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Climate and habitat interact to shape the thermal reaction norms of breeding phenology across lizard populations

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Summary

1. Substantial plastic variation in phenology in response to environmental heterogeneity through time in the same population has been uncovered in many species. However, our understanding of differences in reaction norms of phenology among populations from a given species remains limited.

2. As the plasticity of phenological traits is often influenced by local thermal conditions, we expect local temperature to generate variation in the reaction norms between populations.

3. Here, we explored temporal variation in parturition date across 11 populations of the common lizard (*Zootoca vivipara*) from four mountain chains as a function of air temperatures during mid-gestation. We characterized among-population variation to assess how local weather conditions (mean and variance of ambient temperatures during mid-gestation) and habitat openness (an index of anthropogenic disturbance) influence the thermal reaction norms of the parturition date.

4. Our results provide evidence of interactive effects of anthropogenic disturbance and thermal conditions, with earlier parturition dates in warmer years on average especially in closed habitats.

5. Variation in the reaction norms for parturition date was correlated with mean local thermal conditions at a broad geographical scale. However, populations exposed to variable thermal conditions had flatter thermal reaction norms.

6. Assessing whether environmental heterogeneity drives differentiation among reaction norms is crucial to estimate the capacity of different populations to contend with projected climatic and anthropogenic challenges.

Key-words: among-population variation, anthropogenic disturbance, common lizard, parturition date, phenology, plasticity, reaction norm, thermal sensitivity

Introduction

Changes in phenology, the timing of life cycle events, due to climate warming have been well documented during the past decades. A shift in phenology, in particular the onset of breeding, is often considered to be an effective response by which plants and animals can cope with climate warming (Walther *et al.* 2002). Substantial evidence suggests that phenological traits exhibit plasticity and fluctuate from year to year to track prevailing environmental conditions (Menzel & Fabian 1999; Réale *et al.* 2003; Visser & Both 2005; Charmantier *et al.* 2008). For example, a recent meta-analysis estimated that the current increase in temperatures has advanced the phenology of reproduction and migration in 62% of 678 species

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(Parmesan & Yohe 2003). The extent to which a species phenology may respond to climate warming throughout its range depends on spatial variation in the sensitivity of phenology to local climate conditions (Chevin, Lande & Mace 2010; Chown *et al.* 2010). Yet, most shifts in phenology have been observed only within a single natural population. Our current knowledge of temporal variation in phenology across spatially distinct populations is limited to a few long-term studies of breeding dates in avian or mammals populations (Visser *et al.*, 2003; Both *et al.*, 2004; Brommer *et al.*, 2005; Nussey *et al.*, 2005; Husby *et al.*, 2010; Porlier *et al.*, 2012; Sheriff *et al.*, 2011; Visser, te Marvelde & Lof 2012)

An efficient way to explore plasticity in breeding phenology is the study of the 'reaction norm' that expresses variation of the breeding dates along an environmental gradient, such as thermal conditions (Brommer *et al.* 2005; Nussey *et al.* 2005; Garant *et al.* 2008). Comparison of the thermal reaction norms for breeding date among populations allows one to estimate the extent of spatial variation in phenotypic plasticity. Studies of multiple populations also provide insights into the causes of variation in thermal reaction norms. Moreover, the understanding of variation in phenology among populations is a unique opportunity to predict how populations should respond to climate change given the anticipated exposure of species to novel combinations of climatic and anthropogenic conditions (Travis 2003; Baumann & Conover 2010; Chown *et al.* 2010).

Several studies have highlighted the potential for strong selection on the timing of breeding phenology (Chuine 2010). First, energetically demanding activities associated with breeding should coincide with periods of suitable food availability, and match the temporal dynamics of prey species in the environment (match–mismatch hypothesis, Sinclair & Tremblay 1984; Miller-Rushing *et al.* 2010; Visser, te Marvelde & Lof 2012). Secondly, phenological traits are often heritable and exhibit significant levels of additive genetic variation, suggesting the potential for an evolutionary response to selection and the local adaptation of breeding phenology traits (Scheiner 2002; Nussey *et al.* 2005; Bradshaw, Holzapfel & Crowder 2006). Different evolutionary and ecological scenarios make different predictions about the degree of variation in breeding phenology reaction norms across populations (Fig. 1). First, breeding phenology may vary across populations even if they share the same reaction norm because populations have different positions on the environmental gradient (Fig 1a). Secondly, breeding phenology may not differ across populations despite environmental variation because selection promotes physiological or behavioural adaptations such that individuals breed on average at the same dates (Fig 1b). Finally, populations may evolve a locally adapted reaction norm, influenced by prevailing local conditions, and thus display a locally adapted response (Fig 1c).

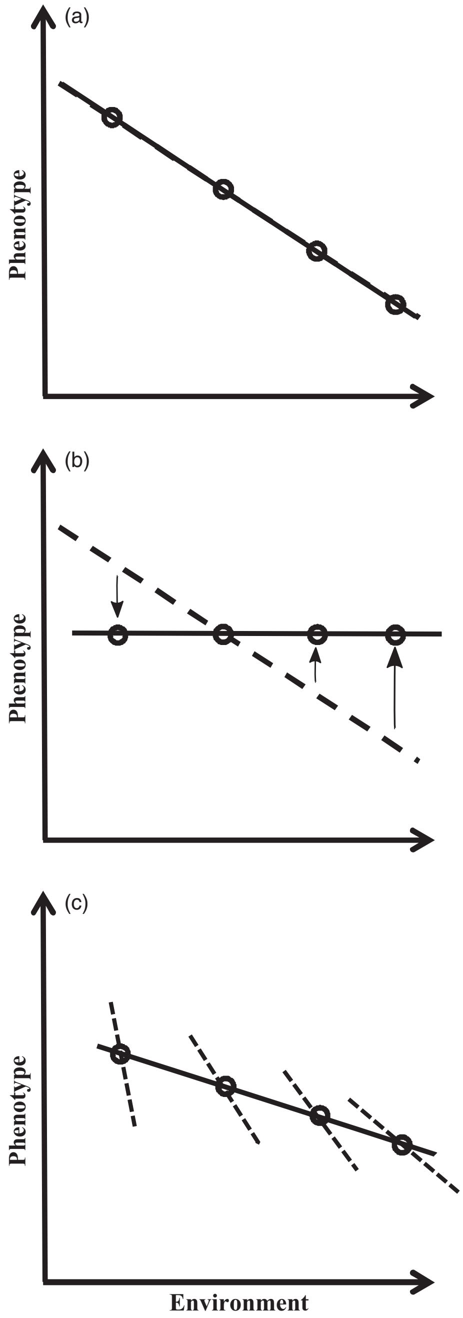

Fig. 1. Evolutionary scenarios to explain potential differences among populations in their plastic response. Each point represents the observed response of a population. Solid lines represent among population reaction norms; dashed lines represent population reaction norm. (a) Populations share a common reaction norm but exhibit local differences in their phenotypes as they are spread at different position on the environmental gradient. Among populations and populations reaction norms are confounded. (b) Populations share a common reaction norm but do not present any differences as selection promotes physiological or behavioural adaptations such that individuals breed on average at the same dates. (1c) Each population evolves a locally adapted reaction norm influenced by local conditions.

When breeding phenology shows a linear relationship with environmental conditions, differences in phenotypic plasticity across populations may be assessed by analysing the intercept and slope of the reaction norm (Baumann & Conover 2010; Baythavong & Stanton 2010; Husby *et al.*, 2010). The extent and the causes of variation in the slope of reaction norms for breeding date remain uncertain, but recent theory predicts that phenotypic plasticity should be greater, and therefore, the reaction norm should be steeper, in populations occupying sites characterized by large, but predictable, temporal environmental variation (Ghalambor *et al.* 2007; Chevin, Lande & Mace 2010). A comparative analysis of multiple populations inhabiting heterogeneous environments provides a unique opportunity to identify putative causal factors of selection on phenology plasticity (Husby *et al.*, 2010; Porlier *et al.* 2012; Klepsatel *et al.* 2013).

Squamate reptiles are ideal models to characterize reaction norms of breeding phenology because of their dependence of key physiological processes to body temperature (Huey & Stevenson 1979; Clusella-Trullas, Blackburn & Chown 2011; Le Galliard *et al.* 2012). Although the effect of climatic conditions on body temperatures may be buffered by compensatory responses of basking behaviour, most physiological performance traits of ectotherms are sensitive to climatic conditions, which in turn affects fitness (Huey, Hertz & Sinervo 2003; Huey *et al.* 2009; Kearney, Shine & Porter 2009; Sinervo *et al.* 2010; Clusella-Trullas, Blackburn & Chown 2011). Here, we analysed temporal and spatial variation in parturition date within and among populations of the common lizard (*Zootoca vivipara*). This lizard is an obligate hibernating species and all reproductive stages (vitellogenesis, ovulation/fertilization, gestation and energetic recovery) occur between early May and late September. Previous studies have demonstrated earlier parturition dates in warmer years (Chamaille-Jammes *et al.* 2006; Lepetz *et al.*, 2009; Le Galliard, Marquis & Massot 2010), but the interpopulation variation in reaction norms with respect to habitat variation has not yet been characterized.

In this study, we determined how environmental conditions affect parturition date using a sample of 11 populations from the Massif Central (France) that occupy an elevation gradient ranging from 1200 to 1450 m a.s.l. This set of populations includes variation in both climatic and anthropogenic conditions encountered by common lizards in the area. The region represents the southern margin of the distribution of the common lizard and local climatic conditions are heterogeneous depending on elevation and prevailing winds. Moreover, the region has a long history of pastoralism, and different levels of human-mediated alteration characterize our study sites. To estimate the impact of such heterogeneity on the reaction norm of parturition phenology, we addressed the following questions: (i) Is local variation in parturition date affected only by climatic factors? (ii) What is the thermal sensitivity of local reaction norms? (iii) How is variation in the reaction norms for parturition date structured according to prevailing weather and habitat conditions?

Materials and methods

NATURAL HISTORY OF *ZOOTOCA VIVIPARA*

The common lizard *Z. vivipara* is a widely distributed lizard species in the family Lacertidae from Eurasia. Most of the European and Asian populations are ovoviviparous except for egg-laying populations inhabiting the very southern and western margin of the distribution (Surget-Groba *et al.* 2001). In our study area, adult males emerge from hibernation in April, before yearlings and adult females. Females emerge in late April to early May. Mating happens immediately after females' emergence. Egg fertilization is initiated shortly after copulation and gestation occurs between the beginning of May and the middle of July. The onset of parturition may be as early as in mid-late July and last through early August. After parturition, females accumulate energy reserves until hibernation which starts on average in October (detailed life cycle and phenology in Bleu *et al.* (2013)).

POPULATION MONITORING AND BREEDING CONDITIONS

The focal populations are located in four mountain chains from the Massif Central, France (exact locations in Table 1 and map in Fig. 2). We sampled 11 populations during mid to late June every two years (i.e. an average of 5 capture episodes per population) from 2003 to 2014. However, some populations were sampled as few as 3 different years and others up to six different years (Table 1). The average date of capture was the 27th of June (SD = 3·5 days). The variation in date of capture was mainly due to poor weather conditions that decreased the efficiency of captures and delayed capture dates. At each sample period, we captured 15 to 20 pregnant females from each population and measured their snout to vent length (SVL, mean = 60·1 ± 4·9 mm) and body mass (mean = 4·76 ± 1·08 g). Pregnant females were brought to the laboratory and individually housed in a separate terrarium (11 × 18 × 11 cm) under standardized conditions (average temperature = 25·19 °C; SD = 2·31), until parturition (Massot & Clobert 2000). The average ambient temperature at each field site during the period of captivity was 22·2 °C (SD = 0·83) but varied between 16·56 °C (SD = 1·23) in the colder population and 24·81 °C (SD = 3·21) in the warmer one. Females were exposed to the local prevailing photoperiod, but provided with access to heat for 6 h per day (two times for 3 h, once in the morning and one in the afternoon). Female mortality during captivity varied between 1 and 3% among years. Parturition date (PD) was calculated from the first of January (e.g. 1 = January 1st; mean PD = 199; SD = 7 days; or 18 July ± 1 week). Three days after parturition, each female was released with her offspring at the exact capture location. Over the 11 years of study, the females spent on average 22·4 days (SD = 6·9 days) in captivity. This period of captivity represents between 25 and −30% of the total gestation period that lasts about two and a half months.

DESCRIPTION OF LOCAL WEATHER DATA AND HABITAT QUALITY

Air temperature data for each population were obtained from the national French meteorological agency (MeteoFrance, MF, http://publitheque.meteo.fr). To explore the impact of temperature on parturition date, we used the mean maximal temperature

Table 1. Position and description of each population with associated mountain chain, sampling opportunities, elevation, forest cover index (FCI), meteorological station and estimated mean daily maximal temperature in June (T_{max6})

Name	Longitude	Latitude	Mountain Range	Number of samples	Meteorological station	Elevation, m	FCI	T_{max6}
BEL	44°40′3·32N	4°01′5·50E	Mont du Velay	7	Loubaresse	1385	0·30	18·82
COP	44°39′3·02N	4°01′7·82E	Mont du Velay	6	Loubaresse	1392	0·07	21·95
BES	44°35′2·81N	3°30′4·81E	Margeride	7	Mende	1200	0·1	21·63
COM	44°40′0·14N	3°31′9·14E	Margeride	6	Mende	1401	0·19	20·04
PAR	44°36′3·06N	2°29′4·79E	Margeride	6	Mende	1454	0·32	20·57
BOU	44°45′4·28N	2°28′9·05E	Margeride	5	Mende	1250	0·12	19·60
TIO	44°35′2·43N	3°06′3·37E	Mont d'Aubrac	6	Nasbinals	1272	0	17·96
USA	44°38′5·45N	3°07′2·33E	Mont d'Aubrac	4	Nasbinals	1219	0·05	15·85
BON	44°33′5·63N	3°07′6·47E	Mont d'Aubrac	6	Nasbinals	1344	0	17·18
JON	44°50′0·98N	4°12′6·49E	Mont du Vivarais	5	Mazzan Abbaye	1381	0·19	22·86
BOB	44°49′4·50N	4°13′6·96E	Mont du Vivarais	3	Mazzan Abbaye	1430	0·04	21·02

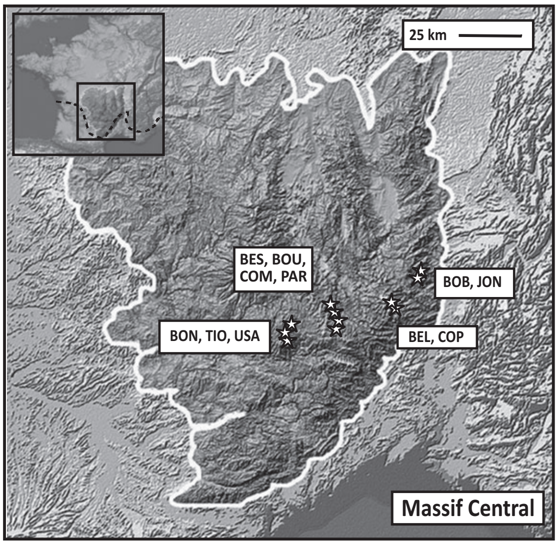

Fig. 2. Location of the common lizard populations in the Massif Central, France. The white line circumscribes the Massif Central. The dashed lines represent the southern margin of viviparous common lizard distribution. Localities of the study populations: BES = Lou Bes, BEL = Bel Air, BOB = Bout de la Barre, BON = Col de Bonnecombe, BOU = Baraque du Bouvier, COM = Col du Cheval Mort, COP = Col du Pendu, JON = Gerbier des Joncs, PAR = Lou Paradis, TIO = Tioule and USA = Usanges.

for June (T_{max6}). First, June temperature has been shown as the best proxy of thermal conditions during gestation and is known to influence significantly the length of gestation in the common lizard (Chamaille-Jammes *et al.* 2006; Lepetz *et al.* 2009; Le Galliard, Marquis & Massot 2010). Secondly, Lourdais *et al.* (2004) showed that the period of development the most sensitive to temperature is the middle part of gestation in the viviparous snake *Vipera aspis*. In the common lizard, this middle stage of gestation corresponds to June (Bleu *et al.* 2013). We estimated the value of T_{max6} that matched the period of time lizards were in the field at each study site and prior to capture. That is, we did not include data from days when females were in captivity.

We calculated local temperatures for each population from the closest MF meteorological station. However, we were unable to find a unique MF station for all populations (Table 1). As a consequence, we used temperature data from local conditions to create T_{max6} data that corresponded with MF data. Our approach involved generating a calibration curve between MF values and local conditions. We deployed temperature data loggers (Thermochron iButtons©, Waranet Solution, Auch, France) on the ground at each capture localities from mid June 2014 to the end of July 2014. We used linear regression to relate the temperatures recorded by the dataloggers for each population to those recorded by the nearest meteorological stations (see Fig. S1, Supporting information). We used the regression coefficients from the linear regression analysis to predict climatic conditions for each population from MF data (see details in Table S1). Despite the substantial altitudinal gradient present in our study, we did not use elevation in our statistical models because T_{max6} was a more relevant descriptor of breeding phenology variation than altitude (results not shown). We are not able to exclude the possibility that proxies other than T_{max6} are better in some populations but the fit of our reaction norms was satisfactory in most cases and this approach allows us to use a common model to analyse variation among the eleven populations. Finally, we also calculated an index of Forest Cover (FCI) to assess the effects of anthropogenic activities and thus local habitat quality. In the study populations, the primary source of disturbance is grazing by livestock. Using aerial photographs (scaled Google Earth© views, Mountain View, CA, USA), we measured FCI as the proportion of pixels representing trees or bushes within the total capture area.

AMONG-POPULATION VARIATION IN REACTION NORMS

To study reaction norms of parturition dates (PD) across populations, we performed a three-step analysis. First, we tested whether geographical proximity between populations was important by nesting each population within their individual mountain chain in a mixed regression model with population as a random factor. The goodness-of-fit of this model was then compared using the corrected Akaike Information Criteria (AICc) to a model excluding the effect of local mountain chain and the null model. Secondly, using a linear mixed regression models, we tested patterns of variation in the reaction norms among populations. The full model included fixed effects of T_{max6}, T^2_{max6} (to account for a potential nonlinearity), FCI, female SVL (as in previous studies) and first-order interactions between temperature variables and FCI. All variables were centred and scaled by their standard deviation to facilitate the interpretation of model estimates. We searched for both interpopulational differences in average value of parturition date (intercept of the reaction norms) and in the response to variation in T_{max6} (steepness of the slope) by including random effects of population on the intercept only or on both slope and intercept of the model:

Minimal model:	*PD ˜ fixed effects*
Random intercept:	*PD ˜ fixed effects, random = Population*
Random intercept and slope:	*PD ˜ fixed effects, random = Population +* T_{max6}**Population*

We first evaluated the random part of the model using AICc selection and a likelihood ratio test (LRT). Then, we assessed the significance of fixed effects using backward selection of non-significant terms (threshold of significance <0·05, Zuur *et al.* 2009).

Last, given significant variation in the thermal reaction norms (see below), we assessed whether the position of each population along the thermal and habitat gradient influenced the intercept and slope coefficients. We retained the regression coefficients of a linear model linking parturition date to T_{max6} for each population after temperatures were centred on the mean temperature of the eleven populations. Coefficients of the reaction norms were then regressed against the local mean T_{max6} (mean value from each population), FCI and variance in T_{max6} (VT_{max6}) using multiple linear regression models. We used two variables to represent two different aspects of climatic conditions: T_{max6} represents mean ambient temperature conditions during mid-gestation for each population, whereas VT_{max6} captures the temporal heterogeneity of weather conditions during the 11 years of sampling. However, their values were positively correlated (Spearman correlation coefficient, $r = 0·574$). To check for some collinearity issues, we calculated both Pearson's bivariate correlations predictor ($|r| = 0·67$) and the variance inflation factor ($VIF = 2·00$). These values are below the traditional thresholds ($|r| < 0·7$ and $VIF < 5$, respectively) suggesting no significant collinearity between the two variables. Hence, we retained both variables to determine the impact of climatic conditions on the shape of the reaction norms and employed backward elimination of the non-significant variables to select for the best model.

Results

Average T_{max6} (the mean maximal temperature of June) during the sample period 2003–2014 varied from 15·85 °C to 22·86 °C. Our index of disturbance, FCI, varied from 0% forest cover (fully grazed habitat) to 32% (mesic, mixed open habitat, see Table 1). Average parturition date (PD) varied between day 195 and 203 across populations and years. We found no evidence of a trend towards warmer conditions during the time period of this study (10 years); instead, all populations showed a weak decrease of temperature between 2003 and 2014 (Fig. S1). Females captured from populations located in the 'Mont d'Aubrac' mountain chain had earlier parturition dates despite experiencing cooler ambient temperatures (Fig. 3). However, according to ΔAIC differences, the model with a random population effect (AICc = 6638·8) outperformed both the nested model with a mountain chain effect (AICc = 6782·3) and the null model (AICc = 6713·9). Thus, the population differences override the regional influence among mountain chains. Based on this result, we used the model with a random population as a starting point in our analysis of the reaction norms.

The linear mixed models showed significant interpopulation differences in both the mean and slope of the reaction norm (AICc minimal model = 6472·5, AICc random intercept model = 6134·1, AICc random intercept and random slope model = 5986·1). Selection of fixed effects led to a final model summarized in Table 2. First, females with a larger SVL had earlier parturition dates (slope $b = -0·91 \pm 0·15$; $t_{1032} = -5·98$; $P < 0·0001$). In addition, PD was significantly advanced by T_{max6} ($b = -5·88 \pm 2·54$; $t_{1032} = -2·31$, $P = 0·021$) and was influenced by a two-way interaction between T^2_{max6} and FCI (Table 2). The exact pattern was that T^2_{max6} decreased PD when FCI equals zero ($b = -2·92 \pm 0·41$; $t_{1032} = -7·12$; $P < 0·0001$), but PD is delayed by FCI when T^2_{max6} equals zero, that is climate conditions are average ($b = 4·94 \pm 2·19$; $t_9 = 2·25$; $P = 0·050$). In addition, there is a reduced effect of FCI on the delay of PD at higher values of air temperatures in June ($b = -1·41 \pm 0·62$; $t_{1032} = -2·19$; $P < 0·023$).

We estimated local reaction norms by performing a linear regression between PD and local temperature for each population (see Table S1, for details of regression estimates). All reaction norms exhibited a negative relationship between mid-gestation temperatures and PD (Fig. 3). The one exception was BOB, which had a positive association. We found a significant and positive effect of VT_{max6} on the slope of the reaction norms ($b = 2·281 \pm 0·83$; $t_8 = 2·74$, $P = 0·0254$; Fig. 4e). We also found a significant and positive effect of T_{max6} on the elevation of the reaction norm ($b = 5·89 \pm 0·95$; $t_8 = 6·190$; $P = 0·0002$; Fig. 4b). One notable pattern is the reaction norm for USA. This population is characterized by particularly cold climate conditions and its reaction norm was a significant outlier. We tested whether USA influenced the relationship between coefficients of the reaction norm and environmental conditions by reanalysing the data without USA. However, the qualitative and quantitative pattern remained unchanged with the exclusion of USA (see details Fig. 4).

Discussion

In the present study, we confirmed, at a broad geographic scale, that populations of the common lizard advanced their parturition date (PD) in years with warmer temperatures during the mid-gestation period (June). We also found that PD is influenced by the interaction between variability in climatic conditions and anthropogenic disturbance as assessed by the extent of grazing. Finally, we demonstrated that PD reaction norms vary among several common lizard populations and that differences in both the mean and sensitivity of PD to thermal conditions are correlated with local climatic conditions.

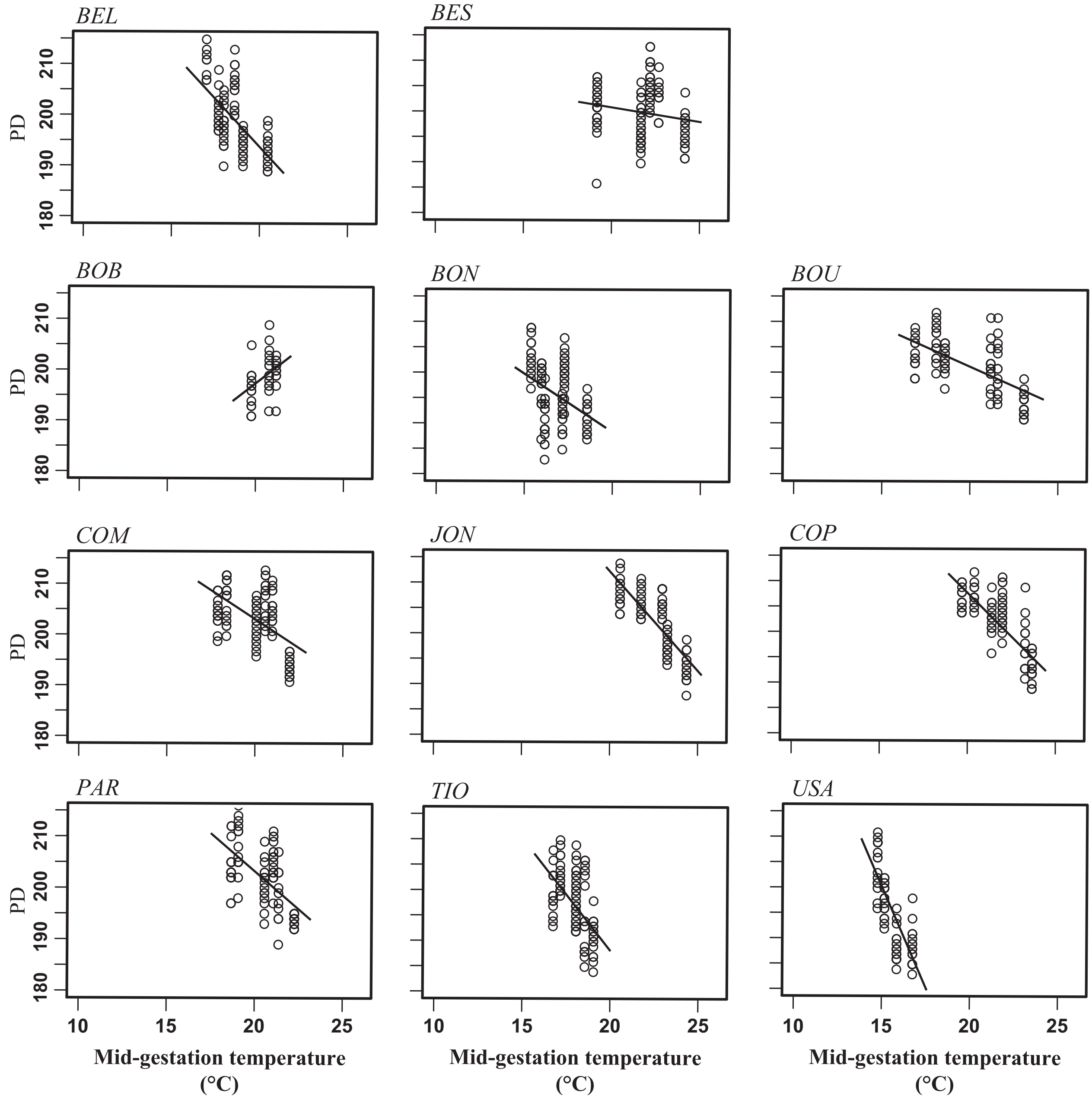

Fig. 3. Population-level reaction norms in each study site of global survey, described as the relation between parturition date and average temperature in mid-gestation (T_{max6}). All relationships were significant ($P < 0{\cdot}05$; with the exception of BES $P = 0{\cdot}06$). We excluded one population from the analysis (BOB) as the relation was positive, which may reflect insufficient sampling opportunities.

IMPACT OF LOCAL CONDITIONS ON PHENOLOGY

Parturition dates of *Z. vivipara* in the Massif Central were generally earlier when females experienced warmer temperatures during mid-gestation. This pattern was evident across all populations in Massif Central and is consistent with previous studies based on a single population on Mont Lozère, which showed that females have specific thermal requirements for gestation during June that are more difficult to attain in cooler years (Chamaille-Jammes *et al.* 2006 and Le Galliard, Marquis & Massot 2010). In our study, we extended this result by showing that the local climate supersedes regional climate conditions when modelling phenological reaction norms across populations at a broad geographic scale. Indeed, some populations included in our sample were spatially clustered in mountain regions and sometimes only few kilometres apart (Fig. 2). However, local conditions, and in particular thermal conditions, were stronger determinants of PD than spatial proximity. Furthermore, we detected the effects of climate and anthropogenic disturbance on PD even though females were maintained in captivity during the last third of their gestational period. The warm and homogeneous laboratory conditions may have introduced

Table 2. Best linear mixed effects model summary table for parturition date vs. snout to vent length (SVL), forest cover index, mid- and squared mid-gestation conditions (T_{max6}, T^2_{max6}) and first interaction terms. Temperature was nested within populations as a random effect

Predictor Variables	Estimate	SE	d.f.	*t*-value	*P*-value
Intercept	196·96	3·88	1032	50·74	<0·0001
SVL	−0·91	0·15	1032	−5·99	<0·0001
FCI	4·94	2·19	9	2·26	0·050
T_{max6}	−5·89	2·55	1032	−2·31	0·006
T^2_{max6}	−2·93	0·41	1032	−7·13	0
CFI * T^2_{max6}	−1·41	0·62	1032	−2·27	0·042

Random effects	SD	Corr
Population (intercept)	12·79	
Population (slope)	4·52	0·84

a bias in our estimation of PD reaction norms through buffering differences among individuals and populations. For example, such conditions would be expected to result in more homogeneous patterns of the timing of parturition. Yet, we recovered significant variation in PD among individuals and populations that is consistent with local climate conditions. Thus, the sampling of females during the latter period of gestation (when thermal effects are less critical, Lourdais *et al.* 2004) may have resulted in our underestimating the magnitude of plasticity in breeding phenology.

Our results also show that anthropogenic activities have a direct effect on the breeding phenology but also an effect in relation with the effect of ambient temperature. This is suggested by the significant interaction between local temperature and the forest cover index. The interaction between these factors exacerbates the effects of ambient temperatures during mid-gestation and may be a consequence of differences in the ability of common lizards to cope with temperature in fully open vs. partially covered habitats. Our analyses suggest stronger effects of temperatures in open, that is, heavily grazed areas. Economic activity in the Massif Central is, in large part, dependent on meat and milk production, pastoralism and agriculture. In the next few decades, the increase in temperatures and the new economic dynamic in the region by promoting livestock production hence grazing activities should lead to an increasingly disturbed and open landscape, enhancing the effects revealed in our analyses. Moreover, different species of livestock (e.g. cows, sheep, horses) do not pose a direct threat to lizards, but may have severe indirect effects by disturbing basking behaviour, reducing the availability of thermal refugees or by carrying parasites that may affect lizard performance.

It is difficult to assess the fitness consequences of accelerating embryogenesis because shifts in parturition date

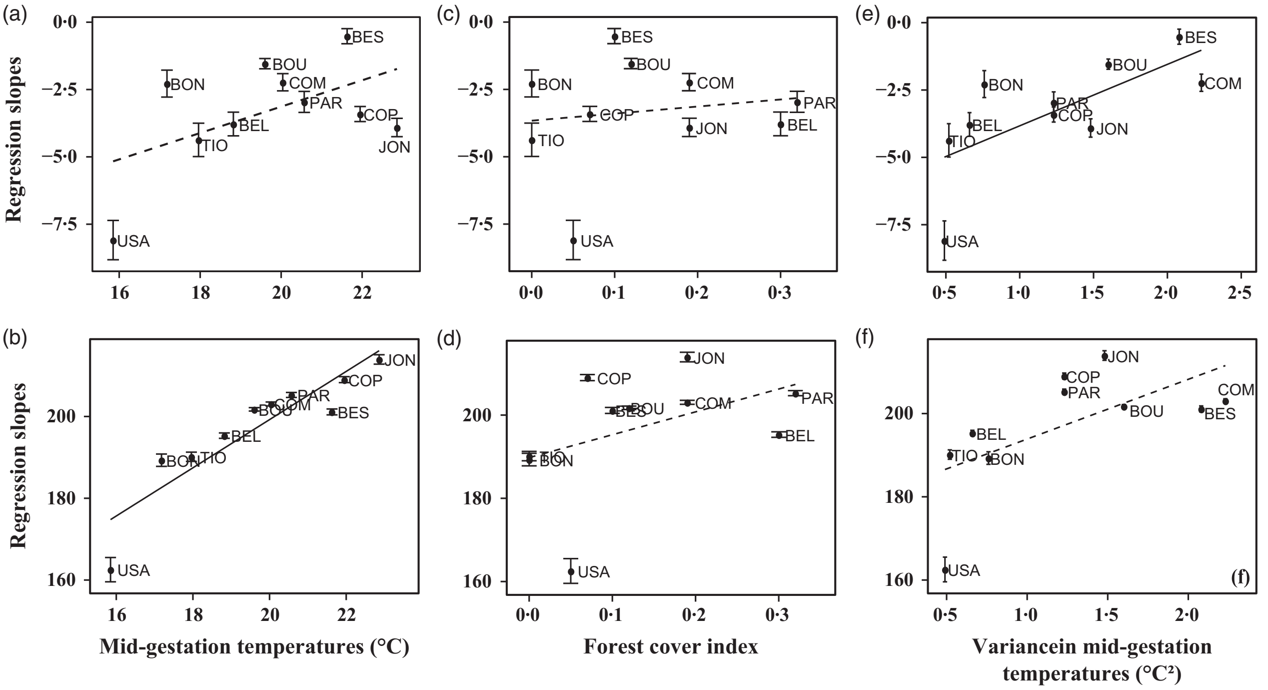

Fig. 4. Slope of the population reaction norms (‘Regression slope’; a., c., e.) and intercept (‘Regression intercept’; b., d., f.) against temperature during mid-gestation (a. and b.), Forest Cover Index (c. and d.) and Variance in Mid-gestation temperatures (e. and f.). Solid lines represent significant relationships ($P < 0·05$); dashed lines represent non-significant relationships. We note that the USA population may drive observed relationships. However, the population experiences cooler environmental conditions than other population, because of the constant windy. We hypothesize that this extreme environment is relevant to consider when comparing phenotypes among different. However, we repeated our analyses with USA removed from the data set and the results remained unchanged (The slope of the reaction norms remain correlated with VT_{max6}, $P = 0.034$; and the elevation is still influenced by T^2_{max6}, $P = 0.004$).

can have either positive or negative consequences on fitness components in common lizards. On the one hand, earlier PD should enhance the growth rate of neonates Bestion *et al*. 2015 and increase offspring survival (Le Galliard, Marquis & Massot 2010), as well as maternal survival (Chamaille-Jammes *et al*. 2006). Yet, a shorter gestation period is also linked with warmer temperatures that, if associated with drought, could be lethal for neonates, as experimentally demonstrated by E. Bestion, A. Teyssier, M. Richard, J. Clobert, J. Cote (in preparation). All things considered, we can expect a mixture of habitat and climatic factors to not only impact phenology as shown in our analysis but to affect population dynamics and age structure (Townroe & Callaghan 2014), individual parasite loads (Pounds *et al*. 2006) and species distribution (Krockenberger, Edwards & Kanowski 2012).

The negative quadratic effect of temperature during gestation on mean parturition date across populations suggests an accelerating effect of thermal conditions on the speed of gestation. High body temperature is known to enhance physiological performance in ectotherms up to a given temperature threshold, called optimal temperature (T_o) for performance (Huey & Stevenson 1979). This nonlinear sensitivity to temperature could be one hypothesis to explain the pattern of accelerating progressively gestation timing. Because sampling opportunities in our study system was limited to a maximum of six parturition years, it is challenging to disentangle whether the observed nonlinearity was due to nonlinear intrapopulation plasticity rather than differences in reaction norm slopes among populations (see Fig. 3). Detailed data from a long-term study of one population of *Z. vivipara* on Mont Lozère monitored by capture–recapture protocols continuously from 1986 to 2012 (see Massot, Clobert & Ferrière 2008 for a complete description) offered a unique opportunity to test for the existence of a quadratic, decelerating reaction norm in the same population. Supplementary analyses based on this population showed that the temperature during gestation ranged from 18·4 to 25·1 °C, but that parturition date was linearly, and not quadratically, related to mid-gestation temperature in this population (see Fig. S3 and Table S4). This result suggests that the nonlinearity observed in our large sample of populations may be a consequence of differences among populations rather than a truly, nonlinear plasticity (see next section).

AMONG-POPULATION VARIATION IN REACTION NORMS

One goal of our study was to explore the environmental characteristics that shape among-population variation in the reaction norm for parturition date including mean thermal conditions, variance in thermal conditions and forest cover. We found that consistent exposure to warm temperatures a heterogeneous pattern of advanced parturition dates depending on local weather conditions. In contrast with theoretical predictions (Ghalambor *et al*. 2007; Chevin, Lande & Mace 2010), parturition dates decreased more quickly with local temperature in populations characterized by a lower variance in mid-gestation thermal conditions. These results are surprising as they show a significant negative relationship between the magnitude of the plasticity and environmental heterogeneity. In other words, sites with low interannual variation in mid-gestation conditions show the strongest response to climate (greatest negative slope of the reaction norm), whereas sites with higher variation display weaker responses (flatter reaction norms; see Figs 3 and 4). This result is of particular importance in the context of current global change, which may enhance variations in weather conditions and alter environmental stability (IPCC 2013). Indeed, an increased instability of climatic conditions may lead populations that are used to stable conditions (and that present the strongest reaction norms) to produce disproportionate or maladapted responses (Ghalambor *et al*. 2007). Given enough time, those populations may shift to flatter reaction norms through behavioural, physiological or genetic adaptation. Alternatively, failure to adjust to new environments may results in local extinctions (Sinervo *et al*. 2010).

The observed divergence in the magnitude of the plastic response may partially be explained by the predictability of ambient conditions during mid-gestation rather than the variance *per se*. The few studies that have compared PD reaction norms between different populations of a same species (Lind & Johansson 2007; Husby *et al*. 2010; Porlier *et al*. 2012) and some theoretical models (Ghalambor *et al*. 2007; Chevin, Lande & Mace 2010) suggest that unpredictable environments will impede the evolution of plasticity as the probability to produce a maladapted (or miss-matched) response is enhanced when heterogeneity is too great. In our case, environments with higher levels of variability in mid-gestation temperatures may be less predictable; however, it is difficult to statistically assess the predictability of the climate with available data and we cannot confirm that predictability is the factor that drives the relation. A second hypothesis might be that females are more responsive in colder populations. For example, populations with the least variable thermal conditions during gestation tend to be the coldest in our data set (Fig. 3e, marginal correlation: $P = 0{\cdot}11$). The observed differences could thus reflect local adaptation that enhances the ability of females to benefit from advantageous thermal conditions when they occur. Indeed, a shortened gestation period may have been selected to release the pressure on the post-gestation period that drives preparation to hibernation of the adults and the juveniles (E. Bestion, A. Teyssier, M. Richard, J. Clobert, J. Cote, in preparation).

In conclusion, our results (i) provide evidence of interactive effects of anthropogenic disturbance and climatic conditions on parturition date, (ii) suggest that variation in PD reaction norms is correlated with local environmental conditions at a broad geographical scale and (iii) indicate that local climate variation is a major driver of spatial variation in breeding phenology plasticity. Altogether, these results emphasize the need of considering multiple factors that could drive local adaptation of reaction norms (i.e. temperature, human activities) when trying to assess how local adaptation may help populations to cope with climate change. Our study also underlines the need to take into account variation in reaction norms in the management strategy of populations threatened by climate warming and caution against the use of stable thermal reaction norms to predict the future ranges of species with climate niche models.

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Authors' contributions

All authors contributed to acquisition of field data; AR carried out the statistical analysis and drafted the manuscript; DBM, JFG and JC contributed to statistical analysis and interpretation of data; MR, DBM, JFG contributed to writing the manuscript. AR, JC and BS designed the study. All authors gave final approval for publication.

Data accessibility

Field data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.qd5gj (Rutschmann *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Air temperatures during mid-gestation conditions for each population in the study.

Figure S2. Regression between Meteo-France (MF) temperature and the temperatures obtained from iButton® data loggers deployed at each study site.

Figure S3. Relation between Parturition date (PD) and mid-gestation conditions on the long term capture mark recapture study site ROB. Despite an accelerating effect at the inter-population level, the relation does not significantly exhibit such an acceleration at the population level.

Table S1. Characteristics of each population.

Table S2. Predictor coefficients for a mixed effect model confronting parturition date (PD) to snout-vent length (SVL), mid-gestation temperature (T_{max6}), squared mid-gestation temperature (T^2_{max6}) on a 23 years old dataset.