

Altitudinally divergent adult phenotypes in Iberian wall lizards are not driven by egg differences or hatchling growth rates

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Abstract The interplay between ecological conditions and life histories has been widely acknowledged in vertebrates, particularly in lizards. Environmental conditions may exert different selective pressures and produce divergent phenotypes even in geographically and genetically close populations. The Iberian wall lizard constitutes a perfect model organism as it is considered a species complex with a complicated evolutionary history. Here, we focus on two proximate populations in which we examined adult morphology and reproductive investment of wild-caught lizards along a 500-m altitudinal gradient with contrasting environmental conditions, where adults show marked morphological differences in spite of being closely related. Also, we performed a common garden experiment to examine embryonic and hatchling growth. We focused on reproductive investment per clutch, incubation time, egg size, morphology and growth rate of hatchlings. Results showed clutch size differences between populations that were independent of the larger body size of highland females. However, there were no egg morphological differences between populations, except for egg width, and this difference disappeared after controlling for female body size. Hatchling lizards from both populations did not differ in morphology. Moreover, we did not observe differences between populations or sexes in hatchling growth. Overall, we provide evidence that the differences in adult body size and clutch size are not driven by size at hatching which is not contributed

to by egg size, nor are intrinsic hatchling growth rates associated with the environmental conditions experienced in our common garden experiment, suggesting that adult phenotypes are not the result of intrinsic differences between populations.

Keywords Common garden · Growth · Lacertids · Phenotypic plasticity · *Podarcis hispanicus*

Introduction

A central tenet of evolutionary biology is that natural selection acting on heritable phenotypic variation will result in adaptation and differentiation among local populations inhabiting environments with different selective regimes (Edwards and Kot 1995; Endler 1977; Herrel et al. 2006; Linhart and Grant 1996). Life histories are a crucial part of the ecology of species and play a central role in evolutionary theory (Stearns 2000; Du et al. 2013). Life histories show variation at three levels: within populations, among populations of the same species, or between species (Bauwens and Damme 1995). This variation in life history phenotypes can originate from different sources. In some cases, adaptive changes may be environmentally induced by extrinsic factors (phenotypic plasticity) (Losos et al. 2000; Via and Lande 1985), in others they are mediated by intrinsic differences linked to geographically variable conditions (local adaptation) (Travis 1994); or a combination of both (Sears and Angilletta 2003). Regardless, environmental variables are of utmost importance to understanding life history variation in ectotherms, and lizards in particular (Adolph and Porter 1993). For instance, temperature, humidity and food availability may exert different selective pressures for the maximization of reproductive tactics

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(Boyce 1979; Bonnet et al. 2001; Angilletta et al. 2006). Thus, life histories vary widely between species and populations (Roff 1992; Stearns 1992; Du et al. 2005).

As a major component of life histories, growth patterns have profound fitness consequences through age and size at maturity and fecundity and/or adult survival (Roff 1992; Stearns 1992). Therefore, growth rates themselves can be honed by natural selection and adjusted to the ecological context (Adolph and Porter 1993; Du et al. 2012). Geographic variation in growth has complex sources, depending on the interplay among resource availability and the efficiency with which an organism can assimilate energy (Congdon 1989; Ferguson and Talent 1993; Niewiarowski and Roosenburg 1993; Arendt 1997).

Because these factors change with altitude, altitudinal variation in life histories, including growth rates, has been commonly studied in lizards (Niewiarowski 2001; Caley and Schwarzkopf 2004; Telemeco et al. 2010). Most studies assume that environmental conditions (temperature and activity period) should be more restrictive as altitude increases (Olsson and Shine 1997; Sears 2005). However, environmental restrictions for ectotherms in Mediterranean mountains pose different problems than in temperate areas. Drought becomes less restrictive as altitude increases due to milder temperatures and higher precipitation, which increases productivity (Nahal 1981; Iraeta et al. 2012). Thus, because restrictions differ altitudinally between Mediterranean and temperate areas, the study of body size variation in the Mediterranean region from a life history perspective could improve our understanding of altitudinal and latitudinal trends (e.g., Bergmann's clines).

The Iberian wall lizard, *Podarcis hispanicus* (Steindachner 1870), is an heliothermic, insectivorous and small diurnal lacertid lizard that is variable in both morphology and life history characteristics (Pérez-Mellado 1998). It is distributed throughout the Iberian Peninsula, and North-West Africa (Guillaume 1987), associated with rock cliffs and boulders, and even lives in close association with human constructions (Van Damme et al. 1997). Recent molecular studies revealed the complex evolutionary history of *P. hispanicus*, considered as a species complex with at least five monophyletic lineages and some well-recognized species, and suggest the existence of speciation within taxa previously considered to be conspecific (Guillaume 1987; Harris and Sa-Sousa 2002; Sá-Sousa et al. 2002; Pinho et al. 2007; Kaliontzopoulou et al. 2011; Carretero 2008; Renoult et al. 2009; Geniez et al. 2014). Even morphological analysis reveals high levels of variation both within and between mitochondrial lineages, and clear diagnostic characters are lacking (Kaliontzopoulou et al. 2012).

Here, we focus on two proximate *P. hispanicus* populations in which we examined adult morphology and reproductive investment of wild-caught lizards. Also we report

the results of a common garden experiment to examine embryonic and hatchling growth. These two populations are separated along a 500-m altitudinal gradient without clear geographical barriers but with contrasting environmental conditions. We selected these two populations because lizards differed in morphology, coloration and chemical sexual signals, in spite of being genetically closely related (Martin and López 2006; Gabirot et al. 2012, 2013). Indeed, the two populations studied here belong to the *P. hispanicus* type 1, which has just been named *Podarcis guadarramae* by Geniez et al. (2014). Specifically, in these populations, lizards from higher altitudes attain a larger body and head size and have more femoral pores (Gabirot et al. 2012). We do not know whether this pattern of high morphological variability among populations is caused by proximate effects of local conditions or local adaptation, and this constitutes a crucial question in adaptation research (Berven and Gill 1983). We hypothesized that, if divergent adult phenotypes are the result of either genetic and/or maternal differences among populations (intrinsic factors), we would expect size at hatching and growth rate differences under a common environment. On the other hand, if lizards plastically respond to the contrasting climatic conditions between Mediterranean highland and lowland sites (extrinsic factors), as has been previously demonstrated in other lacertid lizards (Iraeta et al. 2006), we would not find differences in embryonic development and size at hatching. Moreover, growth rates of hatchlings from both populations should not differ in the laboratory when controlling food, temperature and humidity in a common garden experiment.

Materials and methods

Study sites

During April and May 2011 and 2012 we captured male and gravid female lizards in two proximate populations by noosing in the Guadarrama Mountains (Central Spain). Gravidity was assessed by ventral palpation; all the females found were gravid. These population are separated 6 km by air at different altitudinal ranges. The 'lowland' locality is located in an oak forest (La Dehesa de la Golondrina) near the village of Cercedilla (40°44'N, 04°02'W; 1,250 m altitude), where lizards can be found on granite rocky outcrops inside the forest. This locality has a mean annual temperature of 10.9 °C and a mean annual rainfall of 674 mm (data from Embalse de Navacerrada meteorological station, less than 1 km from the study site). The 'highland' locality is found in the upper part of a mountain valley (Fuenfría) (40°47'N, 04°03'W; 1,750 m altitude) occupying granite rock walls and rock piles at the edge of a pine forest. In this

population, mean annual temperature is 6.2 °C, and mean annual precipitation is 1,170 mm (data from Puerto de Navacerrada meteorological station, 3 km from the study site).

Adult husbandry and morphology

Immediately after capture, individuals were transported to El Ventorrillo field station facilities about 5 km away from the capture localities. Lizards from each population were kept separately in two identical climatic chambers (Ibercex V-450-D walk-in chambers; ASL, Madrid) where temperature (diurnal = 21 °C, nocturnal = 15 °C) and photoperiod (12 h:12 h, light:dark) were easily controlled automatically. Adult lizards from the two populations were maintained separately to prevent the transmission of diseases and parasites between populations. Thus, the factors population of origin and adult husbandry chamber could not be initially partitioned. However, because gravid females were kept in the chambers for just a few days (mean + SE = 12.3 ± 0.6 days), and because the two chambers and the conditions inside were identical, we were confident that it was very unlikely that any differences between populations resulted from potential uncontrolled small differences in captivity conditions. Lizards were individually housed in plastic terraria (40 × 30 × 25 cm) filled with a moistened coconut fiber substrate and provided with a water bowl and a brick (24 × 11 × 8 cm) that allowed shelter and climbing opportunities. A 50-W halogen lamp was suspended over one end of the terrarium providing a diurnal temperature gradient (21–45 °C) allowing thermoregulation of lizards within the preferred temperature range of this species [34.4 °C (Bauwens and Damme 1995)]. In addition, a fluorescent bulb on each shelf provided ambient lighting mimicking the natural photoperiod, and mercury vapor bulbs (Exoterra Solar Glow 125 W) provided ultraviolet radiation during 1.5 h per day (from 1400 to 1530 hours). Adult lizards were watered daily, and fed crickets (*Acheta domesticus*) and mealworms (*Tenebrio molitor*) ad libitum, dusted with a commercial vitamin and calcium supplement.

We measured body size of adult lizards using a ruler [snout-vent length (SVL) to the nearest 1 mm]. We used a digital caliper to measure (to the nearest 0.05 mm) the following morphological variables: 'head length', the distance between the tip of the snout and the posterior side of the parietal scales; 'head width', the greatest distance between the external sides of the parietal scales; 'head height', the greatest distance from the highest portion of the head to the bottom of the lower jaw. 'Femoral length' was the mean distance from the hip to the knee measured in both hind limbs. We used general linear models (GLMs) to analyze whether these morphological variables (log transformed) differed between population of origin and sex as fixed effects.

Reproductive investment

Cages were carefully checked for the presence of eggs twice daily. In all cases females laid eggs in the wet substrate under the brick or the water bowl. Females laid all their eggs in a single day, except one female from the lowland population that laid one egg and then two more at an interval of 3 days. We measured immediately clutch size (number of eggs), egg size (length and width, using a digital caliper to the nearest 0.01 mm) and egg weight (using a digital scale to the nearest 0.01 g). Egg volume was calculated using the equation for volume of an ellipsoid, $V = (4/3)\pi ab^2$, where a is half the longest axis and b is half the shortest axis (Mayhew 1963). Clutch volume was calculated as the product of mean egg volume and clutch size. We calculated relative clutch size of each female (i.e., clutch size adjusted for female SVL) using the residuals of the regression of log clutch size on log female SVL. Eggs were individually placed in 60-mL closed plastic cups filled with 10 g of moistened perlite (10 g perlite:10 g water) and transferred to an incubator at 27.5 °C (IRE-160; 94 × 60 × 60 cm; Raypa, Barcelona). Eggs were randomly distributed in the incubator and shelves rotated each week to control for possible position effects (Telemeco et al. 2010). Hence, we standardized incubation conditions to examine embryonic development as a first step in our common garden experiment during the 2011 breeding season.

When incubation was about to end, we searched daily for newborns, and the duration of incubation was noted. Laying date was referred to 1 May, and thus transformed into a continuous variable like Julian days (Warner and Shine 2009). Of 74 females 12 laid clutches with at least one infertile egg and no female laid a clutch composed entirely of infertile eggs. Infertile clutches were discarded so only the remaining 62 females were considered in subsequent analyses. Deformed hatchlings were excluded from the analyses. Adult lizards were returned to their capture sites in late June, and juveniles released to their mothers' capture sites in November prior to winter.

We focused our analysis on first clutches as they potentially reflect the field conditions (e.g., food availability) experienced by females in the wild before we captured them, minimizing captivity effects in our experiment. To test for differences between populations in mean egg size, clutch size, clutch mass and clutch volume, we analyzed these variables as dependent variables in GLMs, with the population of origin as a fixed effect. To test whether there were size-independent mean egg size and clutch size differences between the populations, we also ran similar GLMs but with female body size added as a covariate.

Hatchling husbandry, morphology and growth

Immediately after hatching, juveniles were measured in a fashion identical to adults (see above) and their body mass determined with a digital scale (to the nearest 0.01 g). Body condition was estimated using the residuals of the regression of log body mass on log SVL at hatching. Thereafter, we standardized environmental conditions in the laboratory to examine post-hatching growth in a common garden experiment. Hatchling lizards from both populations were kept in the same climatic chamber under identical environmental conditions as adults (see above), but fed smaller prey, such as pinhead crickets (*Acheta domesticus*), fruit flies (*Drosophila hydei* and *Drosophila melanogaster*) and small waxworms (*Galleria mellonella*). Hatchling cages were rotated along shelf rows every 3 days and among shelves each week to control for position effects (Telemeco et al. 2010). A subset of hatchlings ($n = 49$) was measured again 130 days after hatching to get a rough estimate of juvenile growth prior to the onset of their first winter. The size-specific (SVL), mass-specific, head and femoral length growth between the hatching date and 130 days of age were expressed as the proportionate increase in size or mass [$\ln(\text{size at the end}/\text{size at the beginning})/(\text{end date} - \text{initial date})$], measured in units of days^{-1} (Iraeta et al. 2006, 2012). Sex was assessed, and confirmed several times during the experiment, by the highly developed femoral pores in males compared to females.

We analyzed growth rates with a nested design in GLM using the statistical package Statistica 8.0 (StatSoft, Tulsa, OK). The mixed model tested the significance of clutch (female identity as a random factor, nested in population) to control for possible familial effects, sex and population (fixed factors) on hatchling phenotypes. It used Satterthwaite's method of denominator synthesis and required leaving the random effects independent of the fixed effects (Searle et al. 1992). As fractions of variance components were used to synthesize error terms for significance testing, the df for the denominator mean square can be fractional rather than integer values (Iraeta et al. 2012). All variables were log transformed prior to analysis to meet the requirements of parametric tests.

Results

Adult morphology

Overall, highland lizards were bigger (GLM—population, $F_{1,123} = 46.8, P < 0.001$; sex, $F_{1,123} = 8.3, P = 0.005$; sex \times population, $F_{1,123} = 0.1, P = 0.709$), had more robust heads (GLMs for head length, head width and head height—population, all $P_s < 0.001$; sex, all $P_s < 0.001$; sex \times population, all $P_s > 0.163$) and had longer femora than those from the lowland population (GLM—population, $F_{1,123} = 87.45, P < 0.001$; sex, $F_{1,123} = 139.03, P < 0.001$; sex \times population, $F_{1,123} = 0.45, P = 0.506$), with independence of sex, as this was for males compared to females in both populations. These differences were not caused by a larger body length of highland lizards, as adding SVL as a covariate did not change significance, which indicated that highland lizards, and males from both populations, were also more robust (GLMs for all variables with SVL as a covariate—SVL, all $P_s < 0.001$; population, all $P_s < 0.002$; sex, all $P_s < 0.001$; sex \times population, $P_s > 0.094$; Table 1).

Reproductive investment

There were no significant differences between populations in laying dates (highland, mean \pm SE = 8 June \pm 2.1 days; lowland, 12 June \pm 2.1 days; GLM, $F_{1,60} = 2.04, P = 0.159$). The egg incubation period did not differ between populations (GLM, $F_{1,60} = 0.01, P = 0.946$; Fig. 1). Clutch size was larger in the highland than in lowland population (GLM, $F_{1,60} = 24.96, P < 0.001$; Table 2). However clutch size differences were not driven by the larger SVL of highland females (GLM—SVL, $F_{1,59} = 2.48, P = 0.121$; population, $F_{1,59} = 5.78, P = 0.019$; Table 2) despite clutch size being positively correlated with female SVL ($r = 0.51, F_{1,60} = 20.63, P < 0.001$) even after controlling for differences between populations ($\beta = 0.57, F_{1,59} = 14.03, P < 0.001$). Clutch weight and clutch volume were greater in the highland population (GLMs—clutch weight, $F_{1,60} = 28.13, P < 0.001$; clutch volume,

Table 1 Mean (\pm 1 SE) values for adult morphological variables in highland and lowland *Podarcis hispanicus* lizard populations

	Highland		Lowland	
	Females $n = 45$	Males $n = 20$	Females $n = 45$	Males $n = 17$
Snout–vent length (cm)	6.3 \pm 0.1	6.7 \pm 0.1	5.7 \pm 0.1	5.9 \pm 0.1
Head length (mm)	11.69 \pm 0.13	14.28 \pm 0.19	10.63 \pm 0.13	12.71 \pm 0.20
Head width (mm)	7.33 \pm 0.08	9.19 \pm 0.12	6.68 \pm 0.08	8.06 \pm 0.13
Head height (mm)	4.94 \pm 0.06	6.13 \pm 0.09	4.39 \pm 0.06	5.23 \pm 0.09
Femoral length (mm)	9.69 \pm 0.12	11.98 \pm 0.18	8.37 \pm 0.12	10.16 \pm 0.19

Fig. 1 Population means (± 1 SE) for clutch size (a), mean incubation time (b), mean egg volume (c) and mean egg mass (d) of *Podarcis hispanicus*

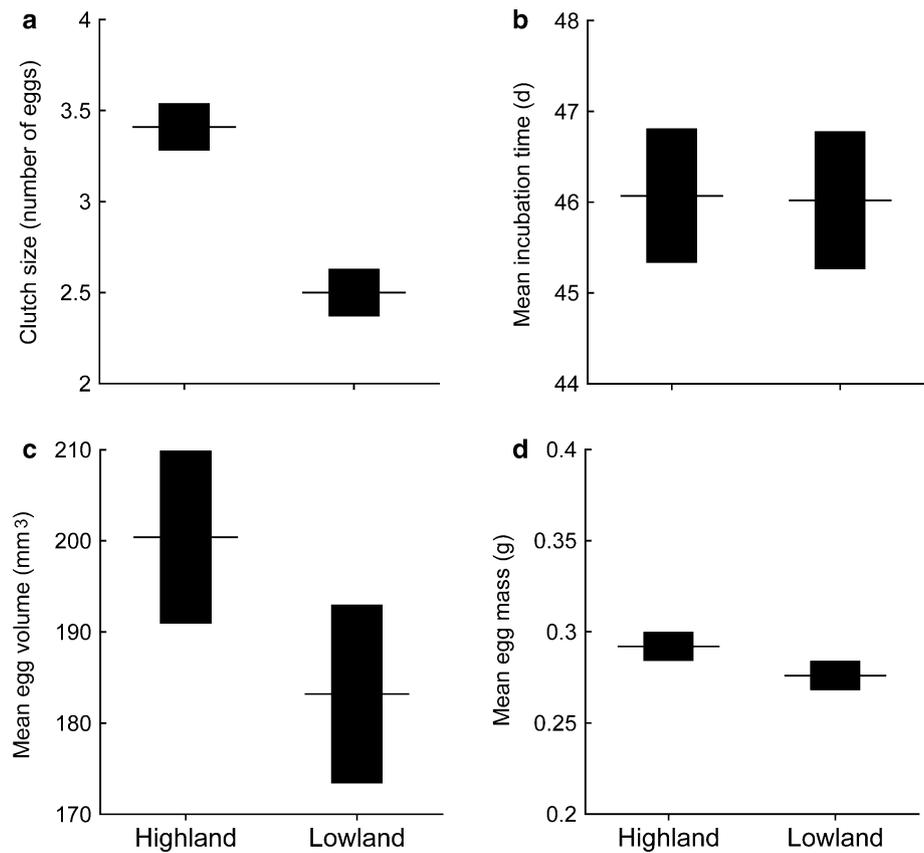


Table 2 Mean (± 1 SE) values for clutch and hatchling characteristics in highland and lowland *Podarcis hispanicus* lizard populations (n = number of clutches)

	Highland ($n = 32$)	Lowland ($n = 30$)
Eggs		
Clutch weight (g)	0.99 \pm 0.04	0.69 \pm 0.04
Clutch volume (mm ³)	688.54 \pm 37.51	450.68 \pm 38.74
Egg length (mm)	11.15 \pm 0.17	11.34 \pm 0.18
Egg width (mm)	6.72 \pm 0.08	6.49 \pm 0.08
Hatchlings		
Mass (g)	0.39 \pm 0.01	0.38 \pm 0.01
Snout–vent length (cm)	2.86 \pm 0.04	2.90 \pm 0.04
Body condition (g cm ⁻¹)	0.011 \pm 0.008	-0.011 \pm 0.008
Head length (mm)	7.07 \pm 0.05	7.10 \pm 0.05
Head width (mm)	4.00 \pm 0.03	4.01 \pm 0.03
Head height (mm)	2.87 \pm 0.02	2.79 \pm 0.02
Femoral length (mm)	4.36 \pm 0.06	4.41 \pm 0.07

$F_{1,60} = 20.47$, $P < 0.001$). Both clutch weight and clutch volume remained different between populations after controlling for female SVL (GLMs, clutch weight, SVL— $F_{1,59} = 5.64$, $P = 0.021$; population, $F_{1,59} = 4.59$, $P = 0.036$; clutch volume, SVL, $F_{1,59} = 1.12$, $P = 0.294$; population, $F_{1,59} = 15.36$, $P < 0.001$; Table 2).

Mean egg length did not differ between populations (GLM, $F_{1,60} = 0.51$, $P = 0.478$; Table 2) but the eggs of highland lizards were wider (GLM, $F_{1,60} = 4.09$, $P = 0.048$; Table 2), which seemed to be a direct effect of a large female body size in this population (GLM—SVL, $F_{1,59} = 2.50$, $P = 0.119$; population, $F_{1,59} = 0.09$, $P = 0.769$). Overall, there were not significant differences between populations in mean egg mass (GLM, $F_{1,60} = 2.12$, $P = 0.150$; Fig. 1) or mean egg volume (GLM, $F_{1,60} = 2.00$, $P = 0.162$; Fig. 1).

Hatchling morphology and growth

Lizards from both populations showed a high hatching rate (lowland, 90.7 %; highland, 91.7 %). Deformed newborns were extremely rare (three newborns from the lowland and two from the highland site). Deformities were localized in the tail (shorter with a kinked or curved tip) and/or the hands and feet, affecting finger or toe number and position.

Hatchling lizards from both populations were morphologically similar in body size (GLMs on hatchling SVL—population, $F_{1,76} = 1.38$, $P = 0.244$; sex, $F_{1,76} = 17.87$, $P < 0.001$; population \times sex, $F_{1,76} = 0.27$, $P = 0.606$; see clutch averaged values in Table 2), body mass (GLM—population, $F_{1,76} = 2.03$, $P = 0.160$; sex, $F_{1,76} = 1.61$, $P = 0.209$; population \times sex, $F_{1,76} = 0.60$, $P = 0.441$),

Table 3 Mean (± 1 SE) growth rates (days⁻¹) for the morphological variables measured, for hatchlings from two populations of *P. hispanicus* lizards reared under a common garden experiment

	Highland		Lowland	
	Females (<i>n</i> = 14)	Males (<i>n</i> = 13)	Females (<i>n</i> = 12)	Males (<i>n</i> = 10)
Mass-specific growth (days ⁻¹)	-0.00371 \pm 0.00081	-0.00331 \pm 0.00084	-0.00334 \pm 0.00087	-0.00399 \pm 0.00095
Size-specific growth (days ⁻¹)	0.00053 \pm 0.00051	0.00043 \pm 0.00052	0.00036 \pm 0.00055	0.00120 \pm 0.00060
Head length growth (days ⁻¹)	0.00342 \pm 0.00064	0.00354 \pm 0.00067	0.00278 \pm 0.00069	0.00362 \pm 0.00076
Head width growth (days ⁻¹)	0.00297 \pm 0.00044	0.00336 \pm 0.00046	0.00316 \pm 0.00048	0.00294 \pm 0.00053
Head height growth (days ⁻¹)	-0.00055 \pm 0.00073	-0.00048 \pm 0.00075	0.00016 \pm 0.00079	-0.00056 \pm 0.00086
Femoral growth (days ⁻¹)	0.00604 \pm 0.00037	0.00633 \pm 0.00039	0.00631 \pm 0.00040	0.00668 \pm 0.00044

Table 4 Effect of population, sex, clutch, and population \times sex and sex \times clutch interactions (mixed-model general linear model) on growth for six morphological variables of hatchlings from two populations of *P. hispanicus* lizards reared under a common garden experiment

	Population	Sex	Clutch	Population \times sex
Mass-specific growth	$F_{1,31.27} = 1.55$ $P = 0.222$	$F_{1,19} = 0.07$ $P = 0.797$	$F_{26,19} = 2.46$ $P = 0.024$	$F_{1,19} = 0.99$ $P = 0.333$
Size-specific growth	$F_{1,31.80} = 0.41$ $P = 0.526$	$F_{1,19} = 0.04$ $P = 0.847$	$F_{26,19} = 2.22$ $P = 0.038$	$F_{1,19} = 0.01$ $P = 0.975$
Head length growth	$F_{1,30.88} = 1.58$ $P = 0.218$	$F_{1,19} = 0.13$ $P = 0.718$	$F_{26,19} = 2.67$ $P = 0.016$	$F_{1,19} = 0.11$ $P = 0.742$
Head width growth	$F_{1,36.05} = 0.71$ $P = 0.404$	$F_{1,19} = 0.06$ $P = 0.807$	$F_{26,19} = 1.21$ $P = 0.341$	$F_{1,19} = 0.75$ $P = 0.398$
Head height growth	$F_{1,36.02} = 0.15$ $P = 0.704$	$F_{1,19} = 0.19$ $P = 0.664$	$F_{26,19} = 1.21$ $P = 0.338$	$F_{1,19} = 0.95$ $P = 0.343$
Femoral length growth	$F_{1,32.04} = 0.01$ $P = 0.964$	$F_{1,19} = 0.14$ $P = 0.708$	$F_{26,19} = 2.13$ $P = 0.047$	$F_{1,19} = 0.53$ $P = 0.475$

body condition (GLM—population, $F_{1,76} = 0.89$, $P = 0.349$; sex, $F_{1,76} = 5.55$, $P = 0.021$; population \times sex, $F_{1,76} = 2.79$, $P = 0.099$), head shape (GLMs for head length, head width and head height—population, all P s > 0.053 ; sex, all P s > 0.155 ; sex \times population, all P s > 0.304) and femoral length (GLM—population, $F_{1,76} = 0.28$, $P = 0.601$; sex, $F_{1,76} = 4.28$, $P = 0.042$; population \times sex, $F_{1,76} = 0.33$, $P = 0.253$). Hatchling females were larger and had longer femora but lower body condition than males (see the previous GLMs). However, after controlling for hatchling SVL, males had relatively longer and wider heads (GLM—head length, SVL, $F_{1,75} = 119.28$, $P < 0.001$; population, $F_{1,75} = 0.52$, $P = 0.473$; sex, $F_{1,75} = 16.25$, $P < 0.001$; population \times sex, $F_{1,75} = 0.89$, $P = 0.350$; head width, SVL, $F_{1,75} = 122.33$, $P < 0.001$; population, $F_{1,75} = 0.83$, $P = 0.365$; sex, $F_{1,75} = 7.52$, $P = 0.008$; population \times sex, $F_{1,75} = 0.79$, $P = 0.376$) while relative head height was similar between sexes (GLM—SVL, $F_{1,75} = 33.86$, $P < 0.001$; population, $F_{1,75} = 2.43$, $P = 0.123$; sex, $F_{1,75} = 3.61$, $P = 0.061$; population \times sex, $F_{1,75} = 2.50$, $P = 0.118$).

A mixed-model GLM of the different growth variables (see Table 3), with clutch as a random factor and population and sex as fixed factors did not show significant differences between populations in mass-specific growth, size-specific growth, head growth or femoral growth, or between sexes (see Table 4). There were no significant differences in sex and population body condition at the end of the experiment (GLM—population, $F_{1,45} = 0.05$, $P = 0.826$; sex, $F_{1,45} = 0.02$, $P = 0.889$; population \times sex, $F_{1,45} = 0.27$, $P = 0.107$).

A significant effect of clutch was found for mass-specific growth, size-specific growth, head length growth and femoral growth (Table 4). This clutch effect only disappeared after controlling for relative clutch size (mixed model GLM—clutch, $F_{26, 18.00} = 1.92$, $P = 0.078$) and egg weight (mixed model GLM—clutch, $F_{26,18.00} = 2.02$, $P = 0.063$) in the case of femoral growth. The rest of the growth variables remained significant after controlling for both effects (all P s < 0.05). However, the relationships between femoral growth and relative clutch ($r = 0.24$, $F_{1,47} = 2.87$, $P = 0.097$) and egg weight ($r = 0.06$, $F_{1,47} = 0.15$, $P = 0.701$) were not clear.

Discussion

Our study provides clear evidence that altitudinal divergent adult body size in two proximate populations of Iberian wall lizards is not caused by contrasting reproductive investment per egg or different pre- and post-hatching growth rates. High-altitude adult lizards were larger with a robust head morphology and had longer femora. Hence, our lizard populations follow Bergmann's rule (i.e., larger body size in colder environments). This result is in sharp contrast with the vast majority of squamates which exhibit reversed Bergmann's clines (Ashton and Feldman 2003). However, different trends can be found within a genus (Ashton and Feldman 2003; Sears 2005) or even within the same species [e.g., *Sceloporus undulatus* (Ferguson and Talent 1993; Niewiarowski and Roosenburg 1993)]. Geographical variation in body size can be produced by mechanisms not necessarily related to Bergmann's rule (Palkovacs 2003) and a life history perspective can enrich our understanding of Bergmann's clines (Roff 1980, 1986). In this context, we did not find differences in growth between high- and low-altitude hatchling lizards or between sexes in our common garden experiment. Thus, our results agree with those studies where growth differences among populations and adult body size are likely a plastic response and not a product of intrinsic differences (Niewiarowski and Roosenburg 1993; Sorci et al. 1996; Lorenzon et al. 2001). Deviations from the reversed Bergmann's size clines in squamates are likely to arise by two different processes: environmental limitation of growth in warmer climates [through resource limitation or process limitation (Congdon 1989; Dunham et al. 1989)] or selection for a specific body size or growth rate via age-specific mortality (Stearns and Koella 1986).

Resource limitation exists when an individual cannot acquire sufficient resources from the environment to support maximal growth. One form of resource limitation is process limitation (Congdon, 1989). Even when food availability is high, lizards may not take advantage of it due to thermal constraints on ingestion and assimilation. This has been described in the lizard *Sceloporus merriami*, where the prolonged exposure to nighttime cool temperatures limits the rate at which food items pass through the gut (Dunham et al. 1989). However, this possibility alone is in contrast to our findings of highland *P. hispanicus* attaining a larger body size. Apart from behavioral interferences of environmental origin, such as predation risk, a common cause of resource limitation is produced when material resources (e.g., food or water) are limited in the environment (Dunham, 1978). Several studies support a link between growth rates and habitat production via climate effects (Bauwens 1985; Bauwens and Verheyen 1987; Heulin 1985). If these effects persist over time, they could generate differential body size and life histories among

populations like those reported here (Buckley et al. 2007; Díaz et al. 2011). That would imply two alternative mechanisms to explain the absence of an origin effect in growth under our common garden experiment. First, environmental constraints such as thermoregulation opportunities or food abundance may be correlated with humidity and could, in turn, limit growth rate because of limited energy availability (Stamps and Tanaka 1981). Second, growth plasticity itself (physiologically) may not be adaptive, and may be the consequence of adaptive plasticity at the behavioral level enabling lizards to avoid dehydration (Jones et al. 1987; Lorenzon et al. 1999).

Our study cannot tease apart the intrinsic and extrinsic factors that shape reproductive investment differences but, as clutch size, clutch volume and clutch weight were shown to be independent of the larger size of highland females, it is interesting to speculate how environmental conditions could potentially drive these differences. As with body size, there is growing evidence that this pattern of variation in reproductive traits (i.e., larger lizards laying big clutches) may be caused by environmental differences in productivity. Tropicidurid lizards show a positive relationship of clutch and female body size with precipitation, possibly via effects on primary production (Brandt and Navas 2011). In the lacertid lizard *Psammotromus algirus*, female body size and clutch size were larger and positively associated with a gradient of increasing humidity and decreasing temperature (Díaz et al. 2011). Similarly, female *P. hispanicus* from our highland population laid larger clutches of wider eggs. Iraeta et al. (2006) showed that food availability was higher in a high-altitude site than in a low-altitude site in the same geographical area as our study. Also, preliminary surveys indicate that food availability is higher in our highland population in early spring (unpublished data). Moreover, in late September, at the end of the breeding season, when summer drought was more evident, soil humidity was still high and lizards and insects were still abundant at the highland site; whereas at the lowland site, the soil was completely dry and lizards and their prey were very rarely observed (unpublished data). This pattern seems likely in Mediterranean lowlands where 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 grow to larger sizes (Iraeta et al. 2006). In addition, higher productivity and reproductive investment are tightly linked to high precipitation (Jordan and Snell 2002). Female *P. hispanicus* may lay several clutches during the breeding season (Galan 2003) so it remains unknown if the annual total reproductive effort of these lowland and highland populations differ. In line with this, Aragón and Fitze (2014) acknowledged primary productivity as an important predictor of body size in another lacertid, the Spanish sand racer, and suggested

how higher juvenile survival due to higher food availability might outweigh the costs of delayed maturation, or higher growth rates due to a higher food intake might counteract growth retardation at lower temperatures.

Classic models of life history evolution predict that when juvenile mortality is high, fast growth is favored (Stearns, 1992, 2000). Hence, Bergmann size clines can be produced by mortality schedules that favor earlier reproduction in warmer environments than in cooler environments (Angilletta et al. 2004). Often, fast growth incurs the cost of maturing at a relatively smaller adult body size. Because longer potential periods of activity, such as those found in warmer environments, can produce higher rates of mortality (Wilson 1991), selection may produce faster growing lizards that achieve smaller adult body sizes, resulting in a Bergmann size cline. However our results do not offer any evidence to support selection for a specific body size or growth rate via age-specific mortality as we did not find growth differences under a common garden experiment. Large body size results from either faster growth, a longer duration of growth, or both (Angilletta et al. 2004). Since ectotherms grow more slowly at lower temperatures, prolonged growth and delayed maturation have been invoked as the proximate mechanism for a larger body size in colder environments (Atkinson 1994; Morrison and Hero 2003). In keeping with this, survival tends to be higher in colder environments (than in warmer lowlands, for instance) in some lizard species which delay maturation until reaching larger body sizes (Angilletta et al. 2004). In addition, individuals with a longer activity season are therefore expected to grow more quickly and attain maturation at smaller size and earlier age (Adolph and Porter 1993; Sears 2005). For example, length of activity season, and not temperature per se, is the main environmental factor constraining growth rate and annual rates of mortality in *Zootoca vivipara* (Horváthová et al. 2013). Thus, the relative contribution of activity period and survival to explain the adult body size differences observed in our lizard populations should be further explored.

In conclusion, the work presented here is the first attempt to experimentally unravel the causes of morphological variation within the *P. hispanicus* species complex. We provide clear evidence that the divergent adult body sizes are not driven by size at hatching, which is not contributed to by egg size, nor are intrinsic post-hatching growth rates associated with the environmental conditions experienced in our common garden experiment. Thus our results suggest that adult phenotypes are not the result of intrinsic differences but the consequence of a plastic response. Further research should aim to determine which factors could drive this phenotypic plasticity. Environmental conditions and their effects on primary production, activity period or survival, could play a key role in maintaining phenotypic

divergence. The relative contribution of phenotypic plasticity and local adaptation to different climatic conditions remains to be assessed by an ongoing reciprocal transplant experiment (unpublished data). More research is needed to clarify the role of phenotypic plasticity as a trigger of divergence within and among populations or as a buffer against it. Because an evolutionary change in body size can be regarded as an important component of the speciation processes (Sistrom et al. 2012), we propose the *P. hispanicus* species complex as a good model to investigate the relative importance of phenotypic plasticity along the speciation continuum.

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