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LETTER

Climate warming: a loss of variation in populations can accompany reproductive shifts

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Abstract

The most documented response of organisms to climate warming is a change in the average timing of seasonal activities (phenology). Although we know that these average changes can differ among species and populations, we do not know whether climate warming impacts within-population variation in phenology. Using data from five study sites collected during a 13-year survey, we found that the increase in spring temperatures is associated with a reproductive advance of 10 days in natural populations of common lizards (*Zootoca vivipara*). Interestingly, we show a correlated loss of variation in reproductive dates within populations. As illustrated by a model, this shortening of the reproductive period can have significant negative effects on population dynamics. Consequently, we encourage tests in other species to assess the generality of decreased variation in phenological responses to climate change.

Keywords

Climate change, phenology, population variation, reproduction, *Zootoca vivipara*.

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INTRODUCTION

Although variability between individuals affects the properties and adaptive potential of populations (Olsen *et al.* 2009; Gibert & DeLong 2015; Pettorelli *et al.* 2015), population-level changes in trait variation have been much less well studied than changes in mean trait values (Olsen *et al.* 2009). This observation is particularly true in the study of climate change responses (Møller & Merila 2006). Among the hundreds of studies considering the impact of climate warming on phenological traits, the most documented response of organisms to climate warming (Walther *et al.* 2002; Root & Hughes 2005; Menzel *et al.* 2006; Parmesan 2006), we found only one that tested a response in phenological variation (Winkler *et al.* 2002). This response is also suggested by some studies that found that climate warming influences the variation in phenological plasticity between individuals (Nussey *et al.* 2005; Husby *et al.* 2010). Overall, whether phenological shifts are associated with changes in variation within populations is neither known nor discussed. However, we expect these changes to be widespread because they can be generated through a variety of processes, including phenotypic plasticity, selection, dispersal, and population dynamics. Considering phenotypic plasticity, a shift in seasonal activities can lead to an increase in variation if phenological plasticity differs among individuals (with varying responses to warming) or if individuals exhibit a bet-hedging strategy (higher variance in individual responses to fluctuating temperature, Simons 2014). However, a decrease in variation is also possible if the variance in phenological traits is dependent on their mean value (for example if seasonal shifts are increasingly constrained by the biology of species). Variation in phenological traits can also depend on evolutionary changes in response to selection by climate change (Reale *et al.* 2003; Nussey *et al.* 2005; Springate *et al.* 2011). Another possible cause of changes in phenological variation can come from the effect of climate change on dispersal when immigrants and population residents differ in phenology (Møller & Merila 2006). This dispersal hypothesis is likely of secondary importance because it requires quite strong differences to impact populations significantly. Finally, variation within populations is expected to be low because of the high genetic drift in newly colonised populations at the expanding margins of species ranges (Hallatschek *et al.* 2007) and in declining populations suffering from climate warming.

Variation within populations of phenological changes are important to consider because the timing of seasonal activities is a key trait that influences the fitness of individuals and population dynamics (Reale *et al.* 2003; Nussey *et al.* 2005; Parmesan 2006). Here, we analyse data on reproductive phenology (parturition dates) of the common lizard (*Zootoca vivipara*) from five study sites located on the same mountain massif (see Fig. S1 in Supporting Information). Like many lizards (*Sinervo et al.* 2010), the common lizard shows responses to the climate warming. We have previously demonstrated dramatic changes in body size, fecundity and dispersal paralleling the rise in spring temperatures in our study area (Cévennes National Park, southern France) (Chamaillé-Jammes *et al.* 2006; Massot *et al.* 2008; Lepetz *et al.* 2009). In the present study, we report a loss of variation in reproductive dates correlated with an earlier average date of reproduction. Because testing the causality of correlations between phenological traits and temperature is critical (Lyon *et al.* 2008;

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Visser *et al.* 2009; Paull & Johnson 2014), we experimentally tested these responses. We also investigated the causes and consequences of the loss of variation in the common lizard. To be more general on the expected consequences of the loss of variation in reproductive dates on population dynamics, we also modelled the life cycles of short-lived and long-lived species with an individual-based model.

MATERIALS AND METHODS

Species

Zootoca vivipara is a cool temperate lizard whose geographic range extends throughout Eurasia and is probably the largest of living reptiles (Avery *et al.* 1982; Surget-Groba *et al.* 2001). This small lacertid (adult snout–vent length 50–70 mm) is a live-bearing species, except in the extreme south of Europe where oviparous populations have been recorded (Surget-Groba *et al.* 2001). In our study region (Southern France, 44°30′ N 3°45′, 1420 m a.s.l.), hibernation lasts from October to April. Males emerge from hibernation in April, and mating occurs soon after female emergence in early May. Females reproduce once a year and parturition occurs in July and August. Average litter size is of 5 shell-less eggs, and females give birth to fully formed juveniles that emerge from the foetal membrane within one or two hours after laying. There is no parental care, and juveniles are independent from birth. The activity season ends in late September.

Population monitoring

We studied five populations (CHA, ERM, PIM, ZDE, ZFD) located in southern France (Mont-Lozère; Fig. S1). The vegetation structure and composition varied among the populations, from dry heath land (*Calluna vulgaris*) to more humid meadows. Between 1989 and 2001, we temporarily removed 2040 pregnant females and kept them in the laboratory under standard conditions until parturition (Massot & Clobert 2000). Each female was housed in an individual terrarium (18 × 12 × 12 cm) with damp soil and a shelter. Females were exposed to natural daylight and were allowed to thermoregulate for 6 h per day under an incandescent lamp (25 W). Each female was supplied with water and *Pyralis* larvae. Terraria were checked three times per day for freshly laid litters. We did not include fully aborted litters in the data, which are laid earlier on average than successful litters. The data are provided in Fig. S2 and Table S1. We performed complementary analyses on the sites ZDE and ZFD for which we have enough data and made a survey of juveniles 1–2 months after birth (recapture session in September). We have monitored these sites using capture-mark-recaptures. All animals were individually marked by toe-clipping, when neonates in the laboratory or at first capture on the field. Toe-clipping and handling has no significant influence on subsequent recapture and survival probabilities in the common lizard (Massot *et al.* 1992). Neonates born in the laboratory were released with their mother 3 days following birth at the point of capture of the mother. Before their release, neonates were sexed according to their ventral scales (Lecomte *et al.* 1992). During capture sessions, animals were identified or marked, measured for snout-vent length (to the nearest millimetre), and located with a 1 m precision. We obtained dispersal data from the distance moved between release and last recapture within the following year (Massot & Clobert 2000).

Climate data

The monthly temperature in June was measured as the mean of the daily maximum air temperature, as recommended for reptiles (Huey 1982). Daily temperatures were collected at a local weather station (50 m from the field site PIM) and at a more distant one (50 km away). Throughout the analyses, we used temperatures from the more distant weather station because they were available for the whole 13-year study period and were closely correlated with local temperatures ($r = 0.82$, $n = 11$, $P = 0.002$). In a previous study (Massot *et al.* 2008), we found a rise in June temperature both in a time series of 29 years from 1976 to 2004 ($r = 0.53$, $P = 0.003$) and in a shorter period of 16 years from 1989 to 2004 ($r = 0.72$, $P = 0.002$). In the present study, we considered only 13 years of reproductive data available from 1989 to 2001. As it can be expected from a lower statistical power, we found only a marginally significant temporal trend ($P = 0.074$). However, this yearly trend is still robust with a correlation coefficient of 0.51 that remains very close to the correlation of 0.53 we found in the time series of 29 years. To note also that the study is focused only on relationships with June temperature because of the lack of temporal autocorrelation between temperatures in May and June ($r = 0.14$, $P = 0.645$).

Experiment

We tested the influence of temperature during gestation on the parturition date in an experiment in 2005. We captured 57 pregnant females on June 6, in a population located close to the other study populations (see the population EXP in Fig. S1), and set up three experimental groups. Females were kept in individual terrariums (10 × 20 × 15 cm) with 1 cm of damp soil, and they were exposed to natural daylight. Heat was provided by a bulb (25 W) hanging at one corner of the terrarium. A shelter allowed the females to thermoregulate. Water was provided by spraying three times per day, and females were fed once per week with one larva of *Pyralis farinalis*, according to standardised rearing conditions for this species (Massot & Clobert 2000). We provided heat 6 h day^{-1} (from 9:00 to 12:00 h and from 14:00 to 17:00 h) in the high-heat group and 3 h per day (from 9:00 to 12:00 h) in the intermediate-heat group, while we left the females in the low-heat group at laboratory temperature (ranging between 19 and 26 °C from 9:00 to 17:00 h). The thermal gradient in the warmed terraria was between 28 and 32 °C.

Statistical analyses

We analysed the mean and standard deviation (SD) of parturition dates using ANCOVAS. The independent factors we tested in these statistical models were the year or June temperature, and their interaction with the study site effect. We checked the residuals of these models for normality and homoscedasticity. To investigate the causes and consequences of variation in parturition dates, we performed complementary analyses on adult female density, phenotypic plasticity, dispersal, juvenile size, and survival rates. These analyses were on the sites ZDE and ZFD for which we have enough data. We performed a test on adult female density with abundance estimates obtained from capture–recapture models for open populations (Seber 1982). We modelled survival and capture probabilities of adult females with year dependence (Clobert *et al.* 1987) using the program MARK (White & Burnham 1999), and estimated female abundance in each year from the number of adult females captured divided by their capture probability. We tested for a change in plasticity of reproductive dates across years from 208 females present several years in our reproductive survey (153 females present 2 years, 45 females present 3 years, 9 females present 4 years, and 1 female present 6 years). We performed a mixed model with the female's identity as a random effect, spring temperature and year as fixed effects, and the interaction between the female's identity and year. Our test on dispersal was based on 59 females present in our reproductive survey and for which we were able to identify their dispersal status as juvenile (dispersal is mainly observed < 10 days after birth in our populations, Massot & Clobert 2000). Dispersing and non-dispersing juvenile females were defined as in our previous studies (Massot & Clobert 2000; Massot *et al.* 2008; Massot & Aragón 2013). We searched for a response in body size (snout–vent length) of juveniles recaptured 1–2 months after birth from the residuals of the relationship between body size and recapture date ($r = 0.29$, $F_{1,355} = 32.3$, $P < 0.0001$) to correct for the length of the growth period. We studied the variation in body size during this first period of life using SD estimated per year and sex in the site ZDE for which we have enough data (we used the values of SD when they were based on at least five juveniles recaptured per year and sex). Our analysis on juvenile survival was performed from the survey of 1699 males and 1518 females in ZDE, 561 males and 514 females in ZFD. We analysed the survival rates estimated from birth to September that we obtained from capture–recapture models for open populations (Clobert *et al.* 1987), using the program MARK (White & Burnham 1999). We modelled survival and recapture rates with age and year dependence for each study site. We log transformed the survival estimates to satisfy the normality assumption of our analysis.

Individual-based simulation of variance in reproductive dates

We investigated the influence of the variation in reproductive dates using an individual-based demographic model in discrete time. The time step is of 1 day in order to simulate finely the tempo of reproduction. The model is built from a female-based age-classified life cycle (Caswell 2001) where transitions last 1 year. For each age class, survival is expressed as a daily survival rate. The population is regulated by density according to a Ricker function acting on survival (see Appendix S1). The environment is assumed to be either constant or to vary periodically. In the periodic environment, the cyclic fluctuation of resource abundance is described by a Gaussian curve repeated over each 1 year period. Resource abundance affects survival (see the function in Appendix S1): the more abundant the resource, the less stringent the reduction on survival.

The date of reproduction of each female individual is drawn according to the normal distribution with mean θ and SD σ. At the given day, the female produces a number of offspring drawn according to a Poisson distribution. The number of female offspring is then drawn according to a binomial distribution with a sex-ratio of 0.5. When resource abundance varies periodically, reproduction is tuned to the timing of the resource in our reference scenario (with the values reported in Table 1 of Appendix S1): the mean date of reproduction θ is such that the peak of population size matches the date θ_{res} of the peak of the resource. The peak of population occurs close to the date $\theta + 2\sigma$, when most offspring is born (in fact, 95% of the offspring by the 2σ criterion). For the same reason, the half width of the population peak is 2σ. Accordingly, the Gaussian function modelling the resource in the reference scenario is chosen to have mean $\theta_{\text{res}} = \theta + 2\sigma$ and SD $\sigma_{\text{res}} = 2\sigma$.

Two typical and contrasted life cycles were considered: a short-lived species (Table 2 in Appendix S1) and a long-lived species (Table 3 in Appendix S1) (Legendre *et al.* 1999). A small lizard like *Z. vivipara* has a life cycle similar to the one used for the short-lived species. To explore the various scenarios, 10 000 trajectories are cast over a time horizon of 50 years. The number of extinct trajectories divided by the total number of trajectories gives an estimate of the probability of extinction. Demographic stochasticity is accounted for by the design of an individual-based model. The other source of stochasticity is in the individual date of reproduction.

RESULTS

Temporal and thermal trends of reproductive phenology

As shown in Fig. 1a, we observed a clear advance in reproduction during the survey ($F_{1,48} = 26.4$, $P < 0.0001$ for the yearly linear trend). Reproductive dates were similar among study sites ($F_{4,48} = 0.9$, $P = 0.462$), and the reproductive advance across years did not significantly differ between study sites (Yearly trend × Site interaction: $F_{4,48} = 2.0$, $P = 0.108$). The average advance of reproduction was 8.1 days per decade. Reproductive dates and spring temperatures were tightly correlated ($F_{1,48} = 47.5$, $P < 0.0001$), with the advanced reproduction paralleling the warmer conditions experienced by pregnant females (Fig. 1b). This relationship was similar among study sites (Temperature × Site interaction: $F_{4,48} = 0.4$, $P = 0.785$). Once the effect of temperature was corrected (test on residuals of the relationship between reproductive dates and spring temperatures), a residual year effect was still significant ($F_{12,41} = 8.0$, $P < 0.0001$).

The effect of spring temperatures on the mean reproductive dates was accompanied by a decrease in variation in reproductive dates. We found that SD decreased across years (Fig. 1c; $F_{1,48} = 21.9$, $P < 0.0001$). SD did not differ between study sites ($F_{4,48} = 2.0$, $P = 0.117$), and the yearly trend did not differ significantly between sites ($F_{4,48} = 2.2$, $P = 0.081$). The single site that did not show a decrease in SD (see site

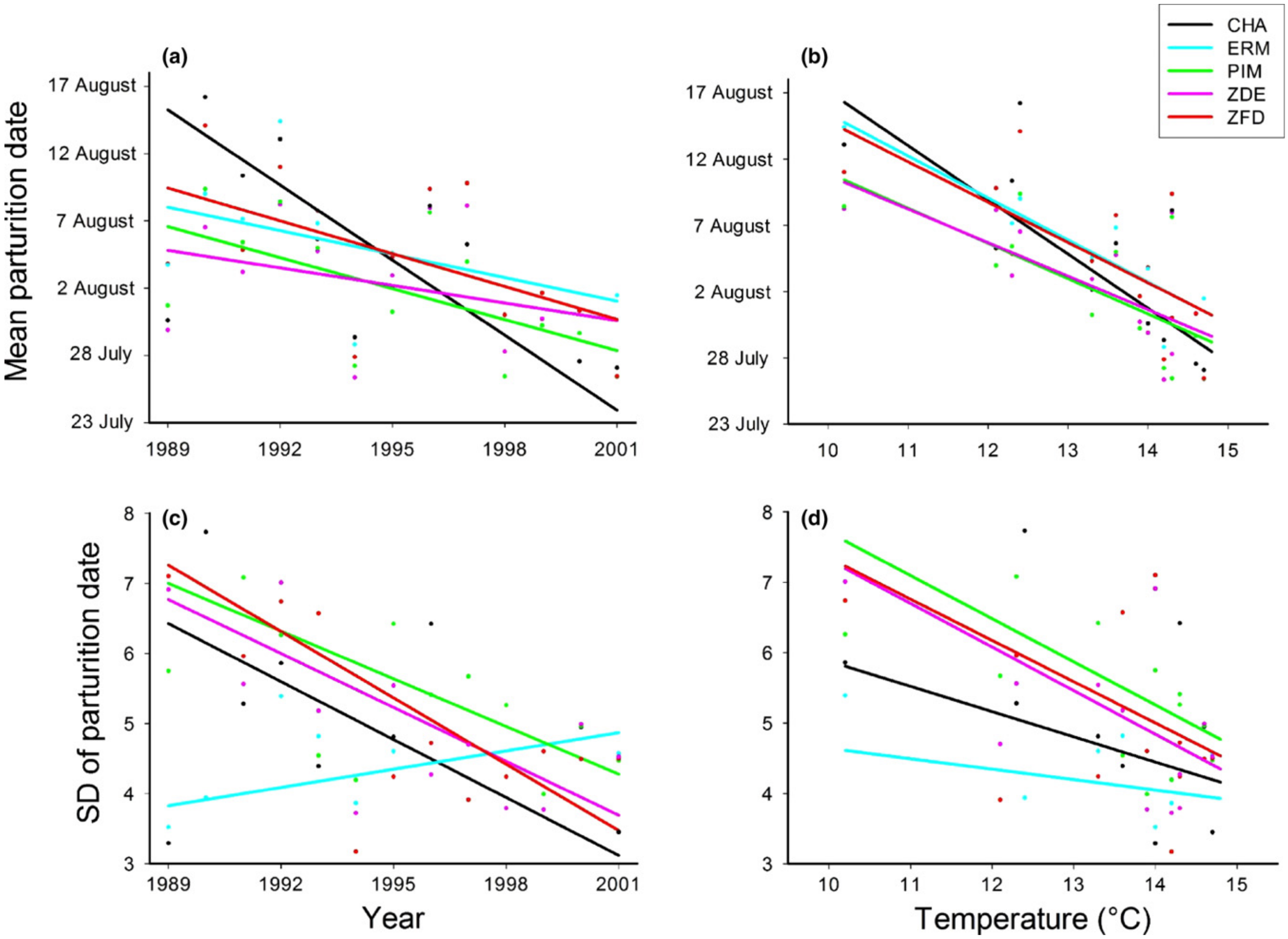


Figure 1 Temporal and thermal trends of reproductive phenology in natural populations of the common lizard at Mont-Lozère (France). (a) Advancement of the mean parturition date from 1989 to 2001 in five study areas. (b) Negative relationships between the mean parturition date and the mean of daily maximum air temperature in June. (c) Change in the standard deviation (SD) of the parturition date during the survey. (d) Negative relationships between the SD of the parturition date and the mean of daily maximum air temperature in June. Data, sample sizes and statistics are provided in Fig. S2, Tables S1 and S2.

ERM in Fig. 1c and in the Table S2) was the one that already exhibited low SD at the beginning of the study. Similarly to the pattern observed in the mean reproductive dates, SD was negatively correlated with spring temperatures (Fig. 1d; $F_{1,48} = 10.9$, $P = 0.002$). This relationship did not differ between sites ($F_{4,48} = 0.4$, $P = 0.822$). A residual year effect was still significant ($F_{12,41} = 4.8$, $P < 0.0001$) once the effect of spring temperatures was corrected. The changes in mean and variation in reproductive dates were not accompanied by other changes in the shape of the frequency distributions of parturition dates (Forrest & Miller-Rushing 2010). The skewness and kurtosis of the distributions were not dependent on the year ($P = 0.341$ for skewness, $P = 0.594$ for kurtosis) or temperature ($P = 0.470$ for skewness, $P = 0.302$ for kurtosis).

Experiment

To test the causality of the observed relationships between reproductive dates and temperature, we experimentally tested the influence of temperature during gestation on parturition dates. We observed an advance in reproductive dates with warmer conditions of gestation ($F_{2,54} = 7.8$, $P = 0.001$), showing a direct effect of temperature: mean parturition date was 16 July in a cold group, 14 July in an intermediate-heat group, and 11 July in a warm group ($n = 19$ in each experimental group). However, we did not find a significant treatment effect on the variability between individuals ($P = 0.171$, one-tailed Bartlett's test for equal variance), although the SD values were compatible with the expected decrease under increasing temperature: SD = 4.48 in the cold group, 3.99 in the intermediate-heat group, and 3.15 in the warm group. Because these values were close to the minima observed in recent years (see Fig. 1c and S3), they could not be decreased much further by temperature. These low SD values could be explained by the very early parturitions observed during our experiment in 2005 (Fig. S3) because of the positive relationship between SD and mean reproductive dates ($P < 0.0001$, Fig. S3).

Causes of the decreased variation in reproductive dates

To take into account the relationship between SD and mean reproductive dates (Fig. S3) and go further to search a cause of the decreased variation in reproductive dates, we performed a test on the coefficient of variation CV (SD divided by the mean date) estimated in our five study sites. Our goal was to test whether the negative correlation between SD and spring temperatures (Fig. 1d) was an indirect effect of the negative correlation between mean reproductive dates and spring temperatures (Fig. 1b). Although CV differed between sites ($F_{4,48} = 4.3$, $P = 0.005$), we did not find a correlation with temperature (Temperature effect: $F_{4,48} < 0.1$, $P = 0.981$; Temperature x Site interaction: $F_{4,48} = 0.6$, $P = 0.678$). This means that temperature did not have an effect on variation in reproductive dates when it is corrected by the mean date. Consequently, the relationship between SD and spring temperatures (Fig. 1d) seems to arise only from the advance in mean reproductive dates due to spring warming. This suggests that the decrease in variation in reproductive dates observed in parallel with the spring warming was an indirect effect of the mean reproductive advance. We also tested some other possible causes of the decreased variation in reproductive dates. This was not a sampling effect because the variation in reproductive dates SD was unrelated to sample sizes ($F_{1,48} = 0.3$, $P = 0.574$). We also did not find a relationship between SD and adult female density ($F_{1,22} = 3.0$, $P = 0.100$). The variation in reproductive dates SD was also unrelated to the SD in spring temperatures ($F_{1,56} = 0.3$, $P = 0.570$), and this estimate of climate variation did not change across years ($F_{1,11} = 1.1$, $P = 0.315$). To search for a response to selection or a change in phenotypic plasticity during the study, we used data from 208 females present during several years in our reproductive survey. We modelled the female's identity as a random effect and found a significant variance between females (likelihood ratio test: $X^2 = 28.4$, $P < 0.001$). However, this variability between females did not significantly change across years ($X^2 < 0.1$, $P = 0.820$). Finally, we tested if the decreased variation in reproductive dates come from the effect of spring warming on dispersal. We already know that dispersal declined over the last years and was related to spring temperatures (Massot *et al.* 2008; Lepetz *et al.* 2009). Here, we found that females that dispersed as juvenile have later in adulthood their reproductive date negatively related to spring temperatures ($F_{1,18} = 11.2$, $P = 0.004$, $n = 20$), while non-dispersing females have their reproductive date independent of temperature ($F_{1,37} = 1.8$, $P = 0.184$, $n = 39$). However, the observed pattern between dispersing and non-dispersing females shown in Fig. S4 (with differences mainly around extreme temperatures), coupled with the decline of dispersal in our populations, makes difficult to relate these responses to the decreased variation in reproductive dates.

Consequences of the decreased variation in reproductive dates

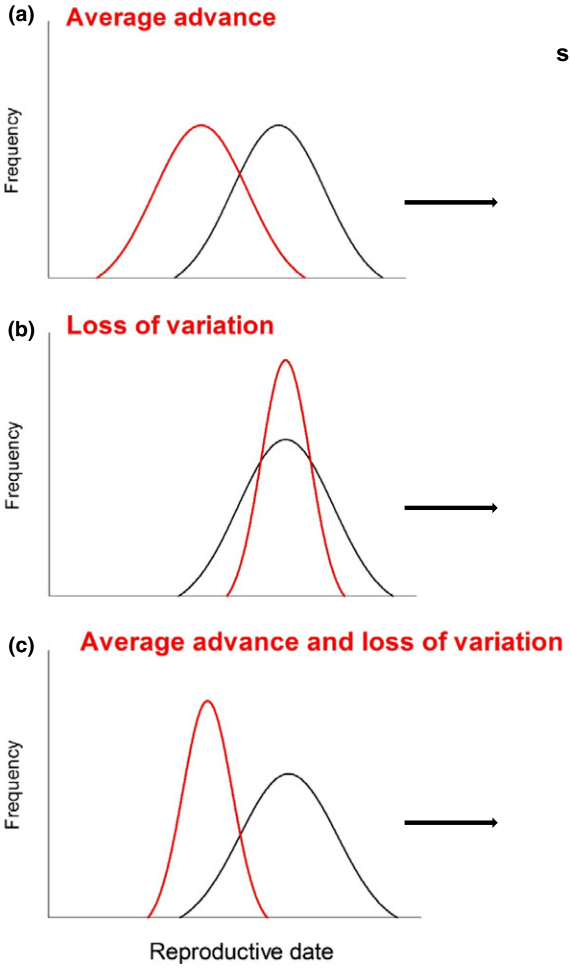
To investigate the consequences of the decreased variation in reproductive dates, we tested for its influence on the variation in body size of juveniles early in life, and also on juvenile survival that is the most influential parameter on the population growth rate in the common lizard (Le Galliard *et al.* 2010). As we could expect, the decreased variation in reproductive dates promoted a decreased variation in juvenile body size. The SD of the body size of juveniles recaptured 1–2 months after birth (body size corrected for recapture date) was indeed positively related to the SD of the reproductive dates ($r = 0.41$, $F_{1,19} = 5.0$, $P = 0.037$, $n = 21$). In spite of the decreased variation in juvenile body size, and of the relationship between juvenile body size and survival (Le Galliard *et al.* 2004), we found that juvenile survival rates were unrelated to the SD of the reproductive dates ($F_{1,38} = 0.6$, $P = 0.442$). Survival rates only differed between juvenile males and females ($F_{1,39} = 7.6$, $P = 0.009$; average survival rate [95% confidence interval] = 0.26 [0.14–0.38] in males, 0.43 [0.29–0.58] in females). Juvenile survival rates were also not significantly related to the mean reproductive dates ($F_{1,37} = 0.8$, $P = 0.374$).

To predict more generally the consequences of the decreased variation in reproductive dates on population dynamics, we modelled the life cycles of short-lived and long-lived species with an individual-based model (see Appendix S1). In the model, daily survival rates are affected by population density with a carrying capacity that varies to simulate the periodic fluctuation of a resource. In a reference scenario of synchrony, the peak and spread of resource abundance match the reproductive period, and do not match in alternative scenarios of earlier or delayed reproduction. We also considered a constant environment with no peak of resource abundance. The environments (constant or periodic) and the life cycles (short- or long-lived) were explored independently so that the probabilities of population extinction must be compared only within a given environment and for a given life cycle, not across. We found effects on the probability of extinction only for short-lived species (Fig. 3). This is expected because the most sensitive parameters in short-lived species are fecundity and juvenile survival whereas the most sensitive parameter is adult survival in long-lived species (Legendre *et al.* 1999). For short-lived species, the probability of extinction increases with the loss of synchrony between the reproductive period and the peak in resource. A shorter reproductive period also increases the risk of population extinction. We observed this negative impact of the decreased variation in reproductive dates on population dynamics whatever the synchrony of reproduction with a peak in resource (average date in reproduction modelled earlier, in synchrony or delayed with respect to the peak of resource), and even in the constant environment with no peak of resource abundance.

DISCUSSION

In parallel with the spring warming observed in the study area (Massot *et al.* 2008), we report a substantial advancement of reproductive dates in several natural populations of the common lizard. This reproductive shift is correlated with spring temperatures, in agreement with the response of many species in the Northern Hemisphere (Walther *et al.* 2002; Root & Hughes 2005; Menzel *et al.* 2006; Parmesan 2006). As indicated by our test on experimental groups showing a causal effect of temperature during gestation, this shift is also in agreement with the expected response in embryos of ectotherms, where the developmental rate increases with temperature (Lourdais *et al.* 2004). The salient result of our study is the finding of a decrease in the variation in reproductive dates accompanying spring warming. This phenological response in variability appeared likely as an indirect effect of the average shift in reproduction. We expect this indirect effect to be common because variance could often be positively related to the mean in reproductive dates, which will be especially true if the reproductive shifts with climate warming become increasingly limited because of the biology of species (phylogenetic constraints, or dependence of reproduction on environmental factors unrelated to temperature). In addition, as indicated previously, variation in phenological responses can also be affected by other processes (phenotypic plasticity, bet-hedging, response to selection, dispersal, genetic drift). However, we did not find that phenotypic plasticity and selection relate to variation in reproductive dates. Dispersal might have contributed at least partly to this variation. Indeed, dispersal declines in our populations (Massot *et al.* 2008; Lepetz *et al.* 2009) and we found that females that dispersed as juvenile have later in adulthood their reproductive date negatively related to spring temperatures.

What might be the consequences of a decrease in variation in reproductive dates combined with an average shift? First, consider a simple average shift (Fig. 2a), which is expected to have direct effects (1) by decreasing the synchrony with seasonal factors that are important for the species (Parmesan 2006) such as feeding resources (Visser & Both 2005), (2) by modifying the interactions with natural enemies (predators, competitors, parasites, pathogens) (Parmesan 2006; Paull & Johnson 2014). Indirect effects on competition with conspecifics are also possible as a result of the reduction in available resources caused by a decrease in synchrony. Similarly, changes in the species density caused by a shift in certain interactions with natural enemies will affect intraspecific competition. Now, if we consider the consequences of the decrease in variation in reproductive dates (Fig. 2b), we would expect direct effects on competition with conspecifics (Forrest & Miller-Rushing 2010), synchrony with seasonal conditions, and relationships with natural enemies. Indeed, the lower variation in reproductive dates means shortening of the reproductive period within populations. This narrower spreading of birth dates



	Synchrony with seasonal conditions	Competition with conspecifics	Natural enemies
(a)	Decrease	No direct effect	Various effects
(b)	Increase	Increase	Various effects
(c)	Decrease	Increase	Various effects

Figure 2 General expectations of the consequences of an average advance in reproduction (a), a loss of variation in reproductive dates (b), and their combined effects (c). Regarding consequences for synchrony with seasonal conditions (Parmesan 2006), we refer particularly to seasonal matching with food availability (Visser & Both 2005). Regarding competition with conspecifics, we restrict our expectations to competition with the same birth cohort. Natural enemies are defined here as predators, competitors, parasites, and pathogens. For the sake of simplicity, we limit our expectations to direct effects that do not take into account the relationships between different types of influences. For instance, a decrease in synchrony with a peak in food availability will increase competition with conspecifics. As a result of the combined effects of average reproductive dates and variation in reproductive dates, we expect that the increase in competition with conspecifics will exacerbate the detrimental effect of the decrease in synchrony with food availability.

should increase intraspecific competition, increase synchrony with seasonal conditions (more individuals born close to the average date), and change interactions with natural enemies (less frequent interactions around extreme dates, more frequent interactions close to the average date). We predict that the loss of variability, combined with the average advance in reproduction (Fig. 2c), will have a significant impact on natural populations. Indeed, the decrease in synchrony with seasonal conditions induced by the average shift is amplified by the loss of variation (individuals born close to the ideal seasonal date are even less frequent than in Fig. 2a); the increase in intraspecific competition makes this negative impact of the loss of synchrony even worse; and the effects of the average advance in reproduction and loss of reproductive variation are combined concerning the interactions with natural enemies.

In the common lizard, we found that the decreased variation in reproductive dates promoted the homogenisation of juvenile body size. Although this homogenisation might have led to a higher competition between juveniles, juvenile survival was unrelated to variation in reproductive dates. This relationship might have been masked by the great sensitivity of juvenile survival of the common lizard to water constraints and precipitations (Le Galliard *et al.* 2010). Moreover, it is challenging to find such a specific relationship in populations that have responded to climate warming for multiple parameters like in our studied populations (Chamaillé-Jammes *et al.* 2006; Massot *et al.* 2008; Lepetz *et al.* 2009). In particular, the negative effect of the body size homogenisation of juveniles might have been offset by the benefit to grow longer within their birth year because of the average advance in reproduction (Le Galliard *et al.* 2010). To overcome these limitations of the studied case and provide a wider view of the expected impact of a decreased variation in reproductive dates on population dynamics, we modelled the life cycles of short- and long-lived species. We found no effect for long-lived species that are known to be mainly sensitive to variation in their adult survival rate (Legendre *et al.* 1999). However, the decreased variation in reproductive dates is predicted to have a negative effect on populations of short-lived species. We found that this detrimental effect plays independently of the responses to the average reproductive shift (Fig. 3), and this illustrates the potential general impact of the increased competition between juveniles born within a shorter period (Fig. 2; Forrest & Miller-Rushing 2010).

Further studies on others species testing that a loss of variation accompanies reproductive shifts will allow to assess the generality of this phenomenon. Beyond the indirect effect of the relationship between the mean and variance of reproductive dates, these studies will allow to investigate the other processes that may impact variability in populations. Tests on others species could be conducted very easily and quickly because SD can be extracted from the hundreds of studies that have previously demonstrated reproductive shifts in response to climate change. A meta-analysis testing this hypothesis in the future will be especially interesting but would not be particularly valuable at present because almost all papers reporting results on average phenological responses to climate change have not reported estimates of their variance. As a repeated suggestion (Olsen *et al.* 2009; Gibert & DeLong 2015; Pettorelli *et al.* 2015), we encourage researchers to pay more attention to variability among individuals.

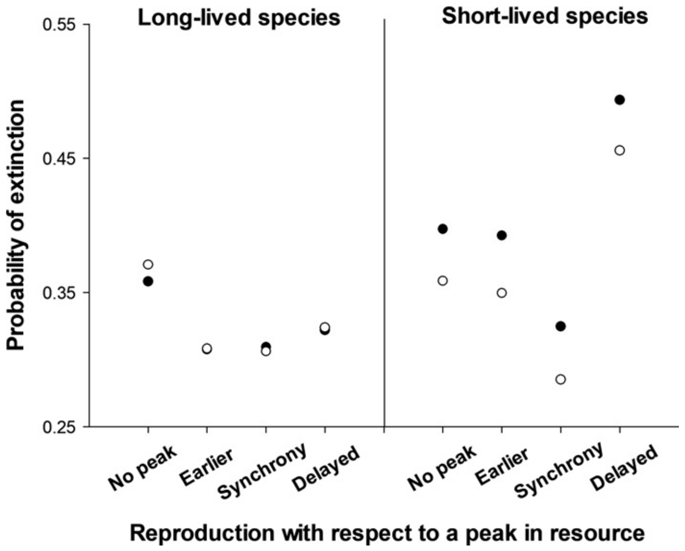


Figure 3 Influence of the loss of synchrony of reproduction with a peak in resource and of the variation in reproductive dates on population dynamics of long-lived and short-lived species. We compared three scenarios varying the average timing of reproduction (earlier, in synchrony, and delayed with respect to a peak in resource), and a scenario with a constant environment (no peak). For each of these scenarios, we compared shorter (filled circles) vs. longer reproductive periods (open circles) to investigate the influence of variation in reproductive dates. The probability of population extinction under the different scenarios were estimated from simulations of individual-based models (see Appendix S1).

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AUTHORSHIP

MM and JC conceived the idea, conducted fieldwork and developed the database. SL developed the model and performed numerical simulation. PF and MM performed the experiment in 2005. MM performed statistical analyses and wrote the paper with revisions from JC and SL.

DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.2np3s

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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