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Cohort variation, climate effects and population dynamics in a short-lived lizard

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Summary

1. Demographic theory and empirical studies indicate that cohort variation in demographic traits has substantial effects on population dynamics of long-lived vertebrates but cohort effects have been poorly investigated in short-lived species.

2. Cohort effects were quantified in the common lizard (*Zootoca vivipara* Jacquin 1787), a short-lived ectothermic vertebrate, for body size, reproductive traits and age-specific survival with mark–recapture data collected from 1989 to 2005 in two wetlands. We assessed cohort variation and covariation in demographic traits, tested the immediate and delayed effects of climate conditions (temperature and rainfall), and predicted consequences for population growth.

3. Most demographic traits exhibited cohort variation, but this variation was stronger for juvenile growth and survival, sub-adult survival and breeding phenology than for other traits.

4. Cohort variation was partly explained by a web of immediate and delayed effects of climate conditions. Rainfall and temperature influenced distinct life-history traits and the periods of gestation and early juvenile life were critical stages for climate effects.

5. Cohort covariation between demographic traits was usually weak, apart from a negative correlation between juvenile and sub-adult body growth suggesting compensatory responses. An age-structured population model shows that cohort variation influences population growth mainly through direct numerical effects of survival variation early in life.

6. An understanding of cohort effects is necessary to predict critical life stages and climatic determinants of population dynamics, and therefore demographic responses to future climate warming.

Key-words: cohort effect, life history, rainfall, reptiles, temperature

Introduction

An accurate description of population trajectories requires some understanding of individual variation and life-history plasticity (e.g. Beckerman *et al.* 2002; Benton, Plaistow & Coulson 2006). Plasticity is often caused by immediate, short-term effects of the environment, but environmental conditions experienced during early development can also have delayed, long-lasting consequences (Mousseau & Fox 1998; Lindström 1999; Beckerman *et al.* 2002). In long-lived species, parental effects, offspring characteristics and post-natal conditions experienced early in life are critical determinants of temporal variation in life-history traits (e.g. Gaillard, Festa-Bianchet & Yoccoz 1998; Lindström 1999; Benton, Plaistow & Coulson 2006). For example, in several long-lived species of birds and mammals, population density, food and climate are important factors of life-history plasticity that can influence entire birth cohorts and cause cohort effects (e.g. Albon, Clutton-Brock & Guinness 1987; Forchhammer *et al.* 2001; Reid *et al.* 2003; Descamps *et al.* 2008 and references therein). In comparison, we know relatively little about cohort effects in short-lived animal species (reviewed by Gaillard *et al.* 2000; Beckerman *et al.* 2002; Lindström 1999) and plants (e.g. Roach 2003). Short-lived squamate reptiles (lizards and snakes) are good model systems for this purpose because they are directly sensitive to climate conditions due to ectothermy (Shine 2005).

Two main types of cohort effects have been identified in natural populations of animal and plant species with annual breeding cycles (Beckerman *et al.* 2002; Gaillard *et al.* 2003). Temporal variation in environmental conditions may cause effects on pre-breeding survival and body growth and therefore variable recruitment rates, hereafter called *numerical cohort effects* after the terminology of Gaillard *et al.* (2003). Numerical cohort effects can be due to immediate or short-term delayed effects of environmental variation and are

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therefore often difficult to distinguish from annual variation. In addition, environmental conditions experienced early in life may have long-term delayed effects on the performances of breeding adults, which generates *delayed quality cohort effects* (Gaillard *et al*. 2003). Numerical and delayed quality cohort effects have been well demonstrated in some long-lived mammals and birds (e.g. Gaillard *et al*. 2003; Reid *et al*. 2006) and two critical issues in their analysis have been recognized. First, studies should quantify the demographic consequences of cohort effects (e.g. Gaillard *et al*. 2003; Wittmer, Powell & King 2007). In an age-structured population, contribution of life-history variation to population growth depends on variance and covariance of demographic traits (e.g. Coulson, Gaillard & Festa-Bianchet 2005). Thus, we need to measure cohort effects for survival, reproduction and other vital rates at several ages, which have seldom been done in a single species. Secondly, studies of cohort effects should also identify the crucial environmental factors and the most sensitive life stages (e.g. Benton, Plaistow & Coulson 2006). This demonstration requires long-term monitoring programmes and detailed individual-based data that are not always available (discussed in Grosbois *et al*. 2008).

Climate conditions affect all individuals of a population at the same time and are good candidate factors of cohort effects in squamate reptiles whose physiological processes are closely tuned to heat and water availability. Here, we examined cohort variation caused by climate conditions (temperature and rainfall) in a short-lived reptile inhabiting relatively cool-climate wetlands throughout Europe, the common lizard (*Zootoca vivipara*). Based on our understanding of population demography in short-lived reptiles and this species, we anticipated three major demographic patterns. First, we expected that warmer environments should be associated with longer activity and growth periods as well as faster growth rates (reviewed in Adolph & Porter 1993) and predicted that increased temperatures should be associated with earlier breeding, faster growth and better body condition, as well as increased reproductive performances and/or survival (Sorci, Clobert & Bélichon 1996; Chamaillé-Jammes *et al*. 2006). Furthermore, air humidity influences activity and growth opportunities and rainfall influences habitat quality and food availability (e.g. Lorenzon *et al*. 1999; Jordan & Snell 2002; Marquis, Massot & Le Galliard 2008). Thus, we predicted lower growth, survival and reproductive performances when rainfall is low. On the other hand, stronger rainfall may also be a proxy for poor basking conditions and cause negative fitness effects (Marquis, Massot & Le Galliard 2008). These climate effects are likely to be more pronounced during gestation (i.e. maternal effects, Lorenzon, Clobert & Massot 2001 and references therein) and during early growth stages. The second major demographic pattern we expected is a larger cohort variation earlier in life than later in life (Gaillard & Yoccoz 2003) and potential difference between males and females due to sexual differences in physiology, morphology and behaviour (Le Galliard, Ferrière & Clobert 2005). We also anticipated that heterogeneity in body size and birth date would cause a substantial demographic variation within each age class (Shine 2005). Third, the covariation between demographic traits and the demographic consequences of cohort effects should depend on plasticity and life-history trade-offs. Climate variation may cause 'silver spoon' effects (Grafen 1988), induce positive covariation among life-history traits and result in large temporal variation in population growth (e.g. Madsen & Shine 2000; Reid *et al*. 2003). On the other hand, growth catch-up and other compensatory demographic responses are feasible in continuous growers like common lizards (Metcalfe & Monaghan 2001; Le Galliard, Ferrière & Clobert 2005). Compensatory responses would cause negative correlations among demographic traits and should buffer the demographic consequences of cohort effects.

To test these predictions, individual-based mark–recapture data were collected from 1989 to 2005 in two contiguous habitats from the Mont Lozère in southern France, which faces local warming and variable rainfall conditions (Chamaillé-Jammes *et al*. 2006; Marquis, Massot & Le Galliard 2008). In a first set of analyses, cohort effects were quantified for body size, reproduction (breeding phenology, clutch size, reproductive failures and offspring size) and age-specific survival. We reported previously on significant cohort variation for fecundity (6·6% of the trait variance) and offspring size (17·2% of the variance, see Marquis, Massot & Le Galliard 2008), and do not present these analyses here. Next, the effects of individual traits (age, sex, habitat, body size and birth date) were disentangled from the effects of birth cohort and yearly conditions for each life-history trait. We tested whether temperature and rainfall contributed to cohort effects, including both immediate and delayed effects of climate conditions experienced before birth (i.e. intergenerational effects) or after birth early in life (i.e. early environmental effects, see Fig. 1). Finally, cohort covariation in life-history traits was tested and consequences of cohort effects for population growth rate were assessed with an age-structured population model.

Materials and methods

STUDY SITES AND LIFE-HISTORY DATA COLLECTION

Mark–recapture data were obtained from 1989 to 2005 in two study sites located in the same glade (1420 m a.s.l.) from the Mont Lozère area, southern France (44°30′N, 3°45′E). Physical heterogeneity differs between a habitat with high structural diversity made out of rocks, trees and grasslands (habitat $F+$, 4300 m^2) and a habitat with low structural diversity (habitat $F-$, 4700 m^2). These sites also differed for density ($F+$, 700 adults ha^{-1} vs. $F-$, 430 adults ha^{-1}) and life-history patterns (see Clobert *et al*. 1994). Each year, sites were sampled for sub-adults and adults in a capture session done ca. 1 month before parturition (June–July). Juveniles were also captured in another session 1 month after parturition and before wintering (September). During each session, captured animals were located, identified or marked by toe-clipping and measured for body length from the snout to the vent (snout-vent length, SVL). Individuals were released at the capture location, except in June–July where gravid females were transported to a laboratory and kept in individual cages

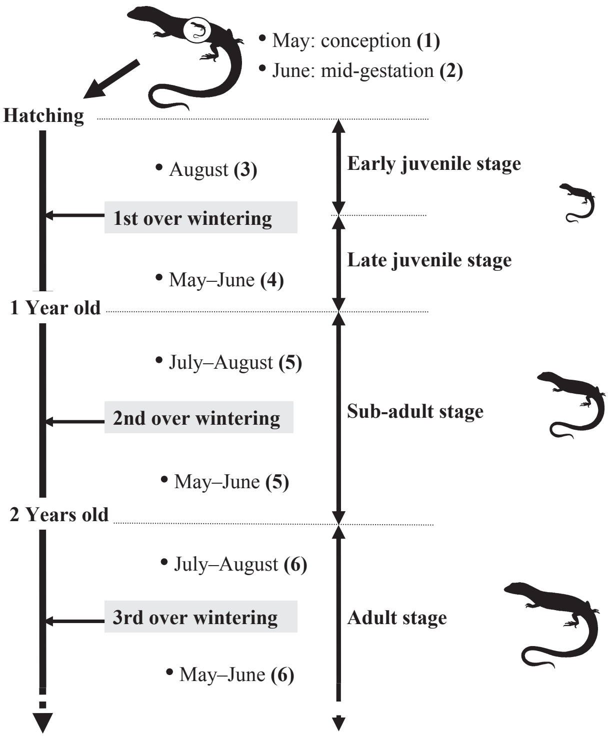

Fig. 1. The life cycle of the common lizard was decomposed into six life stages for the analysis of climate effects on cohort variation in life-history traits. For each birth cohort, rainfall and temperature conditions were calculated at six distinct life stages until adulthood: (1) around conception time, i.e. in May of birth calendar year, (2) during the middle of gestation, i.e. in June of birth year, (3) during the first month of life, i.e. in August of the birth year, (4) during the spring (i.e. in May–June) of the calendar year following birth, (5) during the sub-adult activity season (i.e. in July–August–May–June) and (6) during the adult activity season (i.e. in July–August–May–June). For the sake of brevity, we refer to these life stages as conception, past mid-gestation (to distinguish from current mid-gestation during the reproductive year), early juvenile, late juvenile, sub-adult and adult stage.

until parturition. Parturition date and total clutch size were recorded, and the total number of unhatched eggs, dead hatchlings and live hatchlings was counted. Alive hatchlings were marked by toe-clipping, sexed according to their ventral scales and measured for SVL. Mothers were weighted after parturition, and released together with their offspring at the capture location 3–5 days after parturition. Individuals could be attributed to a birth cohort in three instances: they were born in the laboratory, they were first seen as a juvenile in September of their birth year, or they were first seen as a sub-adult in June–July of the year following their birth (Massot *et al.* 1992).

CLIMATE DATA COLLECTION

Temperature and rainfall were recorded continuously by Météo-France from 1989 to 2005 at a meteorological station situated 50 km south at a similar altitude than the study sites (Mont Aigoual, 1567 m a.s.l., 44°07′N, 3°35′E). This station provided high quality and long-term meteorological data that are highly correlated with meteorological data in the study sites ($r > 0{\cdot}83$), which were only available for a shorter and discontinuous time period (see Chamaillé-Jammes *et al.* 2006). For temperature data, we used means of daily maximum temperature. For rainfall data, we used cumulative amount of precipitation. Analysis of insolation data available from 1990 to 2007 at a nearby meteorological station in Mende-Chabrits (44°32′N, 3°27′E, 932 m a.s.l.) shows that maximum daily temperatures are more strongly correlated with insolation, hence with basking opportunities, than rainfall (see Marquis, Massot & Le Galliard 2008). For each climate variable and each birth cohort, we calculated stage-specific data (Fig. 1). For the analysis of female reproductive traits, we also calculated current climate conditions during gestation (cumulative rainfall and temperatures during June of the reproduction year). Supplementary information on temporal variation and correlation patterns between climatic variables is reported in Appendix S1 (Supporting information). To address potential colinearity issues caused by correlation between climatic variables, we tested whether an effect attributed to one climatic covariate was robust to inclusion of a correlated climatic covariate, especially for rainfall and temperature during mid-gestation (see Appendix S1, Supporting information). Effects were all robust and colinearity was therefore not a strong issue in these analyses.

BODY SIZE AND REPRODUCTIVE TRAITS

To analyse body size, we used SVL like in our previous studies (see Le Galliard *et al.* 2006 for justification) and calculated stage-specific growth rates (body size change divided by the time interval). Similar qualitative results were obtained when we calculated relative growth rates (i.e. daily change in size as a proportion of current size, see Sinervo & Adolph 1989). We calculated juveniles' growth rates during the first year of life (i.e. from hatching to June of the year following birth) and sub-adults' growth rates (i.e. from June of the year following birth to June of the next year). We included initial body size as a covariate in models describing growth rates. For adults, we gathered repeated observations of individual body size after the age of 2 years. Since adult growth curves are well fitted by a function where growth rate decelerates with age, adult body size was analysed with a model for repeated measurements assuming a quadratic effect of age. For reproductive traits, we calculated for each breeding event: (i) parturition date; (ii) reproductive failures (proportion of unviable eggs within the total clutch); and (iii) post-parturition body condition (residuals of a linear regression of post-parturition body mass against body size).

Cohort variation was examined with mixed effects linear model in R 2·7·0 software (http://cran.r-project.org/) following Pinheiro & Bates (2000) and Venables & Ripley (2002). The random part included cohort identity and, when repeated measures from the same individual were included, an individual identity effect nested within the cohort effect. For juvenile growth, we also included a random litter identity effect nested within the cohort identity effect. Using a random effect model, we first calculated variance components as the % of the sum of residuals and random effects, hereafter named R^2_rand in the main text. We then added the fixed part of the model, which included additive effects of individual covariates (habitat, sex, age, body size) and climate variables that are defined in the legend of Fig. 1. From this, we calculated estimates for fixed effects and standard deviations for random effects, selected a minimum adequate model with a stepwise procedure by exact AIC (Akaike Information Criterion) and tested the significance of fixed effects with marginal F tests (Venables & Ripley 2002). For normally distributed responses, we used a maximum likelihood approach in the *lme* procedure. The normality and homogeneous variance of residuals and random effects were satisfactory in all cases. For analysis of reproductive failures, we used a Laplace approximation of the maximum likelihood implemented in *glmer* procedure with a binomial distribution and a logit link function.

SURVIVAL PROBABILITIES

Mark–recapture models and data

We used capture–mark–recapture models for open populations to measure 'apparent' survival (i.e. including disappearance due to emigration and death) and capture probabilities (Lebreton *et al.* 1992). However, since a dense forest that severely constrains lizards' movements surrounds the study area, our estimates of apparent survival probabilities reflect mostly variation in mortality (Massot *et al.* 1992). For juveniles, we used recapture histories of offspring born in the laboratory and recaptured 1 month (September), 10 months (June–July) and 22 months (June–July) later. We discarded recaptures done less than 3 weeks after birth to reduce variation in age at recapture (mean = 42 days, range = 22–70 days). Yet, ages at recapture varied due to changes in birth dates (see below), which could potentially bias juvenile survival estimates. We included birth date as a covariate in this analysis to control for this heterogeneity. For sub-adults and adults, we used recapture histories including all yearly observations of June–July from the age of 1 year until the age of five. This allows estimating annual survival until the age of 4 years, which includes sexual maturation, prime age and senescence (Ronce, Clobert & Massot 1998). We calculated capture effort during a session as the number of days spent in the field (Massot *et al.* 1992).

Goodness-of-fit tests of the general models

We based our goodness-of-fit (GOF) tests on a general model with variation in survival and capture probabilities between age classes and cohorts for juveniles and between age classes, sexes and cohorts for sub-adults and adults. We ran the general model in M-SURGE 1·8 software to diagnose convergence and detect redundant parameters (Choquet *et al.* 2005) and performed GOF tests with a parametric bootstrap test (1000 simulations) in MARK version 4·3 to estimate the amount of over-dispersion (White & Burnham 1999). The bootstrap GOF tests found no over-dispersion for juvenile recapture histories ($P = 0{\cdot}229$) and a slight over-dispersion for sub-adult and adult recapture histories ($P = 0{\cdot}07$). We calculated the over-dispersion parameter from the deviance of bootstrap simulations.

Model selection and hypotheses tests

Model selection and hypotheses tests were conducted with a maximum likelihood approach for juveniles and a quasi-likelihood approach for sub-adults and adults, the logit link, and the Akaike Information Criterion corrected for small sample size (AICc or QAICc) in MARK. The best model was chosen among models with the lowest AICc values and we calculated for each model the ΔAICc (difference with AICc of the best model), AICc weight (a measure of the degree of support of the model) and model likelihood (a measure of the degree of support relative to the best model). Generally, when the ΔAICc between two models is < 2, both models have approximately equal support in the data. If $2 < \Delta\mathrm{AICc} < 7$, then there is support for a real difference, and if $\Delta\mathrm{AICc} > 7$, then there is considerable evidence to support the conclusion of differences between models (Burnham & Anderson 1998).

We followed the methodology of Lebreton *et al.* (1992) to select a minimum adequate model. We first selected the best models describing variation in capture probabilities according to age, sex, cohort effects and capture effort. Next, we selected the best models describing variation in survival according to age, sex and cohort effects. From this, we used a variance components approach to calculate the mean survival (± SE) and cohort variance in survival (White & Burnham 1999). In a third and last step, we tested for the effects of climate and individual covariates on survival by forward selection. We included only additive and linear effects and tested first separately for individual and climate covariates. For climate covariates, we combined model selection based on AICc (or QAICc) scores and tests of specific null hypotheses as recommended by Grosbois *et al.* (2008). Following the methodology and notations of Grosbois *et al.* (2008), we tested for the effects of covariates with (i) a likelihood-ratio test (LRT) of the presence of temporal variation in survival unexplained by the covariate ($LRT_{cov/cohort}$); (ii) a LRT test or an analysis of deviance test of the effects of the covariate ($LRT_{cov/const}$ and $F_{cov/cohort/constant}$, which compares deviance between the covariate relative to the constant and cohort models); and (iii) a partitioning of variation in survival using a fixed-effect model approach (R^2_dev from Skalski, Hoffmann & Smith 1993). Once the best climate model was selected, we added significant individual covariates and again assessed the significance of climate covariates.

PROJECTION MATRIX MODEL

We used a matrix projection model to calculate the asymptotic growth rate (λ) of an age-structured population parameterized with cohort-specific vital rates. This method can predict the potential impact of each demographic trait and of each birth cohort to population growth when the population is at equilibrium. A stable age structure may not be reached when cohort effects are strong (e.g. Wittmer, Powell & King 2007), but our field observations indicate that the assumption of stable population is reasonable (Massot, unpublished data). The model assumes a post-breeding census, birth pulse dynamics and included only the female portion of the population. We considered three age classes in a transition matrix (juveniles, sub-adults and adults) that included juvenile survival, sub-adult survival, adult survival and fecundity. We calculated λ as the dominant eigenvalue of the transition matrix and estimated the 95% confidence limits of λ with Monte Carlo simulations to account for uncertainty in the mean demographic rates (5000 projection matrix, see Alvarez-Buylla & Slatkin 1991). Estimates of λ were approximately normally distributed and were compared with the percentile method and parametric statistics. We first used the long-term mean of each vital rate to calculate the mean population growth rate, as well as sensitivities and elasticities to each vital rate (Caswell 2001). Next, we calculated a transition matrix for each birth cohort to assess cohort variation in population growth. We included cohort-specific estimates for early juvenile survival, sub-adult survival and fecundity.

Results

BODY SIZE

Juvenile growth

Using a random effect model, we found that growth rates varied significantly between cohorts ($R^2\_rand = 37{\cdot}5\%$ of the residuals and random effects variance) as well as among litters ($R^2\_rand = 61{\cdot}5\%$). An analysis of the determinants of cohort variation in growth rates further demonstrated significant effects of both climate conditions and individual covariates (Table 1). First, initially larger juveniles grew more slowly than smaller lizards and juveniles grew more slowly in the *F*− habitat. Growth rates were also influenced by additive effects of rainfall experienced by the mother during mid-gestation and rainfall experienced by juveniles during the first month of life (early juvenile stage). The first significantly increased the growth of juveniles (Fig. 2a), while the second had a negative effect (Fig. 2b). Interestingly, there were no detectable effects of temperature on growth (temperature during past mid-gestation: $F_{1,9}$ = 2·34, *P* = 0·16; early juvenile temperature: $F_{1,9}$ = 0·02, *P* = 0·89). The absence of detectable thermal effects was confirmed by an analysis of body growth rates from birth to the age of 1 month (age = 22–71 days) that included more birth cohorts and observations (445 offspring, 16 birth cohorts; early juvenile temperature: $F_{1,14}$ = 0·03, *P* = 0·87).

Body size at the end of juvenile stage varied significantly among birth cohorts (R^2*_rand* = 28·2%) and among families (R^2*_rand* = 69·8%) but none of the climate variables had detectable effects on body size (all *P* > 0·05). Body size at the end of juvenile stage corrected for capture date varied also significantly with habitat ($F_{1,302}$ = 32·10, *P* < 0·0001), birth date ($F_{1,302}$ = 21·45, *P* < 0·0001) and sex ($F_{1,302}$ = 7·46, *P* = 0·007). At the end of the juvenile stage, lizards from habitat *F*+, lizards from litters born early in the previous year, and female lizards were larger, respectively, than lizards from habitat *F*−, than lizards from litters born late in the previous year and than males.

Sub-adult growth

A significant variation among cohorts of sub-adult growth rates was detected (R^2*_rand* = 19·8%). In the mixed effects model, initially larger sub-adults grew less than smaller lizards (Table 1). In addition, growth rates differed between sexes, with males growing less than females. Surprisingly, climate conditions experienced by yearlings during growth did not influence their growth rates (rainfall: $F_{1,10}$ = 0·08, *P* = 0·77; temperature: $F_{1,10}$ = 0·08, *P* = 0·98), but growth rates were affected by a delayed effect of temperature during the early juvenile stage (Table 1). Sub-adults exposed to higher temperatures during their first month of life grew faster (Fig. 2c). Body size at the end of sub-adult growth varied significantly between cohorts (R^2*_rand* = 28%). At the cohort level, temperature experienced during the early juvenile stage had a positive effect on body size at the age of 2 years ($F_{1,11}$ = 12·72, *P* = 0·004) but none of the other climate variables were influential (all *P* > 0·05). At the individual level, body size at the end of sub-adult stage

Table 1. Cohort variation in juvenile growth rate (mm day^{-1}, 323 observations from 14 cohorts, cohorts of 1997 and 2004 were not included) and sub-adult growth rates (mm day^{-1}, 374 observations from 13 cohorts, cohorts of 1996, 1997 and 2003 were not included in the analysis because of a lack of suitable data to calculate growth rates). The model was obtained by backward selection from a full model including effects of climate conditions (rainfall and temperature) and additive effects of initial body size, sex and habitat

Fixed effects	Estimate ± SE	$F_{\text{ndf,ddf}}$	*P*-value
Juvenile growth rates			
Initial SVL	−0·0027 ± 0·0006	16·55 $_{1,304}$	0·0001
Habitat	*F*−: −0·0076 ± 0·0017	19·02 $_{1,304}$	< 0·0001
Past mid-gestation rainfall	0·00009 ± 0·00002	17·56 $_{1,11}$	0·0015
Early juvenile rainfall	−0·00021 ± 0·00006	11·63 $_{1,11}$	0·0058
	Estimate [95% CI]	LRT test	*P*-value
Random effects			
Cohort identity	0·0054 [0·0032, 0·0091]	24·83	< 0·0001
Mother identity in cohort	0·0130 [0·0120, 0·0141]	7·26	0·0071
	Estimate ± SE	$F_{\text{ndf,ddf}}$	*P*-value
Sub-adult growth rates			
Initial SVL	−0·0019 ± 0·0001	501·83 $_{1,358}$	< 0·0001
Habitat	*F*−: −0·0019 ± 0·0010	3·43 $_{1, 358}$	0·06
Sex	M: −0·0104 ± 0·0009	131·11 $_{1, 358}$	< 0·0001
Early juvenile temperature	0·0034 ± 0·0012	8·16 $_{1,11}$	0·02
	Estimate [95% CI]	LRT test	*P*-value
Random effects			
Cohort identity	0·0038 [0·0022, 0·0056]	37·31	< 0·0001

F− = low-density site; M = males; SVL = snout-vent length; LRT = likelihood-ratio test.

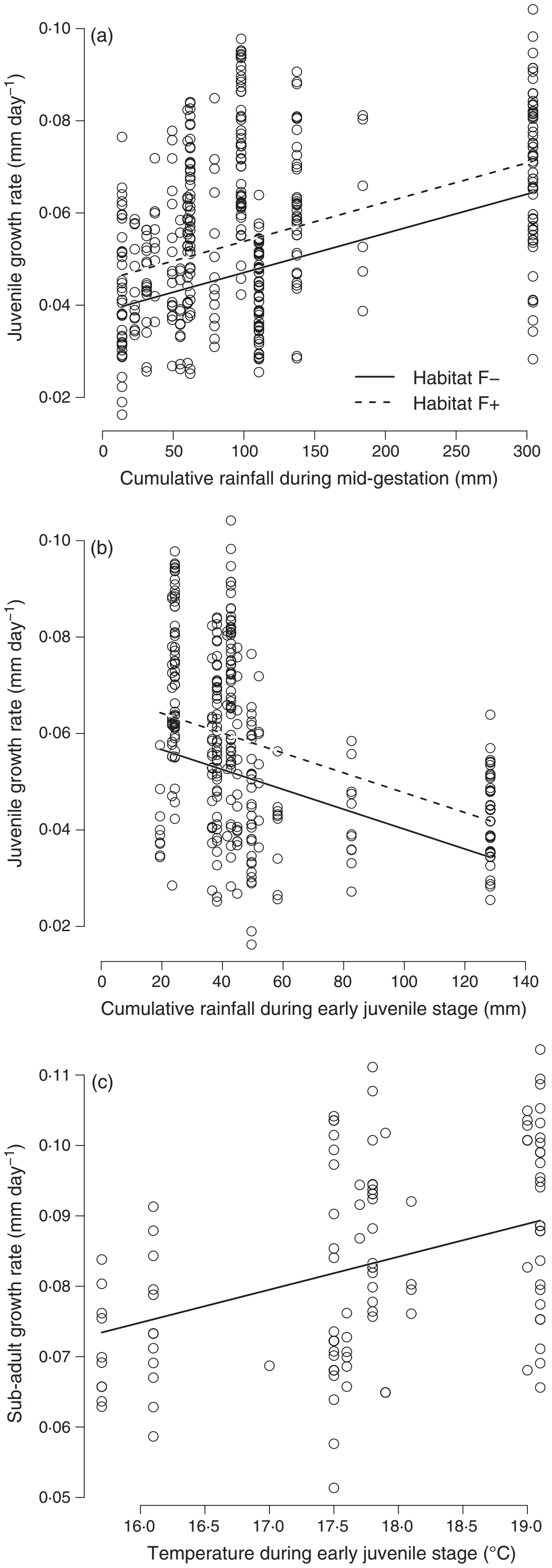

Fig. 2. Cohort variation in body growth rates of juveniles and sub-adults. (a, b) Differences in rainfall before and during growth generated cohort variation in juvenile growth rates. Juvenile growth rates increased significantly with rainfall during past mid-gestation (a), but decreased with rainfall experienced during growth (b). These effects were robust to exclusion of highest values of rainfall during past mid-gestation (year 1992, $F_{1,10}$ = 9·04, P = 0·01) and the early juvenile stage (year 2002, $F_{1,10}$ = 7·47, P = 0·02). Plots show juvenile growth rates controlled for body size at birth against cumulative rainfall. Separate regression lines for each habitat are given. (c) In addition, sub-adult growth rates increased significantly with temperature experienced during the early juvenile stage. Data are sub-adult growth rates controlling for initial body size, sex and habitat effects plotted against temperature.

corrected for the effect of capture date was larger in females ($F_{1,355}$ = 103·61, P < 0·0001) and in habitat $F+$ ($F_{1,355}$ = 11·57, P = 0·0007). Growth rates at the sub-adult stage were also negatively correlated with growth rates at the juvenile stage (n = 86, Pearson's r = −0·48, P < 0·0001).

Adult growth

The SVL of 182 adults was measured from two to eight times depending on the number of recaptures. Cohort variation in body length amounted to 18% of the residuals and random effects variance (χ^2 = 113·76, d.f. = 1, P < 0·0001), which was smaller than the inter-individual variation within cohorts (R^2*_rand* = 39%). In the mixed effects model, body length kept increasing with age though a negative quadratic term indicated decelerating growth rates (Appendix S2, Supporting information). We found no effect of climate conditions experienced before and during adulthood on adult body size and growth rates (all P > 0·05).

REPRODUCTIVE PERFORMANCES

Parturition date

Parturition dates varied significantly among birth cohorts (R^2*_rand* = 29·2%, χ^2 = 85·6, d.f. = 1, P < 0·0001) as well as between females within cohorts (R^2*_rand* = 10·5%). In the mixed effects model, larger females usually gave birth earlier and parturition dates were influenced by current climate conditions during gestation (Appendix S2, Supporting information). In particular, cooler climates during mid-gestation induced delayed parturitions (Fig. 3). None of the climate conditions experienced prior to the reproduction year had delayed effects on parturition dates.

Reproductive failures

Reproductive failures (proportion of unviable eggs within a litter) were infrequent (*c.* 10% of the litter). There was a strong variation in reproductive failures among females within a birth cohort (R^2*_rand* = 58%) but not among cohorts (R^2*_rand* < 1%). In the mixed effects model, the proportion of reproductive failures increased with rainfall during mid-gestation of the breeding year, but was not influenced by other climatic or individual factors (Appendix S2, Supporting information).

Post-parturition body condition

Post-parturition body condition (PBC) varied strongly among individual females within a cohort (R^2*_rand* = 36%) and not significantly among cohorts (R^2*_rand* = 10%). In the mixed effects model, we identified a quadratic relationship between PBC and age (Appendix S2, Supporting information). Qualitatively, PBC increased up to 4 years of age and then decreased in older females. When these effects of age were accounted for, none of the climate conditions experienced by females early in life influenced their PBC and females exposed to higher temperatures during mid-gestation of the breeding year had a higher PBC (Appendix S2, Supporting information).

JUVENILE SURVIVAL

We studied cohort variation in juvenile survival for hatchlings born in the laboratory. The most informative model describing variation in capture probabilities was the age- by-cohort model (Appendix S3, Supporting information). From this model, we detected significant variation in survival among birth cohorts during the early juvenile stage but not during the late juvenile stage (see Appendix S3, Supporting information and Fig. 4a). Thus, our best model predicted variable survival during the early juvenile life stage (mean = 0·42 ± 0·04, σ^2 = 0·014 [0·0048, 0·051] 95% CL, CV = 0·30) and a constant late juvenile survival (mean = 0·93 ± 0·09).

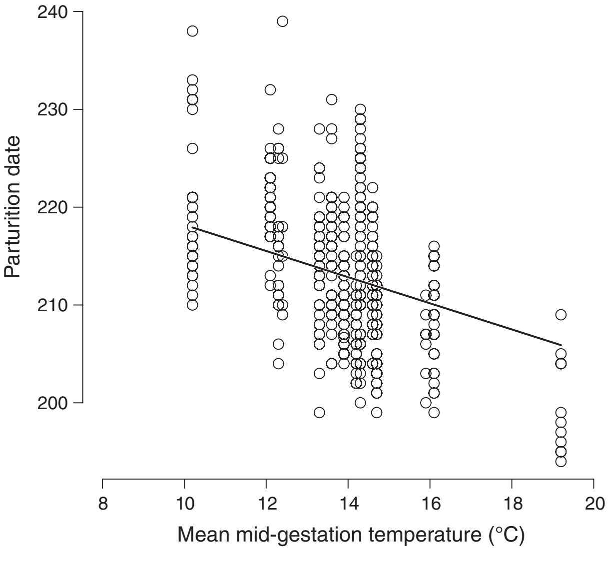

Fig. 3. Variation in climate conditions during gestation cause variation in the timing of parturitions (day of the year). Higher temperatures during mid-gestation in June of the breeding year were associated with earlier parturition dates.

We tested for the effects of climate conditions during conception, past mid-gestation and early juvenile life for early juvenile survival. Model selection led to a most parsimonious model with two climate covariates (model 19 in Appendix S3, Supporting information). This model included positive, additive effects of rainfall during past mid-gestation (logit slope = 0·19 ± 0·08 per one SD in rainfall; $LRT_{cov/const}$: χ^2 = 6·18, d.f. = 1, P = 0·01; Fig. 4b) and of rainfall during the first month of life (logit slope = 0·31 ± 0·08 per one SD in rainfall; $LRT_{cov/const}$: χ^2 = 20·91, d.f. = 1, P < 0·0001; Fig. 4c). There was little unexplained temporal variation in survival after accounting for the two significant climate covariates ($LRT_{cov/cohort}$: χ^2 = 15·2, d.f. = 9, P = 0·09). An analysis of deviance also showed that effects of rainfall conditions during past mid-gestation and early juvenile life explained as much as 70% of the cohort variation ($F_{cov/cohort/constant}$: $F_{2,9}$ = 10·74, P = 0·004), with rainfall during the juvenile stage ranking first (R^2*_dev* = 58%) and rainfall during gestation ranking second (R^2*_dev* = 12%). The positive survival effect of rainfall during past mid-gestation was robust to exclusion of the highest rainfall year (birth cohort 1992, see Fig. 4). The best model fitted with this restricted data set was the same model than the best model fitted with the full data set (model 19 in Appendix S3, Supporting information; AICc weight = 0·52, second best model ΔAICc = 1·04) and the $LRT_{cov/const}$ test of rainfall effect was still nearly significant (χ^2 = 3·08, d.f. = 1, P = 0·08). However, the effect of rainfall during the first month of life vanished when the strongest rainfall year was excluded from the analysis (birth cohort 2002 excluded, $LRT_{cov/const}$: χ^2 = 0·07, d.f. = 1, P = 0·80).

Early juvenile survival increased also significantly with body size at hatching (logit slope in model 15 = 0·35 ± 0·09 per one SD in body size; $LRT_{cov/const}$: χ^2 = 19·45, d.f. = 1, P < 0·0001), and decreased with birth date (logit slope = −0·61 ± 0·09 per one SD in birth date; $LRT_{cov/const}$: χ^2 = 65·80, d.f. = 1, P < 0·0001). Effects of rainfall variables on juvenile survival were robust to the inclusion of birth date and hatchling size in the statistical model (see model 13 in Appendix S3, Supporting information).

SUB-ADULT AND ADULT SURVIVAL

We analysed sub-adult and adult survival with recapture histories from age 1 to 5 years. The most informative model describing capture probabilities included only the effect of capture effort. Furthermore, all but one of the best models describing capture probabilities included the effect of capture effort (Appendix S3, Supporting information). We therefore used the capture effort model as a starting point to select a model describing variation in survival probabilities (Appendix S3, Supporting information). According to our best survival model, annual survival probabilities varied among cohorts and age classes, as well as between sexes. Females survived better than males (logit contrast = 1·54 ± 0·18) and the survival advantage of females was similar across age classes (Appendix S3, Sup-

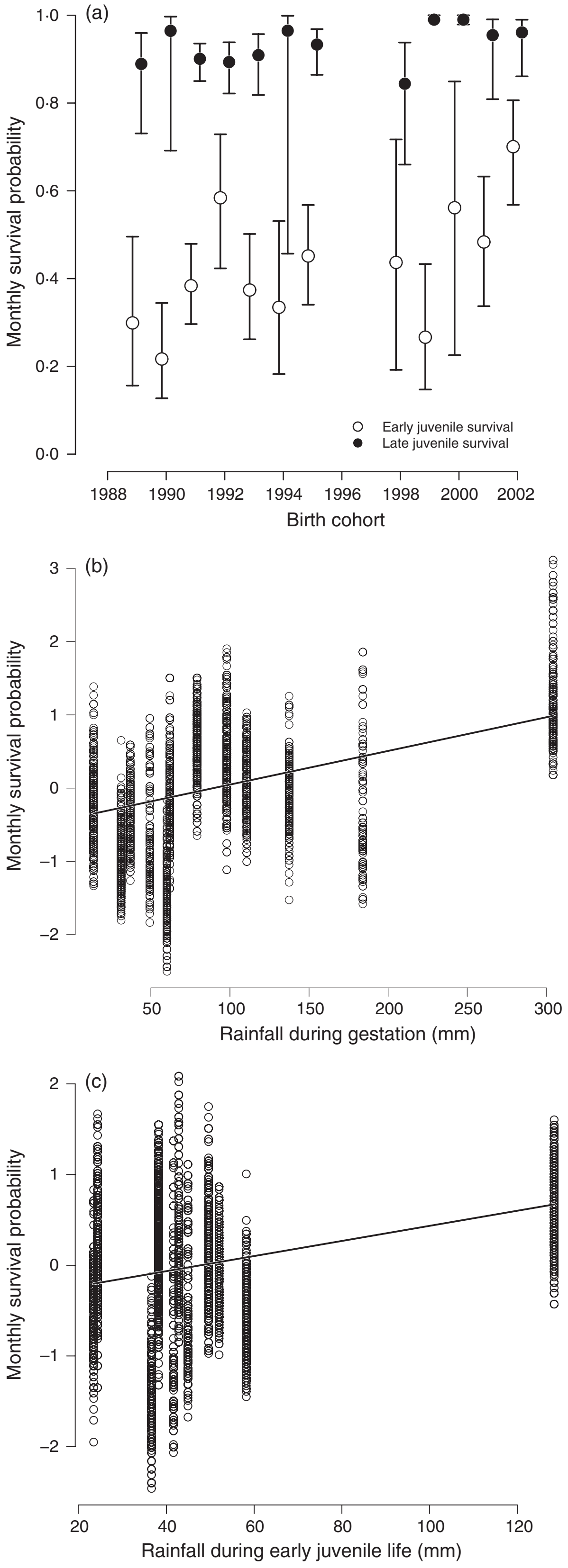

Fig. 4. Variation in juvenile survival among birth cohorts. (a) Mean (and 95% CI) monthly survival probability per birth cohort and age class for juvenile common lizards. Estimates were obtained for early juvenile survival from model 7 and for late juvenile survival from model 1 in Appendix S3 (Supporting information). (b, c) Effects of climate conditions on early juvenile survival probability. Individual estimates of survival were obtained from the best model in Appendix S3 (Supporting information) and regressed against rainfall during gestation (b) and rainfall during the first month of life (c). Data are partial residuals of a model controlling for size at birth, birth date and rainfall. Robustness to exclusion of rainfall extremes is reported in the main text.

porting information). Based on the best survival model selected in Appendix S3 (Supporting information), the variance component approach suggested decreasing cohort variation with age (Appendix S3, Supporting information). An additional model selection procedure was done to test this pattern (Appendix S3, Supporting information). This confirmed that survival varied significantly among cohorts at the sub-adult stage, that survival varied not so importantly in older age classes and that cohort variation in survival of sub-adults was similar between sexes. We then proceeded to test the effects of climate conditions during conception, gestation, juvenile and sub-adult life stages on sub-adult survival. According to QAICc scores (Appendix S3, Supporting information), none of the climate variables explained a significant portion of the cohort variation in sub-adult survival ($F_{cov/cohort/constant}$: $F_{1,9} < 2{\cdot}65$, $P > 0{\cdot}14$, $R^2\_dev < 23\%$). Adding individual covariates habitat and origin (born in laboratory or in the field) did not change our conclusions since these covariates were not significant (Appendix S3, Supporting information).

COHORT COVARIATION IN LIFE-HISTORY TRAITS

Correlations between cohort-specific means of date of birth, hatching size, juvenile growth rate, sub-adult growth rate, early juvenile survival, sub-adult survival, adult fecundity and adult body size are reported in Appendix S4 (Supporting information). Apart for the expected positive correlation between adult body size and fecundity, only one significant negative correlation between juvenile growth rate and sub-adult growth rate was found (Pearson's $r = -0{\cdot}687$, $P = 0{\cdot}009$).

COHORT VARIATION AND POPULATION GROWTH

Monte Carlo simulations with an age-structured population model indicate that the asymptotic growth rate (λ) does not differ from 1 (λ = 0·95, 95% CL 0·80–1·15). The asymptotic growth rate was most sensitive to juvenile survival, followed by adult survival and sub-adult survival, and then fecundity (Appendix S5, Supporting information). We also calculated λ simulated with estimates of vital rates from each cohort. The predicted λ ranged among cohorts from 0·66 to 0·99 without any apparent temporal trend (variance components from a random effect model, $R^2\_rand = 65\%$). Of the influential climatic factors for life-history traits, none had a significant correlation with λ (Spearman's correlation, temperature during gestation: $r = -0{\cdot}25$, $P = 0{\cdot}46$; rainfall during gestation: $r = -0{\cdot}05$, $P = 0{\cdot}87$; rainfall during early juvenile life: $r = -0{\cdot}44$, $P = 0{\cdot}18$). We further tested the effects of cohort variation in early juvenile survival, sub-adult survival and fecundity on cohort variation in λ. To do so, we calculated the λ for each cohort when one of these vital rate was constant (overall mean) instead of different among cohorts. This calculation indicated that juvenile survival, sub-adult survival and fecundity explained 25%, 33% and 4%, respectively, of the cohort variation in λ.

Discussion

Long-term studies and individual-based demographic data are invaluable to assess temporal variation in life-history traits and the demographic effects of climate change (Benton, Plaistow & Coulson 2006; Grosbois *et al.* 2008). Yet, correlative studies of demographic variation are not immune to false inferences and must therefore be interpreted with caution because of a possible uncertainty in the relevant drivers, life stages and mechanisms of climate effects. For example, Grosbois *et al.* (2008) pointed out that the outcomes of model selection may be questionable when complex climate drivers are investigated and a limited time series is available. However, our analysis was built upon relatively good prior knowledge of the species biology and life cycle to limit the number of climate factors tested. We also investigated the effects of climate conditions on life-history traits while controlling for important structuring factors in populations of the common lizard, such as body size, age, sex or habitat. Hopefully, this makes our main conclusions more robust. Hereafter, we discuss the observed patterns of cohort variation and climate effects in the light of available information from natural history, life history and population ecology.

GENERAL PATTERNS OF COHORT VARIATION

Among the 10 demographic traits tested here and the two traits previously tested in Marquis, Massot & Le Galliard (2008), we found significant cohort variation for nine of them. The strength of cohort effects quantified by a variance component approach allowed to separate traits with strong cohort variation (ca. 30–50% of the variation) such as juvenile growth and survival, breeding phenology and sub-adult survival, traits with intermediate cohort variation (ca. 10–20%) such as sub-adult growth, adult body size and offspring size and traits with negligible cohort variation such as post-parturition body condition (NS), fecundity (significant), reproductive failures (NS) and adult survival (NS). Sexual differences in cohort effects and structuring demographic factors have been found in other species (e.g. Rose, Clutton-Brock & Guinness 1998), but cohort variation did not differ between sexes in the common lizard. This species develops a clear sexual dimorphism from the sub-adult stage; yet, the degree of sexual dimorphism may not be strong enough to cause significant sexual differences in cohort effects (see also Le Galliard *et al.* 2006). Absence of sex-dependent environmental sensitivity was also found in our previous studies (Massot *et al.* 1992; Le Galliard, Ferrière & Clobert 2005).

Following on the terminology of Gaillard *et al.* (2003), both numerical cohort effects before recruitment and delayed quality effects after recruitment were detected in the common lizard. Delayed cohort effects were found for adult fecundity and offspring size in a previous study (Marquis, Massot & Le Galliard 2008), but not for the other adult traits investigated here. Direct numerical cohort effects were observed here for juvenile survival, juvenile growth and sub-adult survival – these demographic traits determine the number and size of recruits. However, our study indicates that numerical cohort effects had a stronger impact than delayed quality effects. Firstly, delayed quality effects of rainfall conditions experienced early in life on female reproductive traits were significant in a previous study (Marquis, Massot & Le Galliard 2008), but these effects were weak relative to numerical cohort effects and no delayed quality effects were found for adult survival (this study). Secondly, the asymptotic growth rate of the population was more sensitive to variation in survival early in life, hence recruitment, than to variation in fecundity or adult survival. In other species investigated so far, delayed quality effects were caused by long-lasting maternal effects or long-term effects of environmental conditions experienced early in life. Delayed maternal effects and effects of early environmental conditions have been demonstrated for juvenile growth and survival previously (Lorenzon, Clobert & Massot 2001; Le Galliard, Ferrière & Clobert 2005; Meylan, Clobert & Sinervo 2007), but were apparent only for fecundity and offspring size in this study that examined life-history effects from birth to adulthood.

Delayed quality effects are generally expected when environmental conditions influence permanently a quality trait, such as body size, that causes positive covariation among life-history traits (the ‘silver spoon’ effect, Grafen 1988; Madsen & Shine 2000; Reid *et al.* 2003). However, body size was not the most critical determinant of cohort variation in the common lizard: (i) body size was positively associated with juvenile survival and adult fecundity but contributed only partly to cohort variation in these traits; (ii) climate factors that influenced body size before sexual maturation were not correlated with adult performances; (iii) there was more variation in adult body size within cohorts than between cohorts; and (iv) we found no positive correlation between life-history traits among cohorts. On the contrary, juvenile and sub-adult growth rates were negatively correlated among cohorts and also among individuals within cohorts. Altogether, these results suggest flexible growth trajectories and compensatory responses inside natural populations of the common lizard. These results contrast with those of previous studies indicating lasting effects of food deprivation early in life on body size at the juvenile stage (Le Galliard, Ferrière & Clobert 2005) and the absence of growth catch-up in adults (Massot *et al.* 1992). Yet, previous studies did not investigate growth at the sub-adult stage, which seems critical for growth compensation here. In short-lived continuous growers such as the common lizard, compensatory growth at the sub-adult stage may be beneficial because of strong selection pressures for increased size at a given age (Le Galliard, Clobert & Ferrière 2004; Fitze & Le Galliard 2008). This growth strategy may be flexible enough to cancel long-term effects of climate conditions experienced early in life on body size.

THE ROLE OF CLIMATE VARIATION FOR COHORT EFFECTS

Cohort variation was partly explained by a web of immediate and delayed effects of climate conditions that involved both temperature and rainfall (this study and Marquis, Massot & Le Galliard 2008). Rainfall and temperature influenced distinct life-history traits and the effects of climate conditions were significant during embryogenesis (past mid-gestation) and during early juvenile life, but not during conception, sub-adult life or adult life apart for the direct effect for adult females of climate conditions experienced during gestation. We expected that warmer climates would enhance growth and reproduction, possibly together with a lower survival (Adolph & Porter 1993; Chamaillé-Jammes *et al.* 2006 and references therein). Our analyses showed that effects of temperature were more limited than we anticipated. Significant effects of thermal conditions during mid-gestation of the breeding year were found for breeding phenology and post-parturition body condition (this study), but not for fecundity and offspring size (Marquis, Massot & Le Galliard 2008). This indicates that thermal requirements are crucial for the thermoregulation and energy balance of mothers during current gestation, but not for reproductive effort (see Lourdais *et al.* 2004 for a similar result in a viviparous snake). Laboratory experiments have also consistently reported positive effects of heat on the speed of embryonic development in lizards, but not necessarily on fecundity and offspring size (e.g. Wapstra 2000 and references therein).

In addition to these thermal effects on reproduction, higher temperatures during early juvenile life had positive delayed effects on sub-adult growth but no direct effects on growth and survival. In reptiles, the post-hatching thermal environment influences development with potential long-term consequences (e.g. Qualls & Shine 2000). Delayed effects of juvenile temperatures on sub-adult growth may come from such lagged developmental effects involving storage and capitalization of energy for structural growth but may also come from indirect effects on trophic resources. However, the absence of direct thermal effects on fecundity, size growth and survival suggests either a lack of substantial variation in thermal conditions or some buffering effects of lizards' behavioural and physiological responses. Good active thermoregulation capacities in the face of climate warming may be expected in the common lizard because of its low thermal needs and ovoviparous reproductive mode, which are adaptation to live in relatively cool and variable thermal environments (Le Galliard, Le Bris & Clobert 2003; Shine 2005).

Rainfall had distinct and substantial effects on demographic traits relative to thermal conditions, which confirms the importance of water constraints in the common lizard (Lorenzon *et al.* 1999; Lorenzon, Clobert & Massot 2001). Females experiencing more rainfall during gestation had more reproductive failures, gave birth slightly later, and produced smaller offspring that displayed a higher survival and a higher body growth when controlling for their body size (this study and Marquis, Massot & Le Galliard 2008). In addition, rainfall during the first month of life was associated with higher juvenile survival but poorer growth. The positive effect of rainfall during the first month of life on survival must however be interpreted with caution since it was contingent upon the inclusion of one extremely rainy birth year. Altogether, these results suggest that rainfall is an important determinant of juvenile performances with positive, lagged effects through body growth and survival, and also negative, immediate effects through offspring size and body growth. The negative, immediate effects of rainfall may be due to reduced basking, locomotor activity and food intake during rainy and cloudy days. Maternal effects and/or indirect effects through habitat quality or food availability could explain the lagged effects of rainfall (Marquis, Massot & Le Galliard 2008). In a combined laboratory and field experiment, Lorenzon, Clobert & Massot (2001) found no effects of water availability during gestation on offspring growth and survival in the field, but observed improved juvenile growth and survival in wetter habitats. It is therefore more likely that the lagged, positive effects of rainfall on juvenile growth and survival found here are caused by indirect effects. For example, rainfall could improve habitat humidity, plant growth and insect productivity in the wetlands inhabited by common lizards.

DEMOGRAPHIC CONSEQUENCES OF COHORT VARIATION

Attempts to quantify consequences of cohort effects for population dynamics are rare (Benton, Plaistow & Coulson 2006). On the theoretical side, Lindström & Kokko (2002) modelled an iteroparous population where differences in a quality trait at birth affect the susceptibility of individuals to a density increase. This model predicted that quality cohort effects cause a delayed density dependence that destabilizes population dynamics. Subsequently, Beckerman *et al.* (2003) used populations of mites to demonstrate that a delayed life-history effect of food quantity on individual quality can generate density dependence in a manner consistent with this model. However, most field studies published so far indicate cohort effects on the mean value of demographic traits rather than on density dependence (e.g. Albon, Clutton-Brock & Guinness 1987; Rose, Clutton-Brock & Guinness 1998; Forchhammer *et al.* 2001; Descamps *et al.* 2008). The contribution of density-independent life-history variation to population growth depends on variance and covariance of demographic traits and can be assessed with matrix population models (see Coulson, Gaillard & Festa-Bianchet 2005). We used such a simulation approach to measure the effects of each demographic trait on cohort variation in population growth rate (see also Gaillard *et al.* 2003; Wittmer, Powell & King 2007). This analysis yielded three major results: (i) we found significant cohort variation in asymptotic growth rate; (ii) cohort variation is predicted to impact population dynamics due to direct numerical effects of survival variation early in life rather than due to delayed quality effects on adult performances; and (iii) none of the climate variables explained satisfactorily cohort variation in asymptotic growth rate. These results agree with the sensitivity analysis of the mean life history, with the larger environmental variation observed for survival at younger ages than for survival at older ages, fecundity and reproductive failures, and with the absence of a single, major climatic determinant of life-history variation in the common lizard.

SYNTHESIS: DEMOGRAPHIC RESPONSES TO GLOBAL CLIMATE WARMING

The population examined here faces local air temperature warming with an increase of *c.* 3·7 °C of the mean spring and summer temperatures from 1976 to 2004 – this warming trend is predicted to continue for the next decades. We did not observe trends for rainfall during that period but most climate scenarios predict an increase in rainfall variability during the summer and a long-term decrease in mean rainfall in southern France. Previous studies of local warming have shown positive fitness effects in populations of the common lizards, such as an increase in mean body size and fecundity (Chamaillé-Jammes *et al.* 2006). According to our results, these positive effects of warming on body size and fecundity may be due to two non-exclusive mechanisms. Increased local temperatures have caused earlier birth within a season, allowing juveniles to grow longer within their birth year and reach a larger body size at the sub-adult stage. Thus, phenological changes have allowed lizards to capitalize on longer growing seasons and reach a larger body size, and therefore fecundity, at adulthood. In addition, phenological changes were enhanced by a delayed positive effect of summer temperature on sub-adult growth. However, we also predict negative fitness effects if drought periods become more frequent during the summer and if precipitations tend to decrease on the long-term. In particular, our results indicate that drought during the early summer can cause mortality and growth restriction in juveniles, and could ultimately drive the population to extinction. Thus, to predict the impact of climate change on this species over its entire range, we need mechanistic models of humidity and temperature constraints on demography and additional data from populations facing water constraints at their distribution margins.

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Supporting Information

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

Appendix S1. Supplementary information on climate variation.

Appendix S2. Supplementary tables for analyses of adult growth and reproductive traits.

Appendix S3. Descriptions and tables of statistical models for mark–recapture analyses.

Appendix S4. Detailed information on cohort covariation between life-history traits.

Appendix S5. Supplementary information on the matrix projection model.