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Population ecology

Warmer temperatures attenuate the classic offspring number and reproductive investment trade-off in the common lizard, *Zootoca vivipara*

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Life-history traits involved in trade-offs are known to vary with environmental conditions. Here, we evaluate the response of the trade-off between 'offspring number' versus 'energy invested per offspring' to ambient temperature in 11 natural populations of the common lizard, *Zootoca vivipara*. We provide evidence at both the intra- and interpopulation levels that the trade-off is reduced with an increase in air temperature. If this effect enhances current individual fitness, it may lead to an accelerated pace of life in warmer environments and could ultimately increase adult mortality. In the context of global warming, our results advocate the need for more studies in natural populations to explore interactions between life-history traits' trade-offs and environmental conditions.

1. Introduction

Trade-offs among reproductive traits represent a fundamental principle of life-history theory [1]. Because females have a finite amount of energy available for reproduction, they have to make crucial decisions regarding the optimal allocation strategy to adopt. For over 50 years, numerous studies have attempted to explain observed trade-offs between survival and reproduction, current and future reproduction or number and quality of offspring (e.g. [2]). In most situations, negative correlations emerge, because a female cannot simultaneously optimize all life-history traits. However, null or positive correlations are also found, suggesting that constraints on life-history traits can potentially be released [3,4].

Patterns of selection acting on life-history traits are known to vary between habitats [5,6]. For example, the balance between number and size of offspring may depend on the ecological context: females should invest more in fewer offspring if juvenile survivorship is poor, but may enhance their litter size (LS) in high-quality environments [7]. As a consequence, interactions between traits may circumstantially magnify, diminish or disappear along environmental gradients. The influence of environmental conditions on the intensity of trade-offs has been considered in theoretical works [3,8] or tested experimentally [5], but studies of natural populations are still scarce [9].

In this work, we examined how trade-offs between LS and energy invested per juvenile varied across 11 populations of the common lizard, *Zootoca vivipara*, in the Massif Central, France. Maternal effects are known to vary among lizard populations according to environmental conditions [10], and particularly for the common lizard [11,12]. Here, the sampled populations are distributed along a thermal gradient and allow us to address the following questions regarding the intensity of the trade-off: (i) is there evidence of

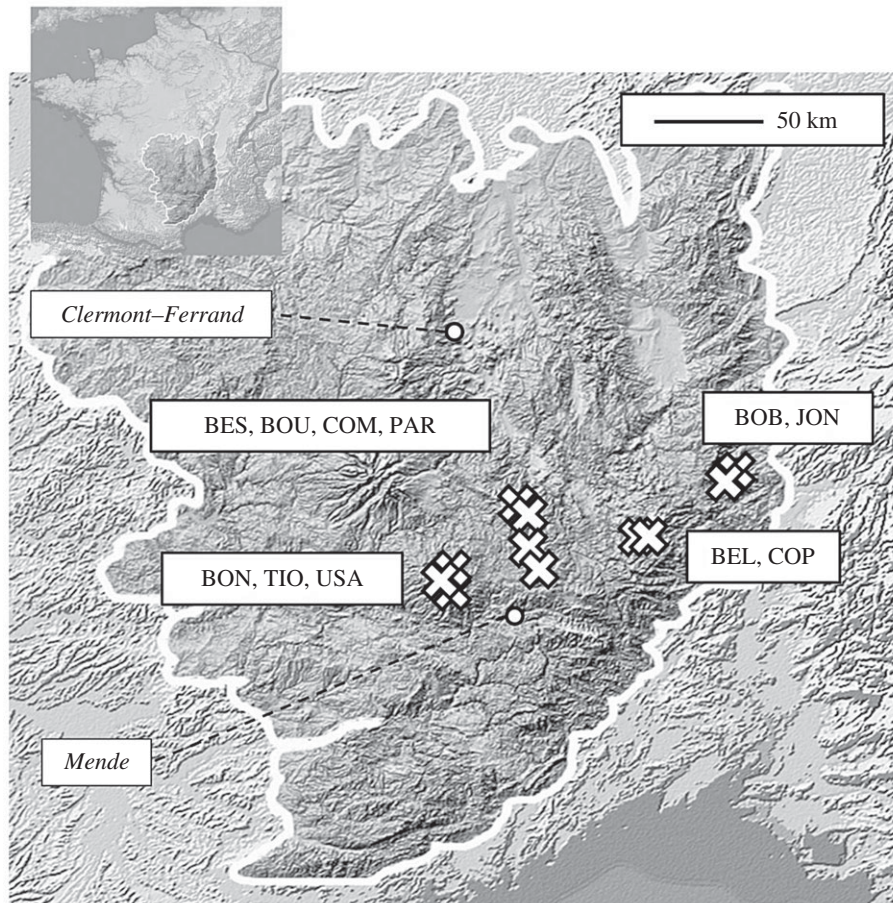


Figure 1. Capture sites in the Massif Central, France.

variation among populations?; (ii) if so, is this variation structured according to thermal characteristics?

2. Material and methods

The common lizard, *Z. vivipara* (Lacertidae), is widely distributed across Eurasia. Mating takes place in May, immediately after female emergence. LS is fixed in early gestation, but investment per progeny is still flexible according to mid-gestation conditions. Parturition occurs between mid-July and early August, after which individuals accumulate energy to prepare for hibernation [12].

We obtained between 15 and 30 females from 11 populations in the Massif Central (France), between 2003 and 2015 (figure 1, average date of capture: 27th of June (± 3.5 days)). We measured snout-to-vent length (SVL, mean \pm s.d. = 62.4 ± 4.3 mm) and body mass (BM_p , 5.14 ± 1.18 g) at the time of capture. We subsequently brought all females to a laboratory facility. Each lizard was individually housed in a plastic terrarium with a sterilized soil substrate and a shelter. Lizards were allowed to thermoregulate under a bulb (25 W) for 6 h a day. We provided water three times a day and fed lizards with two crickets every 2 days. Immediately after parturition, the females were weighed again (BM_{pp} , 3.14 ± 0.62 g). Because females are not captured at the same stages of pregnancy, we corrected BM_p by the time necessary for females to finish their gestation (see the electronic supplementary material, appendix S1). We estimated an index of reproductive investment (RI) as the difference between the mass of a female when pregnant BM_p and her post-parturition mass BM_{pp} [13]. We derived the energy invested per offspring by dividing RI by the total LS of each female. Thus, the *per capita* investment in offspring is $Inv = [BM_p - BM_{pp}]/LS$.

We obtained local weather conditions from the National Meteorological Agency (MeteoFrance, MF, <http://publitheque.meteo.fr>). Because some sample sites shared a common MF station and the distances between MF stations and capture sites can sometime be large (several kilometres), we adjusted the weather data according to *in situ* weather forecasting in order to match local temperatures (see the electronic supplementary material, appendix S2). We used average daily maximal temperatures for June (T_{max6}) that describe the thermal conditions during mid-gestation. This is the period in which temperatures have been demonstrated to be critical for juvenile development in an oviparous snake [14]. To estimate T_{max6} , we used the average temperature for all of June, which ensured we overlapped the mid-gestation period for all populations and therefore compensate for potential asynchrony between individuals in gestational stage.

All statistical analyses were performed with R software (R Development Core Team, v. 3.2.0). To study the variation on the trade-off between Inv and LS across the 11 populations, we first estimated inter-population differences in the magnitude of the trade-off. To do so, we used mixed effect models where the random effect structure of the model was hierarchically extended from a model without inter-population differences (mod1) to a model where populations' trade-offs were allowed to vary in their slope (mod2). Because several factors other than temperature may contribute to the variation in the intensity of the trade-off, we added year as a random factor in the model and female size and reproductive stage (time before parturition) as covariates. Second, we assessed whether the position of each population along the thermal gradient influenced the intensity of local trade-offs. Thus, the *per capita* investment (Inv) in offspring is calculated as: $Inv = [BM_p - BM_{pp}]/LS$. Then, for each population, we calculated the linear regression

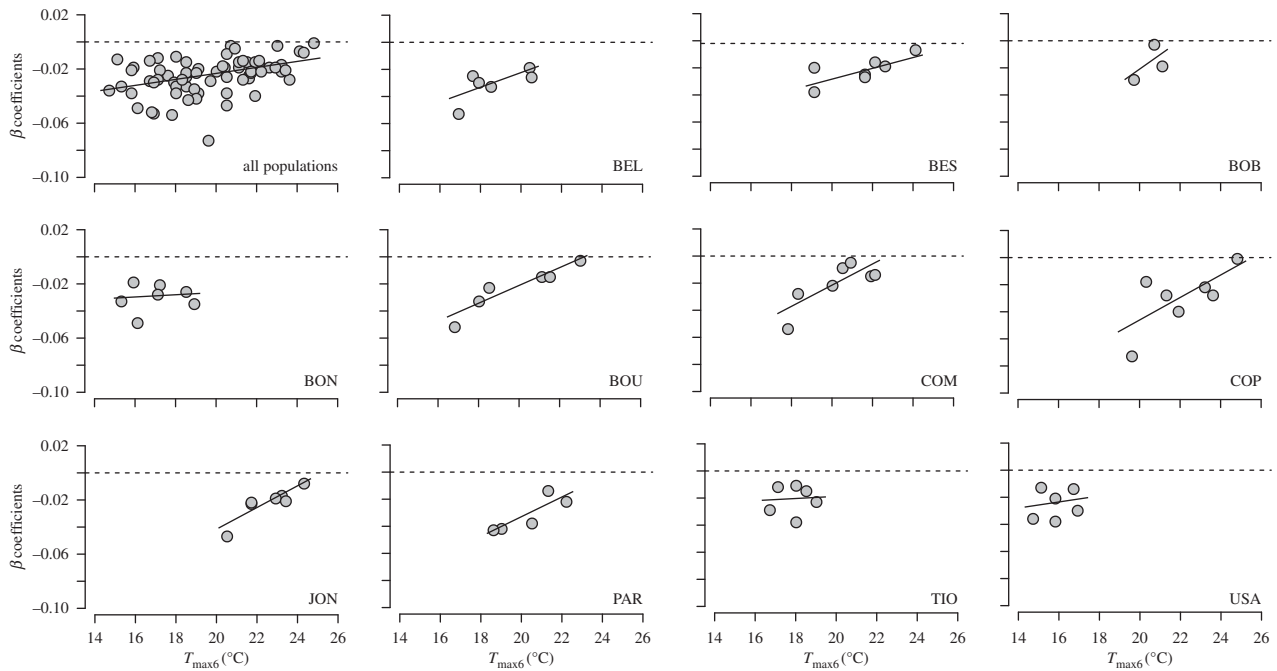


Figure 2. Influence of mid-gestation temperature on the intensity of the trade-offs: β coefficients are calculated as the slope coefficients of a linear regression model between Inv and LS. Top-left panel represents all β regrouped along the global thermal gradient. Other panels: for each population, we calculated α coefficient (linear regression coefficient) that measures the flexibility of β according to local $T_{\max 6}$. We found positive coefficients for all populations, suggesting that constraints on the trade-off are weaker in warmer years (dashed lines for $\beta = 0$).

coefficient α between the different β and average $T_{\max 6}$ to measure the flexibility of the trade-off to mid-gestation temperature.

3. Results

We found an overall negative relationship between RI *per capita* (Inv) and LS ($b = 0.011 \pm 0.001$; $t_{657} = -10.42$; $p < 0.001$). However, the random regression model showed significant interpopulation differences in the intensity of the trade-off between Inv and LS, even if we consider that other annual specific or individual specific factors can directly affect the trade-off intensity. Indeed, the best model was a model where each population's trade-off could vary in its slope (AICc mod1 = -17957.30 ; AICc mod2 = -18232.29). Complete models and significance of fixed effects are provided in the electronic supplementary material, appendix S3.

The analysis of variation in the intensity of trade-offs revealed a positive relationship between β and $T_{\max 6}$ for all populations (figure 2). This result suggests that the trade-off is less intense in warmer conditions. An additional linear model between α coefficients and the population's average temperature confirmed that colder populations are less flexible and therefore cannot adjust the trade-off to inter-annual thermal conditions as well as warmer ones (table 1; $b = 0.001 \pm 0.0003$; $t_{657} = 3.178$; $p = 0.011$).

4. Discussion

We have shown that local conditions influence the allocation of energy that a female makes in current reproduction. Indeed, despite a general negative relationship observed between LS and energy invested per juvenile, our results show significant differences in the intensity of this trade-off between populations. For all populations, we detected a

Table 1. Description of each population. Comparison between α coefficient and average mid-gestation temperatures on each population (mean $T_{\max 6}$). We also provide information about the number of sampling attempts and the Mountain Massif.

site	A	mean $T_{\max 6}$	sampling attempts	Mountain Massif
BEL	0.0055	18.63 (± 0.45)	6	Vivarais
COP	0.0084	22.1 (1.87)	6	Vivarais
BES	0.0040	21.46 (1.82)	6	Vivarais
BOU	0.0067	19.82 (2.4)	6	Margeride
COM	0.0079	20.21 (1.66)	6	Margeride
PAR	0.0073	20.32 (1.52)	5	Margeride
BOB	0.0108	20.5 (0.72)	3	Velay
JON	0.0082	22.53 (1.29)	7	Velay
BON	0.0008	17 (1.34)	7	Aubrac
TIO	0.0008	17.88 (0.86)	5	Aubrac
USA	0.0022	15.93 (0.86)	6	Aubrac

positive relationship between the intensity of annual trade-offs (β) and mid-gestation temperatures $T_{\max 6}$, which demonstrates that the trade-offs are more intense in poor years, but become reduced when temperature increases. This result corroborates results from previous experimental work that revealed a positive correlation between environmental quality and the slope derived from the association of egg size and number [15]. In ectotherms, both physiological activity and metabolic rate increase with ambient temperature [16]. Higher efficiency in resource acquisition or digestion and higher metabolic rate could facilitate the ability of females to accumulate sufficient energy reserves

and to complete gestation, regardless of the number of fertilized eggs. However, three populations surprisingly showed a relationship between β and $T_{\max 6}$ that was almost null (BON, TIO, USA). These populations are situated in the coldest locations of our survey and, even in warm years, climatic conditions may probably be too restrictive to allow any attenuation of the trade-off. We are also aware that additional factors to temperature, specific to each individual (i.e. size, growth) or population (i.e. precipitation, predation), may also influence the trade-off intensity.

Our analyses furthermore suggest that the relaxing effect of warmer temperature observed at the intrapopulation level also exists at a larger scale: colder sites impose restrictions in resources allocation, whereas at warmer sites females have the opportunity to maximize both LS and litter quality as soon as conditions turn favourable. In the context of current climate change, the positive effect of temperature might have important consequences for common lizards' population dynamics. For example, Bestion *et al.* [17] experimentally demonstrated a switch of demographic strategies in a warming experiment conducted in semi-natural conditions. Their results showed that warmer temperatures led to an accelerated pace of life (e.g. increased probability of pregnancy, larger juvenile mass) and would ultimately induce a rapid collapse in population density by increasing adult mortality. In our situation, the relaxing effect of temperature on the offspring number–quality trade-off may paradoxically strengthen other trade-offs too (e.g. present versus future reproduction and RI versus future survival or growth). Conflicts between

trade-offs are very well described and are known to sometimes influence species evolution [18]. For example, environmentally dependent reorganization of trade-offs has been documented for spatial and temporal variation in food abundance [19,20]. Although we cannot confirm this hypothesis here, our results highlight the crucial importance of considering the major effect of variation in environmental characteristics on the evolution of life-history traits, specifically in the current context of global change.

Ethics. This study was carried out in accordance with institutional guidelines, under licence from the French Ministry of the Environment and the veterinary and environmental services of every region where we sampled lizards (permits 81-2013-05; 2013274-0002 and 2013/DREAL/259).

Data accessibility. The dataset used for statistical analyses is available in the electronic supplementary material.

Authors' contributions. A.R. carried out the statistical analysis and drafted the manuscript; A.R. and M.R. designed the study and all authors contributed to acquisition of data, contributed to interpretation of data and helped revise the manuscript. All authors gave final approval for publication and agreed to be held accountable for the content herein.

Competing interests. We have no competing interest.

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