

Mediterranean hatchling lizards grow faster at higher altitude: a reciprocal transplant experiment

P. IRAETA,* C. MONASTERIO,‡ A. SALVADOR‡ and J. A. DÍAZ*†

*Dpto. de Zoología y Antropología Física (Vertebrados), Facultad de Biología, Universidad Complutense, E-28040 Madrid, Spain, and ‡Dpto. de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, C.S.I.C., José Gutiérrez Abascal 2, E-28006 Madrid, Spain

Summary

1. In reptiles, growth is subject to proximate environmental influences, such as food availability and temperature, that may be crucial during the early stages of postnatal development. Mediterranean regions, with their severe summer drought, offer an excellent opportunity to examine the effects of environmental variations in precipitation and productivity on the timing of reproduction and growth rates of lizards.
2. In this study, we compared the incubation time, size at hatching, growth rates and changes in juvenile body condition of two nearby populations of the lizard *Psammotromus algirus* separated by 600–700 m altitude in central Spain. We combined a reciprocal incubation experiment at 27 and 30 °C with a reciprocal transplant experiment to distinguish between environmental and population-specific sources of geographical variation.
3. At both temperatures, eggs from the high-elevation site hatched sooner. Several important phenotypic traits of juveniles were primarily determined by the growing environment: the high-elevation site provided more food and allowed hatchlings to grow faster and reach larger size.
4. Environmental effects overrode familial ones, as shown by the larger growth rate of half-sibs released at the high-elevation site. However, both the size and the growth rate of juveniles were also influenced by their mother's site of origin, which means that population differences may reflect a genetic differentiation and/or different maternal effects.
5. Low precipitation and associated food scarcity were seemingly the main factors constraining the growth rates of juveniles at the lowland site.

Key-words: Drought, food availability, geographical variation, *Psammotromus*

Functional Ecology (2006) **20**, 865–872
doi: 10.1111/j.1365-2435.2006.01162.x

Introduction

Growth is an important component of the life histories of animals (Stearns 1992). It has major fitness implications through its effects on body size, that influence competitive ability (Civantos 2000; Downes & Bauwens 2002), fecundity (Sinervo *et al.* 1992; Downes 2001) and survival (Ferguson & Fox 1984; Civantos, Salvador & Veiga 1999; Díaz *et al.* 2005). In reptiles, growth is indeterminate, and it is subject to proximate environmental effects that may be crucial during the early stages of postnatal development (Dunham 1978; Sinervo & Adolph 1994; Lorenzon, Clobert & Massot 2001). In fact, phenotypic plasticity

of lizard growth rates represents one of the most acknowledged sources of variation in their life histories (Niewiarowski & Roosenburg 1993; Sinervo & Adolph 1994; Sorci, Clobert & Belichon 1996; Lorenzon *et al.* 2001; Sears & Angilletta 2003). Thus, the interpretation of interpopulation differences in growth rates along geographical gradients requires distinguishing between the environmental and genetic determinants of growth.

Environmental variation, in turn, has two main sources, since both food availability and temperature are likely to have strong proximate effects on the growth rates of lizards (Sinervo & Adolph 1989). However, precipitation (a main cue of food availability) and temperature tend to be negatively related in temperate regions. Thus environments where thermal constraints limit activity and thereby foraging

opportunities may be either hot and food-restrictive, such as deserts (Dunham 1978; Grant & Dunham 1990), or food-rich but with a short and relatively cool summer season, as may be the case of the altitudinal or latitudinal limits of distribution ranges (Olsson & Shine 1997). This implies that the interaction between resource levels and biophysical constraints may greatly influence interpopulation differences in life histories (Grant & Dunham 1990). Within this framework, Mediterranean climatic zones offer an excellent opportunity to examine the effects of environmental variations in temperature, precipitation and food availability on lizard growth rates. Mediterranean climates are characterized by a summer drought that persists no less than 2 months, and there is great variability in monthly and yearly rainfall from year to year, which accentuates the severity of these climates for vegetation and associated arthropod faunas (Nahal 1981). Thus, the main problem for Mediterranean reptiles during the summer (late reproductive season) should be food scarcity rather than thermal constraints. On the one hand, the summer drought should favour early reproducing females by allowing them to synchronize ovogenesis with the spring peak of productivity; but, on the other hand, their offspring could face serious difficulties for growing owing to food shortage in the late summer.

This could widen the views about the selective forces that may have shaped the reproductive phenology of temperate reptiles. It is usually assumed that the fitness consequences of variations in the timing of reproduction are most significant in cold environments, where summers are brief and the time available for incubation and subsequent hatchling growth prior to winter is severely limited (Olsson & Shine 1997). In Mediterranean areas, however, the summer drought may be the outstanding factor determining the laying date, duration of incubation and/or clutch frequency of lizard populations.

In this study, we compare the incubation time, size at hatching, growth rates and changes in body condition of juveniles of two nearby populations of the lizard *Psammodromus algirus* separated by 600–700 m altitude in central Spain. We combined a reciprocal incubation experiment at 27 and 30 °C with a reciprocal transplant experiment to distinguish between environmental and population-specific sources of geographical variation in the phenotypic traits examined (Niewiarowski & Roosenburg 1993; Qualls & Shine 2000; Lorenzon *et al.* 2001). By manipulating incubation temperatures, we can explore the effects of variations in hatching date on the growth rate and body condition of juveniles from different origins and reared at different environments. Our goal is to test the hypothesis that lizards will grow faster at the high-elevation site because of the better growth environment driven by higher precipitation levels, associated types of vegetation (i.e. deciduous forests) and, ultimately, higher productivity.

Materials and methods

STUDY SPECIES

Psammodromus algirus (Linnaeus, 1758) is a medium-sized (adult snout–vent length 60–90 mm; mass 6–16 g), heliothermic, insectivorous lacertid that inhabits shrub and woodland habitats of the Iberian Peninsula, south-eastern coastal region of France and north-west Africa (Arnold 1987; Díaz and Carrascal 1991). In central Spain, its elevational range is approximately 450–1400 m. Hibernation takes place from October through February, courtship and egg-laying occur between April and June, and hatchlings are born in August–September (Veiga and Salvador 2001). Clutch size ranges between 3 and 12 eggs and clutch frequency varies between one and two clutches per year.

STUDY AREAS

Our low-elevation study area was located at ‘El Pardo’ (Madrid, central Spain: 40°31′ N, 03°47′ W; 650 m elevation), a holm oak (*Quercus ilex* L.) broad-leaved, evergreen forest in which offshoots of *Q. ilex* dominate the shrub layer together with Rockroses *Cistus ladanifer* L. The site has a mean annual temperature of 12.5 °C and a mean annual rainfall of 438 mm, but meteorological conditions vary extensively on a seasonal basis and among years (Díaz & Cabezas-Díaz 2004).

The high-elevation site was located at Navacerrada (Cerro de la Golondrina, Sierra de Guadarrama, central Spain: 40°44′ N, 4°00′ W; 1300 m elevation), at a linear distance of 32 km from the lowland site. It is a deciduous Pyrenean Oak (*Quercus pyrenaica* Willd) forest in which shrub patches (mainly of oak saplings and Rockroses) are interspersed with grasslands and rocky outcrops. Mean annual temperature at the nearby meteorological station ‘Puerto de Navacerrada’ is 6.2 °C, and mean annual precipitation is 1170 mm. *Psammodromus algirus* is the most abundant lizard species in both study areas. Long-term climatic data (>18 years) for the second half of the 20th century indicate that summer drought is much shorter and less intense at the high-elevation site (where it spans from late June to early August) than at the lowland site (where it spans from mid-May to mid-September).

At each site, lab-born hatchlings were released in a 600 m² plot (30 × 20 m²) with homogeneous vegetation cover.

HUSBANDRY OF ADULTS, EGGS AND JUVENILES

In May 2005, 70 adult lizards (El Pardo: 22 gravid females (mean SVL ± SE = 80.4 ± 0.7 mm; mean body mass = 10.7 ± 0.3 g) and 11 males; Navacerrada: 26 gravid females (mean SVL = 80.8 ± 0.8 mm; mean body mass = 10.5 ± 0.4 g) and 11 males) were captured and transported on the same day to the Department

of Zoology (Universidad Complutense de Madrid). Lizards were housed in white opaque wall terraria covered by a green net that prevented escape, let daylight enter the cages, and provided a shrubby-like shelter. Terraria were filled with moistened earth covered by leaf litter. A 60 W lamp suspended over one end of the cage created a photothermal gradient (c. 25–50 °C) allowing thermoregulation within the preferred temperature range (Díaz & Cabezas-Díaz 2004). Lizards were fed crickets (*Acheta domestica*) and mealworms (*Tenebrio molitor*), dusted with a commercial vitamin and calcium supplement. All cages were watered *ad libitum*.

Gravid females were daily monitored to detect egg-laying. When a female had laid, it was removed from the cage and the eggs were carefully searched for. Upon finding the clutch, eggs were counted (mean clutch sizes were 5.8 ± 0.24 and 6.8 ± 0.35 for El Pardo and Navacerrada, respectively), weighed and individually placed in 150-ml closed plastic cups filled with c. 35 g of moistened vermiculite (10 g vermiculite: 8 g water, equivalent to -200 kPa; Tracy, Packard & Packard 1978). Eggs of the same clutch were distributed evenly over two incubators (Friocell, Königswinter, Germany) set at constant temperatures of 27 and 30 °C. These temperatures are not intended to represent the incubation conditions of any of the two sites (lowland females select nest temperatures of c. 26 °C; authors, unpublished), but to allow manipulation of hatching date. When incubation was about to end, newborns were searched for daily. Hatchlings were weighed, measured (snout–vent length, SVL) and individually toe-clipped.

All newborns (sample size = 246 lab-born lizards) were released in the field the day after hatching (i.e. between 17 July and 19 August 2005). Half of the hatchlings from a given clutch and incubator were assigned to the release plot at the low-elevation site ($n = 123$), and the other half to the high-elevation site ($n = 123$). Thus, we used a split-clutch design both for incubation temperature and release site.

FIELD PROCEDURES

Between 5 September and 29 September 2005 both study sites were visited regularly, and all juveniles found while walking slowly across the study plots were captured by hand. To control for hatchling dispersal, our search area was expanded to a belt 30 m wide outside the plots, which exceeds the mean distance moved by juveniles of this species (14.8 ± 3.0 m, Civantos *et al.* 1999). The same recapture effort was made at both study sites (low-elevation: 55.9 person-hours; high-elevation site: 56.4 person-hours).

Each captured lizard was examined to determine whether it was marked or not. If not, it was toe-clipped and identified as field-born. All captured juveniles were measured (SVL) and weighed before being released at their site of capture.

At the end of the sampling period, food availability was estimated by tossing a 20×20 cm² wooden frame 24 times at each study site and counting and identifying all arthropods contained within it during 1 min of search (see Díaz & Carrascal 1990 for details).

ANALYSES

Growth rates of lab-born juveniles were expressed on a size-specific basis [$\ln(\text{SVL}_{\text{recapture date}}/\text{SVL}_{\text{hatching date}})/(\text{recapture date} - \text{hatching date})$] or a mass-specific basis [$\ln(\text{body mass}_{\text{recapture date}}/\text{body mass}_{\text{hatching date}})/(\text{recapture date} - \text{hatching date})$]. These estimates reflect the proportionate increase in size or mass on a per-day basis (Sinervo 1990). The body condition of juveniles was estimated using the residuals of the regression of $\log(\text{body mass})$ on $\log(\text{SVL})$. Unless otherwise stated, all statistical analyses were performed using general linear models after having checked the assumptions of parametric tests and, when necessary, log-transforming the corresponding variables. Data are given as mean \pm 1 SE.

Results

More juveniles were captured at the high-elevation than at the lowland site, both for lab-born ($n = 26$ and 14 individuals at Navacerrada and El Pardo, respectively) and field-born lizards ($n = 35$ and 27). Thus, recapture rates of lab-born hatchlings were lower at the lowland site ($\chi^2 = 4.30$, $df = 1$, $P = 0.038$).

INCUBATION PERIOD

Incubation times were shorter at higher temperature and, remarkably, they differed significantly between populations (ANOVA with the data shown in Table 1; incubation temperature: $F_{1,36} = 349.1$, $P < 0.001$; site of origin: $F_{1,36} = 24.6$, $P < 0.001$; interaction: $F_{1,36} = 0.39$, $P = 0.538$): at both temperatures, incubation times of Navacerrada lizards were on average about 94% as long as those of El Pardo lizards. As a consequence, although laying occurred earlier for the lower elevation clutches (ANOVA: $F_{1,38} = 12.4$, $P = 0.001$; mean laying dates = 27 May and 1 June for recaptured juveniles from El Pardo and Navacerrada

Table 1. Incubation period (in days) of the eggs that hatched into recaptured juveniles as a function of incubation temperature and population of origin: mean, standard error, range, and sample size (N)

	Mean	SE	Range	N
El Pardo 27 °C	67.0	1.34	64–72	5
Navacerrada 27 °C	63.1	0.93	60–68	8
El Pardo 30 °C	53.6	0.37	52–55	10
Navacerrada 30 °C	50.6	0.41	48–54	17

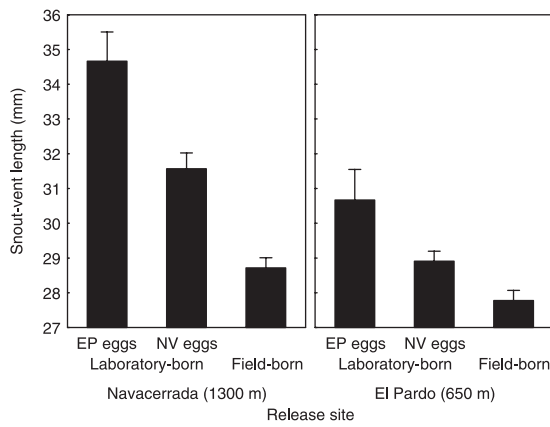


Fig. 1. Mean (± 1 SE) snout-vent length (in mm) of juvenile lizards captured at each study site, classified as field-born or lab-born (hatched in captivity and released into the field the day after hatching). Recaptured lab-born lizards, in turn, are classified according to their mother's site of origin as coming from Navacerrada (NV) eggs or from El Pardo (EP) eggs.

clutches, respectively), hatching dates did not differ significantly between both populations ($F_{1,38} = 0.2$, $P = 0.637$; mean hatching dates = 24 and 25 July), even after controlling for the effects of egg mass ($F_{1,37} = 2.0$, $P = 0.162$; egg mass: $\beta = 0.341$, $P = 0.089$).

SIZE OF JUVENILES

Because the first observations of field-born hatchlings took place on the second week of August at both localities, when 85.7% of lab-born juveniles had already been released, we can assume that lab-born lizards were older than field-born ones. As a consequence, this age difference should translate into body-size differences when (re)captured. A two-way ANOVA with release site and condition (field vs lab-born) as factors and SVL as the dependent variable (Fig. 1), showed that, as expected, lab-born juveniles were larger than field-born ones ($F_{1,98} = 51.2$, $P < 0.001$). More importantly, juveniles captured at the high-elevation site were larger than those captured at the lowland site ($F_{1,98} = 31.4$, $P < 0.001$), especially in the case of lab-born, presumably older lizards (site \times field vs lab-born interaction: $F_{1,98} = 9.9$, $P = 0.002$; see Fig. 1). A second ANOVA considering only the lab-born juveniles, with release site and site of mother's origin as

factors, and with SVL as the dependent variable, showed significant differences due not only to release site but also to site of origin (release site: $F_{1,36} = 20.7$, $P < 0.001$; site of origin: $F_{1,36} = 10.9$, $P = 0.0023$; interaction: $F_{1,36} = 0.52$, $P = 0.475$): at both sites, juveniles from lowland clutches were larger than those from high-elevation clutches (Fig. 1). This effect decreased, but remained significant, after controlling for the effects of SVL at hatching (ANCOVA; site of origin: $F_{1,35} = 8.0$, $P = 0.008$) or egg mass (site of origin: $F_{1,35} = 4.3$, $P = 0.045$). In fact, SVL and body mass at hatching were larger for lowland newborns (SVL: 28.7 ± 0.29 mm; body mass: 0.58 ± 0.02 g) than for high-elevation ones (SVL: 27.6 ± 0.23 mm; body mass: 0.51 ± 0.01 g). However, this significant difference (SVL: $F_{1,38} = 7.3$, $P = 0.010$; body mass: $F_{1,38} = 10.7$, $P = 0.002$) was mainly due to the higher per-offspring investment of lowland females (ANCOVAs; SVL: $F_{1,37} = 0.2$, $P = 0.662$; body mass: $F_{1,37} = 0.6$, $P = 0.461$), the eggs of which had a larger mass than those of high-elevation females (El Pardo: 0.48 ± 0.01 g, $n = 15$; Navacerrada: 0.40 ± 0.01 g, $n = 25$; $F_{1,38} = 20.4$, $P < 0.001$).

Since eggs incubated at 30 °C hatched earlier than those incubated at 27 °C (see above), we should expect incubation temperature to affect the age and hence size, of the lab-born juveniles recaptured in the field. However, incubation temperature had a small and non-significant effect on juvenile size (incubation effect in the two-way ANOVA with release site and temperature as factors: $F_{1,36} = 2.8$, $P = 0.104$) that only in the high-elevation site was closer to statistical significance (30 °C: 33.8 ± 0.65 mm, $n = 16$; 27 °C: 31.7 ± 0.83 mm, $n = 10$; $F_{1,24} = 3.8$, $P = 0.064$). In summary, juvenile size was determined by the environmental conditions of the growing environment and (to a lesser extent) by maternal per-offspring investment, rather than by incubation temperature or hatching date.

GROWTH RATES AND BODY CONDITION

Neither incubation temperature nor date of capture influenced size-specific growth rate of lab-born juveniles (both $P > 0.35$), but there was a clear effect of release site: juveniles grew faster at higher elevation (Table 2). With respect to the site of origin, juveniles from El Pardo tended to grow faster at both sites (release site: $F_{1,36} = 20.8$, $P < 0.001$; site of origin:

Table 2. Mean (± 1 SE) size-specific growth rates (days⁻¹) and the same means adjusted for (log) SVL at hatching. *N* = sample size

Release site	Site of origin	Mean \pm SE	Adjusted mean \pm SE	<i>N</i>
Navacerrada	El Pardo	0.0034 \pm 0.0003	0.0037 \pm 0.0003	12
	Navacerrada	0.0028 \pm 0.0003	0.0027 \pm 0.0002	14
El Pardo	El Pardo	0.0018 \pm 0.0006	0.0017 \pm 0.0005	3
	Navacerrada	0.0009 \pm 0.0003	0.0007 \pm 0.0003	11

$F_{1,36} = 4.0$, $P = 0.054$; interaction: $F_{1,36} = 0.25$, $P = 0.618$). This difference became larger and significant when controlling for the effect of hatchling size (ANCOVA with data in Table 2; release site: $F_{1,35} = 33.3$, $P < 0.001$; site of origin: $F_{1,35} = 8.7$, $P = 0.006$; interaction: $F_{1,35} = 0.01$, $P = 0.933$; hatchling SVL: $\beta = -0.373$, $F_{1,35} = 10.3$, $P = 0.003$), because size-specific growth rates were higher for smaller juveniles, and size at hatching was larger for lowland lizards.

We also compared the size-specific growth rates of half-siblings released at different sites, to control for possible familial effects. Four females (one from El Pardo and three from Navacerrada) had a recaptured offspring at each site, another one (from Navacerrada) had two recaptured offspring at the lowland site and one at the high-elevation site, and another one (also from Navacerrada) had six recaptured offspring, three at each site. A repeated measures ANOVA comparing the (average) growth rates of half-sibs reared at both sites showed that size-specific growth rates were consistently higher at the high-elevation site (El Pardo: $0.0012 \pm 0.0003 \text{ day}^{-1}$; Navacerrada: $0.0030 \pm 0.0004 \text{ day}^{-1}$; $F_{1,5} = 14.8$, $P = 0.012$). Moreover, the three juveniles from the same clutch that were recaptured at Navacerrada had grown faster than their three half-sibs released at El Pardo ($F_{1,4} = 38.3$, $P = 0.003$). Thus, juveniles grew faster at the high-elevation site after controlling for familial effects.

Concerning changes in body mass, hatchlings released at the high-elevation site gained mass more rapidly (mass-specific growth rate: $0.0074 \pm 0.0008 \text{ days}^{-1}$, $n = 25$) than those released at the lowland site ($-0.0014 \pm 0.001 \text{ day}^{-1}$, $n = 14$), independent of their site of origin (two-way ANOVA; release site: $F_{1,35} = 33.4$, $P < 0.001$; site of origin: $F_{1,35} = 0.72$, $P = 0.400$; interaction: $F_{1,35} = 0.15$, $P = 0.697$). In fact, hatchlings released at the high-elevation site increased their mass during the study period (one-sample *t*-test against the null hypothesis that the mean mass-specific growth rate is equal to zero: $t = 10.2$, $df = 24$, $P < 0.001$), whereas those released at the lowland site did not manage to do so ($t = -1.2$, $df = 13$, $P = 0.259$).

Because lab-born juveniles released at the lowland site increased their size without gaining mass accordingly, their body condition was eventually worse than that of juveniles released at the high-elevation site ($F_{1,38} = 10.4$, $P = 0.003$; see data in Fig. 2). In fact, the body condition of both field-born and lab-born juveniles was better at the high-elevation site, and the site effect was somewhat larger, though not significantly so, for the older, lab-born lizards (two-way ANOVA with data in Fig. 2; field vs lab-born: $F_{1,97} = 3.0$, $P = 0.086$; site: $F_{1,97} = 9.1$, $P = 0.003$; interaction: $F_{1,97} = 2.2$, $P = 0.141$).

FOOD AVAILABILITY

The availability of arthropods was higher at the high-elevation site (Navacerrada: 1.71 ± 0.23 prey per

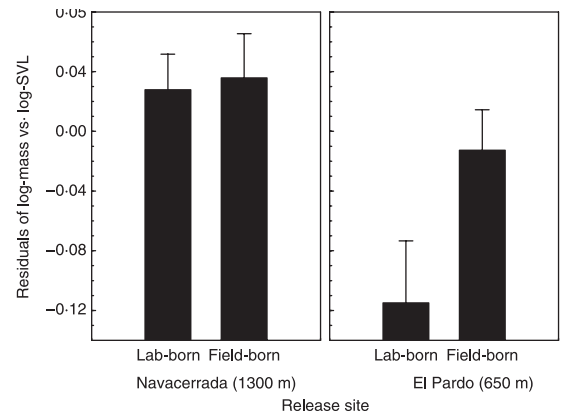


Fig. 2. Mean (± 1 SE) body condition (estimated using the residuals of the regression of body mass on snout-vent length) of juvenile lizards captured at each study site, classified as field-born or lab-born (hatched in captivity and released into the field the day after hatching).

minute of search, $n = 24$; El Pardo: 0.62 ± 0.23 prey per minute, $n = 24$; Mann-Whitney's *U*-test: $U = 444.5$, $Z = 3.11$, $P = 0.002$). Although there were no significant between-site differences in the mean number of prey taxa, overall prey diversity was lower at the lowland site, where we found four major prey types (Formicidae, Araneae, Blattidae and Homoptera) vs eight at the high-elevation site (the former ones plus Diptera, Gryllidae, Heteroptera and insect larvae).

Discussion

Our most interesting result is that lizard growth rates were higher at the cooler, higher altitude environment, thus differing from what would be expected on the basis of thermal opportunity for activity (Sinervo & Adolph 1989; Grant & Dunham 1990; Sears 2005a). Instead, differences in food resources appeared to be the main cause of faster growth rates at higher altitude. The environmental factors that determine energy budgets of ectotherms (absolute resource availability and the rate at which energy can be harvested and processed; Congdon 1989) interact in complex ways that prevent single expectations about how growth rates will vary along altitudinal or latitudinal gradients (Sears 2005a). Thus, growth rates of lizards may increase at higher (Sinervo 1990; Sears 2005a), lower (Sorci *et al.* 1996; Rohr 1997) or intermediate (Grant & Dunham 1990) elevations. The mechanisms that promote faster growth may also vary among taxa or environments, so that variation in growth rates may result from differences in thermal opportunity (Niewiarowski & Roosenburg 1993; Sinervo & Adolph 1994), food availability (Dunham 1978), a combination of the two (Grant & Dunham 1990), metabolic expenditure (Grant & Dunham 1990; Sears 2005b) or activity constraints imposed by predation risk (Sears 2005a).

In our system, the high elevation site provided more food and allowed hatchlings to grow faster and reach

larger size, even though it presumably offered shorter potential daily activity periods. Thus, the growing environment was the main determinant of several traits of juveniles, such as growth rate, size or body condition, which may be related to their fitness (Civantos *et al.* 1999; Díaz *et al.* 2005). The preponderance of environmental effects, which is consistent with previous studies of lizard growth rates (Niewiarowski & Roosenburg 1993; Sinervo & Adolph 1994; Sorci *et al.* 1996; Qualls & Shine 2000; Lorenzon *et al.* 2001), was confirmed by the fact that they clearly overrode familial ones, since half-sibs released at Navacerrada grew faster than those released at El Pardo in all possible comparisons.

On the other hand, both the size and the growth rate of juveniles were also influenced by their mother's site of origin, independently of the growing environment. This influence was mainly determined by differences in maternal investment, because its magnitude became much smaller after controlling for the effects of egg mass (Sinervo 1990). However, it remained significant, at least in the case of growth rate. Thus, we cannot reject the hypothesis that population differences in growth rate reflect a genetic differentiation in the underlying physiology of growth (Sinervo 1990; Bronikowski 2000) and/or different maternal effects, aside from egg mass, in both populations (Bernardo 1996). Growth rates were higher for lab-born juveniles of lowland origin at both release sites. Thus, hatchlings from lowland clutches were larger and grew faster than their conspecifics from high-elevation clutches incubated under the same conditions. This is in contrast with previous studies that have reported higher mass-specific growth rates for lizard populations with smaller hatching sizes (Sinervo 1990). Perhaps the larger size and higher growth rates of our juveniles of lowland origin may be related to the selective advantage of large-sized juveniles in years of drought and food scarcity (Ferguson & Fox 1984; Sinervo & DeNardo 1996). However, rapid growth early in life may have associated costs (Metcalf & Monaghan 2001). Juvenile lizards that increase foraging activity may suffer higher predation (Warner & Andrews 2002). Also, individuals that grow more rapidly as neonates may experience higher mortality later in life if they allocate resources among different body components in ways that compromise their subsequent survival (Olsson & Shine 2002).

With respect to the timing of reproduction, previous research has emphasized the advantage of early hatching at high altitude or in cold environments (Schwarzkopf & Shine 1991; Olsson & Shine 1997), assuming that delayed hatching is negatively selected because of the short time available for energy storage before wintering. Our data suggest an alternative interpretation for our two study sites, because summer drought at the lowland site may represent a serious challenge for early hatchlings, whereas the higher productivity of the montane site may allow early hatchlings to grow faster

and reach larger size than later newborns. Two lines of evidence support this interpretation. First, the size difference between lab-born (older) and field-born (younger) juveniles was much larger in the montane site (Fig. 1). Second, the body condition (i.e. size-adjusted body mass) of lab-born juveniles was inferior at the low-elevation site (Fig. 2). In fact, hatchlings released at the lowland site did not manage to increase their body mass during the study period. As a consequence, only the juveniles released at the high-elevation site were able to grow without losing body condition.

The superior habitat quality for juvenile lizards of the high-elevation site was confirmed by the fact that even field-born lizards were larger at higher altitude. This is surprising because, as previously discussed, our lab data indicate that hatching size was smaller for high-altitude clutches. Thus, either hatching occurred earlier at higher elevation (which could be suggested by shorter incubation times, but was not confirmed by field observations), or the environmental component of the variance in growth rates was large enough to override the between-sites difference in hatching size. Our data support this later interpretation, because the age of recaptured lab-born lizards did not differ significantly between both recapture sites (El Pardo: 53.2 ± 3.1 days; Navacerrada: 49.4 ± 2.0 days; $F_{1,38} = 1.2$, $P = 0.287$). In any case, rapid growth may be advantageous at the high-elevation site both in terms of survival (Civantos *et al.* 1999) and intraspecific competition (we made sporadic observations of larger, lab-born juveniles chasing smaller, field-born ones).

Both mean prey availability and mean size-specific growth rates were about three times higher at the high elevation site, which suggests that low precipitation and associated food scarcity are proximate factors constraining the growth rates of juveniles at the lowland site (Dunham 1978; Lorenzon *et al.* 2001). This response may be reinforced by low activity levels, enabling lizards to avoid dehydration (Jones, Waldschmidt & Potvin 1987; Lorenzon *et al.* 1999; Sears & Angilletta 2003). Accordingly, activity of released hatchlings seemed lower at the lowland site. On the other hand, operative temperatures available were probably adequate for long-day activity at both sites (Díaz 1997; Díaz & Cabezas-Díaz 2004), which implies that thermal opportunities were not the main factor explaining between-site differences in growth rates. In fact, the study year was characterized by conditions of high temperature and extreme summer drought (2005 was the driest year in the Madrid region since 1912), which may have represented a particularly intense episode of selection. Moreover, if the lower resource availability at lower elevation restricts growth potential, selection may favour bigger eggs and hatchlings in this environment, thus compensating for reduced growth rate. Previous studies indicate that the survival advantage of large offspring is greater under conditions of food

shortage (Ferguson & Fox 1984) and/or in drought years (Sinervo *et al.* 1992; Sinervo & DeNardo 1996).

Finally, it should be stressed that, because our study compares only two sites that differ in altitude, precipitation, type of vegetation and arthropod abundance, inferences drawn from the results of our experiment are, in a strict sense, restricted to the two sites used. However, our reciprocal transplant results are still useful for examining the relative importance of genetic *vs* environmental effects as sources of variation in lizard growth rates (Niewiarowski & Roosenburg 1993). Moreover, our two-site comparison may be representative of altitudinal effects in the Mediterranean region of the Iberian peninsula, and our results may suggest general patterns that could be tested with future work. Thus, our findings may be relevant for understanding the distribution of this widespread lizard species because growth rate may contribute to between-sites differences in body size, fecundity and, ultimately, population size. The abundance of *P. algirus* on a regional scale was positively correlated with food availability when holding for the effects of habitat structure (Díaz & Carrascal 1991), and lizards were more abundant at a high-altitude site similar to the one reported here than at our lowland study site, despite the lower temperatures of the former (Díaz 1997). All this evidence suggests that Mediterranean mountains, owing to their mild climate and high levels of food abundance, could represent patches of higher habitat quality for lizards than surrounding xeric lowlands.

Acknowledgements

This paper is a contribution to the project CGL2004-01151 funded by the Spanish Ministry of Education and Science. Permissions to capture lizards were provided by the Patrimonio Nacional (owner of El Pardo) and the 'Dirección General del Medio Natural' of the Madrid region. We thank Javier Pérez-Tris, Tomás Santos, Peter Niewiarowski and two anonymous reviewers for useful comments on a previous version.

References

- Arnold, E.N. (1987) Resource partition among lacertid lizards in southern Europe. *Journal of Zoology B* **1**, 739–782.
- Bernardo, J. (1996) Maternal effects in animal ecology. *American Zoologist* **36**, 83–105.
- Bronikowski, A.M. (2000) Experimental evidence for the adaptive evolution of growth rate in the garter snake (*Thamnophis elegans*). *Evolution* **54**, 1760–1767.
- Civantos, E. (2000) Home-range ecology, aggressive behaviour, and survival in juvenile lizards, *Psammodromus algirus*. *Canadian Journal of Zoology* **78**, 1681–1685.
- Civantos, E., Salvador, A. & Veiga, J.P. (1999) Body size and microhabitat affect winter survival of hatchling *Psammodromus algirus* lizards. *Copeia* **1999**, 1112–1117.
- Congdon, J.D. (1989) Proximate and evolutionary constraints on energy relations of reptiles. *Physiological Zoology* **62**, 356–373.
- Díaz, J.A. (1997) Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two

- temperate lizard populations. *Functional Ecology* **11**, 79–89.
- Díaz, J.A. & Cabezas-Díaz, S. (2004) Seasonal variation in the contribution of different behavioural mechanisms to lizard thermoregulation. *Functional Ecology* **18**, 867–875.
- Díaz, J.A. & Carrascal, L.M. (1990) Prey size and food selection of *Psammodromus algirus* (Lacertidae) in central Spain. *Journal of Herpetology* **24**, 342–347.
- Díaz, J.A. & Carrascal, L.M. (1991) Regional distribution of a Mediterranean lizard: influence of habitat cues and prey abundance. *Journal of Biogeography* **18**, 291–297.
- Díaz, J.A., Pérez-Tris, J., Tellería, J.L., Carbonell, R. & Santos, T. (2005) Reproductive investment of a lacertid lizard in fragmented habitat. *Conservation Biology* **19**, 1578–1585.
- Downes, S. (2001) Trading heat and food for safety: cost of predator avoidance in a lizard. *Ecology* **82**, 2870–2881.
- Downes, S. & Bauwens, D. (2002) An experimental demonstration of direct behavioural interference in two Mediterranean lacertid lizard species. *Animal Behaviour* **63**, 1037–1046.
- Dunham, A.E. (1978) Food availability as a proximate factor influencing growth rates in the iguanid lizard *Sceloporus merriami*. *Ecology* **59**, 770–778.
- Ferguson, G.W. & Fox, S.F. (1984) Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana* – its causes and evolutionary significance. *Evolution* **38**, 342–349.
- Grant, B.W. & Dunham, A.E. (1990) Elevational covariation in environmental constraints and life histories of the desert lizard *Sceloporus merriami*. *Ecology* **71**, 1765–1776.
- Jones, S.M., Waldschmidt, S.R. & Potvin, M.A. (1987) An experimental manipulation of food and water: growth and time-space utilization of hatchling lizards (*Sceloporus undulatus*). *Oecologia* **73**, 53–59.
- Lorenzon, P., Clobert, J., Oppliger, A. & John-Adler, H. (1999) Effect of water constraint on growth, activity and body temperature of yearling common lizard (*Lacerta vivipara*). *Oecologia* **118**, 423–430.
- Lorenzon, P., Clobert, J. and Massot, M. (2001) The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. *Evolution* **55**, 392–404.
- Metcalfe, N.B. & Monaghan, P. (2001) Compensation for a bad start: grow now, pay later? *Trends in Ecology and Evolution* **16**, 254–260.
- Nahal, I. (1981) The Mediterranean climate from a biological viewpoint. *Mediterranean-Type Shrublands* (eds F. di Castri, D.W. Goodall & R.L. Specht), pp. 63–86. Elsevier, Amsterdam.
- Niewiarowski, P.H. & Roosenburg, W. (1993) Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. *Ecology* **74**, 1992–2002.
- Olsson, M. & Shine, R. (1997) The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why earlier clutches are better. *Journal of Evolutionary Biology* **10**, 369–381.
- Olsson, M. & Shine, R. (2002) Growth to death in lizards. *Evolution* **56**, 1867–1870.
- Qualls, F.J. & Shine, R. (2000) Post-hatching environment contributes greatly to phenotypic variation between two populations of the Australian garden skink, *Lampropholis guichenoti*. *Biological Journal of the Linnean Society* **71**, 315–341.
- Rohr, D.H. (1997) Demographic and life-history variation in two proximate populations of a viviparous skink separated by a steep altitudinal gradient. *Journal of Animal Ecology* **66**, 567–578.
- Schwarzkopf, L. & Shine, R. (1991) Thermal biology of reproduction in viviparous skinks, *Eulamprus tympanum*: why do gravid females bask more? *Oecologia* **88**, 562–569.

- Sears, M.W. (2005a) Geographic variation in the life history of the sagebrush lizard: the role of thermal constraints on activity. *Oecologia* **143**, 25–36.
- Sears, M.W. (2005b) Resting metabolic expenditure as a potential source of variation in growth rates of the sagebrush lizard. *Comparative Biochemistry and Physiology A* **140**, 171–177.
- Sears, M.W. & Angilletta, M.J. (2003) Life-history variation in the sagebrush lizard: phenotypic plasticity or local adaptation? *Ecology* **84**, 1624–1634.
- Sinervo, B. (1990) The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* **44**, 279–294.
- Sinervo, B. & Adolph, S.C. (1989) Thermal sensitivity of growth rate in hatchling *Sceloporus* lizards: environmental, behavioural and genetic aspects. *Oecologia* **78**, 411–419.
- Sinervo, B. & Adolph, S.C. (1994) Growth plasticity and thermal opportunity in *Sceloporus* lizards. *Ecology* **75**, 776–790.
- Sinervo, B. & DeNardo, D.F. (1996) Costs of reproduction in the wild: Path analysis of natural selection and experimental tests of causation. *Evolution* **50**, 1299–1313.
- Sinervo, B., Doughty, P., Huey, R.B. & Zamudio, K. (1992) Allometric engineering: a causal analysis of natural selection on offspring size. *Science* **258**, 1927–1930.
- Sorci, G., Clobert, J. & Belichon, S. (1996) Phenotypic plasticity of growth and survival in the common lizard *Lacerta vivipara*. *Journal of Animal Ecology* **65**, 781–790.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Tracy, C.R., Packard, G.C. & Packard, M.J. (1978) Water relations of chelonian eggs. *Physiological Zoology* **51**, 378–387.
- Veiga, J.P. & Salvador, A. (2001) Individual consistency in emergence date, a trait affecting mating success in the lizard *Psammodromus algirus*. *Herpetologica* **57**, 99–104.
- Warner, D.A. & Andrews, R.M. (2002) Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. *Biological Journal of the Linnean Society* **76**, 105–124.

Received 4 January 2006; revised 10 May 2006; accepted 1 June 2006

Editor: Peter Niewiarowski