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Original Article

Plastic responses to warmer climates: a semi-natural experiment on lizard populations

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Abstract

Facing warming environments, species can exhibit plastic or microevolutionary changes in their thermal physiology to adapt to novel climates. Here, using semi-natural mesocosms, we experimentally investigated over two successive years whether a 2°C-warmer climate produces selective and inter- and intragenerational plastic changes in the thermal traits (preferred temperature and dorsal coloration) of the lizard *Zootoca vivipara*. In a warmer climate, the dorsal darkness, dorsal contrast, and preferred temperature of adults plastically decreased and covariances between these traits were disrupted. While selection gradients were overall weak, selection gradients for darkness were slightly different between climates and in the opposite direction to plastic changes. Contrary to adults, male juveniles were darker in warmer climates either through plasticity or selection and this effect was strengthened by intergenerational plasticity when juveniles' mothers also experienced warmer climates. While the plastic changes in adult thermal traits alleviate the immediate overheating costs of warming, its opposite direction to selective gradients and to juveniles' phenotypic responses may slow down evolutionary shifts toward phenotypes that are better adapted to future climates. Our study demonstrates the importance of considering inter- and intragenerational plasticity along with selective processes to better understand adaptation and population dynamics in light of climate change.

Keywords: climate change, ectotherm, lizard, phenotypic plasticity, natural selection, thermal physiology

Introduction

Ongoing climate change threatens species persistence and biodiversity (Walther, 2010). Species can respond to such change by improving the match between their phenotype and the novel climatic conditions. The phenotypic modifications, spanning various traits such as reproductive features (Parmesan, 2006) and morphology (Sheridan & Bickford, 2011; Zeuss et al., 2014), may enhance species' adaptations to warming climates (Boutin & Lane, 2014, often imperfectly: Radchuk et al., 2019) and may result from a combination of intra- and intergenerational plasticity and microevolution. Despite the different possible outcomes for biodiversity under climate change, only a few studies have disentangled evolutionary from plastic drivers of species' responses to changing climates (Bonnet et al., 2019; Bradshaw & Holzapfel, 2006; Charmantier et al., 2008; Gienapp et al., 2008; Sauve et al., 2019; Urban et al., 2014). For example, a long-term study on red squirrels revealed that 62% of the change in breeding phenology resulted from phenotypic plasticity, while 13% was attributed to microevolutionary changes (Berteaux et al., 2004). Further, intra- and intergenerational plasticity in response to climate can interact (Wadgymar et al., 2018), and both levels of plasticity can interact with selection (Chevin et al., 2010). For example, when plastic changes are in the same direction as the optimal value favored by selection, which is usually defined as adaptive plasticity (Ghalambor et al., 2007; Gibert et al., 2019), they can delay extinction and allow enough time for populations to evolve (Ghalambor et al., 2007; Gibert et al., 2019). However, they can slow down evolutionary change by reducing the strength of selection, although in directionally changing environments, the benefits of plasticity should exceed the cost of slower adaptation (Chevin et al., 2013). In contrast, non-adaptive plasticity, when a plastic response is in the opposite direction to the optimal selective value, can lead either to the rapid extinction of the population or to a rapid evolutionary response by increasing the strength of selection (Ghalambor et al., 2007; Gibert et al., 2019). To complicate matters further, plasticity can itself evolve (Kelly, 2019; Svensson et al., 2020). The grounds for a conflict between plastic and evolutionary responses particularly exist for ectotherm thermal physiology. Ectotherms may indeed respond to climatic conditions through both a high degree of phenotypic plasticity in response to air temperature (Urban et al., 2016) and selection on heritable traits linked to thermal physiology (Angilletta Jr. et al., 2002).

Ectotherms adjust their thermoregulatory behavior to environmental temperature over time. A lower thermal preference appears to be an efficient plastic response to prevent organisms from experiencing damaging temperatures (i.e., overheating costs; Gvoždík, 2012; Huey et al., 2003). However,

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ectotherm thermal physiology depends upon multiple thermal traits (e.g., thermal optimum and tolerance width, heat absorption, and coloration), that can be linked together and form thermal syndromes (a.k.a thermal types, Goulet et al., 2017). Thus, higher thermal preferences could be correlated with higher thermal optima and critical thermal limits, and thus be positively selected for in warmer temperatures. Some thermal traits have a reduced potential for climate-dependent plasticity and may only change through selection when their evolution is not genetically constrained (Addo-Bediako et al., 2000; Araújo et al., 2013; Buckley & Kingsolver, 2021). Therefore, plastic thermoregulatory behavior may buffer populations against selection on these traits and slow down population shifts toward higher thermal optima and larger tolerances (the "Bogert effect"; Gunderson & Stillman, 2015; Huey et al., 2003; Logan et al., 2019). Given the pessimistic forecasts for ectotherm species (Deutsch et al., 2008; Sinervo et al., 2010), an important challenge is to accurately estimate the complementary and conflicting contributions of plastic and evolutionary responses of thermal phenotypes to species adaptation.

Here, we simulated present-day and warmer climatic conditions in 16 semi-natural mesocosms during a 2-year experiment (Figure 1, Bestion et al., 2015b), and studied three main thermal phenotypic traits (i.e., dorsal skin darkness, color contrast, and preferred temperature) and body size in the most widespread terrestrial reptile species, *Zootoca vivipara* (Roitberg et al., 2013). We first estimated the repeatability and the genetic and environmental variance components of these traits using a quantitative genetics design. We then estimated phenotypic changes in response to climatic conditions and the mechanisms underlying these changes (i.e., degree of intragenerational plasticity and selective gradients). Last, we studied how climatic conditions experienced by mothers the year before gestation affected juvenile traits through inter-generational plasticity. In previous studies, we found strong detrimental effects of warmer climates on adult lizards' survival with potential consequences on population dynamics and structure (Bestion et al., 2015b; Pellerin et al., 2022). However, lizards might be able to acclimate and/or adapt to warmer climates to a certain extent through changes in their thermal traits and syndromes. We expect lizards in warmer climates to display lower thermal preferences (Gvoždík, 2012; Huey et al., 2003), lower dorsal darkness to reduce heat gain (thermal melanism hypothesis, Clusella-Trullas et al., 2007), and lower dorsal contrast (as found in a short-term nocturnal warming experiment, Rutschmann et al., 2021), either through plasticity or selection. Finally, we expect that trait covariation, i.e., thermal syndromes, may be affected by climate as individuals that have both higher thermal preferences and darker skins may be at heightened risk of overheating, and thus potential positive covariation between traits may be lowered either through plasticity and/or selection.

Materials and methods

Studied species

The viviparous subspecies of the common lizard (*Zootoca vivipara*; Jacquin 1787) exhibits intraspecific variation in dorsal darkness patterns (Lepetz et al., 2009) and preferred temperatures (Artacho et al., 2015; Bestion et al., 2015a; Van Damme et al., 1986). Juveniles are visually almost completely dark at birth and variation in darkness increases over the first years of life. Lizards reproduce once a year in the spring, with a an average lifespan of 4–6 years (Romero-Diaz et al., 2017).

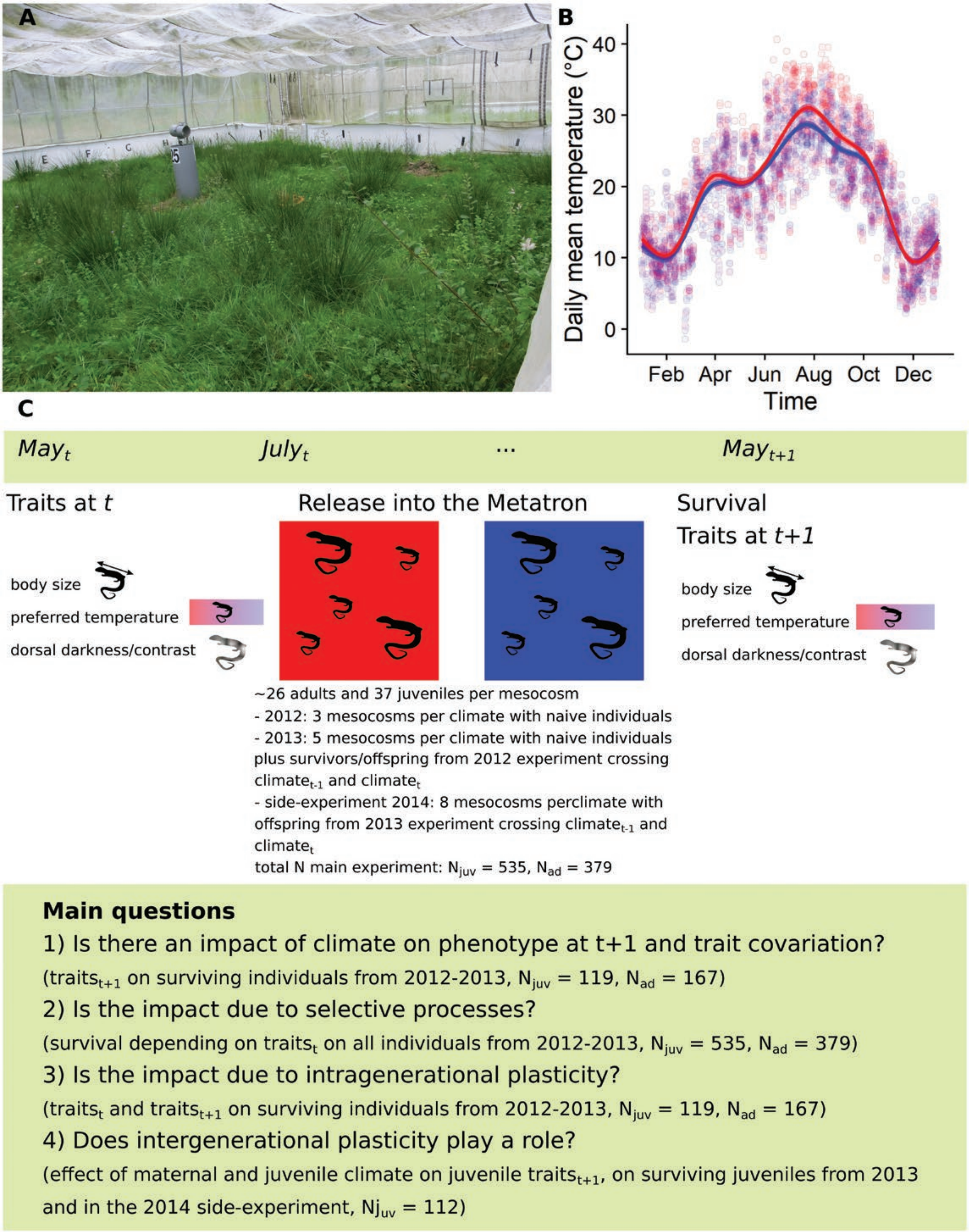
Experimental system and climate manipulation

We performed our experiment in the Metatron, an ensemble of 10 × 10 m semi-natural mesocosms fully enclosed by tarpaulin and fine-meshed nets (Ariège, France, 43°01′ N, 1°05′ E; Legrand et al. 2012). Mesocosms act as mini-ecosystems that are typical of lizard habitats, with diverse natural vegetation (39 ± 9 plant species per mesocosm), invertebrate communities (37 ± 4 insect families per mesocosm) and thermal micro-habitats (shaded, dense and diverse vegetation, hides, sun-battered rocks, and logs and small ponds; Bestion et al., 2015b), but hold no lizard predators. Climatic conditions within the mesocosms are monitored continuously and can be manipulated using motor-driven shutters (Bestion et al., 2015a, 2015b).

Lizards were captured in 2010 from natural populations (France, 44°27′ N, 3°44′ E), marked by toe-clipping, translocated to the Metatron, and maintained for two years prior to the experiment in "present-day climate" conditions, allowing acclimation. Between May 2012 and 2014, we performed two studies that manipulated summer climatic conditions and monitored the consequences on lizard populations (Bestion et al., 2015b). We used data from these two 1-year experiments to test for intra-generational plasticity and selection in response to warming. In addition, we used data from on offspring in 2013 and 2014 from mothers who have participated in the warming experiment in 2012 and 2013, respectively, to study the impacts of inter-generational plasticity in response to warming. Note that the experiments included the possibility for lizards to disperse through 20 m-long corridors opened between mesocosms (Bestion et al., 2015b). Dispersing lizard were caught in pit-fall traps at the end of the corridor, identified and released in another mesocosms. For the purpose of this study, we focus only on resident lizards.

Over the 2 years of the experiment, we manipulated climatic conditions inside several Metatron mesocosms. We originally created three climate treatments in 2012, a "present-day climate" (PC), an 'intermediate climate" (IC), and a "warm climate" (WC), but in the course of running the 2012 experiment, we realized that the intermediate climate treatment induced similar temperatures to the warm climate treatment. We thus decided to drop this intermediate treatment in the 2013 experiment. For the purpose of the study, we focus only on the present-day and warm climates, resulting in three mesocosms per climate in 2012 and five mesocosms per climate in 2013 (Figure 1). Mesocosms were randomly assigned a treatment each year so that present-day mesocosms in 2012 could become either present-day or warm climate mesocosms in 2013. We further chose the mesocosms to be initially homogeneous among treatments in respect to plant cover ($F_{1,14}$ = 0.24, p = .63), plant composition ($F_{1,14}$ = 1.69, p = .21), and invertebrate diversity ($F_{1,14}$ = 0.11, p = .74).

Climatic conditions inside of the mesocosms were manipulated with automatic shutters above the mesocosm, that were allowed to close when temperature exceeded 28°C for the present-day climate and 38°C for the warm climate. Enclosed habitats are warmer than outside habitats. Closing the shutters both stopped temperature from rising and caused temperatures to drop, evening out temperature peaks. The present-day climate mesocosms thus corresponded to the local area's climate, while the warm climate mesocosms were on



~26 adults and 37 juveniles per mesocosm

- 2012: 3 mesocosms per climate with naive individuals
- 2013: 5 mesocosms per climate with naive individuals plus survivors/offspring from 2012 experiment crossing climate_{t-1} and climate_t
- side-experiment 2014: 8 mesocosms perclimate with offspring from 2013 experiment crossing climate_{t-1} and climate_t

total N main experiment: $N_{juv} = 535$, $N_{ad} = 379$

Main questions

1) Is there an impact of climate on phenotype at t+1 and trait covariation?

(traits$_{t+1}$ on surviving individuals from 2012-2013, $N_{juv} = 119$, $N_{ad} = 167$)

2) Is the impact due to selective processes?

(survival depending on traits$_t$ on all individuals from 2012-2013, $N_{juv} = 535$, $N_{ad} = 379$)

3) Is the impact due to intragenerational plasticity?

(traits$_t$ and traits$_{t+1}$ on surviving individuals from 2012-2013, $N_{juv} = 119$, $N_{ad} = 167$)

4) Does intergenerational plasticity play a role?

(effect of maternal and juvenile climate on juvenile traits$_{t+1}$, on surviving juveniles from 2013 and in the 2014 side-experiment, $Nj_{uv} = 112$)

Figure 1. The Metatron, climatic treatments and experimental design. (A) Picture of the inside of one mesocosm. Each mesocosm is 100 m² with natural vegetation and insects. (B) Daily mean temperature during lizard activity period (10:00–18:00) in the mesocosms over the year for the two climatic treatments (blue: present-day climate (PC), red: warm climate (WC), points and smoothed curve from a gam model with cubic splines with the default ggplot method). Climatic treatments are active from June to the end of September using automatic shutters (see Bestion et al. (2015b) for details). The present-day climate mesocosms corresponded to the local area's climate, while the warm climate mesocosms had on average 2°C warmer mean daily temperatures (mean daily temperature between mid-June and mid-September: PC, 26.4 ± 0.3°C and WC, 28.3 ± 0.3°C) and 3°C warmer maximum daily temperatures (Fig. 1, SA1, maximum daily temperature: PC, 29.2 ± 0.3°C and WC, 32.3 ± 0.3°C). (C) Experimental design and main questions. The same procedure was applied every year for 2 years, in 2012 (experiment beginning in May 2012 and finishing in May 2013), and in 2013 (experiment beginning in May 2013 and finishing in May 2014). In addition, a side experiment in 2014, added to the 2013 dataset, allowed testing the effects of intergenerational plasticity. Please note that the total *N* for each step may slightly vary as we missed some data points for some traits at some time points, please refer to the *N* reported in each table for more details.

average 2°C warmer during the summer (mean daily temperature between mid-June and mid-September: PC, 26.4 ± 0.3°C and WC, 28.3 ± 0.3°C [mean ± SE], $F_{1,238} = 22.1$, $p < .001$; maximum daily temperature: PC, 29.2 ± 0.3°C and WC, 32.3 ± 0.3°C, $F_{1,238} = 54.4$, $p < .001$; Bestion et al., 2015b; Figure 1, Supplementary Figure SA1), which is consistent with Intergovernmental Panel on Climate Change projections for southern Europe in 2080 (IPCC, 2021), while the treatments effects were negligible during winter and spring. Importantly, maximum temperatures are below the critical thermal limits of common lizards (Van Damme et al., 1991), and the mesocosms provide many opportunities for thermal refuges, thus selection is unlikely to act through strong physiological damage. However, climate warming could act through increased metabolic demands increasing the risk of physiological exhaustion, potential increases in intraspecific competition, or reduced thermal windows for activity and foraging before retreating into thermal refuges (Sinervo et al., 2010), which could all affect lizard survival and mediate selection on thermal traits.

Experimental design and procedures

We used the same experimental procedure in both 2012 and 2013 (Figure 1). Mid-May, we captured all surviving lizards from the mesocosms. The lizards were measured for snout-vent length, weighed, and a tail tip (for paternity analyses, see below), and a dorsal picture were taken to measure dorsal darkness and dorsal contrast (see below). The lizards were kept in individual terraria following the methods described in Bestion et al. (2015b). After 1 week of acclimation to laboratory conditions, we measured their preferred temperature in a thermal gradient (see below). Between early June and mid-July, females laid eggs in the terraria. Offspring were marked and measured for natal snout-vent length and body mass, sexed (Lecomte et al., 1992), and a tail tip was taken. Three days after birth, we measured their preferred temperature.

Lizards were released into the mesocosms from June to early July following the experimental design described in Bestion et al. (2015b), to form 16 small populations in total released into 3 mesocosms per climate (i.e., 6 mesocosms) in 2012, and 5 mesocosms per climate (i.e., 10 mesocosms) in 2013. Each mesocosm contained 11 ± 1 two-or-more-year-old (2+ yo) females, 6 ± 1 (2+yo) males, 9 ± 2 one-year-olds (1yo) and 37 ± 4 juveniles (<1yo). There were no statistically significant differences between treatments in a suite of phenotypic traits at release (body size [adults: $F_{1,423}= 0.10$, $p = .75$, $R^2 < 0.001$; juveniles: $F_{1,589} =0.68$, $p = .41$, $R^2 = 0.001$], preferred temperature [adults: $F_{1,420} = 1.76$, $p = .19$, $R^2 = 0.004$; juveniles: $F_{1,583} = 0.11$, $p = .75$, $R^2 < 0.001$], adult dorsal darkness [$F_{1,355} = 0.29$, $p = .59$, $R^2 = 0.001$], and adult dorsal contrast [$F_{1,355} = 1.62$, $p = .20$, $R^2 = 0.005$]). Populations from the 2012 and 2013 experiments were formed slightly differently. The initial populations in 2012 were formed by lizards translocated to the Metatron in 2010 and maintained for 2 years prior to the experiment in holding mesocosms in present-day climate conditions. For this experiment, juveniles from each clutch were released together in the same mesocosm. In 2013, populations were composed of both surviving lizards from the 2012 experiment and offspring from those lizards, and from lizards maintained in holding mesocosms in present-day climate conditions throughout 2012. Adult and yearling lizards surviving the 2012 experiment (i.e., alive in May 2013) were re-assigned randomly a temperature treatment in 2013, so that half of the lizards from each treatment were assigned the present-day climate and half were assigned the warm climate. Further, juveniles born from the mothers that had survived the 2012 experiment were distributed among mesocosms leading to a split-clutch design crossing maternal and juvenile climates and thus allowing us to test the interactive effects of maternal and juvenile exposure to a warmer climate on the development of juvenile traits. This dataset was supplemented by a side experiment in 2014, in which juveniles born from the mothers that had survived the 2013 experiment were released into the mesocosms for a different experiment on climate and connectivity, similarly splitting clutches of juveniles among climates. We used juveniles released into this side experiment together with the 2013 juveniles in order to study how traits developed depending on maternal and juvenile climates on a larger sample size and on juveniles from all mothers included in main analyses. This design allowed us investigate intergenerational plasticity and its interaction with climatic conditions experienced by juveniles on their phenotypic traits at 1-year old.

Lizards spent the summer, winter and spring in the mesocosms, and the following May, we re-captured all survivors during repeated capture sessions (>10 sessions). The lizards were measured, weighed, assessed for their preferred temperature and dorsal darkness and contrast again, and maintained in the laboratory until female parturition.

Phenotypic traits

Preferred temperature

Preferred temperature was measured following Bestion et al. (2014, 2015a). Tests were performed in eight 100 × 20 × 40-cm glass terraria in a controlled temperature room (18°C, Supplementary Figure SA2). Marks on the floor divided the terraria into ten 10-cm zones, and a movable divider created a 10-cm acclimatization zone at one end. A light bulb (60 W) was set at the opposite end, which created a temperature gradient from 45.8 ± 0.8°C to 19.4 ± 0.6°C. We quantified temperature gradients using thermometers placed every 10 cm in an additional terrarium. Individuals were maintained in the controlled temperature room without heat or light on the morning of the test and were tested within a few hours, avoiding differences in the motivation of lizards to thermoregulate. Lizards were individually placed in each terrarium in the acclimatization zone at the coolest part of the gradient, and left for 10 min before the divider was removed. A video camera above the terrarium recorded the individuals' positions for 30 min, and each zone's temperature was recorded at the end of each trial. The videos were analysed using The Observer software to calculate the preferred temperature as the mean of the temperatures in each zone in which the focal lizard stayed during the experiment weighted by the time spent at each position. The preferred temperature was strongly correlated to mean body temperature (intercept = 0.42 ± 0.79, slope = 0.99 ± 0.03, $R^2 = 0.90$, $F_{1,118} = 1016$, $p < .001$), which was measured during the test in 2014 using an ultra-thin thermocouple (Omega T-type 5SC-TT-T-40–72) taped onto the belly of 119 adults and connected to a computer with Omega PT-104A software through a data acquisition module (Omega TC-08). The preferred temperature is repeatable over 2 weeks in juveniles ($R = 0.43$ [0.19, 0.54], Bestion et al., 2015a), and over pre- and post-laying in gravid females ($R = 0.25$ [0.09, 0.39], $p = .002$ on 132 females).

Dorsal darkness and contrast

The lizards were scanned using a computer scanner (Canon Canoscan Lide 110, resolution 400 dpi) lined with high-density foam to protect them. Using a computer scanner prevented luminosity differences between pictures. Dorsal darkness was determined using ImageJ (Supplementary Figure SA3; Schneider et al. 2012). We delimited a section on the median part of the back between the legs and two lateral sections on the flanks, transformed the pictures into 32-bit black-and-white ones, and measured darkness as the proportion of black pixels in the delimited parts using the greyscale threshold option (threshold: 45). We calculated mean dorsal darkness as the mean of the median and lateral parts, and dorsal contrast as the absolute darkness difference between the flanks and median parts divided by median darkness. Such measurements were reliable (repeatability of mean dorsal darkness $R = 0.94$ [0.90, 0.97], $p < .001$, of dorsal contrast $R = 0.90$ [0.83, 0.94], $p < .001$ on 46 individuals), and strongly correlated with visual melanism scores blindly taken by an experienced observer (Pearson's $r = 0.60$ [0.58, 0.71], $p < .001$ for 354 individuals).

Genetic data and paternity analyses

Lizard genomic DNA was extracted from tail tips using a QIAquick 96 Purification Kit (QIAGEN) following the manufacturer's instructions after a proteinase K digestion. Individuals were genotyped using eight microsatellite markers (Richard et al., 2012). We checked for perfect matches between juveniles and their mothers and assessed paternity using CERVUS v.3.0 (Bestion et al., 2015b; Kalinowski et al., 2007). This allowed creating a pedigree with a total of 722 individuals, including 187 founders (87 males and 100 females). The pedigree included 535 dam-offspring links, 480 sire-offspring links (some paternities missing due to issues in attribution), with 62% of full-sib clutches and 38 % of half-sib, a mean maternal sibship size of 4.2, a mean paternal sibship size of 4.6, and a maximum pedigree depth of 3 generations with 44 individuals pertaining to the third generation. The pedigree was used in the animal models to calculate additive genetic, maternal and environmental variances of offspring traits.

Statistical analyses

Analyses were done in R v4.0.5. Data and code are available on Zenodo (Bestion et al., 2023). We investigated the effects of the climatic treatments on individual phenotype (mean dorsal darkness, dorsal contrast, preferred temperature, and body size) and on selective and plastic processes involving these traits with linear and generalized linear mixed models using *lmer* package (Bates et al., 2015). We analyzed data for 379 adults (including 1yo and 2+yo, $N = 154$ in 2012 and 225 in 2013) and 535 juveniles (228 in 2012 and 307 in 2013), but the exact sample size varied with the analysis (e.g., on all individuals or survivors only), and is thus presented for each table. All mixed model analyses followed the same fitting and simplifying procedures, with a full model and all derived simpler models compared through AIC (see model fitting subsection, and Supplementary Figure SA5 for equations of each model). Mixed modeling allowed the inclusion of various random intercepts, depending on the model (see individual model descriptions): (a) a clutch effect in juveniles to account for family non-independence; (b) population identity to account for variation among populations; and (c) individual identities for adults when individuals appeared in both experimental years. We first investigated whether there was an impact of climatic conditions on phenotype measured the year after (at t+1), both on individual traits and trait covariation (i.e., thermal syndrome). Second, we assessed whether traits were likely to evolve in response to selection, by (a) testing the heritability of these traits, (b) testing whether survival differs in each climate, and (c) measuring selection gradients in each climate. Third, we considered whether intragenerational plasticity could play a role, by testing the interaction between time (t or t+1) and climatic treatments on the trait values taking only the individuals surviving until t+1 (see Supplementary Figure SA4 for a flow diagram). It therefore analyses temporal phenotypic changes resulting only from differential plastic responses among climates. Finally, we investigated intergenerational plasticity by testing the additive and interactive effects of maternal climatic treatments the year before and juvenile climatic treatments on juvenile traits at 1 year old.

Effect of climatic conditions at time *t* on phenotype at time *t*+1

We investigated whether summer climatic conditions at time t affected the phenotype measured the year after (t+1) using linear mixed models (Supplementary Figure SA4, N_{juv} ~119, N_{ad} ~ 167). Dorsal contrast was log-transformed. Full models for adults included climatic treatment and its interaction with age class (1yo or 2+yo) and sex, plus body size, year of experiment as fixed covariates, and random intercepts for population and adult identities. For juveniles, we included climatic treatment and its interaction with sex and birthdate plus body size, year as fixed covariates, and random intercepts for clutch and population identities.

We also investigated how climate affected covariation between traits (i.e., thermal syndrome) through structural equation modeling using the *lavaan* package, both for juveniles and adults. We tested for the presence of phenotypic covariation between traits within the present-day and warmer-climate treatments, as well as differences in trait covariation between present-day and warmer climates. We created a path model that included dorsal darkness, log-transformed contrast, preferred temperature and body size, and all two-way covariations. We compared covariances among traits between present-day and warmer climates using a nested model approach, which compared a null model (with all covariances being equal between climates) to sub-models in which one of the covariances (e.g., body size-preferred temperature covariance) differed between climates. Models were ranked by ΔAIC. When two models with one covariance differing between climates had lower AIC than the null model, we created a model with two covariances differing between climates. We also provided covariances from the model with all covariances differing between the climates, as well as from the best model.

Variance components and heritability

We used an animal model with MCMCglmm (Hadfield, 2017; Riska et al., 1985; Wilson et al., 2010) to partition the additive (V_A), maternal (V_M), and—for traits measured at 1-year old—environmental components of variance (V_E, i.e., population effect), for the preferred temperature and body size (at birth and at 1-year old), and dorsal darkness/contrast at 1-year old. We included year as a fixed effect and the random effects of animal (pedigree-derived relatedness), mother, and for traits measured at 1-year old, population identity (Supplementary Figure SA4, N_{juv} ~535). We ran the analyses with three sets of priors, one non-informative, one weakly informative and one strongly informative (Supplementary Table SF1). We ran 1,000,000 iterations with a burn-in of 3,000 and a thinning of 1,000.

Selection

We first tested whether selection was influenced by climatic treatments, and then we measured selection gradients (Janzen & Stern, 1998) and differentials for phenotypic traits separately in the two climatic treatments. To do so, we investigated whether phenotype at time *t* (i.e., dorsal darkness, dorsal contrast, preferred temperature, and body size for adults, and only preferred temperature and body size for juveniles, as juveniles appear completely black at birth) affected annual survival between time *t* and time *t*+1 in the two climates using GLMMs (family: binomial, Supplementary Figure SA4, N_{juv} ~529, N_{ad} ~ 312).

First, we studied how climate could affect selection through multivariate regressions (Lande & Arnold, 1983). We centered and scaled the phenotypic traits by year to zero mean and unit variance (Lande & Arnold, 1983). We checked for impacts of climate on directional selection by using a global model including all interactions between climate and each trait of interest (e.g., climate × darkness) or between climate and covariates (sex and either age class [adults] or birthdate [juveniles]), and added year as a fixed effect and random intercepts (population and, for juveniles, family identity).

Second, we measured selection gradients and selection differentials on survival separately by climate. Assessing selection gradients separately by climate allowed taking into account differences in mean fitness between climates and thus get scaled coefficients. Selection differentials analyze the change in the mean value of a trait produced by within-generation selection and quantify the effects of all sources of selection (direct and indirect), while selection gradients measure the direct influence of selection on a trait holding other traits constant (Lande & Arnold, 1983). Thus, presenting the two allows distinguishing selection acting directly on the trait from potential indirect selection caused by phenotypic correlations with other traits under direct selection. Directional selection gradients were calculated separately for present-day and warm climate by modeling survival as a function of the traits of interests plus random intercepts (population and, for juveniles, family identity). We centered and scaled the phenotypic traits by year and by climatic treatment to zero mean and unit variance prior to running the models (Lande & Arnold, 1983). Selection gradients were transformed from logistic regression coefficients to average gradient (βavggrad) following Janzen and Stern (1998) and scaled by mean survival fitness of the individuals in each climate treatment. Directional selection differentials were calculated as the difference in the mean trait value (centered and scaled) before (i.e., at *t*, on all individuals) and after selection (i.e., at *t*+1, on surviving individuals), following Lande and Arnold (1983).

Intra- and intergenerational plasticity

We first checked the repeatability of each trait between *t* and *t*+1 by climate with *rptR* package.

Then, we tested climatic effects on plasticity for dorsal darkness and contrast (on adults) and preferred temperature and body size (adults and juveniles) using a repeated-measures linear mixed model (Supplementary Figure SA4, N_{juv} ~119, N_{ad} ~ 166) in which we studied how the trait depended on the interaction between climate and time (i.e., trait measured at *t* or *t*+1, only on individuals alive at *t* and *t*+1), thus explicitly excluding effects of selection. Full models for adults included time, climate, age class, sex and up to three-way interactions with time, plus year as a covariate and random population and individual identity. Models for juveniles included time, climate, birthdate, sex and up to three-way interactions with time, as well as body size plus year as a fixed factor and random intercepts for population, family, and individual identities.

We then used juveniles in the 2013 + 2014 experiment to test the inter- and intragenerational plasticity with linear mixed models. Global models for each trait included maternal and juvenile climates and their interaction, the interactions between juvenile climate and sex and between birthdate and sex, and body size and year as covariates, plus random intercepts for family and juvenile population identities (Supplementary Figure SA4, N_{juv} = 112).

Model fitting

Models for phenotype at *t*+1, selection and plasticity were fitted with the same procedure. Following Zuur et al. (2009), we fitted global models with maximum likelihood and all relevant fixed variables (i.e., the variables and interactions that we deemed biologically relevant, and not all possible variables and interactions, Burnham et al., 2002) and random intercepts. We checked the global models for residual normality, homoscedasticity, and the absence of collinearity between predictors through variance inflation factors. We then compared the global models with all derived simpler models with AIC using the *dredge* function from *MuMIn* to fit all fixed-variable combinations. If several models fell within ΔAIC < 2, we used model averaging (Grueber et al., 2011) to produce averaged parameter estimates using conditional averages and relative parameter importance with *model.avg* (Barton, 2012). We checked our results' robustness to an increase in the ΔAIC threshold to 4, yielding very similar results (Supplementary Appendix G). We further fitted a model containing all the predictors present in the averaged model to calculate R^2m and R^2c (Nakagawa & Schielzeth, 2013) and random component SD.

Results

Heritability of thermal traits

All traits were moderately to substantially heritable (Supplementary Table SE1), with a narrow-sense heritability of traits ranging depending on the choice of priors from 0.10 [0.02, 0.20] to 0.13 [6e-6, 0.26] (median [95% credible interval]) for thermal preference at birth, from 0.57 [0.39, 0.74] to 0.71 [0.55, 0.85] for body size at birth, from 0.11 [3e-6, 0.70] to 0.18 [0.02, 0.47] for dorsal darkness at 1-year old and from 0.19 [0.01, 0.62] to 0.41 [2e-4,0.97] for dorsal contrast at 1-year old. Heritability of traits measured at 1-year old was difficult to assess due to mortality before trait measurement, thus they were quite sensitive to priors, with heritabilities close to zero with non-informative priors (Supplementary Table SE1).

Effect of climatic conditions on thermal phenotype

At the end of the experiment, adults from the warmer treatments preferred lower temperatures and displayed lighter colors with lower contrast than those in present-day climates and adult females were larger than in present-day climates (Figure 2, Supplementary Table SB1).

A path analysis supported a difference in covariances between preferred temperature and dorsal darkness and between preferred temperature and dorsal contrast (ΔAIC = 1.63, Supplementary Table SB2). The positive covariation between preferred temperature and dorsal darkness in present-day climates (Figure 2, Supplementary Tables SB2–SB4) was halved in warmer climates, but the negative covariation between preferred temperature and dorsal contrast was not significantly different between climates (Figure 2, Supplementary Tables SB2–SB4).

There were no effects of climate on juvenile preferred temperature and on dorsal contrast at the end of the experiment while male juveniles were darker and all juveniles were larger in warmer than present-day climates (Supplementary Figure SB1, Supplementary Table SB1). We found a positive covariation between darkness and preferred temperature, as in adults, but this covariation did not depend on climatic conditions (Supplementary Figure SB1, Supplementary Tables SB2–SB4). There was also a positive covariation between body size and preferred temperature in both climates, but it was only significant in present-day climates (Supplementary Figure SB1, Supplementary Tables SB2–SB4).

Climate-dependent selection

Body size positively affected adult yearly survival, with the interaction between climate and dorsal darkness retained in the best averaged model on survival with a non-significant *p*-value and a low RI (Supplementary Table SC1). When analyzing each climate separately, there was a positive directional selection gradient for body size that was only significant in warm climate, while dorsal darkness had non-significant positive and negative selection gradient in warm and present-day climate, respectively. Dorsal contrast and preferred temperature had non-significant positive selection gradients in both climates (Figure 3, Supplementary Tables SC2–SC3).

Juvenile survival tended to be affected by an interaction between body size and climate, with non-significant positive selection gradients for body size in present-day climate (Supplementary Figure SC1, Supplementary Tables SC1–SC3).

Climate-dependent intragenerational plasticity

Thermal traits in adults were overall repeatable over a year (Supplementary Table SD1), however this was due to a high repeatability in present-day climate, with a tendency for a

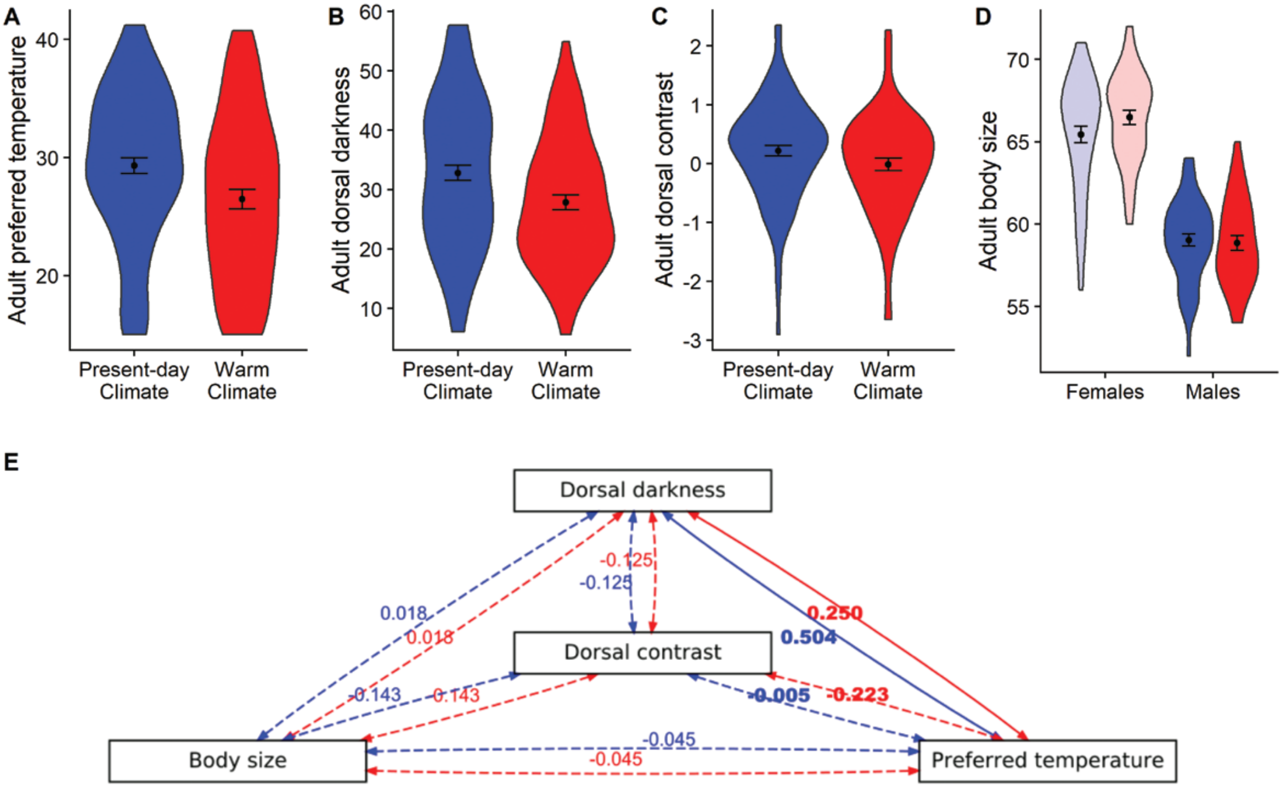


Figure 2. Adult phenotype one year after climatic treatments. (A-D) Effect of climate on single traits. (A) Adult preferred temperature (°C). (B) Adult darkness (%). (C) Adult dorsal contrast (log-transformed). (D) Body size (mm, separated by sex; light color: females, dark color: males) seven months after a three-month climatic treatment. Means ± SEM and violin plots are presented. Warmer climates resulted in significantly lower preferred temperatures, dorsal darkness, and dorsal contrast, and an increased body size in females (see Supplementary Table SB1). (E) Path analysis of the links between the phenotypic variables and climatic condition in adults. Numbers represent covariances between variables in present-day (in blue) and warmer climates (in red), from the best model from a selection of path models with constrained covariances between climates (Supplementary Table SB4). Significant covariations between traits are represented by full lines, non-significant by dashed lines (see Supplementary Table SB4), and covariations that significantly differed between present-day and warmer climates are represented in bold (see Supplementary Table SB2). Warmer climates resulted in a weaker covariation between dorsal darkness and preferred temperature, and a stronger negative covariation between log-transformed dorsal contrast and preferred temperature, although non-significant. *N* = 99 surviving adults were in the present-day climate (95 for preferred temperature) and *N* = 74 surviving adults were in the warmer climate (73 for dorsal darkness and contrast and 72 for preferred temperature).

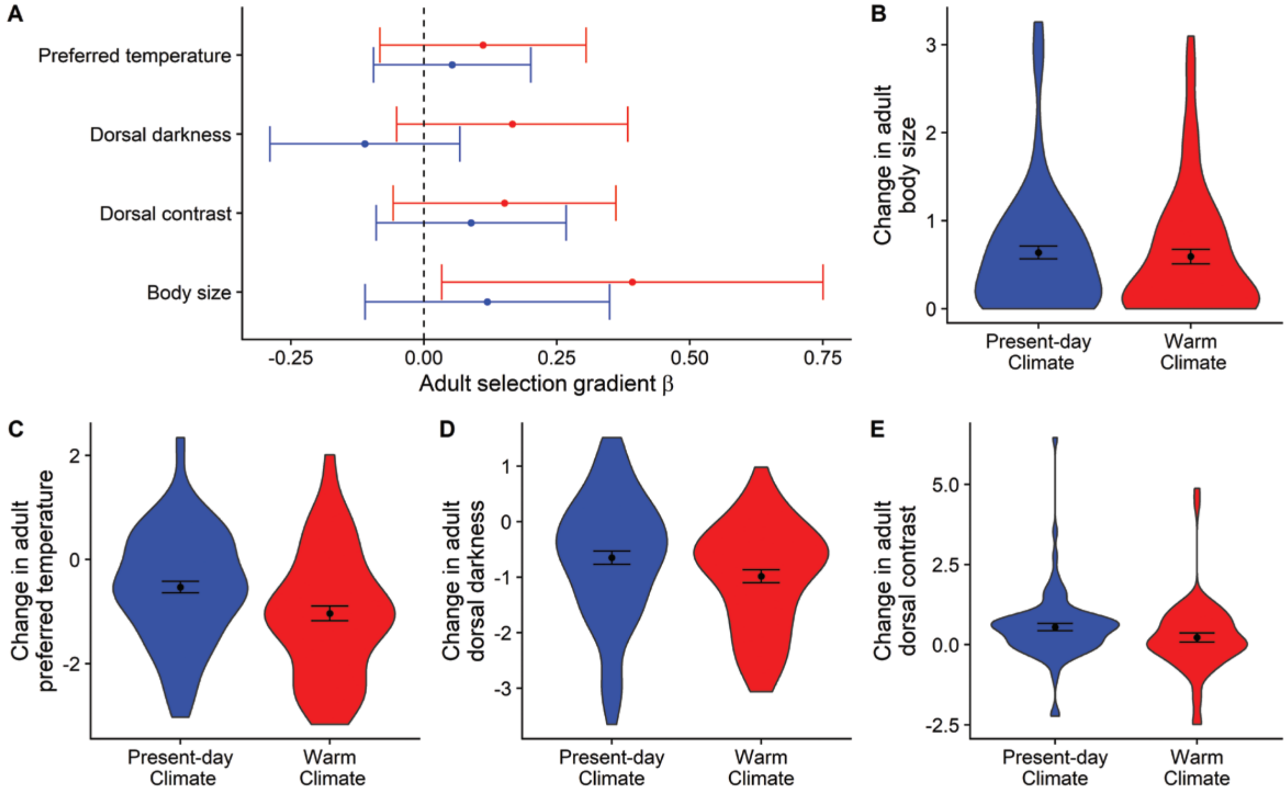


Figure 3. Selection gradients (A) and plastic phenotypic changes (B–E) of adult lizard phenotypic traits in present-day and warmer climates. (E) Selection gradients (and 95% confidence intervals) on adult phenotypic traits in present-day (blue) and warmer (red) climates. Although not always significant, there was a positive directional selection gradient for body size, dorsal contrast and preferred temperature in adult, while there was a reversal in selection for dorsal darkness from negative in present-day climate to positive in warm climate (Supplementary Table SC2). N = 160 adults in present-day and N = 152 in warmer climates. (B–E) Effect of climate on adult plasticity. (B) Changes in adult body size, (C) Changes in adult preferred temperature, (D) Changes in adult darkness, (E) Changes in adult contrast over the course of the experiment. Scaled values, means ± SEM and violin plots are presented. Blue bars: present-day climate; red bars: ~2°C-warmer climate. N = 99 surviving adults were in the present-day climate (95 for preferred temperature), N = 74 surviving adults were in the warmer climate (73 for dorsal darkness and contrast and 72 for preferred temperature). Warmer climates resulted in adults plastically decreasing their preferred temperature, dorsal darkness, and dorsal contrast (see Supplementary Table SD2).

lower repeatability in warm climate likely due to plasticity. Indeed, repeated measures on survivors show that adult preferred temperature, dorsal darkness, and dorsal contrast depended on an interaction between climate and time. There was no difference between climates at time t but all these traits decreased more between time t and time t+1 and so had lower values at time t+1 in warmer climates than in present-day climates (Figure 3, Supplementary Table SD2). Plasticity for dorsal darkness and contrast could not be assessed for juveniles, as they appear completely dark at birth, but we were able to assay plasticity for preferred temperature and body size (i.e., growth). There was no interaction between climate and time on preferred temperature, showing no differential plasticity on preferred temperature between climates (Supplementary Figure SD1, Supplementary Table SD2). However, there was a strong interaction between climate and time on body size indicating a faster growth in warmer than in present-day climates (Supplementary Figure SD1, Supplementary Table SD2).

Climate-dependent intergenerational plasticity

When investigating maternal effects (Supplementary Table SF1, Fig. 4), juvenile dorsal darkness and contrast at 1-year old depended on the interaction between maternal and juvenile climates, whereby juveniles from mothers in warm climates were darker and less contrasted when they lived themselves in warm climates and conversely for juveniles from mothers in present-day climate. Maternal climate did not significantly influence preferred temperature and body size.

Discussion

Warmer climates led to differences in lizard body size and thermal traits. Adults preferred lower temperatures, were paler and less contrasted and the positive covariance between the preferred temperature and dorsal darkness (i.e., thermal syndrome) was halved. Survival analyses showed that differential selection between climates did not explain phenotypic differences between climates, even if there were positive directional selection gradients for body size in warm climate only, and a slight differential selection between climates on dorsal darkness. In contrast, differences in adult thermal traits between climates resulted from differential phenotypic plasticity between climates, with a stronger decrease in preferred temperature, dorsal darkness, and dorsal contrast of adults over time in warmer climates. As shown in other species (Artacho et al., 2013; Clusella-Trullas et al., 2007; Paranjpe et al., 2013; Roulin, 2014), thermal preferences and skin darkness consistently vary among individuals, with some individuals preferring higher temperatures and being darker than others. Thermal traits can form a thermal syndrome along a cold-hot continuum of thermal adaptation

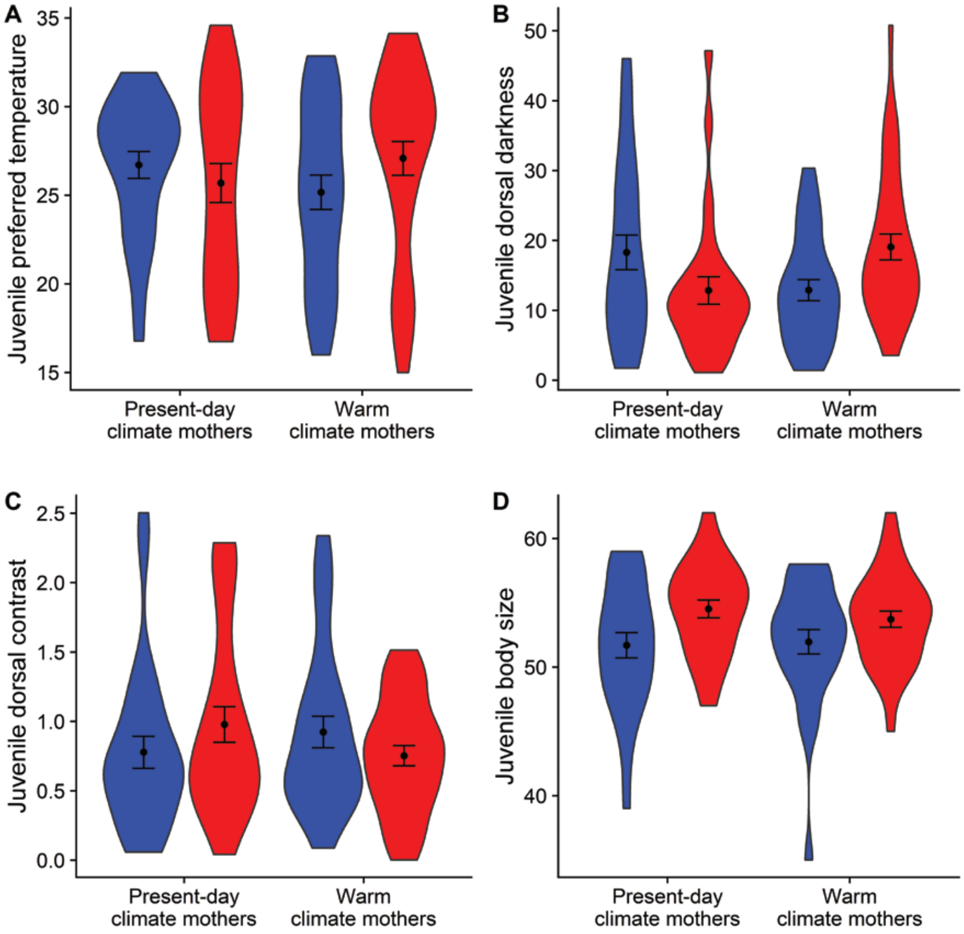


Figure 4. Effect of maternal and juvenile climate on juvenile traits. (A) Juvenile preferred temperature (°C), (B) Juvenile dorsal darkness (%), (C) juvenile dorsal contrast (log-transformed), and (D) juvenile body size (mm) at 1-year old depending on both maternal and juvenile climates. Means ± SEM and violin plots are presented. Blue bars: present-day climate; red bars: ~2°C-warmer climate. N = 26 juveniles from mothers in present climates and that lived themselves in present climates, 27 juveniles from mothers in present climates that lived in warm climates, 27 juveniles from mothers in warm climate that lived in present climate, and 32 juveniles from mothers in warm climates that lived in warm climate. Juveniles issued from mothers in warmer climates were darker and less contrasted when they were subjected to warmer climates themselves, the reverse being true for juveniles from mothers in present-day climates (see Supplementary Table SF1).

(Goulet et al., 2017), as supported by the positive covariation between dorsal darkness and preferred temperature here and by results in *Cordylus cordylus* lizards (Aguado & Clusella-Trullas, 2021). A side controlled heating experiment shows that darker adult individuals heated up faster than lighter ones (Supplementary Appendix H), in accordance with the thermal melanism hypothesis (Clusella-Trullas et al., 2007). Consequently, in this species, some individuals prefer higher temperatures, warm up faster thanks to their darker skin and so should have a higher thermal optimum.

If thermal traits are partly genetically determined, warmer climates may exert an upward selection on these thermal traits that favors higher thermal optima in warmer environments, and species adaptation to warmer climates. Current evidence suggests that there is low additive genetic variation in behaviors related to thermal preference (Logan et al., 2018; Paranjpe et al., 2013), which dramatically limits the rate of evolutionary response under projected levels of climate change (Sinervo et al., 2010), while melanism is more heritable in several species (Roulin, 2016). Here, additive genetic effects inherited from both parents, and to a lesser extent, maternal effects, explained a proportion of the variance in the thermal preference, and dorsal color traits (darkness and contrast). We found that selection gradients and differentials for darkness were overall weak, but tended to be different between climates and in the direction of darker skin in warmer climates. However, a plastic response on these traits may have changed the strength of selection. Thermal traits can indeed be highly plastic, in particular the behavioral choices of thermal microhabitats (Basson & Clusella-Trullas, 2015). Lizards can retreat to cool refugia when operative temperatures on the surface exceed their physiological limits (Sinervo et al., 2010). This plastic response prevents increased energy expenditure and the risk of overheating that excessive warming of the body would induce (Angilletta Jr. et al., 2002; Artacho et al., 2013), but reduces the time spent foraging (Sinervo et al., 2010). For example, climate warming increases the amount of time that *Sceloporus* lizards spend hiding in cool refugia to prevent overheating, which restricts their activity budget and precipitates contemporary extinctions (Sinervo et al., 2010). However, if heatwaves are chronic or continuous, lasting plastic responses may reduce survival rates. In our study, lizards indeed altered their thermal traits and this alteration was still visible seven months after encountering warmer conditions, as our climatic treatments were only active from July to early October and lizard phenotype was assessed the following June. Therefore, plastic changes in lizard traits may allow them to avoid overheating during the summer, but may come at the cost of achieving body temperatures farther from the optimum during autumn and spring. Another possible cost of such mitigation responses is that selection pressure on these traits is decreased, so evolutionary adaptation to future warmer climates is weakened (Buckley & Kingsolver, 2021; Logan et al., 2019).

How can the plastic changes we observed interact with selection to drive evolution in the long term? Effects of plasticity on the speed of evolution depend upon whether plasticity is adaptive or not (Coulson et al., 2017; Ghalambor et al., 2007; Gibert et al., 2019), and on the difference between the environmental sensitivity of selection and phenotypic plasticity (Chevin et al., 2010). While selection gradients were relatively weak and so the results should be cautiously interpreted, we found that plastic changes in adult thermal phenotype were in the opposite direction to the mean value of the selection gradients observed for dorsal darkness. This is usually defined as maladaptive plasticity (Ghalambor et al., 2007; Gibert et al., 2019), even if the adaptiveness of plasticity will depend on, e.g., the autocorrelation between environments in which development and selection occur and the time window to estimate fitness (Chevin & Lande, 2015). For example, in our study, plastic changes tended to temporarily improve individual survival to warmer climates. Indeed, individuals displaying a greater decrease in dorsal darkness and contrast tended to have improved survival the following year in warmer climates only, although these results should be interpreted cautiously due to the low sample size (see side experiment in Supplementary Figure SD2, Supplementary Table SD3). Further, as plastic changes conjointly occurred with selection, our estimates of selection were probably influenced by plastic responses and conversely, with potential for such maladaptive plasticity increasing the strength of selection (Ghalambor et al., 2007; Gibert et al., 2019). We hypothesize that in ambient climatic conditions, a higher thermal preference and skin darkness positively affects lizard survival by allowing a more efficient thermoregulation, provided air temperature does not exceed a given threshold. Above this threshold, warmer preferences and a darker skin become detrimental and plasticity may become beneficial. Male juveniles were darker at one-year-old in warmer climates. This could have resulted from plasticity being in the same direction as the optimal selective value (i.e., adaptive optimum) for juveniles, or from selective processes toward darker coloration. In contrast to their negative effect on adult survival, warmer climates do not induce overheating costs and are actually beneficial for juveniles with a faster growth rate (and thus larger body size at 1-year old), an earlier access to reproduction and even a better survival (Bestion et al., 2015b; Pellerin et al., 2022). Therefore, we should see a selective advantage for warmer phenotypes in juveniles, which could explain the observed differential impact on dorsal darkness between age classes. Unfortunately, we were unable to measure darkness at birth and tease apart plasticity from selection. However, we found that intergenerational plasticity further influenced juvenile responses to climate. In warm climates, juveniles developed darker and less contrasted skins when their mothers were in warm climates as well, while they actually became paler and more contrasted when their mothers were from present-day climates. Intergenerational plasticity is widespread among taxonomic groups (Salinas et al., 2013) and allows rapid responses to fast environmental changes consistent across generations (i.e., predictive environments). Parental effects should be an important mechanism in resilience to changing climates (Meylan et al., 2012; Paranjpe et al., 2013; Visser, 2008). As in adults, juveniles were paler when climates were warmer on a single generation and were darker when climates were repeatedly warmer across generations. An explanation would be the repeated occurrences of warmer conditions over time influencing the costs and benefits of responses to warming; avoiding overheating through a paler color or increasing warmer optimum through a darker color. Regardless of the right explanation, it suggests that both intra- and intergenerational plasticity interacted to influence rapid responses of juveniles to warmer climates.

Warmer climates may further drive adaptation by increasing heritability, and, consequently, responses to selection (Gibert et al., 2019); however, deeper pedigrees with more generations are needed to study potential differences in additive genetic variance and heritability of traits and traits' covariance between climatic conditions. Finally, large environmental changes such as these warmer climates can drive evolution by selecting for increased plasticity, which can accelerate adaptive evolution of the mean phenotype (Lande, 2009). Further studies are needed that investigate longer temporal scales to confirm or invalidate our hypotheses, and elucidate evolutionary responses to warmer climates.

In conclusion, we suggest the existence of thermal syndromes of dorsal darkness and thermal preference that are disrupted by climate, with a lower thermal preference, a lower skin darkness and a lower covariation between the two in warm climates. The response to warmer climates was mainly driven by both intra- and intergenerational plasticity, which was maintained over time as measurements were done eight months after the summer warming experiments. There was only a weak selection that went in the opposite direction to the plastic changes. The observed plasticity might reduce overheating and allow lizard populations to acclimate to climate change in the short term. However, the populations studied were declining, suggesting that acclimation was not strong enough (Bestion et al., 2015b, but see Pellerin et al., 2022). Acclimation could further interact with selection to drive the evolutionary adaptive potential of ectotherm species in a warming world, as evidenced by the plastic changes being in the opposite direction to the selection gradients, thus potentially accelerating adaptation. Current models that investigate the future impacts of climate change tend to ignore the potential for plastic and evolutionary change in species' traits (Deutsch et al., 2008; Sinervo et al., 2010, but see Bonebrake & Mastrandrea, 2010; Huey et al., 2012). Including such potential might allow for a better forecasting of future extinction risks.

Supplementary material

Supplementary material is available online at *Evolution* (https://academic.oup.com/evolut/qpad070)

Data availability

Data and code are available on zenodo (http://dx.doi.org/10.5281/zenodo.7845944).

Ethical statement

Experiments followed French ethics regulations and CNRS institutional ethics guidelines. We applied the 3R rule by reducing the number of lizards to the minimum to form enough populations and providing care appropriate to the species. Lizards were captured from the wild according to the capture licence number 2010-189-16 DREAL and transferred to the laboratory (laboratory use of animals: agreement B09583). Experiments were started before the need of obtaining a permit following French law (article R.214-113, ordonnance 2012-10, décret 2013–118, arrêtés 1er février 2013, transposing EU directive 2010/63/UE), however we then obtained a permit for further experiments following the same procedure (permits number APAFIS#15897-2018070615164391 v3 and APAFIS#19523-201902281559649 v3 obtained from the ethics comity n°068).

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Author contributions

EB and JuCo designed the study, EB, LDG, OC, OG, and JuCo performed the experiment, MR performed the extractions, the polymerase chain reaction and analyzed the paternity data. EB and JuCo analyzed and interpreted the data. BS, JeCo, and LSJ provided assistance with the animal models. EB and JuCo wrote the first draft and LSJ, BS, MR, and JeCo significantly contributed to redrafting.

Conflict of interest: The authors declare no competing interests.

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