

Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*

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Abstract

Recent global warming threatens many species and has already caused population- and species-level extinctions. In particular, high risks of extinction are expected for isolated populations of species with low dispersal abilities. These predictions rely on widely used 'climatic envelope' models, while individual responses, the ultimate driver of a species response to climate change, have been most often neglected. Here, we report on some changes in life-history traits of a dispersal-limited reptile species (a poorly studied taxa) living in isolated populations. Using long-term data on common lizards collected in southern France, we show that individual body size dramatically increased in all the four populations studied over the past 18 years. This increase in body size in all age classes appeared related to a concomitant increase in temperature experienced during the first month of life (August). Daily maximum temperature in August increased by 2.2 °C and yearling snout-vent-length increased by about 28%. As a result, adult female body size increased markedly, and, as fecundity is strongly dependent on female body size, clutch size and total reproductive output also increased. For one population where capture–recapture data were available, adult survival was positively related to May temperature. All fitness components investigated therefore responded positively to the increase in temperature, such that it might be concluded that the common lizard has been advantaged by the shift in temperature. We contrast these short-term results with the long-term habitat-based prediction that these populations located close to mountain tops on the southern margin of the species range should be unable to cope with the alteration of their habitat. To achieve a better prediction of a species persistence, one will probably need to combine both habitat and individual-based approaches.

Keywords: body size, fitness, global warming, life-history trade-offs, lizards, mountain habitat reproduction, survival

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Introduction

Assessing species' responses to climate change is one of the greatest challenges for ecologists because global warming is expected to be a major threat for biodiversity in coming years (Hughes, 2000; McCarty, 2001; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Thomas *et al.*, 2004). A recent study showed that up to 37%

of species on Earth might be threatened by extinction because of the recent rise in temperature (Thomas *et al.*, 2004). Climatic shifts and establishments of isotherms at higher latitudes will cause numerous species distribution shifts with the consequence of disrupting communities, altering species' abundance, increasing fragmentation of habitats and therefore increasing probabilities of population extinctions (Brown *et al.*, 1997; Davis *et al.*, 1998; Peterson *et al.*, 2002). In that context, isolated (e.g. island, mountain) populations or species with limited dispersal abilities appear at especially high

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risk as available altitudinal or latitudinal gradient is limited. Global warming-driven extinction in these situations indeed has already been reported (Pounds *et al.*, 1999).

Multiple life-history traits have been demonstrated to respond to the fast increase in temperature (e.g. clutch size: Winkler *et al.*, 2002; overall breeding success: Barbraud & Weimerskirch, 2001; Sanz *et al.*, 2003 and sex-ratio: Post *et al.*, 1999). In particular, advancement in phenology is among the most widely reported effect (Beebee, 1995; Crick & Sparks, 1999; Dunn & Winkler, 1999; Gibbs & Breisch, 2001; Peñuelas *et al.*, 2002; Réale *et al.*, 2003; Visser *et al.*, 2003; Gordo *et al.*, 2005; Sparks *et al.*, 2005). However, a striking conclusion of these studies is the evidence that (1) the reported effects are clearly species and populations dependent, and (2) in some cases, populations responded in a nonlinear way to a rise in temperature. In turn, this is likely to cause changes in community compositions and mismatches within the environment (Harrington *et al.*, 1999; Visser & Holleman, 2001; Stenseth & Myserud, 2002; Sanz *et al.*, 2003). This highlights the urgent need to document species response to climatic change in as many taxa and ecological frameworks as possible to build global predictions at the ecosystem level. However, most of the available information on the impact of climate change are on endothermic vertebrates (e.g. birds: Barbraud & Weimerskirch, 2001; Sanz *et al.*, 2003; Visser *et al.*, 2003; Sparks *et al.*, 2005; and mammals: Post *et al.*, 1997; Réale *et al.*, 2003), while research on poikilotherm terrestrial vertebrates have mainly focused on temperature dependent embryonic development and sex determination (Janzen, 1994; Robert & Thompson, 2001; Hays *et al.*, 2003).

In this study, we aimed to provide an example of the *in situ* effect of a temperature warming on some key life-history traits in an ectotherm, the common lizard *Lacerta vivipara*, using data from four unconnected populations located in mountain habitats of southern France.

In reptiles, individual body size, of which many other life-history traits are dependent (age at maturity, fecundity, survival, dispersal: Bauwens & Verheyen, 1987; Léna *et al.*, 1998; Lorenzon *et al.*, 1999, 2001), shows important variations with respect to humidity, temperature and food supply (Andrews, 1982; Sinervo & Adolph, 1989; Niewiarosky & Roosenburg, 1993; Sinervo & Adolph, 1994; Sorci *et al.*, 1996). In the common lizard, body size and other life-history traits were also found to be highly geographically variable and dependent on climatic conditions (Pilorge *et al.*, 1983; Bauwens *et al.*, 1986; Van Damme *et al.*, 1986; Bauwens & Verheyen, 1987; Sorci *et al.*, 1996). The large phenotypic plasticity of this species' life-history traits is seen as an adaptative strategy to cope with environmental varia-

bility (Sorci *et al.*, 1996; Lorenzon *et al.*, 1999, 2001; Massot *et al.*, 2002). However, our study sites being at the southern margin of the species' range, the species is likely to be at the border of its phenotypic tolerance with respect to temperature and humidity. The common lizard in our study sites, therefore, appears as a good model for investigating the effect of global warming on terrestrial ectotherms.

Material and methods

The species

The common lizard (*Lacerta vivipara* J.) is a small (adult snout-vent length (SVL) \sim 50–70 mm) live-bearing lacertid living in peat bogs and heath lands. It is widely distributed across Europe and Asia. Life-history traits vary between locations according to climatic conditions (Pilorge *et al.*, 1983; Bauwens *et al.*, 1986; Sorci *et al.*, 1996). In the studied populations, hibernation lasts from October to April. Mating takes place in May, with parturition starting about 2 months later (late July). Three age classes can be distinguished: juveniles (born in the current year), yearlings (born the year before), and adults (\geq 2 years). Growth is mainly restricted to the two youngest stages, whereas reproduction occurs only at the adult stage (Massot *et al.*, 1992). The main prey species are small arthropods (spiders, homoptera, caterpillars). Unfortunately, we had no measure of the food levels across the study period.

Study sites

We studied four unconnected populations (named CHA, ERM, PIM, ZDE) located on top of the Mont Lozère (Fig. 1: \sim 1430 m, 44°30'N, 3°45'E, Massif Central, south-east France) at the southern limit of the species' range (Pilorge *et al.*, 1983). No population exists below 1000 m of elevation in the Massif Central. Vegetation structure and composition vary between populations from dry heath land (*Calluna vulgaris*) to more humid meadows (herbaceous or moss cover). The shortest distance between the studied populations is 500 m (i.e. approximately five times more than the maximum dispersal distance observed in these populations (unpublished data)). In addition, in 16 years of intense individual monitoring by capture–recapture (more than 10 000 recaptures), no individuals were found to move between the two closest populations.

Climatic data

As the Intergovernmental Panel on Climate Change reported a sharp increase in global temperature since

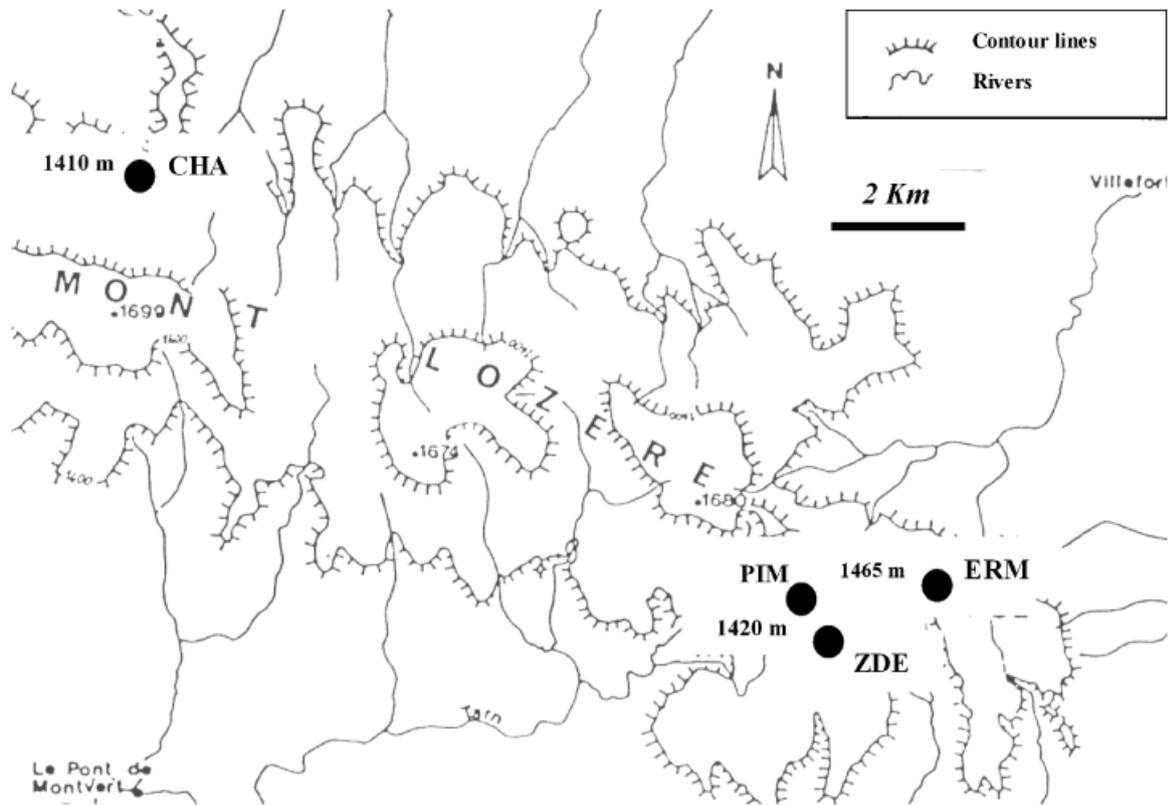


Fig. 1 Localization of study sites on Mont Lozère. Site areas are approximately 0.5 ha.

1976 (IPCC, 2001), we collected temperature data from 1976 to 2004. Temperatures were recorded at a meteorological station situated at the same altitude, but 50 km south from the study sites. We also used temperature data collected from a meteorological station located closer to the study sites (100 m to 12 km). These data were available for a shorter and discontinuous time. As the temperature data of the two meteorological stations were highly correlated for each month ($r = 0.830\text{--}0.887$, $n = 9\text{--}11$, all $P < 0.01$), we only used data from the meteorological station with the complete time series. Following Huey's (1982) recommendation about the description of reptiles' thermal environment, we used monthly means of daily maximum temperature as a descriptor of temperature variation in our analyses. Certainly data on thermoregulation opportunities would have been more meaningful; however, such data were lacking, and are especially difficult to gather.

Local climates are often driven by large-scale climatic influences. Our study region is classified as being part of the Mediterranean biome, of which the climate has been shown to be related to the North Atlantic Oscillation (NAO; Hurrell, 1995) and more recently to the Sahelian climate (Baldi *et al.*, 2003). We, therefore, used previous winter NAO index (calculated as the mean of monthly values from December to March) and present

normalized summer rainfall over Sahel (calculated as the June–October rainfall) as potential large-scale predictors of local climate at our study sites. Both datasets were downloaded for the 1976–2001 period on the NOAA website at the following address: <http://www.cdc.noaa.gov/ClimateIndices/Analysis/>

Biological data collection

Monitoring of life-history traits was conducted from 1984 to 2001 (thereafter referred as the study period) during capture sessions from June to July. Not all populations were sampled every year. Captured yearlings were measured and weighed at capture and immediately released. Gravid females were measured and weighed and then transferred to a field laboratory until parturition (less than 3 weeks). Each female was housed in an individual terrarium with a soil layer and a shelter. Heat and water were provided following a standard protocol (rearing conditions as in Massot & Clobert, 2000). Lizards were allowed to thermoregulate under a bulb (25 W) for 6 h a day. A larva of *Pyralis farinalis* (live weight = 0.189 ± 0.051 SD, dry weight = 0.075 ± 0.025 SD, $n = 30$) was provided once a week as a food item. After giving birth, each female was weighed, and hatchlings were measured and weighed.

Reproductive investment was measured as the total clutch mass (weight before and after parturition) and was calculated only for clutches in which all new-borns were alive at birth. Females and hatchlings were then released in their population of origin at the female's last capture point. Individual identification was performed by a unique toe-clipped code made at first capture. Initial handling and toe-clipping have no effect on the probability of subsequent recapture and survival in the common lizard (Massot *et al.*, 1992). In the same way, toe-clipping does not affect the maximal sprint speed in this species (G. Sorci personal communication) as also demonstrated for two other species of lizard (Huey *et al.*, 1990).

Analyses

We investigated changes in monthly temperature between April and October (i.e. when the lizards are active in our populations). Trends were assessed using second-order polynomial regressions of temperature against time with stepwise backward selection (α threshold $\alpha_{th} = 0.05$). We checked that observed trends during the study period were part of a longer warming by performing similar analysis on the full length of the dataset. We also investigated the correlation of local temperatures with large-scale climatic indexes (NAO, Sahel rainfall) using Pearson's correlations. Temporal trends in life-history traits were similarly assessed using second-order polynomial regressions with stepwise backward selection ($\alpha_{th} = 0.05$). Climatic variables showing a significant trend along the study period were used as independent explanatory variables in multiple regression models to explain changes in life-history traits for each population. To keep all sources of heterogeneity, analyses were conducted at the individual level, with climate as a covariate. Because of a lack of appropriate data, adult survival was estimated for both sexes in only one population (ZDE) for the period 1989–2001 (no data for males in 1998). Survival rates were estimated with capture-mark-recapture models (following Lebreton *et al.*, 1992) with recapture probabilities modelled as a function of year (Massot *et al.*, 1992). We fitted models with constant survival, annual variability in survival (with or without linear trend), and survival linked to independent climatic variables. The best model was chosen using corrected Akaike information criterion (See Lebreton *et al.*, 1992; Burnham & Anderson, 2002).

Results

Temperature trends

Temperature in May, June, and August increased significantly during the study period while temperature of

Table 1 Trends in temperature (1984–2001)

	F-ratio	P
April	$F_{2,16} = 0.254$	0.779
May	$F_{1,17} = 10.63$	0.005
June	$F_{1,17} = 4.570$	0.047
July	$F_{2,16} = 1.146$	0.343
August	$F_{2,16} = 3.870$	0.042
September	$F_{2,16} = 1.346$	0.288
October	$F_{2,16} = 2.224$	0.140

Results from second-order polynomial regressions with stepwise backward selection ($\alpha = 0.05$).

Boldface indicates significant trends.

other months did not show any trend (Table 1). Therefore, we used May, June and August temperature in subsequent analyses. These 3 months experienced a similar increase of around 3.7 °C since 1976 (Fig. 2). From 1976 to 2001 temperature in May and August only were marginally correlated to the NAO index (May: $r = 0.386$, $P = 0.052$; June: $r = 0.139$, $P = 0.497$; August: $r = 0.476$, $P = 0.014$) and correlation with Sahel rainfall was close to significance for all months (May: $r = 0.384$, $P = 0.053$; June: $r = 0.387$, $P = 0.051$; August: $r = 0.346$, $P = 0.083$). When restricted to the study period, temperature in May, June, and August were not related to the NAO index (May: $r = 0.303$, $P = 0.208$; June: $r = -0.015$, $P = 0.952$; August: $r = 0.277$, $P = 0.251$) but were all positively correlated with the Sahel rainfall (May: $r = 0.476$, $P = 0.039$; June: $r = 0.495$, $P = 0.031$; August: $r = 0.494$, $P = 0.032$).

Body length and temperature

All populations showed a consistent increase in yearling SVL over the study period (Fig. 3a). Yearling SVL markedly increased from 1984 to 1996 and stabilized thereafter. As captures of yearlings occurred during the June–July period, temperature in May and June of the year of capture and temperature in August of the previous year were considered as potential climate drivers. Because body size changes rapidly during the yearling stage, we included, as a correcting factor, the date of capture as an individual covariate in all analyses. Temperature in August, May, and June were all related to yearling SVL (Table 2a). The effect of May temperature, however, appeared inconsistent across populations and was therefore removed for further analyses. Both August and June temperature were significantly related to yearling body size in all populations (Table 2b), and were not correlated to one another ($r = -0.005$, $P = 0.985$). Overall explanatory power of August temperature was much higher than June

temperature in three populations out of four, and both were low in the remaining fourth population (Table 2b). August temperature was strongly correlated to yearling SVL in three populations and only weakly in the PIM population (Fig. 4). Fitting a common trend to all populations shows that while August temperature increased by 2.2 °C between 1984 and 2001, yearling SVL increased by 8.7 mm, a rough 28% augmentation. This increase in yearling SVL clearly impacted adult female SVL, which increased in all populations (Fig. 3b). How-

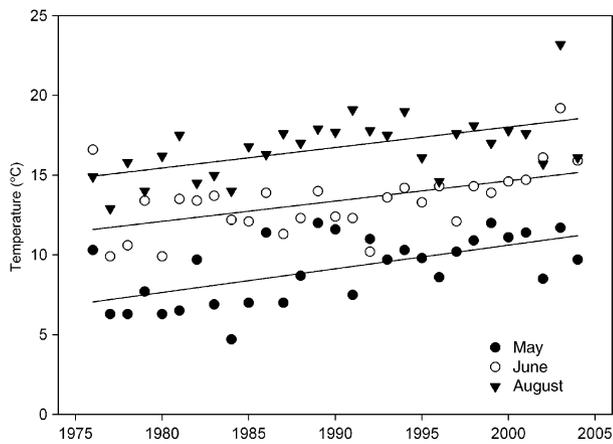


Fig. 2 Temporal trends in May, June and August mean maximum temperature. Slopes do not differ statistically (ANCOVA: year: $F_{1,81} = 36.532$, $P < 0.001$, month: $F_{2,81} = 139.276$, $P < 0.001$; year \times month: $F_{2,81} = 0.089$, $P = 0.915$).

ever, SVL changes in the CHA population slightly differ from the others populations by staying almost stable after the 2 first years (Fig. 3b). Overall, female SVL increased during the first decade, and then stabilized in all populations around 64 mm (Fig. 3b). Body size gain in female SVL was of the same magnitude than the one of yearling individuals (Fig. 3a,b).

Reproductive traits, female body size and temperature

Total reproductive investment (i.e. clutch mass) was highly correlated to clutch size in all populations (Pearson's correlations on yearly standardized and normalized data to remove any year effect; CHA: $r = 0.943$, $n = 185$, $P < 0.001$; ERM: $r = 0.949$, $n = 175$, $P < 0.001$; PIM: $r = 0.927$, $n = 381$, $P < 0.001$; ZDE: $r = 0.939$, $n = 453$, $P < 0.001$). Over the study period, clutch size increased in three populations (Fig. 5a), partly through indirect consequences of change in body size, as indicated by the positive relationship between fecundity and female SVL in all populations (Pearson's correlations on yearly standardized and normalized data; CHA: $r = 0.543$, $n = 249$, $P < 0.001$; ERM: $r = 0.643$, $n = 247$, $P < 0.001$; PIM: $r = 0.533$, $n = 528$, $P < 0.001$; ZDE: $r = 0.602$, $n = 741$, $P < 0.001$). Clutch size, however, decreased in the CHA population (Fig. 5b). Reproductive investment increased in three populations (ERM: $F_{1,174} = 16.16$, $P < 0.001$; PIM: $F_{1,379} = 12.51$, $P < 0.001$; ZDE: $F_{2,450} = 18.13$, $P < 0.001$) and show an

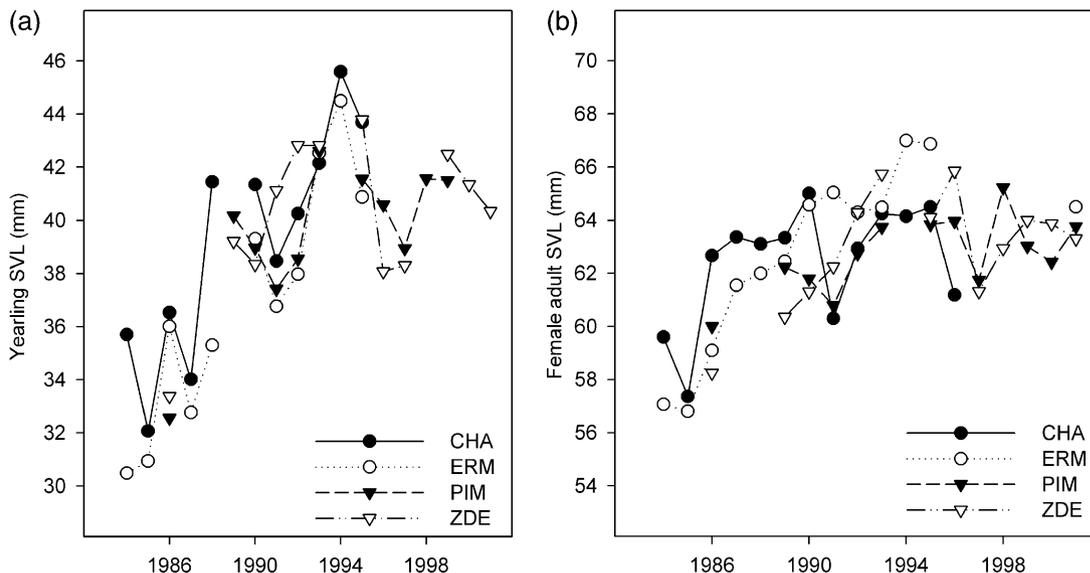


Fig. 3 Temporal changes in a) mean yearling snout-vent-length (SVL) corrected for date of capture and b) mean adult female SVL in the four study populations. SVL significantly increase in both age-classes in all populations (yearlings: CHA: $F_{2,352} = 239.40$, $P < 0.001$; ERM: $F_{2,348} = 223.40$, $P < 0.001$; PIM: $F_{2,415} = 77.60$, $P < 0.001$; ZDE: $F_{2,1124} = 134.40$, $P < 0.001$; adult females: CHA: $F_{2,248} = 17.27$, $P < 0.001$; ERM: $F_{2,248} = 92.44$, $P < 0.001$; PIM: $F_{2,531} = 10.47$, $P < 0.001$; ZDE: $F_{2,742} = 35.70$, $P < 0.001$). SD are not shown for clarity. Same scale apply to both panels.

Table 2 Relationship between yearling snout-vent length (SVL) and date of capture, previous-year August temperature, May and June temperature in the four populations (CHA, ERM, PIM, ZDE)

	Temperature			
	Capture date	August	May	June
<i>(a) Full model</i>				
CHA	$F_{1,350} = 207.875^{***}$	$F_{1,350} = 230.386^{***}$	$F_{1,350} = 2.668^{ns}$	$F_{1,350} = 101.330^{***}$
ERM	$F_{1,346} = 146.624^{***}$	$F_{1,346} = 131.478^{***}$	$F_{1,346} = 4.138^*$	$F_{1,346} = 122.168^{***}$
PIM	$F_{1,413} = 191.908^{***}$	$F_{1,413} = 11.386^{***}$	$F_{1,413} = 1.102^{ns}$	$F_{1,413} = 18.279^{***}$
ZDE	$F_{1,1122} = 956.364^{***}$	$F_{1,1122} = 179.157^{***}$	$F_{1,1122} = 48.146^{***}$	$F_{1,1122} = 7.774^{**}$
<i>(b) Model testing for August and June temperature effects (May removed)</i>				
CHA	$F_{1,351} = 205.730^{***}$	$F_{1,351} = 388.210^{***}$		$F_{1,351} = 101.620^{***}$
ERM	$F_{1,347} = 179.150^{***}$	$F_{1,347} = 364.020^{***}$		$F_{1,347} = 143.140^{***}$
PIM	$F_{1,414} = 213.829^{***}$	$F_{1,414} = 10.335^{***}$		$F_{1,414} = 17.556^{***}$
ZDE	$F_{1,1123} = 930.206^{***}$	$F_{1,1123} = 155.058^{***}$		$F_{1,1123} = 4.848^*$

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, $^{ns}P > 0.1$.

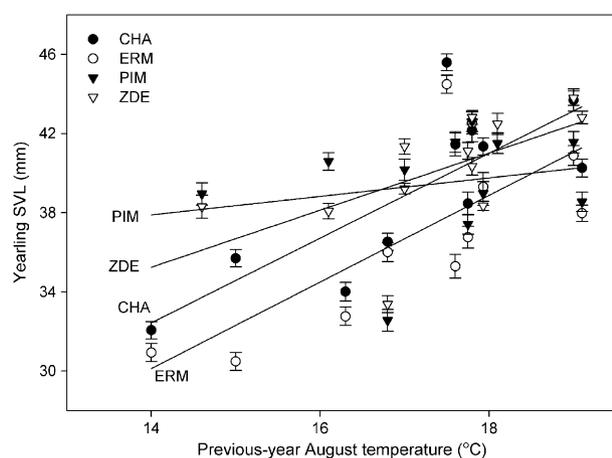


Fig. 4 Relationship between August temperature of the previous year and mean yearling snout-vent length (SVL) (corrected for date of capture) in the four study populations. See Table 2 for statistics.

almost significant decline in CHA ($F_{1,184} = 3.57$, $P = 0.060$, $\beta = -0.010 \pm 0.005$ SE). However, once corrected by female body size, the total clutch mass remained almost constant over years (Table 3).

Survival and temperature

The best fitted model of survival rates for both males and females in the ZDE population was obtained by including an effect of May temperature (Table 4), which was positively correlated to survival rates (Fig. 6). Integration of June or August temperature produced significantly higher AICc ($\Delta AICc > 2$; Burnham & Anderson, 2002), and therefore, did not improve the model (Table 4).

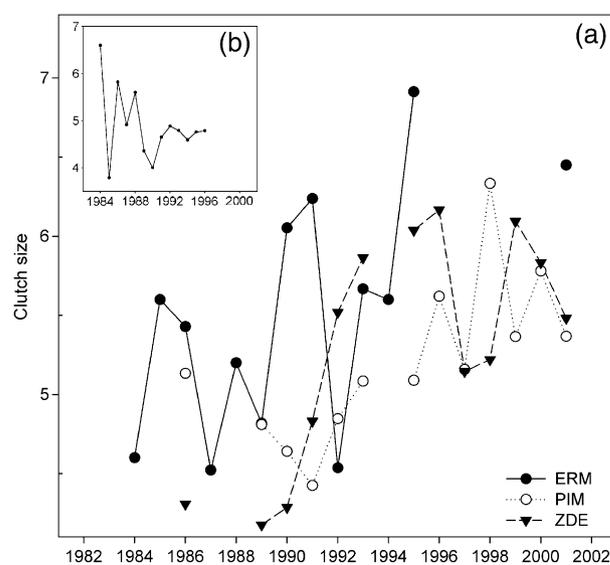


Fig. 5 Temporal changes of clutch size in the four study populations: (a) clutch size significantly increase in three populations (ERM: $F_{1,254} = 17.25$, $P < 0.001$; PIM: $F_{1,530} = 20.91$, $P < 0.001$; ZDE: $F_{2,740} = 35.35$, $P < 0.001$) and (b) clutch size significantly decrease in the CHA population ($F_{1,273} = 3.99$, $P = 0.047$). SD are not shown for clarity.

Discussion

We provide, here, the first comprehensive study on the potential effect of a raise in temperature on fitness changes in an ectothermic terrestrial vertebrate, the common lizard. Temperature during spring and summer rose during the past 29 years on the Mont Lozère. This raise in temperature was correlated with an increase in body size, which induced an increase in the reproductive outcome for most of the sampled

Table 3 Effects of year (as category) and female snout-vent length (SVL) on total clutch mass

	SVL	Year	Year*SVL
CHA	$F_{1,152} = 39.055^{***}$	$F_{11,152} = 1.410^{ns}$	$F_{11,152} = 1.491^{ns}$
ERM	$F_{1,145} = 61.191^{***}$	$F_{11,145} = 1.603^{ns}$	$F_{11,145} = 1.799^{\&}$
PIM	$F_{1,353} = 99.959^{***}$	$F_{12,353} = 1.709^{\&}$	$F_{12,353} = 1.734^{\&}$
ZDE	$F_{1,426} = 273.109^{***}$	$F_{12,426} = 1.072^{ns}$	$F_{12,426} = 1.151^{ns}$

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, & $P < 0.1$, ^{ns} $P > 0.1$.

Table 4 AICc values of survival estimates models

	Males	Females
Phi(year) P (year)	723.85	2770.41
Phi(Tmay) P (year)	713.45	2766.47
Phi(Tjune) P (year)	721.52	2773.91
Phi(Taugust) P (year)	726.26	2773.33
Phi(Trend) P (year)	717.65	2773.75
Phi(Constant) P (year)	724.25	2772.45

Phi; Survival rate; P ; Capture probability. In brackets: modeled source of variability influencing Phi and P .

Boldface indicates lower AICc model for both sexes.

populations. In the same time, adult survival was also positively correlated to the temperature in spring. All the fitness components therefore appeared boosted by local warming.

Climatic evolution in south-east France

The increase in spring and summer temperature observed in our study region matched those reported in other studies at the France (Moisselin *et al.*, 2002) or at the European level (e.g. Crick & Sparks, 1999; Sanz *et al.*, 2003). This corroborates the general finding that, in most geographical parts of Europe, the spring and summer have become warmer in the last decades. Both NAO index and Sahel rainfall revealed positive correlation with local climate in the study region, although Sahel rainfall appears as a more reliable large-scale descriptor for the study area. NAO index has been intensively used to demonstrate climatic-driven population dynamics in northern Europe (see references in Myrnerud *et al.*, 2003), but its effect on local climate is weakened in the south part of Europe (Hurrell, 1995). Our study area is likely to be at the interface of two large-scale climatic regions and is under the influence of NAO and of convective cells determining Sahel rainfall (Giannini *et al.*, 2003). It is likely that many places are under such mixed effects. Although it was beyond the scope of this paper, it poses the question of the value

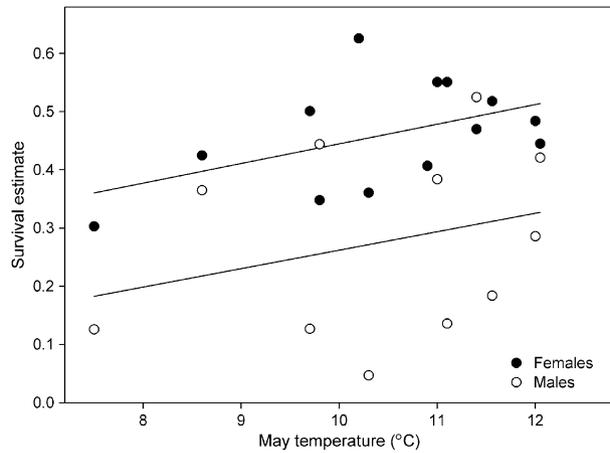


Fig. 6 Relationship between May temperature and adult survival for males (plain dots) and females (full dots) in the ZDE population. See text for details on the model selection and statistics.

and the way to disentangle respective influence of several climate proxys (Almaraz & Amat, 2004).

Climate driver of body size

Global warming has shown to affect the ecology of birds and mammals in most parts of Western Europe (Crick & Sparks, 1999; Dunn & Winkler, 1999; Post *et al.*, 1999; Gibbs & Breisch, 2001; Sanz *et al.*, 2003; Visser *et al.*, 2003; Gordo *et al.*, 2005; Sparks *et al.*, 2005). Not surprisingly, we found the same in the case of the common lizard. Indeed, yearling body size increased by about 28% in 18 years, and this change was correlated to an increase in temperature in August and June. Although body size is one of the easiest life-history trait to describe, studies showing a response of body size or body size index to climate change are rare in terrestrial species (Post *et al.*, 1997; Yom-Tov, 2001; Wikelski & Romero, 2003), while it is more commonly reported in aquatic ecosystems (e.g. Panov & McQueen, 1998; Pypers & Peterman, 1999). However, most of the studied cases in terrestrial ecosystems concern endothermic species where body size is less dependent on ambient thermal conditions compared to ectothermic species (Atkinson & Thorndyke, 2001). Body size variation in reptiles is a common phenomenon and has been related to climatic conditions, both at a geographical (following a converse Bergmann's rule: Ashton & Feldman, 2003) and temporal scale (Avery, 1985; Bauwens & Verheyen, 1987; Sinervo & Adolph, 1994; Wikelski & Romero, 2003). Change in habitat type and structure has also been shown to influence body size (Summer *et al.*, 1999). In the common lizard the direct effect of temperature has been highlighted by many studies. Although reptiles have developed behavioural adaptations which allow

them to actively thermoregulate and, therefore, buffer climatic variations (Avery, 1985), Heulin (1987) showed that, in the field, body temperature of common lizards is highly correlated to environmental temperature. This suggests that thermal conditions variability affects the time a lizard can be active at its preferred body temperature ($\sim 28\text{--}33\text{ }^{\circ}\text{C}$; Avery, 1985). This should be true in particular for the youngest stages as heating and cooling rates are negatively related to body size in lizards (Martín *et al.*, 1995). Moreover, Lorenzon *et al.* (1999, 2001) experimentally demonstrated in the common lizard that growth rate at the juvenile and yearling stages were affected by environmental conditions (temperature, humidity) even when controlling for food. Temperature, therefore, affects the time devoted to foraging activities, as well as the efficiency of the physiological processes involved in growth (Avery *et al.*, 1982; Waldschmidt *et al.*, 1986; Van Damme *et al.*, 1991). It follows that, although we cannot reject the hypothesis of an increase in food resources in the field, a direct effect of the temperature on metabolism might be sufficient to explain the observed increase in yearling body size. Moreover, the raise in temperature can increase thermoregulation opportunities, which in turn could increase diurnal activity and food consumption. However, these results call for experimental manipulations to disentangle between direct (metabolism, thermoregulation constraints) and resource-related (food availability) effects.

Somewhat surprisingly, a temperature change restricted to a very limited period of time (i.e. immediately after birth), had a major effect on individual body size measured at the yearling stage, 6 months later (excluding hibernation). This indicates that higher growth rates were maintained even after the short period of time when temperature increased. In the same species, Massot *et al.* (1992) similarly found that competition experienced early in life affect individual body size up to the adult stage. As physiological processes underlying growth (from digestion to conversion) are almost strictly temperature-dependent (Waldschmidt *et al.*, 1986), the most likely explanation for a sustained difference in growth rate might be that an increase in body size early in life is associated to a permanent increase in either foraging time or efficiency later in life. For example, larger animals move faster (Sorci & Clobert, 1996), are more enduring (Sorci & Clobert, 1996), ingest larger prey (Avery *et al.*, 1982), and their relative metabolic needs are lower.

Fitness components and temperature

In most reptiles, the volume of female abdominal cavity constrains the reproductive output by limiting egg

number, entailing a strong positive relationship between fecundity and body size (Clobert *et al.*, 1998). Although a higher abdominal volume could lead to either numerous or larger eggs, an increase in fecundity is the most dominant response to an increase in female body size (Bauwens & Verheyen, 1987; Sinervo, 1990; Massot *et al.*, 1992). This probably arises from anatomical constraints on egg size at parturition (Sinervo & Licht, 1991; Clark *et al.*, 2001; Bowden *et al.*, 2004) and from the likely higher fitness gain from increasing offspring number rather than their size (but see Lindström, 1999). In this study, the female reproductive output increased in three out of four populations and was partly a byproduct of the increase in female body size, itself because of body size increase at earlier stages. These results confirm that early development can have major effects on lifetime reproductive success of many organisms (Lindström, 1999), and that such cohort effects should be carefully looked for as they could create large delays in species' response to climate change (Post *et al.*, 1997; Forchhammer *et al.*, 2001).

Adult survival rates of males and females were positively related to May temperature. As stated above, an increase in temperature allows for longer and more efficient foraging, and therefore, enhances resource acquisition. This should decrease the relative costs of maintenance and reproduction, and, by relaxing the time constraint, diminish the strength of trade-offs among competing activities. Other nonexclusive mechanisms might also operate, such as a reduction of exposure to predators by the shorter time needed for thermoregulation (Avery *et al.*, 1982; Avery, 1985; Downes, 2001) or by a higher escaping success because of improved speed and endurance (Avery & Bond, 1989; Sorci & Clobert, 1996).

Individual versus habitat-based models

We found that environmental warming had a positive impact on all life-history traits studied. This raises two questions. The first one is why the species did not colonize lower altitude, warmer, habitats? Humidity constraints are likely to be the primary explanation for the absence of populations below a certain elevation (1000 m) in the Massif Central. Indeed, even at our populations elevation, a relative absence of running water or lower precipitation (i.e. a low humidity rate at the ground level), has a strong negative effect on the population density and species presence (Lorenzon *et al.*, 2001). The humidity rate at the ground level is governed by multiple factors, an important factor being temperature. This suggests that more than elevation itself (although being a good proxy), what governs the species presence and density is the interplay between

humidity and temperature. This leads to the second question: can we extrapolate these results to even larger temperature increases? Two lines of arguments strongly militate against this view, one at the individual and one at the habitat level.

At the individual level, a further increase in temperature will most likely result in a restriction of the time devoted to foraging because of increased thermoregulation. Indeed, in ectotherms, the optimal response of morphological, physiological and behavioural functions has a bell-shaped relationship with temperature (Avery, 1985) i.e. after some temperature threshold value the organism functions suboptimally.

At the habitat level, a further raise in temperature could increase evaporation and soil dryness and threaten humid habitats like peat bogs and heath lands (IPCC, 2001), the main habitats of the common lizard in the study region. Persistence of these populations on the long term are, therefore, linked to the ability of the ecosystem to escape global warming by shifting at higher altitude (Pounds *et al.*, 1999; Walther *et al.*, 2002). In the southern part of its range, the common lizard is only present in isolated habitats at a minimum elevation of 1000 m (Pilorge *et al.*, 1983). At these locations potential range elevation for altitudinal shifts is low and such shifts are likely to increase the habitat fragmentation. A continuous rise in temperature could then decrease on the long term the amount of suitable habitats and therefore increase local extinction risks. It was, however, argued that global warming could increase rainfall over Western Europe (IPCC, 2001) and compensate for the effect of the temperature increase. However, data do not support such hypothesis in our study area because of annual rainfall did not increase since 1976 ($F_{1,27} = 1.099$, $P = 0.304$). In a general survey of existing populations in the south part of the region, one common lizard population (located on Mont Caroux, 43°37'N, 2°53'E) is already extinct in a location that experienced dramatic drying (B. Sinervo and J. Clobert, personal observations). Climatic refuges are, therefore, likely to become climatic traps in the context of global warming for species with limited dispersal capacities.

Conclusions

Our results support previous demonstrations of time-lags in biological responses to environmental warming. Here, we identified a correlation between spring temperatures and survival, and a delayed response of reproduction to changes in temperature experienced early in life through an increase in individual body size. A strong background of observations and experiments supports the view that body size response to climate change should be common in terrestrial

ectotherm vertebrates, but very few had been reported before. Because it can have major effect on population dynamics and survival of these species, and because ectotherms in general are at the base of many food webs, we strongly call for more data on these under studied taxa.

Our results also highlight a potential discrepancy between individual and habitat-based predictions. Suitable habitats of common lizard in the study region, at the southern margin of the species distribution, are likely to disappear, and have probably already shrunk. However, the factor driving this decline – the increase in temperature – had only positive effects on individual fitness. Both individual- and habitat-based approaches are necessary to fully understand species' response to climate change.

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