INTERGENERATIONAL EFFECTS OF CLIMATE GENERATE COHORT VARIATION IN LIZARD REPRODUCTIVE PERFORMANCE

OLIVIER MARQUIS,[1] MANUEL MASSOT, AND JEAN FRANÇOIS LE GALLIARD

Centre National de la Recherche Scientifique (CNRS), UMR 7625, Laboratoire Fonctionnement et Evolution des Systèmes Ecologiques, Université Pierre et Marie Curie, 7 Quai St. Bernard, 75005, Paris, France

Abstract. An evaluation of the link between climate and population dynamics requires understanding of climate effects both within and across generations. In ectothermic vertebrates, demographic responses to climate changes should crucially depend on balancing needs for heat and water. Here, we studied how temperature and rainfall regimes experienced before and during adulthood influenced reproductive performances (litter size, offspring size, and survival) in a natural population of the live-bearing common lizard, *Lacerta vivipara*, monitored continuously from 1989 to 2004. Rainfall regime, but not temperature, had both immediate and delayed effects on these reproductive performances. Rainfall during the first month of life was positively correlated with juvenile survival. Females experiencing more rainfall during gestation produced smaller neonates that showed greater survival when controlling for the positive effect of body size on survival. Furthermore, females that experienced heavier rainfall when in utero produced fewer but longer neonates during adulthood. These demographic effects of rainfall on adult reproductive traits may come from maternal effects of climate conditions and/or from delayed effects of rainfall on the environment experienced early in life. Irrespective of the precise mechanism, however, this study provides evidence of intergenerational climate effects in natural populations of an ectothermic vertebrate.

Key words: climate; intergenerational effect; Lacerta vivipara; *life history trait; maternal effect; plasticity.*

INTRODUCTION

The extensive phenotypic variation observed within natural populations can substantially modify the dynamics of ecological systems (Benton et al. 2006). Phenotypic variation can result from an underlying genetic polymorphism, but most life history traits also exhibit substantial plasticity in response to environmental factors (Via and Lande 1985). Plasticity is often caused by immediate, short-term effects of the environment. In addition, environmental conditions experienced at one point in developmental time may have profound, long-lasting consequences on life history performances (Mousseau and Fox 1998a, Lindström 1999, Dufty et al. 2002). The complex web of immediate and delayed life history effects makes it difficult to predict ecological dynamics without a good knowledge of individual sensitivity to environmental fluctuations (Beckerman et al. 2002, Benton et al. 2006). Thus, an evaluation of the link between climate and population demography requires understanding of how climate influences demographic parameters both within and across generations (Stenseth et al. 2002).

Numerous studies have shown that recent climate change directly impacts on species phenology and distribution (Root et al. 2003, Parmesan 2006). Some studies have also pointed out effects of climate change on population dynamics through dramatic, direct effects on life history traits (e.g., Barbraud and Weimerskirch 2001, Chamaillé-Jammes et al. 2006). It is often less appreciated that climate conditions can also have delayed life history effects. Climate conditions experienced early in life may cause sustained physiological and morphological variation among entire cohorts of individuals (hereafter referred to as "cohort effects"; see Lindström and Kokko 2002). Furthermore, the influence of climate conditions experienced by the parents may transfer between generations via maternal or other intergenerational effects (e.g., Anderson 1978, Mousseau and Fox 1998b, McMahon and Burton 2005). The importance of current vs. past climate variations for life history variation in the wild has only been understood in a few study systems, including wild ungulate populations (e.g., Coulson et al. 2001, Forchhammer et al. 2001) and some species of long-lived birds (e.g., Reid et al. 2003). Even in some of those well-documented systems, investigators rarely identify the life stages where climate conditions act predominantly and therefore when climate conditions are more likely to influence population dynamics (Hallett et al. 2004). The detection of life history consequences of climate in the

wild is indeed a difficult task that requires long-term studies combined with detailed individual-level monitoring. Thus, the importance of direct vs. delayed life history effects of climate remains largely an open question (Stenseth et al. 2002).

Ectothermic species rely on external conditions to raise their body temperature and global climate change is suspected to have a great impact on populations of ectothermic vertebrates such as reptiles (Lourdais et al. 2004, Chamaillé-Jammes et al. 2006). Bioclimatic models for reptiles in Europe predict a decline in species range as a result of a decrease in suitable habitats (Araujo et al. 2006), but positive effects of warming have also been observed locally (Lourdais et al. 2004, Chamaillé-Jammes et al. 2006), and some species may expand their range as a result of global warming (Araujo et al. 2006). The demographic consequences of global climate changes on those species could crucially depend on their balancing needs for heat and water, and therefore on projected trends in temperature and rainfall (Araujo et al. 2006). Air temperature is known to be a key climate parameter inducing life history trait variation in reptiles both within and across generations (reviewed in Adolph and Porter 1993). Although less well studied, rainfall is directly relevant to air and habitat humidity, which has been found to influence activity patterns and therefore growth opportunities in lizards (see Lorenzon et al. 1999 and references therein, Sears and Angilletta 2003). Moreover, rainfall may also influence the food web (e.g., prey abundance and composition) and the habitat (e.g., soil moisture) in the long term (e.g., Tinkle et al. 1993). Therefore, besides direct effects through activity patterns, rainfall regimes may potentially have cascading consequences on lizards' demography via a variety of trophic or environmental effects. To our knowledge, however, no long-term study has addressed both the direct and delayed life history consequences of temperature and rainfall for wild populations of ectothermic vertebrates.

The question we aim to address here is whether climate conditions (temperature and rainfall) experienced by females before and during adulthood can have a significant effect on their reproductive performances. To this end, we analyzed variation in fecundity, offspring size, and offspring viability between and within maternal cohorts using life history data collected in a natural population of the common lizard (*Lacerta vivipara*; see Plate 1) monitored continuously from 1989 to 2004 (Massot and Clobert 2000, Chamaillé-Jammes et al. 2006). The species is a small ovoviviparous lizard, i.e., eggs are retained in the abdominal cavity until completion of embryonic development and hatching of non-calcified eggs occurs a few minutes after egg laying, inhabiting humid habitats across northern Eurasia. The population examined here is located in a mountainous habitat at the southern range of the species distribution that faces climate warming with an increase of ~3.7°C of the daily maximal temperature in May, June, and

August from 1976 to 2004 (Chamaillé-Jammes et al. 2006). To assess reproductive performances, we measured total litter size, neonate snout–vent length (SVL), and offspring survival from birth to the age of one year. We first ask whether these three life history traits show significant variation between maternal cohorts. We then examine if cohort variation in reproductive traits can be explained by climate conditions experienced by mothers before and during adulthood. Our analysis builds on previous work with this species that established that there is an effect of climate warming on body size at the population level (Chamaillé-Jammes et al. 2006), that both air temperature and humidity can induce significant immediate life history effects (Lorenzon et al. 1999, 2001), and that conditions experienced by the mother may cause further variation in offspring quality and survival (e.g., Lorenzon et al. 2001). However, no study to date has examined cohort variation induced by climate conditions in the common lizard, and we believe this to be the first such study for any ectothermic vertebrate.

Methods

Study sites and life history data collection

Data were obtained from two long-term study sites located in the same glade (1420 m above sea level [a.s.l.]) in the Mont Lozère area, southern France (44°30′ N, 3°45′ E). These two sites (i.e., F+ and F−) differ in the density of lizard populations (700 adults/ha vs. 430 adults/ha, respectively) and show consistent life history differences, despite juvenile dispersal rates of 10% and thus weak genetic isolation between the two sites (see Massot and Clobert 2000 for more details). For example, neonates from F− have a larger body size at birth and females from F− give birth later in the season (Le Galliard et al. 2006). Each year from 1989 to 2004, both sites were sampled for subadults and adults in June–July and for juveniles in September (i.e., just before hibernation). In July (i.e., at the end of the gestation period of females), adult females were measured for snout–vent length (SVL, to the nearest millimeter) and kept in individual cages until parturition under standardized conditions in the laboratory (see Massot and Clobert 2000 for details on maintenance conditions). On average, we captured 58.2 ± 13.8 pregnant females per year (mean ± SD) in the F+ site (range = 40–95) and 21.4 ± 6.4 females in the F− site (range = 12–32). Cages were searched three times per day for freshly laid eggs, and total litter size was recorded upon completion of birth, which occurs usually within one hour following parturition. Live neonates were marked, sexed according to their ventral scales (Lecomte et al. 1992), and measured for SVL. Less than 3–5 days after parturition, females were released together with their offspring within 1 m of the original capture location. In June–July and September capture sessions, all captured animals were identified or marked by toe-clipping to be identified in the following sessions.

With the exception of adult females in July, individuals were released at the capture location upon completion of measurements. For the purpose of this study, adult females could be aged to the nearest birth year in three instances: birth in the laboratory, first seen as an unmarked juvenile in September of the birth year, or first seen as an unmarked yearling in June–July of the year following birth. It was not possible to age accurately unmarked adults due to overlap in body size between adult age classes (Massot et al. 1992).

Climate data collection

Temperature and rainfall data were recorded by Météo-France from 1989 to 2004 at a meteorological station situated at the same altitude, 50 km south from the study sites (Mont Aigoual, 1567 m a.s.l., 44°07′ N, 3°35′ E). This meteorological station was the closest mountainous site located in the same climatic area for which high quality and long-term meteorological data were available. Furthermore, temperature data from this meteorological station are strongly correlated to the local climate conditions experienced by lizards in the study site for each month ($r = 0.830$–0.887, $n = 9$–11, all $P < 0.001$), but local data were only available for a shorter and discontinuous time period (Chamaillé-Jammes et al. 2006). We used monthly means of daily maximum temperature as a descriptor of thermal conditions. Daily maximum temperatures are a better predictor of thermoregulation opportunities than mean or minimum daily temperatures (Huey 1982). Furthermore, clear increases in maximum daily temperature have been detected in the observed climate, including our study site (Chamaillé-Jammes et al. 2006, Rosenzweig et al. 2007). Analysis of additional data of insolation in June from 1990 to 2007 collected in the meteorological station in Mende-Chabrits (44°32′ N, 3°27′ E, 932 m a.s.l.) shows that maximum daily temperatures were highly correlated with basking opportunities indicated by insolation (Pearson's product-moment correlation, $r = 0.89$, $P < 0.001$). For rainfall data, we used the monthly cumulative amount of precipitation. Significant but weaker correlations were found between maximal temperature and precipitation ($r = -0.60$, $P = 0.01$) and between precipitation and insolation ($r = -0.64$, $P = 0.006$). This indicates that cumulative amount of precipitation integrates both temperature and insolation variations but that maximal temperature is the best predictor of insolation, and therefore basking opportunities. We calculated stage-specific climate data fitted to the life cycle and phenology of the common lizard. Specifically, local climate data were calculated at three distinct life stages: (1) during the time of conception and ovulation (values from May of birth year, hereafter referred to as "conception" life stage), (2) during early development in the middle of gestation (values from June of birth year, hereafter referred to as "in utero" life stage), and (3) during the first month of life after birth (values from

August of birth year, hereafter referred to as "early juvenile" life stage). From 1988 to 2004, temporal autocorrelation of these climate data was weak and nonsignificant for both temperature and rainfall data (autocorrelation functions within each life stage, nonsignificant correlations for positive lags). Furthermore, correlations of cohort-specific climate data between life stages were not significant (Pearson's product-moment correlations, $-0.23 < r < 0.38$, all $P > 0.13$).

Statistical analysis

We analyzed cohort variation in reproductive traits (total litter size, neonate size, and survival) for a total of 13 maternal cohorts (i.e., reproductive characteristics of mothers born in 13 different years). We excluded maternal cohorts that could not be fully characterized until the age of four years (2001–2004). Furthermore, for the survival analysis, we excluded the birth cohort of neonates from 1997 for which survival probabilities could not be properly assessed due to very poor capture effort at the subadult life stage in the following year. We examined cohort variation in litter size and offspring body size at birth with mixed-effects linear models following Pinheiro and Bates (2002). The random part of the models included a maternal cohort effect and, in the case of offspring size, a mother identity effect nested within the maternal cohort effect. This random model fitted the data satisfactorily, and the normality and homogeneous variance of residuals and random effects were fulfilled (Pinheiro and Bates 2002). We next built a full model including the additive fixed effects of climate conditions experienced by the mother early in life (rainfall and temperature during conception, when in utero, and during the early juvenile stage), of climate conditions during gestation (rainfall and temperature in June of the current year), and of maternal traits of the current year (age and size). We also added an effect of habitat because previous studies have reported consistent differences in life history traits between the F+ and the F− sites (Massot and Clobert 2000, Le Galliard et al. 2006). We selected a minimum adequate model with a stepwise procedure by exact Akaike's Information Criterion and tested for significance of fixed effects with F tests based on the usual (restricted maximum likelihood) conditional estimate of the variance. We first selected a model with maternal traits and habitat covariates, and then a model with climate covariates. There was a significant negative correlation between monthly temperature and rainfall data in June and August (Pearson's product-moment correlation $r = -0.63$, $P = 0.06$ and $r = -0.48$, $P = 0.05$, respectively). To avoid a colinearity issue in the statistical models (Quinn and Keough 2002), we therefore chose to select separate minimum adequate models with temperature or rainfall covariates. Once these models were fitted, we assessed the robustness of individual effects when pooling terms from the two models (Quinn and Keough 2002). Only the significant and robust effects are

TABLE 1. Cohort variation in litter size of female common lizards, *Lacerta vivipara* ($N = 450$ from 13 cohorts).

Effect	Estimate†	F	df	LR	P
Fixed					
Female SVL	0.14 ± 0.043	11.58	1, 128		0.001
Female age	-2.75 ± 0.948	8.41	1, 128		0.004
Female age × Female SVL	0.044 ± 0.014	9.35	1, 128		0.003
Past rainfall when in utero	-0.003 ± 0.001	10.0	1, 316		0.002
Random					
Cohort identity	0				
Female identity in cohort	0.45 (0.21, 0.83)			2.17	0.14
Residuals	1.18 (1.07, 1.31)				

Notes: The model was obtained by selection of a full model including effects of past and current climate conditions (rainfall and temperature), female age and snout–vent length (SVL), and habitat (see *Methods: Statistical analysis* for details). The random cohort effect was dropped from the model because the estimate was lying at the boundary of the parameter space ($\sigma = 0$). Female age varied from 2 to 9 years, and female SVL varied from 51 to 77 mm. LR is the likelihood-ratio test.

† The estimate is shown ±SE for fixed effects and with 95% CL for random effects.

reported here. We used the linear mixed-effects model procedure in R version 2.4.0 software with a maximum likelihood approach to estimate parameters and select the best model (Ihaka and Gentleman 1996).

We tested for changes in juvenile survival between maternal cohorts for juveniles born in the laboratory using recapture histories from September of birth year (mean age of one month), June in the year following birth (mean age of 10 months), and June in the second year following birth (mean age of 22 months). The open population model of Cormack-Jolly-Seber (CJS) was fitted to the recapture data using M-SURGE for diagnosis of convergence and detection of redundant parameters (Choquet et al. 2005). Then we used MARK for parameter estimations and model selection (White and Burnham 1999). The CJS model was used to assess variation among maternal cohorts in early juvenile survival (from birth to the age of one month) and late juvenile survival (from the age of one month to the age of 10 months). We also tested for the effects of body size at birth and climate conditions on juvenile survival. Details on statistical procedures and model selection are provided in the Appendix.

RESULTS

Variation in litter size among maternal cohorts

Total litter size varied significantly between cohorts and individual females within each cohort and contributed 6.6% (standard variation, $\sigma = 0.44$ [0.25, 0.77] 95% CL) and 10.3% ($\sigma = 0.55$ [0.30, 1.03]), respectively, of the total variance of litter size. The cohort effect was fully explained by maternal and climate covariates (Table 1). First, larger females produced significantly larger litters and the slope of the relationship between litter size and body size increased with age (interaction term age × SVL; Table 1). Second, stronger rainfall when females were in utero was associated with the production of smaller litters later in their life (Fig. 1a). The relationship between rainfall when in utero and litter size remained
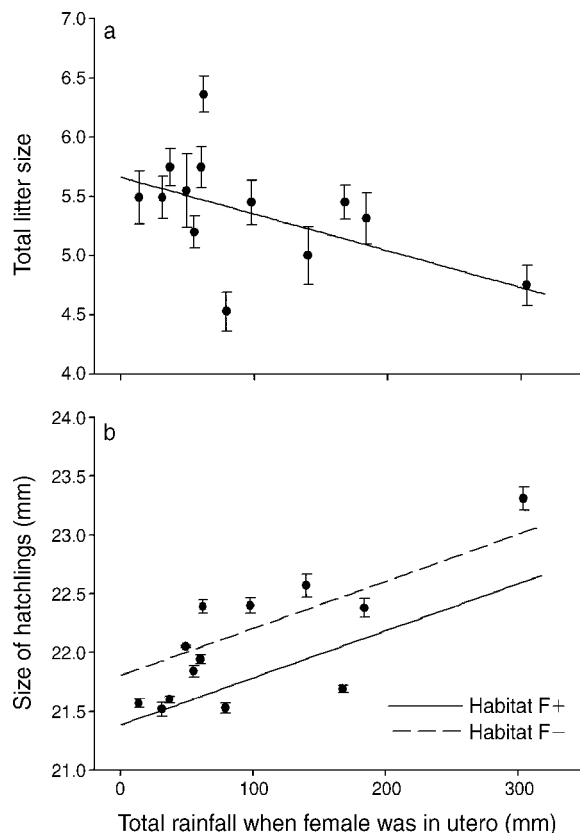

FIG. 1. Rainfall generates maternal cohort variation in total litter size and offspring body size at birth for the common lizard, *Lacerta vivipara*. (a) Total litter size (number of neonates and unhatched eggs) decreased when mothers had experienced high rainfall while in utero. (b) Offspring body size at birth increased with the intensity of rainfall that mothers experienced while in utero. Plots show mean (±SE) per cohort grouped by the total rainfall experienced during the month of the year when mothers were in utero. The regression lines through the data are displayed, and separate regression lines for each habitat (F+, high lizard density; F−, low lizard density) are given in the case of neonates size (see Tables 1 and 2 for statistical details).

TABLE 2. Maternal cohort variation in body size at birth for offspring common lizards ($N = 2139$ from 13 maternal cohorts and 308 individual mothers).

Effect	Estimate†	F	df	LR	P
Fixed					
Mother SVL	0.04 ± 0.009	18.51	1, 1828		<0.0001
Mother habitat ‡	0.41 ± 0.11	12.66	1, 1828		0.0004
Past rainfall when mother was in utero	0.005 ± 0.001	12.62	1, 11		0.004
Current rainfall during gestation	-0.002 ± 0.0005	17.55	1, 1828		<0.0001
Random					
Cohort identity	0.35 (0.21, 0.62)			115.5	<0.0001
Mother identity in cohort	0.87 (0.79, 0.96)			711.11	<0.0001
Residuals	0.87 (0.84, 0.90)				

Notes: The model was obtained by selection of a full model including effects of past and current climate conditions experienced by the mother (rainfall and temperature), mother age and size, and mother habitat (see *Methods: Statistical analyses* for details).

† The estimate is shown ±SE for fixed effects and with 95% CL for random effects.

‡ The estimate is a contrast between the low-density (F−) and the high-density (F+) sites because, by convention, the estimate for F+ was 0. The test statistic columns apply only to the estimate column for this contrast.

significant when the most extreme rainy cohort was excluded from our analysis ($F_{1,294} = 7.52$, $P = 0.006$, slope $= -0.0034 \pm 0.0012$), showing robustness of the linear relationship between rainfall and litter size.

Variation in neonate size among maternal cohorts

Similar qualitative results were obtained for neonate size (SVL). Neonate SVL showed marked variation among cohorts as well as among individual females within each cohort contributing 17.2% ($\sigma = 0.56$ [0.36, 0.88]) and 40.5% ($\sigma = 0.86$ [0.78, 0.95]), respectively, to total variance in neonate size. Again, cohort variation in neonate SVL could be explained, though not fully, by maternal and climate covariates (see Table 2). Neonate SVL increased with mother SVL and was larger in the F− than in the F+ site. Furthermore, mothers produced larger neonates if they had experienced heavy rainfall when in utero (Fig. 1b). The effect of rainfall when mothers were in utero on the size of their offspring became nonsignificant if the most extreme rainy cohort was excluded from our analysis ($F_{1,10} = 2.26$, $P = 0.16$, slope $= 0.0033 \pm 0.0022$). This suggests a nonlinear relationship between rainfall when females were in utero and neonate SVL. In addition, we found that high rainfall during gestation was negatively correlated with SVL at birth.

Variation in juvenile survival among maternal cohorts

The statistical analysis of capture–recapture histories with a CJS model indicated significant cohort variation for early and late juvenile survival ($\chi^2 = 170.93$, df = 36, $P < 0.0001$; see Appendix: Table A1 for more details). The variance among cohorts was 0.07 with 95% CL [0.03, 0.18] for early juvenile survival and 0.002 [0.001, 0.009] for late juvenile survival. There was no indication that cohort variation in juvenile survival could be explained by climate conditions experienced when the mother was in utero (Appendix: Table A2). Rainfall and temperature experienced when the mother was in utero contributed only 5% and 11% of the total variation in juvenile survival among maternal cohorts, respectively. However, juvenile survival was positively correlated with body size at birth (pooled test for early and late juvenile survival probabilities, $\chi^2 = 7.12$, df = 2, $P = 0.03$). Furthermore, early juvenile survival increased with high rainfall during gestation and with high rainfall during the first month of life (pooled test for the two covariates, $\chi^2 = 8.52$, df = 2, $P = 0.01$; see Appendix for more details).

DISCUSSION

Delayed life history effects of climate conditions in the wild have been reported only in a few well-studied animal populations, but, to our knowledge, had never been tested before for ectothermic vertebrates, such as the common lizard investigated here. Despite some evidence for delayed life history consequences of environmental variation in natural and laboratory populations of plants and animals, the demographic importance of cohort and intergenerational effects has been debated (Lindström and Kokko 2002, Beckerman et al. 2006). Climate conditions may not necessarily cause detectable, long-term life history variation in the wild. Individuals may be able to compensate for poor conditions experienced early in life when they face better conditions in their future (reviewed in Metcalfe and Monaghan 2001). Also, variation in climate conditions throughout life has the potential to mask the expression of delayed life history effects of climate. This might explain why intergenerational or cohort effects account only for a minor proportion of the variation in adult life histories in some species (Ergon et al. 2001, Beckerman et al. 2006).

Overall, our results show significant cohort variation for the three reproductive traits examined here, namely litter size, neonate size, and juvenile survival. This

PLATE 1. The common lizard (*Lacerta vivipara*). Photo credit: M. Massot.

cohort variation was partly explained by additive effects of maternal traits. Litter size and neonate size were positively related to maternal body size and the relationship between fecundity and body length was stronger in older females. Moreover, habitat influenced neonate size, which is in line with previous studies showing differences in life history traits between the two study sites (Clobert et al. 1994). More importantly, cohort variation was also associated with past climate conditions when the mother was in utero and with current climate conditions experienced during gestation. Rainfall during gestation had both immediate and delayed effects on reproductive traits, but, contrary to our expectation, air temperature variations were not associated with detectable changes in the reproductive traits examined in the studied population. Thus, rainfall was better at predicting cohort variation in fecundity, neonate phenotype, and neonate survivorship than air temperature (see also Tinkle et al. 1993). This result holds despite the strong correlation between maximum daily temperatures and basking opportunities as indicated by insolation data (see *Methods* for details).

Thermal environment during embryonic development has been reported to influence morphology, physiology, and behavior of neonate reptiles (Shine and Harlow 1993, Shine and Downes 1999, Massot et al. 2002). Two studies found that natural temperature fluctuations can significantly alter neonate phenotype, including morphology in a viviparous snake (Lourdais et al. 2004) and dispersal behavior in the common lizard (Massot et al. 2008). In viviparous reptiles, such as the common lizard,

temperature of embryonic development is directly linked to maternal body temperature that is regulated by basking behavior (Rock et al. 2002, Shine 2004). Furthermore, the body temperature of active common lizards tracks seasonal and daily variations in air temperature (Heulin 1987, Van Damme et al. 1987), and natural variations in air temperatures impacts on body size, dispersal behavior, and reproduction phenology in the study species (Chamaillé-Jammes et al. 2006, Massot et al. 2008; O. Marquis, J. F. Le Galliard, and M. Massot, *unpublished data*). In particular females gave birth earlier when the climate was warmer indicating that gestation lengths were constrained by thermal conditions in the study site (O. Marquis, J. F. Le Galliard, and M. Massot, *unpublished data*). One explanation for the lack of temperature effects on reproductive traits examined here could be that the basking behavior of female common lizards during gestation buffered temperature fluctuations. The capacity of female lizards to maintain constant fecundity and neonates' phenotypes despite significant variation in air temperature may be a consequence of their low thermal needs and reproductive mode (i.e., ovoviparity) being an adaptation to relatively cool climates (Le Galliard et al. 2003).

The lack of immediate temperature and rainfall effects on fecundity suggests that females did not adjust their litter size after ovulation in response to current local climate conditions. This fact could be due to the absence of physiological mechanisms enabling selective abortion and egg resorption at that stage of the reproductive cycle

in viviparous lizards (e.g., Blackburn et al. 2003). Nevertheless, we found evidence that stronger rainfall during gestation led females to produce smaller neonates. Current climate conditions did therefore cause significant changes in offspring quality rather than in offspring quantity (Beckerman et al. 2006).

Effects of rainfall on reptile's life history and population dynamics have been understudied relative to temperature effects and other climate variables. In lizards occupying water limited habitats, rainfall can enhance survival, growth, and litter size as well as neonate success by modifying vegetation cover (Dickman et al. 1999). Moreover, precipitation may have beneficial effects by enhancing water availability or prey abundance (Dunham 1978, Stamps and Tanaka 1981). In the common lizard, low levels of air humidity constrain basking and foraging activities because lizards are less active when the air is drier (Lorenzon et al. 1999). Habitat humidity may even be more important for gravid females because water content increases drastically in the eggs during the three last weeks of gestation (Dauphin-Villemant and Xavier 1986). Common lizards are also typical inhabitants of wet bogs and heathlands, where rainfall may be essential to habitat quality (e.g., vegetation cover, prey abundance; see Lorenzon et al. 2001). On the other hand, in the high altitude environment of our study site, high rainfall may also be indicative of suboptimal climate conditions. For example, rainy episodes impact negatively on insolation, which may constrain both thermoregulation opportunities and food intake by reducing lizard activity (Avery 1971). Our data do indeed suggest that rainfall had both positive and negative effects on reproductive performances depending on the reproductive trait and the life stage examined.

When controlling for the fact that neonate size is positively correlated with juvenile survival in this species, high rainfall during gestation increased juvenile survival during the first month of life. This positive, delayed effect of rainfall may involve trophic effects if prey abundance is water limited during the summer in the study site. Furthermore, females that experienced heavier rainfall when in utero produced larger neonates later in their life. This positive, intergenerational effect of rainfall was compensated by a strong, negative, intergenerational effect of rainfall on offspring quantity. Such climate-induced changes in neonate size and quantity could occur along a potential trade-off between litter size and offspring size (Stearns 1992). However, against this hypothesis, body size at birth was only marginally correlated with total litter size ($F_{1, 1824} = 3.35$, $P = 0.07$, slope $= -0.05 \pm 0.03$), and controlling for this weak trade-off in the models did not change the estimates and test statistics for the main effects listed in Table 2.

The precise mechanisms by which adult breeding performances in terms of offspring quantity and quality were affected by rainfall experienced by females when in utero are still unknown. Yet, our results are consistent with the short-term maternal effects observed in previous studies with this species (Le Galliard et al. 2006). In *Lacerta vivipara*, embryos develop within yolked eggs retained in the oviduct, and a simple placenta allows water, nutrient, and gas exchanges between the mother and eggs (Panigel 1956). For example, maternal stress during gestation causes developmental changes before birth, as well as later life history and behavioral modifications at the juvenile stage (Meylan et al. 2002). Thus, climate conditions experienced when in utero may have cascading effects on adult breeding performances by altering developmental processes early in life (Lindström 1999, Dufty et al. 2002). Another possibility is that rainfall caused delayed effects on the food web or other environmental factors. These delayed effects of rainfall on the food web and the environment are unlikely to persist for more than one field season due to some cumulative effects of environmental noise. However, variable rainfall during gestation may influence the food web and the environment during the summer and therefore the early environment experienced by offspring. The environment experienced early in life by juveniles could have a persistent effect and therefore influence their reproductive traits during adulthood (Lindström 1999, Benton et al. 2006). To discriminate maternal effects from potential delayed effects of rainfall on environment, common garden experiments should be conducted where neonates from mothers experiencing different amounts of rainfall would be reared in the same environment.

In the common lizard, maternal traits and a combination of delayed and direct climate effects generate significant cohort variation in adult females' breeding performances. In particular, rainfall during gestation had both short-term and long-term delayed consequences on neonates' traits (neonate size and survival) and maternal traits at adulthood (fecundity and offspring size). Thus, rainfall during gestation is a key climatic factor influencing breeding performances through delayed effects spanning up to two generations. Such intergenerational effects are suspected to have consequences on population dynamics by acting as a potential source of delayed density dependence (Beckerman et al. 2002, Plaistow et al. 2006). Our study provides one of the first examples of intergenerational climate effect in natural populations of an ectothermic vertebrate. Yet, our results showed contrasting effects of rainfall between and within each life stage. This complex web of climate-induced life history changes should be accounted for in the context of global climate change impacts.

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APPENDIX

Analysis of cohort variation in juvenile survival (*Ecological Archives* E089-145-A1).