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Life-history traits of two Mediterranean lizard populations: a possible example of countergradient covariation

Pablo Iraeta[1,3], Alfredo Salvador[2], and José A. Díaz[1]

[1] *Dpto. de Zoología y Antropología Física (Vertebrados), Facultad de Biología, Universidad Complutense, E-28040 Madrid.*

[2] *Dpto. de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, MNCN-CSIC, José Gutiérrez Abascal 2, E-28006 Madrid.*

[3] *Corresponding author*

email: piraeta@bio.ucm.es

Tel.: +34 91 394 51 36.

Fax: +34 91 394 49 47.

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Abstract

The trade-off between clutch and offspring size, which is a central topic in life-history research, is shaped by natural selection to maximize the number of surviving offspring, but it also depends on the resources available for reproduction. Conspecific populations living in different environments may differ in adult body size, clutch mass, clutch size, offspring size, and/or post-natal growth rates, due either to phenotypic plasticity or local adaptation. Here, we compare these traits and their relationships between two populations of the lizard *Psammodromus algirus* separated by a 600-m altitudinal gradient. We used a common garden design to control incubation temperature and food availability, with two different feeding treatments. Females were larger at the high-elevation site. Although SVL-adjusted clutch mass did not differ between populations, high-elevation females laid more but smaller eggs than low-elevation ones. Hatchlings were larger at lower elevation. Our common garden experiment revealed that low-elevation hatchlings grew faster than high-elevation hatchlings under both feeding treatments. However, higher food availability at higher altitude allows high-elevation lizards to grow faster and attain larger adult sizes, especially in the case of females. The two key adaptations of low-elevation lizards, large eggs and hatchlings and the ability to grow rapidly after hatching, are likely to enhance survival in low-productivity Mediterranean lowlands. Our data support the hypothesis that the reproductive strategies of these populations provide an example of countergradient variation, because the genotypes that encode for fast growth and large body size occured in low food availability habitats where juveniles grew slowly and attained small adult sizes.

Key-words: altitudinal gradients, clutch size, egg size, food availability, growth,

Psammodromus

Introduction

Life-history strategies are coadapted suites of traits that have been shaped by natural selection to maximize reproductive output in a particular environment (Stearns 1976). Therefore, variation in life-history traits is expected to be common among geographically separated populations of widely distributed species (Roff 1992; Stearns 1992). This variation may be the result of phenotypic plasticity, local adaptation to specific environmental conditions, or a combination of both (Berven and Gill 1983; Via and Lande 1985; Conover and Schultz 1995; Sears 2003). Environmental conditions are therefore important to understand intraspecific variation of life-history traits (Grant and Dunham 1990; Mathies and Andrews 1995), because geographically separated populations may experience differences in temperature, seasonality, length of the breeding period, and/or food availability that may favor different strategies to maximize reproductive success (Ballinger 1977; Boyce 1979; Angilletta et al. 2006).

One particular topic that has been central in life-history research is the trade-off between offspring number and quality (Stearns 1992; Roff 1992), because producing more but smaller offspring may result in less offspring surviving to breeding age (Lack 1947). To maximize their reproductive value, females should try to rear as many offspring as possible of the best quality or biggest size. However, the amount of resources a female can devote to reproduction is limited (Ballinger 1983). Therefore, under the assumption of finite resources, allocation to more eggs will necessarily lead to smaller offspring. Within this context, maternal body size is a primary determinant for fecundity in ectotherms with variable clutch sizes (Fitch 1970), because bigger females will have more resources to invest, and will be able to bear more eggs and lay larger clutches (Braña 1996) without a severe reduction of per-offspring investment. Accordingly, natural selection will favour large females due to their fecundity advantage over smaller ones (Fitch 1970; Braña 1996; Olsson et al. 2002). In addition, for a given female size local environmental conditions such as predation risk or food availability will favour different patterns of resource allocation, trading larger clutches for larger offspring (Sinervo 1990; Roff 1992; Stearns 1992).

Another life-history trait that responds readily to environmental variation is post-natal growth rate, that will determine juvenile survival and size at maturity. Growth rates are dependent on food availability and the thermal environment (Adolph and Porter 1993). However, alternative strategies can evolve under conditions of food scarcity to promote faster growth when food is available or to lower activity when conditions are harsh (Iraeta et al. 2006, 2008). Thus, variation in juvenile growth rates among populations of the same or closely related species has been interpreted as adaptive (Lorenzon et al. 2001; Niewiarowski 2001, Caley and Schwarzkopf 2004). However, sometimes the observed differences among populations may be smaller than expected or even remain undetected due to the process known as countergradient variation, where genotypes within a species are distributed in nature such that genetic influences on a trait oppose environmental influences, leading to reduced variance in mean trait expression across the environmental gradient (Levins 1968, 1969). For example, genotypes that code for fast growth are often found in habitats that would otherwise cause slow growth, due to low operative temperatures or food scarcity (Blanckenhorn 1991; Arnett and Gotelli 1999; Jonassen et al. 2000; Ficetola and De Bernardi 2005, 2006). Most studies of countergradient variation in physiological traits of vertebrates use fish or amphibians as model organisms, although a few of them deal with iguanid or scincid lizards (review by Conover et al. 2009).

Altitudinal gradients provide a good example of the above mentioned type of environmental variation. Altitudinal differences in life-history traits have been well established, and they have frequently been interpreted within the framework of countergradient variation (Berven 1982 a, b; Merilä et al. 2000). Most studies of altitudinal variation in the life-histories of ectothermic animals assume that, because temperature decreases with altitude, environmental constraints should be more important at higher altitude, where summers are brief and the time available for hatchling growth prior to winter is more limited than at lower altitude (Olsson and Shine 1997; Sears 2005). However, this assumption does not hold for Mediterranean climates, where summer drought persists more than two months, accentuating their severity for vegetation and associated food webs (Nahal 1981). Thus, the main problem for ectotherms in Mediterranean lowlands during the summer may be food scarcity rather than thermal constraints, where offspring may experience reduced growth due to food shortage (Iraeta et al. 2006). Moreover, such difficulties should decrease with increasing altitude, because precipitation and productivity are higher in Mediterranean mountains, especially in the late breeding season, than in the surrounding xeric lowlands.

In this study, we compare adult body size, clutch mass, clutch size and mean egg mass of wild-caught females from two nearby populations of the lacertid lizard *Psammodromus algirus*, a widely distributed species in the western Mediterranean basin. The lizard populations studied are separated by 600–700 m altitude in central Spain.

Although no genetic differentiation between these populations is apparent according to mtDNA (no more than 3 changes in 843 bp; Verdú-Ricoy et al. 2010), we have previously reported significant differences between them in hatchling size and field growth rates (Iraeta et al. 2006). Here, we experimentally confirm such differences using a common garden design in which we controlled incubation temperature (which may affect growth rates; Caley and Schwarzkopf 2004) and food availability, with two different treatments, to mimic the selective pressures faced by juveniles in the wild. Our goal is to identify patterns of covariation of life-history traits (i.e. female body size, clutch mass, clutch size, egg mass, size at hatchling, and growth rates) and to discuss how these traits are coadapted to maximize reproductive success in the particular environment of each population. Specifically, we address the following hypotheses: 1) the key adaptations of the low-elevation lizards, namely large eggs and hatchlings and high potential post-natal growth rates, are likely to enhance survival in low-productivity Mediterranean lowlands; and 2) the high productivity of Mediterranean mountains should allow females to reach large sizes, achieve higher fecundity and large population densities, and produce small hatchlings that, despite low potential growth rates, grow fast enough to overcome their initial size disadvantage.

Materials and methods

Study species and study areas

Psammodromus algirus is a medium-sized (adult snout-vent length 60-90 mm; mass 6-16 g), ground-dwelling, heliothermic, insectivorous lacertid that inhabits shrub and woodland habitats on both margins of the Western Mediterranean basin (Arnold 1987;

Díaz and Carrascal 1991). It is a widely distributed species in which many life-history traits show large amounts of variation across its distribution range (Díaz et al. 2005; Iraeta et al. 2006, 2008; Díaz et al. 2007). Courtship and egg-laying occur between April and June, and hatchlings are born in August–September (Veiga and Salvador 2001).

Our low-elevation study area was located at ‘El Pardo’ (Madrid, central Spain: 40º31’N, 03º47’W; 650 m elevation), a cleared holm oak (*Quercus ilex*) broad-leaved, perennial forest. The site has a mean annual temperature of 12.5 °C and a mean annual rainfall of 438 mm (meteorological station ‘Madrid-Retiro’). The high-elevation site was located at Navacerrada (Cerro de la Golondrina, Sierra de Guadarrama, central Spain: 40º44’ N, 4º00’ W; 1300 m elevation), at a deciduous Pyrenean oak (*Quercus pyrenaica*) forest 32 km by air from the low-elevation site. 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 in both sites, but it reaches higher densities at higher altitude (Díaz 1997).

Husbandry of adults and juveniles

During April and May of the years 2005, 2006, and 2008, we captured a total of 95 adult lizards either by hand or with a noose (28 females and 22 males from the high-elevation population, and 30 and 15 males females from the low-elevation population) that were transported on the same day of capture to the laboratory at the Universidad Complutense de Madrid. All females were captured between 10 and 20 days prior to egg laying. We recorded weight and snout-vent length (SVL) of each lizard upon arrival. Lizards were housed in white opaque-walled terraria (40 x 60 cm, and 30 cm high) 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 (ca. 25–50 ° C) allowing thermoregulation within the preferred temperature range (Díaz and Cabezas-Díaz 2004). Lizards were fed crickets (*Acheta domesticus*) dusted with a commercial vitamin and calcium supplement. All cages were watered *ad libitum*. We monitored female's reproductive status on a daily basis to determine the laying date. When a female had laid a clutch, we removed it from the cage and we searched carefully for the eggs. Of 79 females, two had laid their clutches unburied and the eggs were slightly dehydrated when we found them, thus making their egg mass data inaccurate. Other 19 females laid clutches with at least one non-viable egg. Of these, 5 were composed entirely of non-viable eggs, and the remaining 14 had an average proportion of 0.45 non-viable eggs (range: 0.17-0.83). Females with non-viable eggs were smaller ($t_{77} = 2.0$, $P = 0.049$; mean ± se = 78.3 ± 0.7 *vs.* 80.4 ± 0.5 mm) and laid their clutches after a longer period of captivity ($t_{77} = 3.5$, $P < 0.001$; 18.3 ±1.6 *vs.*13.2 ± 0.7 days) than did their conspecifics whose eggs were all viable, but there were no significant differences between both groups in mean capture date ($t_{77} = 0.1$, $P = 0.918$, 21st May ± 2.0 *vs.* 22nd May ± 1.4 days). Only the 58 females that buried their clutches and laid all their eggs in good condition were considered in the subsequent analyses.

Eggs were counted, weighed, and individually placed in 150 ml closed plastic cups filled with ca. 35 g of moistened vermiculite. Eggs were incubated in individual plastic containers with moist vermiculite at 28 ºC. After hatching, juveniles were weighed, measured, and placed in individual terraria. In 2008, we performed a common garden experiment with two feeding treatments to determine post-natal growth rates. We used a split-clutch design in which half of the hatchlings from each clutch (9 clutches from low-elevation and 7 from high-elevation) were assigned to one of two possible treatments. In the first treatment (‘restricted food’), they were fed one cricket (*Acheta domesticus*) every other day, only if they had eaten the previous cricket (total food supply of 0.06 ± 0.002 g per week). In the second treatment (‘abundant food’), hatchlings were fed daily up to three crickets (total food supply of 0.18 ± 0.010 g per week). There were no initial differences between feeding treatments in SVL ($F_{1,28} = 0.17$; $P = 0.681$) or body mass ($F_{1,28} = 0.21$; $P = 0.651$). After all laboratory work was completed, all individuals were released at their sites of capture.

Growth rate estimates and statistical analyses

To estimate early post-natal growth rates, we measured all juveniles every four days until an age of ca. 28 days. We calculated size-specific and mass-specific growth rates (i.e. growth in SVL and gain in body mass, respectively) during the experiment using the formula $\ln(\text{measurement}_2/\text{measurement}_1)/(\text{date}_2 - \text{date}_1)$, where date_2 and date_1 are the dates at the end and the beginning of the experiment, respectively. These rates reflect the instantaneous proportionate increase in body size or body mass on a per-day basis (Sinervo 1990).

Unless otherwise stated, all statistical analyses were performed using general linear models (GLMs) after having checked the assumptions of parametric tests and, when necessary, log-transformed the corresponding variables. We analysed growth rates using the Variance Components & Mixed Model ANOVA/ANCOVA module of the statistical package Statistica 7.0. The mixed model, used for testing the significance of clutch (random factor), treatment, and population (fixed factors) on hatchling phenotypes, requires leaving the random effects independent of the fixed effects (Searle et al. 1992). This module uses Satterthwaite's method of denominator synthesis to find the linear combinations of sources of variation that serve as appropriate error terms for each effect. The degrees of freedom for the denominator mean square can be fractional rather than integer values, because fractions of variance components were used to synthesize error terms for significance testing. Data are given as mean ± se.

Results

Adult body size

Overall, body size (SVL) was similar for both sexes and populations, but the interaction between these factors was significant (two-way ANOVA: sex: $F_{1,91} = 0.89$; $P = 0.347$; site effect: $F_{1,91} = 1.45$; $P = 0.232$; sex x site interaction: $F_{1,91} = 4.82$; $P = 0.031$); high-elevation females were larger than low-elevation ones (high-elevation: 81.9 ± 0.7 mm; low-elevation = 79.3 ± 0.7 mm; $F_{1,56} = 6.50$, $P = 0.014$), and there were no significant differences between males (high-elevation = 79.5 ± 0.8 mm, low-elevation = 80.3 ± 0.9 mm; $F_{1,35} = 0.54$, $P = 0.466$). Female body condition did not differ between sites (ANCOVA with body mass as the dependent variable, site as factor, and SVL as the covariate; SVL: $F_{1,55} = 275.72$, $P < 0.001$; site: $F_{1,55} = 2.85$, $P = 0.097$).

Reproductive strategies

Low-elevation females laid smaller clutches, composed of larger eggs, than did high-elevation ones (ANOVAs; clutch size: $F_{1,56} = 16.2$, $P < 0.001$; egg mass: $F_{1,56} = 10.9$, $P = 0.002$; see Fig 1). These differences were not attributable to the larger size of high-elevation females, because they remained significant after controlling for the effects of SVL: despite the positive correlation between clutch size and SVL, high-elevation females still laid more eggs than did low-elevation females (ANCOVA: SVL effect: $F_{1,55}= 41.9$, $P < 0.001$; site effect: $F_{1,55}= 8.56$, $P = 0.005$; see Fig 1), and high elevation females produced relatively smaller eggs (SVL effect: $F_{1,55}= 0.01$, $P = 0.917$; site effect: $F_{1,55}= 9.76$, $P = 0.003$). The trade-off between clutch size and egg size was apparent ($r = -0.543$, $F_{1,56} = 23.41$, $P < 0.001$), even after controlling for differences between sites ($\beta = -0.421$, $F_{1,55}= 12.97$, $P < 0.001$). Although clutch mass was larger for high-elevation than for low-elevation females (Fig. 1: $F_{1,56} = 5.82$, $P = 0.019$), their overall reproductive investment was similar after controlling for the effects of SVL (ANCOVA; SVL effect: $F_{1,55} = 71.14$, $P < 0.001$; site effect: $F_{1,55} = 0.50$, $P = 0.483$; see Fig 1). These results suggest that although the larger clutch mass of high-elevation females was due to their bigger size, the allocation of this investment followed a different strategy (more but smaller eggs) that was largely independent of body size.

Low-elevation newborns were larger and heavier than high-elevation ones (SVL: 28.87 ± 0.21 mm and 27.68 ± 0.17 mm at low and high-elevation, respectively; $F_{1,55} = 18.79$, $P < 0.001$; body mass: 0.568 ± 0.010 g and 0.507 ± 0.012 g at low and high-elevation, respectively; $F_{1,55} = 14.94$, $P < 0.001$), confirming the pattern obtained in previous studies of these populations (Iraeta et al., 2006). Such differences remained significant after controlling for the effects of egg mass, especially in the case of SVL (site effect in ANCOVAs with egg mass as the covariate; hatchling SVL: $F_{1,54} = 14.0$, $P < 0.001$; hatchling mass; $F_{1,54} = 4.11$, $P = 0.047$). The body condition of newborns did not differ significantly between sites (ANCOVA with body mass as the dependent variable, site as the factor and SVL as the covariate; SVL effect: $F_{1,54} = 18.72$, $P < 0.001$; site effect: $F_{1,54} = 2.73$, $P = 0.104$).

Juvenile growth rates

A mixed-model ANOVA (with size-specific growth rate as the dependent variable, clutch as a random factor to control for possible familial effects, and treatment and site of origin as fixed factors) showed that low-elevation juveniles grew faster than high-elevation ones under both feeding treatments (mixed-model ANOVA; feeding treatment: $F_{1,9.52} = 41.10$, $P < 0.001$; site: $F_{1,10.99} = 12.16$, $P = 0.005$; treatment x site interaction: $F_{1,9.58} = 0.45$, $P = 0.519$; see Fig. 2). Neither clutch nor the clutch x treatment interaction had a significant effect on growth rates (both P's > 0.25). The between-sites difference in growth rates was not attributable to the mean number of crickets eaten during the 28-days experimental period, that was similar for both populations (mixed-model ANOVA with the variables in Table 1; feeding treatment: $F_{1,12.07} = 131.67$, $P < 0.001$; site: $F_{1,12.46} = 0.60$, $P = 0.453$; clutch: $F_{14,12.17} = 1.36$, $P = 0.290$; treatment x site interaction: $F_{1,11.79} = 3.71$, $P = 0.078$). However, the marginally non-significant treatment x site interaction indicates that whereas low-elevation juveniles ingested less crickets than high elevation ones when food was restricted ($F_{1,35} = 5.179$, $P = 0.029$), the opposite trend was true when food was abundant ($F_{1,30} = 2.36$, $P = 0.135$; see average values in Table 1). This could explain, at least in part, the lack of between-sites differences in the rate of body mass gain (mixed-model ANOVA with the variables in Table 1; feeding treatment: $F_{1,10.92} = 30.93$, $P < 0.001$; site: $F_{1,11.19} = 2.19$, $P = 0.167$; clutch: $F_{14,12.84} = 1.03$, $P = 0.484$; treatment x site interaction: $F_{1,10.93} = 0.91$, $P = 0.360$; clutch x treatment interaction: $F_{14,37} = 1.17$, $P = 0.340$), because low-elevation lizards, despite growing faster (SVL) than high-elevation ones, seemed to eat less under conditions of food scarcity, which suggests an energy-saving strategy that would not allow them to gain mass. Thus, low-elevation lizards increased their SVL, but not their body mass, significantly faster than high-elevation ones. However, body condition at the end of the experiment (i.e. 28 days after hatching) did not differ significantly between sites (mixed-model ANCOVA with body mass as the dependent variable and SVL as the covariate: SVL: $F_{1,21.93} = 111.91$, $P < 0.001$; feeding treatment: $F_{1,11.00} = 13.60$, $P = 0.004$; site: $F_{1,13.52} = 0.12$, $P = 0.7.34$; clutch: $F_{14,11.70} = 2.20$, $P = 0.091$; treatment x site interaction: $F_{1,8.47} = 2.5$, $P = 0.150$; clutch x treatment interaction: $F_{14,36} = 0.72$, $P = 0.744$).

Discussion

The main result of the current study was that the life-history strategies of two populations of a widespread Mediterranean lizard separated by a 600 m altitudinal gradient differed: high-elevation females were larger and laid more but smaller eggs than low-elevation ones, whereas low-elevation hatchlings were larger and had a faster growth rate under common garden conditions than high-elevation ones. Here, we suggest how these life-history traits can be integrated into adaptive patterns of altitudinal covariation, and we discuss their relevance as an example of countergradient variation. Because our study compares only two sites that differ in altitude, precipitation, type of vegetation, and arthropod abundance (Iraeta et al. 2006), inferences drawn from our results are, in a strict sense, restricted to the two sites used. However, despite this obvious limitation of our design, we believe that our two-sites comparison is representative of altitudinal effects in Mediterranean regions, and our results actually suggest a general pattern of countergradient variation that can be tested with future work.

Differences in size are common among populations of ectotherms living at different altitudes, but the sign of these differences varies among studies. In some species, high-elevation populations are larger than low-elevation ones (Chown and Klok 2003), whereas in other species the opposite pattern is true (Jin et al. 2007; Jin and Liu 2007). A possible explanation for the first pattern (i.e. larger body sizes in colder environments) is that as body mass increases, the surface area to volume ratio gets proportionally smaller, which contributes to reduce the rate of heat exchange with the environment. But this effect, although beneficial for endotherms, has a less clear role in the case of ectotherms inhabiting cool environments, which need to warm as fast as possible to compensate for low ambient temperatures and reduced basking opportunities (Díaz et al. 1996). As a consequence, the reason why some ectotherms conform to Bergmann's rule remains controversial (Sears and Angilletta 2004; Pincheira-Donoso et al. 2008). Another mechanism that could account for larger body sizes in colder environments is delayed maturation (Angilletta et al. 2004 a, b). Nevertheless, our two populations appeared to reach maturity at the same age, i.e. after their second winter. Another possibility, which seems likely in Mediterranean environments, is that precipitation, primary production, and hence food availability for insectivores tend to be higher in mountain ranges than in the surrounding xeric lowlands, allowing lizards to attain larger sizes (Iraeta et al. 2006). However, it is not clear why this difference applied only to females. Perhaps low-elevation males were forced to attain larger body sizes, despite low food availability, due to stronger sexual selection, which is suggested by their brighter coloration and higher number of femoral pores (Iraeta et al. 2011). Also, high-elevation females might be selected to grow larger in order to maximize fecundity (Braña 1996; Cox et al. 2003). This hypothesis is supported by our data, because the absolute reproductive investment of high-elevation females was larger than that of low-elevation females due to their larger size, and this may be an adaptive response. More importantly, this larger investment was partitioned into a higher number of smaller eggs (see below). Finally, another possibility is that the frequency of second clutches could be higher at lower elevation (Díaz et al. 2007). This would produce the deviation of resources from growth to reproduction, which combined with indeterminate growth would lead to smaller body size at lower elevation.

Concerning altitudinal differences in the allocation of resources to the first clutch, low-elevation females traded larger clutches for larger offspring. Interestingly, this is in contrast with several studies of other lizard species in which females produced fewer but larger offspring at higher elevation (Rohr 1997; Jin and Liu 2007). In our system, low-elevation hatchlings were larger and heavier than high-elevation ones, partly as a consequence of the larger per-offspring investment of their mothers, especially in the case of hatchling mass. However, differences in SVL, unlike those in hatchling mass, remained highly significant after controlling for the effects of egg mass. Thus, large propagule size seems to be part of the reproductive strategy favoured by selection in low-elevation females, beyond the survival advantage of large juveniles that has been previously reported for both populations (Civantos and Forsman 2000, Iraeta et al. 2008).

Moreover, differences in growth rates supported the importance of being large at low-elevation. According to the results of our post-natal growth rate experiment, juveniles from low-elevation origin grew faster than high-elevation ones under both feeding treatments, and there was no interaction between these two factors, which suggests that faster growth rates are an intrinsic characteristic of low-elevation lizards. Furthermore, our results indicate that between-population differences in growth rates cannot simply be attributed to different levels of food intake, because the mean number of crickets eaten during the 28-days period of the experiment was similar for both populations. However, when food was restricted low-elevation juveniles ate less frequently than high-elevation ones (which might explain, at least in part, the lack of a significant between-sites difference in the rate of mass gain), whereas the opposite trend was true (though not significantly so) under conditions of food abundance. These results suggest that the modulation of energy savings may be important for maintaining growth rates, especially under food shortage. Metabolic expenditure is expected to be lower in captivity (where newborns are confined to small terraria with no predators and readily accesible heat, food and water) than in the field. Accordingly, only the lizards that grew most rapidly in the field (those of low-elevation origin in the high-elevation environment; Iraeta et al. 2006) managed to grow faster than the ones that grew at a slowest rate in the laboratory (those of high-elevation origin under the restricted feeding treatment), confirming the size advantage of captive-bred juveniles relative to wild-born ones (Santos et al. 2009).

It could be also argued that the similarity of the common garden conditions experienced by eggs or hatchlings to either of their original habitats could have a strong influence on the results due to local adaptation. Unfortunately, there are no data about incubation conditions in the field, because no natural nests have ever been found for this species. However, the soil and within-shrub environments –i.e., the two most likely locations for nest sites– buffer altitudinal variation in temperature, and nearly all temperatures previously registered for these habitats at both sites are well below our lab incubation temperature (unpublished data). Concerning the growth rate experiment, the thermal conditions in the lab were different enough from the thermal environment at both sites to make local adaptation an unlikely explanation of the differences found. Moreover, the similar results obtained in our previous reciprocal transplant experiment also suggest that such differences are population-specific and independent of the growing environment, since low-elevation lizards grew faster than high-elevation ones at both sites (Iraeta et al. 2006).

More importantly, we have some evidence (Iraeta et al. 2008) of the ability of low-elevation juveniles to reduce activity (and, presumably, energy expenditure) more readily than high-elevation ones in response to food scarcity. Thus, in a year of severe drought activity was higher at high-elevation than at low-elevation. Moreover, only the smallest juveniles were recaptured in September (i.e. when food availability is lowest) at low-elevation, because larger hatchlings remained inactive and were not recaptured until the next spring (Iraeta et al. 2008). This suggests that inactivity would be advantageous at low-elevation except for the smallest juveniles (that must acquire sufficient reserves prior to hibernation). However, only juveniles of low-elevation origin were able to modulate their activity levels in response to both food availability and their own body size (Iraeta et al. 2008).

Remarkably, low-elevation juveniles, despite their intrinsic capacity for fast growth, did not manage to reveal such capacity at their location of origin due to food scarcity during the post-natal period (Iraeta et al. 2006). Similar results were obtained with the phrynosomatid lizard *Sceloporus undulatus* (Ferguson and Talent 1993), in which the population that grew faster in the lab failed to do so in the field probably due to suboptimal growth conditions. Previous examples of growth rate variation along bioclimatic gradients support the hypothesis that populations living at cooler sites should either grow faster (Merilä et al. 2000; Caley and Schwarzkopf 2004; Conover et al. 2009), or compensate their slower growth rate with larger eggs and hatchlings and delayed maturity (Berven 1982a). However, our study system exemplifies just the opposite pattern: despite better thermal quality at lower elevation (Díaz 1997), lower food availability at xeric lowlands seems to override temperature as a limiting factor that shapes the variation of growth rates along Mediterranean altitudinal gradients.

To get an idea of the temporal constraints associated with growth, we can use our data to estimate the time needed to reach adult size at both sites. Assuming that SVL at hatching and post-natal growth rates are reliable estimates of population trends, it is easy to show that if Q equals $\ln(\mathrm{SVL}_{\text{adult female}} / \mathrm{SVL}_{\text{hatchling}})$, GR is the size-specific growth rate, and t is the time needed by females to grow from SVL at hatching to mean adult SVL, then $\mathrm{GR}_{\text{site 1}} / \mathrm{GR}_{\text{site 2}} = (Q_{\text{site 1}} / Q_{\text{site 2}}) \times (t_{\text{site 2}} / t_{\text{site 1}})$. Given the mean values of hatchling size and female body size in both populations, the ratio between the highest and lowest growth rates should be about 1.074 times the ratio between the longest and shortest time needed to reach adult SVL. Thus, the time needed to grow to adult size should be 1.28 times longer at higher altitude according to our lab data (both feeding treatments pooled), and 1.64 times longer at lower altitude according to field growth rates under severe summer drought (Iraeta et al. 2006). Clearly, real values must lie between these limits. More generally, we can conclude that field growth rates should increase with altitude in Mediterranean mountain ranges to compensate for the initial small size of high-elevation lizards, their lower intrinsic growth rates, and the lower thermal quality of their habitat (Díaz 1997).

In summary, all population differences reported in this study –smaller females that lay smaller clutches of larger eggs, larger hatchlings and juveniles, and higher potential growth rates at higher altitude– provide a clear example of countergradient variation (Conover et al. 2009), because the genotypes that apparently encode for fast growth and large size were found in a food-poor environment that caused slow growth and small size (Iraeta et al. 2006). In the long run, high-elevation females would attain larger sizes than low-elevation ones due to high environmental production in mountain ranges that combine mild temperatures with higher precipitation levels than in surrounding lowlands. This should allow them to lay more eggs (Fitch 1970; Pincheira-Donoso and Tregenza 2011) and have higher reproductive output, also because their allocation strategy traded off larger hatchlings for larger clutches, leading to higher lizard abundance at higher altitude (Díaz 1997). It is interesting to speculate that, because lizards must have survived the ice ages by descending and ascending mountains (Hewitt 1999), the climatic conditions now prevailing in mountain ranges must have been those present in the Mediterranean valleys that served as refuges during the glacial maxima. If so, it can be assumed that the life-history strategy of high-elevation lizards can be regarded as the ancestral one, and that the traits that characterize low-elevation females (large eggs and hatchlings, and high potential post-natal growth rates) evolved as adaptations to ensure offspring survival under the selective pressures posed by the severe conditions of Mediterranean xeric lowlands.

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Table 1. Mean (± 1 SE) size- and mass-specific growth rates (days^{-1}), and number of crickets eaten, for two populations of *P. algirus* under two treatments of food availability. See text for details.

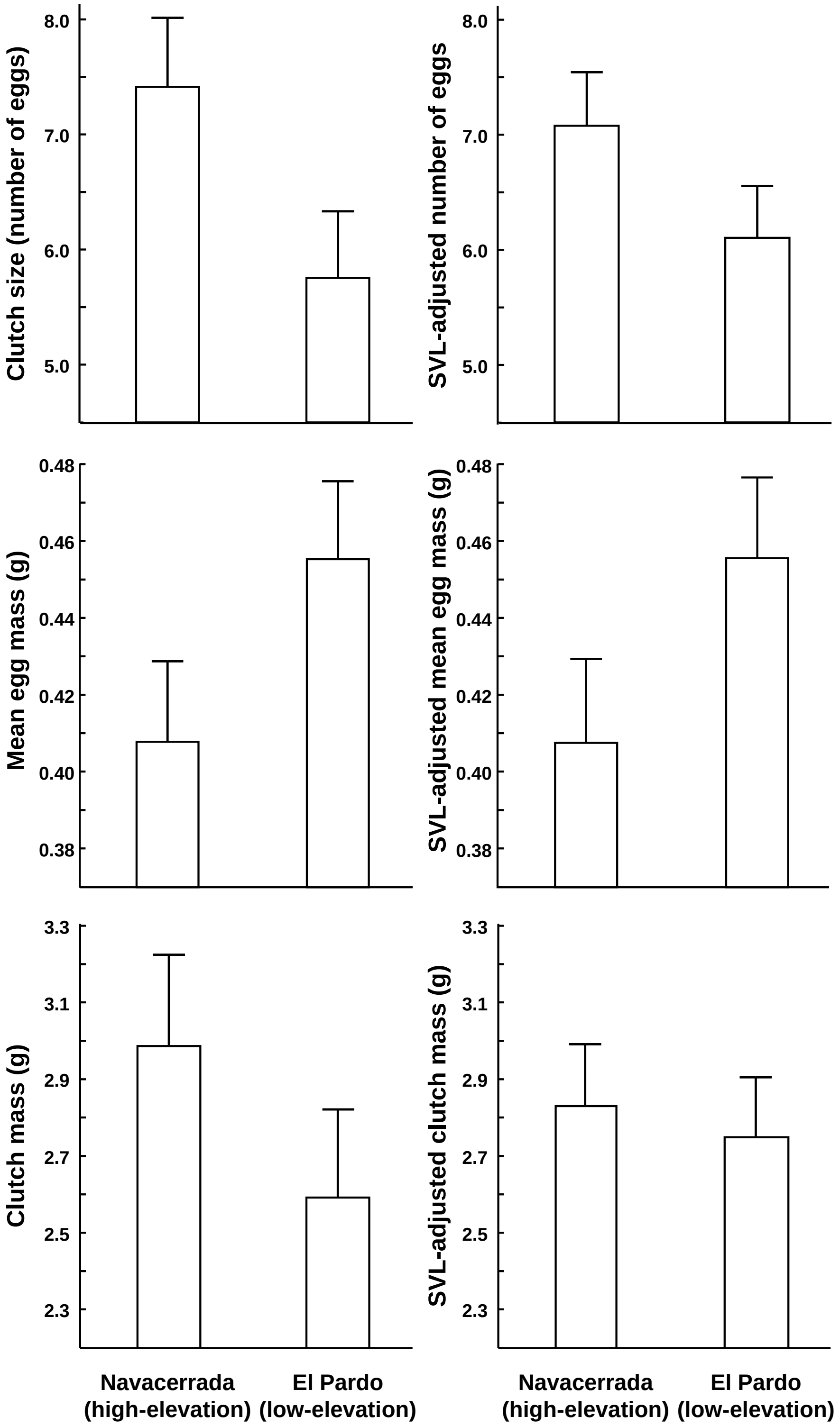
Feeding treatment	Site of origin	Size specific growth rate (days^{-1})	Mass specific growth rate (days^{-1})	Number of crickets eaten	N
Restricted	High-elevation	0.00314 ± 0.00016	-0.00076 ± 0.00078	11.4 ± 0.5	17
Restricted	Low-elevation	0.00376 ± 0.00013	0.00027 ± 0.00081	9.9 ± 0.5	20
Abundant	High-elevation	0.00410 ± 0.00026	0.00516 ± 0.00214	29.1 ± 2.9	15
Abundant	Low-elevation	0.00486 ± 0.00019	0.00797 ± 0.00079	34.5 ± 2.1	17

Figure captions

Figure 1. Population means (with 0.95 CI) for clutch size, mean egg mass, and clutch mass, either unweighted (left) or adjusted for female SVL (right).

Figure 2. Size-specific growth rates of siblings reared under abundant and restricted feeding treatments in a common garden experiment. Each line represents a clutch.

Fig. 1


Clutch size (number of eggs)
8.0
7.0
6.0
5.0
SVL-adjusted number of eggs
8.0
7.0
6.0
5.0
Mean egg mass (g)
0.48
0.46
0.44
0.42
0.40
0.38
SVL-adjusted mean egg mass (g)
0.48
0.46
0.44
0.42
0.40
0.38
Clutch mass (g)
3.3
3.1
2.9
2.7
2.5
2.3
SVL-adjusted clutch mass (g)
3.3
3.1
2.9
2.7
2.5
2.3
Navacerrada (high-elevation)
El Pardo (low-elevation)
Navacerrada (high-elevation)
El Pardo (low-elevation)

616 Fig. 2

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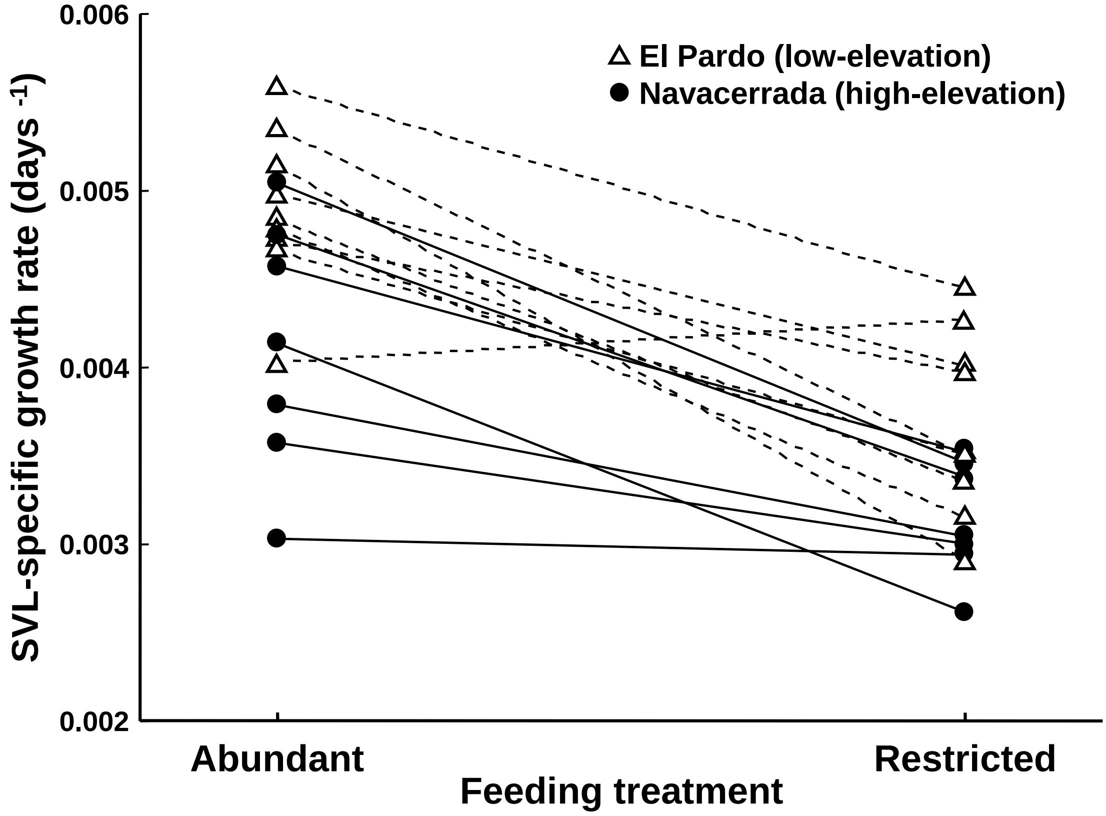

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