating triglyceride rates and body condition were not affected by habitat degradation contrary to our predictions based on the most commonly reported effects of corticosterone on energy metabolism (e.g., Johnson et al. 1992; Sapolsky et al. 2000a). Yet, Peckett et al. (2011) reviewed both positive and negative effects of corticosterone secretion on circulating free fatty acids concentration in humans and rodents depending of fasted state. In particular, under nonfasted state, corticosterone secretion can promote lipid storage by stimulating lipogenesis and adipogenesis. In the common lizard, a prolonged corticosterone elevation promotes behaviors associated with food intake including basking and exploratory activities (De Fraipont et al. 2000; Cote et al. 2006, 2010). Moreover, we have recently shown that 3 weeks of corticosterone application increases liver mass, suggesting that liver may store more fatty acids during a chronic stress (Voituron et al. unpublished). We, therefore, propose that corticosterone elevation in low-quality habitat may have stimulated food acquisition and/or lipid storage, thus explaining the absence of difference in body mass, size growth, and circulating triglyceride concentration between habitat qualities.

In contrast, juveniles from low habitat quality enclosures had higher triglyceride concentrations in the plasma than juveniles from high habitat quality enclosures suggesting more pronounced fatty acid release despite no significant change in corticosterone level, body growth, and body condition. The fitness of male juveniles was not influenced by habitat degradation, whereas juvenile females reaching sexual maturity at the age of 1 year delayed their parturition date by 3–4 days like adult and yearling females. Thus, the physiological responses of juveniles differed from those observed during the pre-winter period only for circulating triglyceride levels. We suggest that allostatic load was too low to cause a detectable rise in corticosterone levels in juveniles, but that stress caused by habitat degradation was strong enough to induce the necessity of mobilizing lipid reserves to maintain homeostasis. In favor of this scenario, which assumes low energetic constraints in juveniles, levels of circulating triglycerides were very high in juveniles compared to yearlings and adults, and sexual maturation of juvenile females (proportion of breeders) was independent of habitat quality.

Altogether, our results were generally in accordance with the "corticosterone-fitness" hypothesis in adults (Bonier et al. 2009). In addition, as suggested by allostatic load model (McEwen and Wingfield 2003), our study demonstrates that life stage and environmental constraints are important factors to take into account to understand effects of perturbations on demographic and physiological responses. This suggests that baseline corticosterone level can be used as an indicator of population health or individual fitness in response to habitat perturbations, but only under certain circumstances.

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Author contribution statement RJ, SM, and JFLG conceived and designed this study, performed statistical analyses and wrote the manuscript. RJ, SM, JFLG, AD, and SA performed the experiment. RJ, AD, and CH provided biochemical analyses.

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