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Christine R. Buckley

Duncan J. Irschick

Stephen C. Adolph

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The contributions of evolutionary divergence and phenotypic plasticity to geographic variation in the western fence lizard, *Sceloporus occidentalis*

CHRISTINE R. BUCKLEY^{1*}, DUNCAN J. IRSCHICK² and STEPHEN C. ADOLPH³

¹Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts at Amherst, Amherst, MA 01003, USA

²Biology Department, University of Massachusetts at Amherst, Amherst, MA 01003, USA

³Biology Department, Harvey Mudd College, Claremont, CA 91711, USA

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Local genetic adaptation and phenotypic plasticity are two mechanisms that can have marked effects on the morphology, performance, and behaviour of animals, producing geographic variation among populations. However, few studies have examined how these mechanisms interact during ontogeny to shape organismal phenotypes. We incubated eggs of the western fence lizard, *Sceloporus occidentalis*, from four populations (representing two latitudes and altitudes) in either a warm or cool environment in the laboratory. We then raised the hatchlings under common laboratory conditions, measured morphological and performance traits until 5 weeks of age, and compared juvenile morphology with that of field-caught adults from each population. The results obtained indicate that some phenotypic traits that contribute to performance (body size, hindlimb length, head shape) were relatively canalized in juveniles and differed among populations in a way that was consistent with adults from their population of origin. However, other traits (forelimb length, inter-limb length, mass, tail length), showed significant effects of incubation temperature, and this environmentally induced variation persisted throughout the experiment. Although selection pressure may be stronger for traits that are integral to survival, developmental effects might still have a lasting impact on traits less important to organismal fitness. We discuss the results obtained in the present study in the context of the life history of these animals. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, 99, 84–98.

ADDITIONAL KEYWORDS: development – incubation – local adaptation – morphology – ontogeny – performance – reaction norm – temperature.

INTRODUCTION

Variation in organismal phenotypes can be caused by local adaptation, which occurs as a result of genetic divergence among populations, and phenotypic plasticity, which results from environmental differences among habitats acting in concert with reaction norms (Brown, 1985; Ford & Seigel, 1989; Sears & Angilletta, 2003). Organisms from different populations within the same species are known to vary greatly in their phenotypes, behaviour, and performance capacities (Gould & Johnston, 1972; Endler,

1977; Huey, Overall & Newman, 1998; Le Galliard, Le Bris & Clobert, 2003; Sears & Angilletta, 2003; Moyaho, Garcia & Manjarrez, 2004). Geographic variation in phenotypes among populations of a species represents the first step toward genetic divergence and eventual speciation (Herrell, Meyers & Vanhooydonck, 2001). Many studies have documented extensive intraspecific variation in organismic traits across geographic space (Sinervo & Adolph, 1994; Jockush, 1997; Arnett & Gotelli, 1999; Buckley, 2008), and realized adult trait values are assumed to be influenced by both genetic and environmental factors. The influence of phenotypic plasticity on long-term trait expression, however, remains largely unknown for wild populations.

*Corresponding author. E-mail: crcbuck@gmail.com

Biologists have long recognized the influence of incubation temperature on the phenotypes and behaviour of hatchling ectotherms (Christian, Tracy & Porter, 1986; Van Damme *et al.*, 1992; Shine, Elphick & Harlow, 1997; Elphick & Shine, 1998; Andrews, Mathies & Warner, 2000; Du & Ji, 2003; Diaz-Paniagua, Andreu & Keller, 2006; Watkins & Vraspir, 2006). For reptiles, substantial phenotypic plasticity in hatchling morphology (Shine *et al.*, 1997; Elphick & Shine, 1998; Qualls & Shine, 2000), performance and behaviour (Marsh & Bennett, 1986; Qualls & Shine, 1998; Du & Ji, 2003), and growth rates (Sinervo & Adolph, 1994; Du & Ji, 2003) can be caused by variation in incubation temperatures. Although this developmental plasticity in response to variable temperature is well documented, few studies have assessed the ecological consequences of this induced variation. Although some studies have shown that nest temperatures induce changes in morphology and performance that persist up into the lifetime of juvenile ectotherms (Elphick & Shine, 1998), others show that the post-hatching environment is more important than incubation conditions in determining juvenile morphology, growth rates and performance (Qualls & Shine, 2000; Nelson *et al.*, 2006; Watkins & Vraspir, 2006; Buckley *et al.*, 2007; Buckley, 2008). Furthermore, maternal behaviours, such as nest site choice, may buffer against the effects of extreme environmental factors (Shine & Harlow, 1996; Warner & Andrews, 2002; Blouin-Demers, Weatherhead & Row, 2004).

Some laboratory and field studies have shown that environmental factors can cause physiological modifications that result in long-term or permanent changes in trait expression (Elphick & Shine, 1998; West-Eberhard, 2003; Lerner, Bjornsson & McCormick, 2007) or growth rates (e.g. Madsen & Shine, 2000). These differences in phenotype can be adaptive: they may give a distinct advantage to some animals that use particular microhabitats (Kawecki & Stearns, 1993; Atkinson & Sibly, 1997; Lindström, 1999; Laurila *et al.*, 2002). Therefore, it is important to determine whether environmental influences early in ontogeny persist into consecutive life-history stages (Angert *et al.*, 2002; Herrel, Meyers & Vanhooydonck, 2002).

Our approach, which examines the relative roles of the incubation and early juvenile stages on lizard phenotypes, is useful because it allows us to examine trait variation over different life-history stages. Most ecomorphological studies of lizards focus exclusively on phenotypic differences among adult individuals (Smith-Gill, 1983; West-Eberhard, 2003), with less attention being devoted to the ontogenetic trajectories that have led to such differences. For example, some animals that are initially poor performers may

exhibit compensatory growth that allows them to 'catch up' to their better-performing conspecifics when subjected to a favourable growth environment (Garland & Losos, 1994; Beuttell & Losos, 1999; Irschick, 2002; Brandley & de Queiroz, 2004). By contrast, some animals may experience a 'silver spoon' effect, in which a favourable growth environment leads to long-term advantages (Madsen & Shine, 2000).

In the present study, we tested the persistence of phenotypic plasticity in morphology and performance across four populations of the western fence lizard, *Sceloporus occidentalis*. Our previous research showed that, between a mountain and a desert population (high and low elevation, respectively) of these lizards, some hatchling traits showed variation based on incubation temperatures, although these differences did not persist over time and were small in magnitude compared to differences between sites (Buckley *et al.*, 2007). Here, we expand upon this study by including two more populations, from a higher latitude, that are larger in body size than those included in our first study (Buckley, 2008); these body size differences led us to examine potential differences in allometry among the populations. Additionally, the two additional populations have altitude and temperature metrics similar to those that we previously examined. We also examined sprint speed in hatchling individuals to provide a performance link between morphology and fitness. Finally, we compared hatchling phenotypes to field-caught adults from each population to examine how the rank order of phenotypes produced during incubation compares with wild individuals. This design allowed us to examine animals at three different points on their ontogenetic trajectory (hatchling, juvenile, adult) and to attribute changes in phenotype to a lizard's population of origin and/or its incubation regime.

The present study addressed three questions. First, do phenotypic and performance traits differ among populations or between incubation regimes (or both) in hatchlings? Second, do these differences persist into the juvenile stage? Third, how do traits differ across the life-history stages of hatchling, juvenile and adult? Based on our previous work, we predicted that body size and appendage lengths will differ based on incubation regimes: lizards incubated in a cool environment should be larger and have shorter limb and tail lengths than those incubated in a warm environment. Furthermore, we predicted that, as hatchling lizards grow in a common environment, they will converge on an intermediate phenotype (Buckley *et al.*, 2007). We also predicted that, if juveniles do converge on a common phenotype, then we should similarly observe no phenotypic differences among adults across the different populations.

MATERIAL AND METHODS

STUDY ORGANISM, COLLECTION, AND CARE

Sceloporus occidentalis is a medium-sized lizard (adults weigh 10–30 g) that ranges from the northern portion of Baja California through Washington state, from sea level to approximately 2700 m in elevation. Individuals of this species select a variety of microhabitats ranging from trees to rocks, and occupy a variety of perch heights (Adolph, 1990a; Asbury & Adolph, 2007). We collected male and female adult lizards from four populations that differ in altitude, latitude and temperature profiles. We then raised 74 female and 66 male hatchlings to 5 weeks of age in a common laboratory environment to test whether the rank order of phenotype produced during the incubation stage persists into the hatchling stage.

During the months of May and June 2006, adult *S. occidentalis* were collected by noose from four populations in central and southern California (Fig. 1): (1) Largo Vista, 8 km east of Valyermo, Los Angeles County, on the edge of the Mojave desert (elevation 1370 m, 34°27'N); (2) Table Mountain, 2 km north-

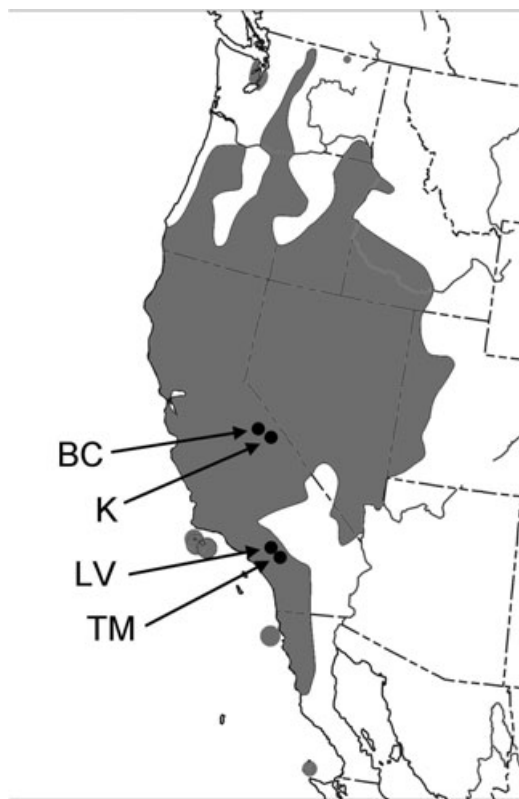


Figure 1. Range map of the lizard *Sceloporus occidentalis* in western North America. Populations sampled in this study are labelled by acronym. LV, Largo Vista; TM, Table Mountain; K, Keough Hot Springs; BC, Bishop Creek. Adapted from Jones & Lovich, 2009.

west of Wrightwood, San Bernardino County, in the Angeles National Forest (elevation 2230 m, 34°24'N); (3) Keough Hot Springs, near Bishop, in the Owens Valley, Inyo County (elevation 1220 m, 37°15'N); and (4) Bishop Creek, in the Inyo National Forest (2135 m, 37°16'N). The Largo Vista and Table Mountain sites are 12 km apart. The Keough Hot Springs (Keough) and Bishop Creek sites are 15 km apart, and are 315 km north of the Largo Vista and Table Mountain sites. We sampled these four sites because they represent two latitudes (south and north) and two altitudes (low and high), which gives a broad sampling of the environments that these lizards occupy within their natural range. Additionally, the two sites within each latitude occupy nearly identical altitudes, which should control for differences such as pressure and oxygen content in the air. The four sites also encompass a range of temperatures. During the summer months in 2006, the two mountain sites, Bishop Creek and Table Mountain, had an average maximum daily temperature of 29.5 °C and an average minimum daily temperature of 10.7 and 12.4 °C, respectively. The two desert sites, Keough and Largo Vista, had average maximum daily temperatures of 35.5 and 36.0 °C and average minimum daily temperatures of 14.4 and 14.6 °C, respectively (D. McMillan, pers. comm.).

Adults were transported to a laboratory within 24 h of capture and housed individually in glass terraria (approximately 38 L) in an animal room (air temperature range 21–23 °C). The female lizards' substrate consisted of mixed peat moss and sand, 4 cm deep, with several pieces of bark for cover. Each lizard was supplied with a heat lamp cycling under a 12 : 12 h light/dark cycle, creating a thermal gradient of approximately 40–20 °C in which the lizards could thermoregulate. Lizards were fed crickets dusted with vitamin powder *ad libitum* and provided with a small bowl of water.

Cages were checked at least once daily for the presence of eggs. We removed eggs from the cages and placed them individually in 200-mL plastic cups filled with moistened vermiculite (10 : 1 ratio of vermiculite to water by mass to produce a water potential of approximately –200 kPa) and sealed with plastic wrap to reduce water loss. Each female laid between two and 12 eggs, and clutches were split and assigned randomly to one of two incubation treatments: warm (30 °C average) or cool (24 °C average). Each temperature cycled daily ± 3 °C around the average temperature to better mimic nest temperatures in the wild (Shine *et al.*, 1997; Qualls & Shine, 2000) and were chosen to represent the extremes of temperatures these animals can withstand and still develop normally (Adolph, 1990a; Adolph, 1990b; Grover, 1996; Asbury & Adolph, 2007). Vermiculite was replaced

every 7 days, and incubators were checked daily for the presence of hatchlings.

Juveniles were housed individually in plastic terraria (28 × 14 × 11 cm) with a damp sand substrate, fed 2-week-old crickets, and supplied with water in excess. The animal holding room was set to a 12 : 12 h light/dark cycle. Each cage was provided with a suspended heat source for 10 h each day to create a gradient of 20–40 °C in which the juveniles could thermoregulate. These conditions allowed the animals to choose their preferred body temperatures in the laboratory and imposed no restrictions on the amount of basking time during the day.

MORPHOLOGY, GROWTH, AND PERFORMANCE

We analysed data obtained from a total of 172 hatchlings from 43 clutches. All but four gravid females laid their eggs in the sand and peat moss substrate. Most of the southern California lizards (71%) laid their eggs before June 15, whereas most of the central California lizards (95%) laid their eggs after 15 June. We measured mass, snout–vent length (SVL), hindlimb length, forelimb length, inter-limb distance (i.e. the distance between the posterior insertion of the forelimb and the anterior insertion of the hindlimb), and tail length of neonates and adults (to ±0.01 cm or 0.001 g) using digital calipers and an analytical balance. We measured body size and limb lengths because they have been shown to be predictors of sprinting speed and survivorship in lizards (Losos *et al.*, 2000). Biting ability can determine animals' prey types (Verwajen, Van Damme & Herrel, 2002; Aguire *et al.*, 2003), and, in these and other territorial lizards, biting ability can also predict winners of male–male aggressive contests (Lailvaux & Irschick, 2007). We measured head length, head width, and head depth because head shape has also been shown to be a predictor of bite force in vertebrates (Verwajen, Van Damme & Herrel, 2002; Herrel *et al.*, 2005). We repeated these morphological measurements at 1, 3, and 5 weeks of age.

Sprinting performance was recorded at one week of age by placing lizards on a 1-m racetrack and inducing them to run the length of the track by gently touching the base of their tail with the bristles of a paintbrush. Photogates were positioned at 25-cm intervals along the walls of the racetrack, and speeds were calculated by a computer program. All lizards were placed in an incubator and held at 35 °C for 30 min before measuring sprint performance; 35 °C is the optimal temperature for sprint performance in *S. occidentalis* (Marsh & Bennett, 1986). Each lizard was raced at 1, 3, and 5 weeks of age; they were raced four times with at least 30 min of rest between trials. Lizards rarely sprinted the length of the racetrack,

so we used the fastest 25-cm interval at each age as a measure of maximum running speed. Because hatchling and juvenile lizards are fragile, and because of the time-intensive nature of measuring sprint performance repeatedly (see Results), we did not measure other metrics of performance. We calculated repeatability of sprint speeds within each of the eight population × incubation treatment groups.

STATISTICAL ANALYSIS

To determine potential correlations among morphological variables at hatching, we performed principal components analysis on the morphological variables measured and analysed the effects of source population and incubation regime on resultant factor loadings. Because we found only one significant principal component (see Results), all further analyses were performed on size-corrected trait measurements. We used a combination of analysis of variance (ANOVA) and regression analysis to assess the relative impacts of each factor (source population and incubation regime) on juvenile morphology and behaviour. To correct for differences in body size, we performed a least-squares regression on each morphological variable against the lizard's SVL. We used these residual values in a two-way ANOVA with source population and incubation environment as factors to determine differences among juvenile traits at hatching. Because the data collected at each 2-week interval were measured from the same animals, and were therefore not statistically independent, we used a two-way repeated measures ANOVA to determine the relative effect each factor has on the morphology of lizards over time. We calculated juvenile body mass indices (BMI) by performing a regression of lizard body mass against SVL for individuals pooled across populations, and used the residual values from this analysis as the lizard's BMI. Analyses were corrected for multiple comparisons using a Bonferroni adjustment. To assess sprint speed relative to body and limb size, we performed two analyses of covariance (ANCOVA) on juvenile sprint speed with SVL and hindlimb length, respectively, as covariates. Repeatability analyses were conducted *sensu* Lessels & Boag (1987) to determine the proportion of variance in sprint speed occurring among individuals.

To compare morphological traits of adult lizards across populations, we used ANCOVA with SVL as a covariate, and Tukey's honestly significant difference (HSD) post-hoc tests to determine differences among the four populations.

RESULTS

For hatchling lizards, we found no significant differences between the sexes in body size or relative

morphometrics over time, and no significant differences in sprinting speed at hatching; therefore, we pooled sexes for the remainder of the analyses. We found that hatchling morphological traits were significantly positively correlated with each other. Principal components analysis on the nine morphological variables resulted in one significant component based on the broken stick model; this factor had an eigenvalue of 5.533 and explained 61% of the variance among variables. Body size characteristics loaded most highly on this factor (mass = 0.903; SVL = 0.898), but there were no other clear patterns of morphological trait loadings (head width = 0.891; inter-limb length = 0.876; head length = 0.802; forelimb length = 0.789; head length = 0.672; tail length = 0.651; head height = 0.456). Population had a significant effect on the factor scores, with lizards from Bishop Creek having the largest average factor score (0.846 ± 1.0), lizards from Keough having intermediate scores (0.210 ± 0.61), and Table Mountain and Largo Vista showing no significant difference between each other and having the lowest scores (TM = -0.644 ± 0.60 ; LV = -0.662 ± 0.50). These scores show that, on average, morphometrics were largest for Bishop Creek lizards, intermediate for Keough lizards, and that Table Mountain and Largo Vista lizards had the smallest morphologies, as reinforced below by the analyses of individual traits.

The average values for juvenile body morphometrics are reported in Table 1. For all comparisons, we set $\alpha = 0.008$ to adjust for the six comparisons. To simplify interpretation, we present all traits affected by source population, then all traits affected by the incubation environment, and, finally, all traits that showed a significant interactive effect. Within each section, we first report significance values for hatchling lizards in the text, and then refer to analyses on juvenile traits over the course of the 5-week experiment in Table 2. Finally, we report analyses on adult lizard morphometrics.

POPULATION EFFECTS: CANALIZED TRAITS

Population had a significant effect on lizard SVL at hatching, with Bishop Creek lizards having longer bodies than Keough lizards, and both having longer bodies than the Table Mountain or Largo Vista populations ($F_{3,168} = 67.01$, $P < 0.0001$). Population influenced hatchling mass, with Bishop Creek animals being larger and Table Mountain animals being smaller than the others, but only marginally ($F_{3,168} = 3.76$, $P = 0.012$; Table 1).

Population had a significant effect on hatchling forelimb length ($F_{3,168} = 4.871$, $P = 0.003$), with lizards from the central California populations and the

Table 1. Summary of morphological measurements at hatching in four populations of *Sceloporus occidentalis*

Trait	Southern California				Central California			
	Largo Vista		Table Mountain		Keough		Bishop Creek	
	Cool	Warm	Cool	Warm	Cool	Warm	Cool	Warm
Snout-vent length	25.87 ± 0.33	26.11 ± 0.32	26.31 ± 0.19	26.09 ± 0.24	28.22 ± 0.25	27.71 ± 0.46	29.86 ± 0.38	29.33 ± 0.27
Mass (g)	0.71 ± 0.02	0.68 ± 0.02	0.71 ± 0.01	0.64 ± 0.01	0.86 ± 0.02	0.82 ± 0.03	1.02 ± 0.04	0.95 ± 0.02
Forelimb length	7.49 ± 0.17	7.5 ± 0.10	7.7 ± 0.08	7.68 ± 0.15	8.32 ± 0.11	8.54 ± 0.14	8.2 ± 0.14	8.99 ± 0.16
Hindlimb length	12.58 ± 0.15	12.64 ± 0.29	12.71 ± 0.18	12.92 ± 0.20	13.67 ± 0.15	13.88 ± 0.27	14.44 ± 0.25	14.7 ± 0.19
Inter-limb length	10.32 ± 0.13	11.29 ± 0.35	10.51 ± 0.09	10.54 ± 0.17	12 ± 0.13	11.64 ± 0.26	11.99 ± 0.22	12.04 ± 0.13
Tail length	33.2 ± 0.86	33.42 ± 2.41	33.66 ± 0.68	34.9 ± 1.20	31.74 ± 0.54	35.12 ± 1.14	35.4 ± 1.16	38.44 ± 0.89
Head length	7.13 ± 0.13	6.6 ± 0.78	7.35 ± 0.09	6.79 ± 0.10	7.68 ± 0.06	7.95 ± 0.10	7.74 ± 0.09	7.76 ± 0.07
Head width	5.89 ± 0.06	5.96 ± 0.06	5.86 ± 0.04	5.86 ± 0.06	6.21 ± 0.04	6.3 ± 0.07	6.34 ± 0.07	6.62 ± 0.07
Head height	4.26 ± 0.08	4.39 ± 0.08	4.05 ± 0.05	4.23 ± 0.06	3.97 ± 0.05	4.26 ± 0.8	4.19 ± 0.06	4.7 ± 0.07
Sprint speed (m/s)	1.61 ± 0.18	1.23 ± 0.09	1.59 ± 0.09	1.58 ± 0.14	1.43 ± 0.07	1.29 ± 0.08	1.45 ± 0.11	1.39 ± 0.09

Values are reported with 1 SE and given in millimetres unless otherwise specified.

Table 2. *F*-values for repeated-measures analyses of variance conducted for all measurements over 5 weeks of life

	Between subjects				Within subjects				
	Population	Incubation	Population × Incubation	d.f.	Age	Age × Incubation	Age × Population	Age × Incubation × Population	d.f.
Snout-vent length	57.402	0.646	0.131	3,88	235.819	26.489	1.948	1.899	3,264
Mass	0.881	7.023	0.451	3,86	4.454	4.097	0.705	0.949	3,258
Forelimb length	2.345	13.260	0.384	3,88	5.609	2.014	1.540	1.715	3,264
Hindlimb length	4.753	0.229	0.233	3,88	0.730	10.479	3.175	1.795	3,264
Inter-limb length	0.976	15.969	1.543	3,88	0.958	2.347	1.004	2.581	3,264
Tail length	11.346	16.164	1.042	3,76	10.978	13.368	2.311	3.652	3,228
Head length	6.383	0.773	1.573	3,88	0.600	2.232	1.945	2.958	3,264
Head width	4.219	12.472	1.589	3,88	21.704	2.568	1.365	4.100	3,264
Head height	1.851	3.279	0.097	3,88	9.855	12.749	5.758	1.933	3,264
Body mass index	5.050	6.984	1.605	3,87	39.307	15.254	2.270	2.100	3,261

Mass, forelimb length, hindlimb length, inter-limb length, tail length, and head shape measurements are size-corrected using residual analysis. Bold indicates significant values ($P < 0.008$).

warm-incubated treatment having longer forelimbs. Hatchling hindlimb length was significantly affected by population (population: $F_{3,168} = 6.57$, $P < 0.0001$). Keough and Largo Vista lizards had longer hindlimbs than those from Table Mountain, and the Keough lizards also had longer hindlimbs than the Bishop Creek lizards. Population had a significant effect on tail length ($F_{3,150} = 17.38$, $P < 0.0001$), with lizards from southern California having longer tails.

Population significantly affected relative head length ($F_{3,168} = 7.60$, $P < 0.0001$), width ($F_{3,168} = 7.21$, $P < 0.0001$), and height (population: $F_{3,168} = 9.53$, $P < 0.0001$). Bishop Creek and Largo Vista lizards had deeper heads (larger head heights) than Keough and Table Mountain lizards. Table Mountain lizards had relatively narrower heads than the other populations, and the central California populations had relatively wider heads than the southern California populations. Keough lizards had relatively longer heads than the other populations.

In the laboratory, we found that juvenile sprinting speed decreased over time, by 21% of their sprinting speed on average at week 1. There was no average decline in body condition index of all lizards over time (see below), ruling out the possibility that the animals' health deteriorated in the laboratory. The decline in sprint speed may be a result of repeated handling, causing the lizards to grow habituated to their handlers and therefore less motivated to sprint quickly. Consequently, we analysed sprinting data for these animals only at 1 week of age. When SVL was used as a covariate, population had a significant effect on sprinting speed at age one week (ANCOVA: $F_{3,150} = 6.00$, $P = 0.001$), with Table Mountain lizards being faster than Bishop Creek (Tukey's HSD test, $P < 0.0001$) and Keough lizards (Tukey's HSD test, $P = 0.009$) and Largo Vista lizards being intermediate. When hindlimb length was used as a covariate, the same trend was observed (ANCOVA: $F_{3,150} = 2.78$, $P = 0.044$), with Table Mountain lizards being faster than lizards from Bishop Creek (Tukey's HSD test, $P = 0.003$) and Keough (Tukey's HSD test, $P = 0.009$). Six of eight treatments had mean sprint speeds that were repeatable over the 0.50 level (Largo Vista: 24 °C, $r = 0.47$; 30 °C, $r = 0.83$; Table Mountain: 24 °C, $r = 0.67$; 30 °C, $r = 0.53$; Keough: 24 °C, $r = 0.31$; 30 °C, $r = 0.65$; Bishop Creek: 24 °C, $r = 0.78$; 30 °C, $r = 0.52$).

Over the duration of the 5-week experiment, population had a significant effect on juvenile SVL and relative hindlimb length. Animals from central California had greater SVLs and relatively longer hindlimbs than those from southern California; animals from Bishop Creek also had greater SVLs than did animals from Keough (Fig. 2, Table 2). Population of origin also affected tail length: lizards from the

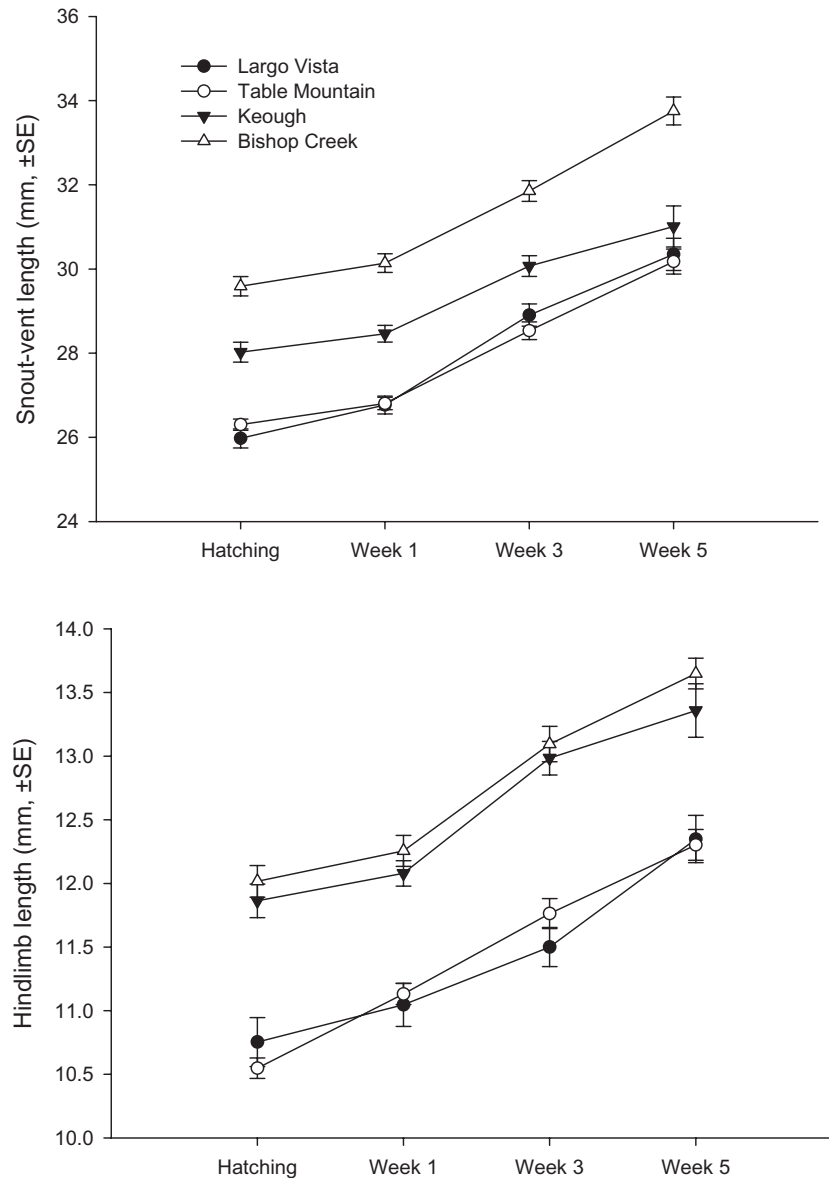


Figure 2. Snout–vent length and hindlimb length differed among populations of juvenile *Sceloporus occidentalis*, and this trend persisted until the animals were 5 weeks old. Error bars indicate 1 SE. Although for hindlimb length statistics were performed (see text) on the lengths of hindlimbs relative to body length, the figures show absolute values for morphometrics.

central latitudes had tails that grew faster than did lizards from the southern latitudes. Relative head length and width significantly varied over time across source populations (Table 2), such that lizards from central California had relatively longer and wider heads than the lizards from southern California.

INCUBATION EFFECTS: PLASTIC TRAITS

Incubation temperature did not affect hatchling SVL ($F_{1,168} = 1.11$, $P = 0.294$), mass ($F_{1,168} = 3.03$, $P = 0.084$),

inter-limb length ($F_{1,168} = 5.43$, $P = 0.021$), or hindlimb length ($F_{1,168} = 6.44$, $P = 0.012$). Incubation had significant effects on forelimb length ($F_{1,168} = 11.23$, $P = 0.001$), with high-latitude animals having longer forelimbs, and on tail length ($F_{1,150} = 63.78$, $P < 0.0001$; Table 1), with lizards from the warm-incubated group having longer tails. Incubation temperature also had significant effects on head length (incubation: $F_{1,168} = 32.27$, $P = 0.0001$), width ($F_{1,168} = 14.92$, $P < 0.0001$), and height ($F_{1,168} = 4.11$, $P = 0.044$), such that warm-incubated hatchlings had

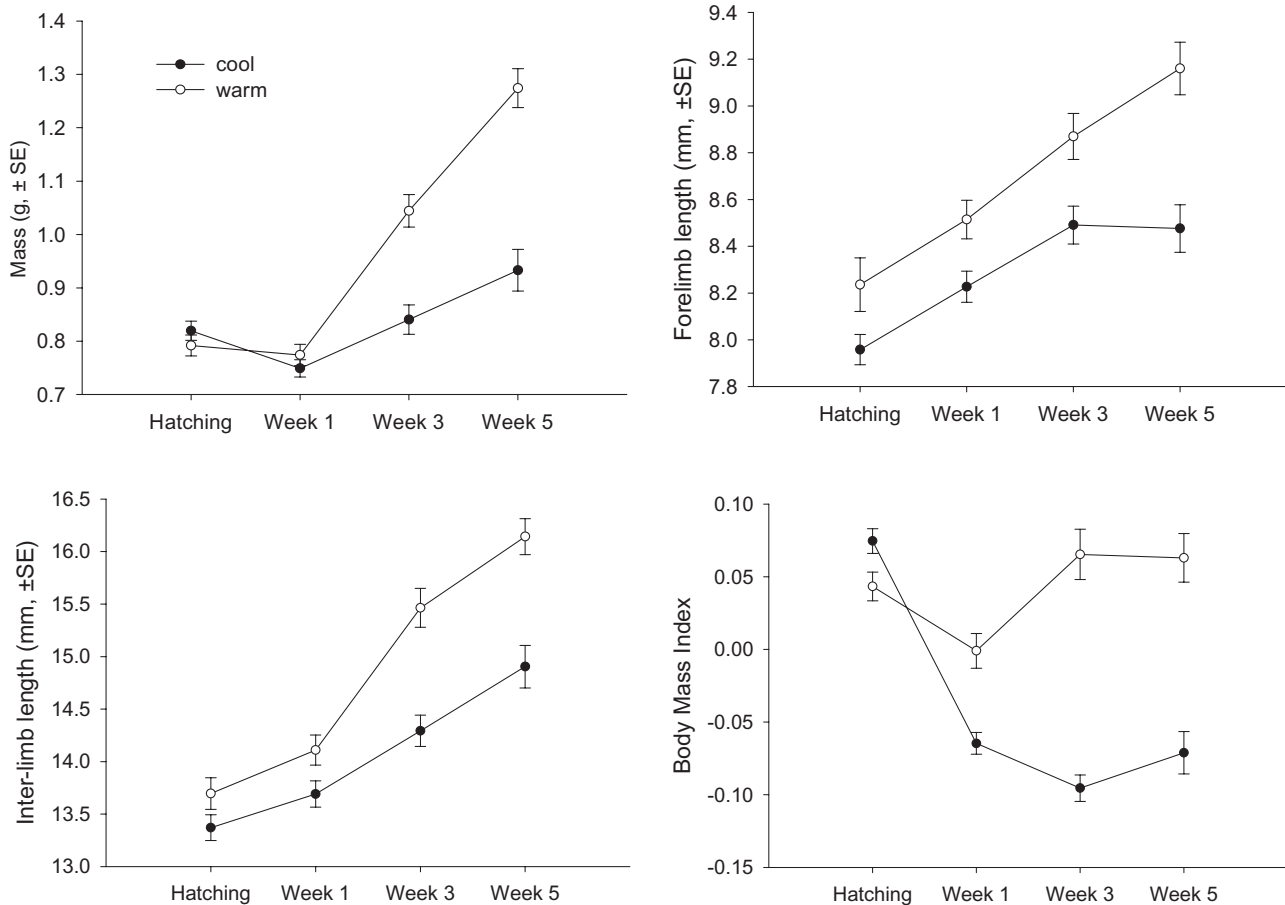


Figure 3. Hatchling mass, forelimb length, inter-limb length, and body mass index (BMI) showed significant variation between incubation temperatures. Error bars indicate 1 SE. Analyses on mass, forelimb, and inter-limb lengths were conducted using snout–vent length as a covariate. BMI was calculated by regressing snout–vent length against mass for all animals and using each animal’s residual value as its BMI. See text for significance values.

deeper, wider, and shorter heads than those that were cool-incubated.

Over the 5-week experiment, the incubation environment affected morphology (Table 2), with significant effects on lizards’ mass, body condition index, relative forelimb lengths and relative inter-limb lengths (Fig. 3). Initially, the two treatments did not differ significantly in mass, but, at the weeks 3 and 5, the warm-incubated lizards were significantly heavier. Lizards from the cool environment initially had significantly higher body condition indices, although this trend reversed for the remainder of the experiment. Lizards from the warm incubation environment consistently had relatively longer forelimbs and inter-limb lengths throughout the 5 weeks. Relative head width was significantly affected by incubation temperature (Table 2); cool-incubated lizards had relatively narrower heads than warm-incubated lizards. Incubation regime also significantly affected

relative tail length: animals from the cooler incubation environment had relatively shorter tails (Table 2).

INTERACTIVE AND WITHIN-SUBJECTS EFFECTS

At hatching, there were no significant interactive effects of population of origin and incubation environment on lizard SVL ($F_{3,168} = 0.466$, $P = 0.706$), mass ($F_{3,168} = 0.20$, $P = 0.895$), hindlimb length ($F_{3,168} = 3.32$, $P = 0.021$), inter-limb length ($F_{3,168} = 0.762$, $P = 0.517$), tail length ($F_{3,150} = 1.61$, $P = 0.189$), or head height ($F_{3,168} = 3.55$, $P = 0.016$). The interaction of population and incubation regime had significant effects on forelimb length ($F_{3,168} = 6.28$, $P < 0.0001$), with warm-incubated lizards having significantly longer forelimb lengths than cool-incubated lizards in the central but not southern latitudes. There were also significant population by incubation interactive effects on

head width ($F_{3,168} = 4.47$, $P = 0.005$) and depth ($F_{3,168} = 11.03$, $P < 0.001$). Warm-incubated hatchlings had deeper heads than those that were cool-incubated, and the interactive effect was likely a result of Bishop Creek animals in the warmer incubation environment having relatively deeper heads compared to their cool counterparts (Table 1). There were no significant population by incubation interactive effects on juvenile traits over time (Table 2).

The within-subjects effects of age, population and incubation environment on juvenile traits over time were complex, and the magnitude and direction of these effects varied throughout the course of the experiment. It is not surprising that age affected SVL as juveniles grew; however, age affected the size-corrected values of mass, forelimb length, tail length, head width and head depth, and BMI (Table 2). This effect implies that allometric growth of morphometric traits was not consistent over time in juvenile lizards. There were significant interactive effects of age and incubation environment on juvenile SVL, hindlimb length, tail length, head height and BMI (Table 2). Many of these traits showed no direct effect of the incubation environment, implying that incubation did have an effect on trait values, but only indirectly across the range of ages. Conversely, the interactive effect of age and population (on hindlimb length, tail length, head depth, and BMI) were mostly confined to traits that had direct population effects (Table 2). Finally, several traits showed a three-way interactive effect of age, incubation and population over time (Table 2).

ADULT MORPHOLOGY

Adult lizards from our four study populations differed in some body shape measurements and not others. We used ANCOVA with SVL as a covariate to correct for body size when comparing morphological variables among adults in the four populations. Adults from the four populations did not differ in forelimb length ($F_{3,88} = 2.362$, $P = 0.077$), interlimb length ($F_{3,88} = 1.694$, $P = 0.174$), or tail length ($F_{3,49} = 3.172$, $P = 0.103$). SVL ($F_{3,89} = 66.04$, $P < 0.0001$) differed significantly among the groups; the populations differed such that Bishop Creek > Keough > Table Mountain = Largo Vista (Tukey's HSD test, $P < 0.001$ for all comparisons but Largo Vista versus Table Mountain; Fig. 4). Hindlimb length also showed a significant population effect ($F_{3,88} = 3.772$, $P = 0.013$), with Keough lizards having longer hindlimbs than Table Mountain lizards (Tukey's HSD test, $P = 0.026$; all other pairwise comparisons were nonsignificant; Fig. 4).

Lizards from the different populations differed in some characteristics of head shape. An ANCOVA with

SVL as a covariate yielded a significant main effect of population on lizards' head height ($F_{3,88} = 3.131$, $P = 0.030$), but a post-hoc test revealed no pairwise differences (Tukey's HSD test, all pairwise comparisons $P > 0.07$). Lizards from the Keough population had relatively wider heads than the other populations ($F_{3,88} = 15.78$, $P < 0.0001$; Tukey's HSD test, all Keough pairwise tests, $P < 0.001$). Finally, Keough lizards had relatively longer heads than Table Mountain lizards ($F_{3,88} = 3.758$, $P = 0.014$; Tukey's HSD test, $P = 0.012$).

DISCUSSION

PHENOTYPES AT HATCHING: GENETIC AND ENVIRONMENTAL EFFECTS

Body size is a predictor of survivorship during the juvenile stage; small animals are poor performers on an absolute scale and their small size makes them more manageable prey (Marsh & Bennett, 1986). Further, hindlimb length and head morphology are, in some species, predictors of sprinting and biting performance, respectively (Carrier, 1996). At hatching, the effects of population and incubation temperature on lizard morphological traits were complex. The observations in the present study demonstrating that several traits (body length, hindlimb length, head shape, sprint speed) were more affected by population of origin than by developmental plasticity suggest that these traits may be more canalized (i.e. resistant to environmental effects).

Although some hatchling traits only varied among populations, other traits were affected by incubation temperature and by their population of origin. The direction and magnitude of their interactive effects were complex for hatchlings; overall, animals from the southern populations and the warmer incubation environment tended to have longer forelimbs, interlimb lengths, and tail lengths. The relationship between hindlimb length and sprint speed is generally well-supported (Mayr, 1956), but the relationships of other body shape characteristics, such as forelimb length and tail length, with sprinting speed, are less clear. Although short forelimbs and long tails are considered to be beneficial to lizards that rely on fast running, they are also thought to hinder climbing ability and sprinting speed on arboreal perches (Irschick & Jayne, 1998; Bonine & Garland, 1999; Vanhooydonck & Van Damme, 2001b; Herrel *et al.*, 2002). Therefore, in comparison to traits that have a direct relationship to performance (i.e. hindlimb length), these less integral traits might have higher variability and more susceptibility to environmental perturbations. The ultimate relationships between habitat use and behaviour may also play a more

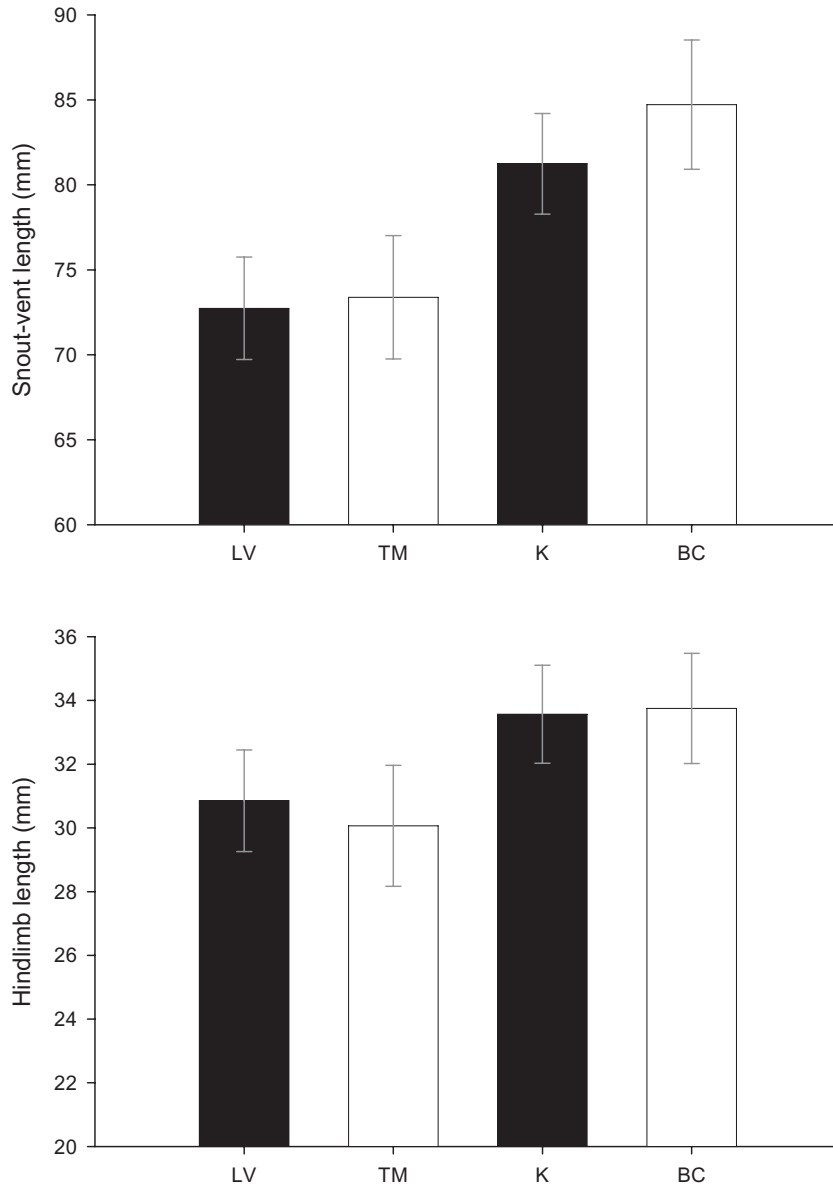


Figure 4. Adult morphologies across populations, showing differences in snout–vent length and hindlimb length. Lizards from the central California populations [Bishop Creek (BC) and Keough Hot Springs (K)] had longer bodies and relative hindlimb lengths than did lizards from the southern California populations [Table Mountain (TM) and Largo Vista (LV)]. Error bars indicate 1 SE. For statistical comparisons, see text.

significant role than these proximate variables (Irschick & Jayne, 1998; Herrel, Meyers & Vanhooydonck, 2001; Vanhooydonck & Van Damme, 2001a; but see also Goodman, Krockenberger & Schwarzkopf, 2007). *Sceloporus occidentalis* displays different levels of arboreality across populations (Adolph, 1990a; Sinervo & Losos, 1991; Asbury & Adolph, 2007); thus, a more flexible phenotype that can perform maximally in many habitats might be advantageous to this species.

We also found a general trend for hatchlings from the central populations and the cool incubation treatments to have larger heads relative to their body size. Lizard head shape is a predictor of bite force, which is important for male–male combat and for capturing prey (Tsuji *et al.*, 1989; Garland & Losos, 1994; Irschick *et al.*, 2005; Herrel, McBrayer & Larson, 2007); however, to date, no studies have examined whether bite force varies with latitude in lizards. Cooler annual temperatures in the central population

may lead to larger invertebrate prey items as predicted by Bergmann's rule, which is defined as a negative association between body size and environmental temperature (Verwajen, Van Damme & Herrel, 2002; Lappin, Hamilton & Sullivan, 2006; Herrel *et al.*, 2007). This pattern might lead to natural selection for relatively large heads in lizards from central California. Although our time and space constraints did not allow more extensive sampling of lizards further north or south of our populations, future studies would benefit from sampling across the entire range of this species.

There are at least two possible explanations for some lizard traits being phenotypically plastic. First, the response may be adaptive. If animals are incubated in a cold environment, limb and body dimensions could be reduced (Davis & Verbeek, 1972; Lillywhite & North, 1974; Adolph, 1990b; Sinervo & Losos, 1991), creating a stouter body shape that has greater thermal inertia, and adjusting the lizard to the cool habitat that its embryo stage 'predicted'. Conversely, the differences in body shape may simply be a byproduct of physiological processes that contribute to the development of muscle mass and bone structure slowing down in a cool incubation environment. Our study design is limited in that it cannot assign levels of importance for fitness to the traits we measured; future studies that measure the propensity for plastic changes in traits with known contributions to an organism's fitness would address this question.

One counterintuitive result was that hatchlings from the southern populations, which had relatively shorter hindlimbs, were the fastest sprinters, with hatchlings from Table Mountain sprinting faster than the others when hindlimb length was factored out. Animals with longer hindlimbs for their size are usually faster sprinters (Burger, 1991). Performance is understood to provide a proximate link between morphology and fitness because of its importance for capturing prey, defending territories, and interacting with conspecifics (Garland & Janis, 1993; Bauwens *et al.*, 1995; Vanhooydonck, Van Damme & Aerts, 2002; Vanhooydonck *et al.*, 2006). Substrate type (e.g. ground, trunk, branch) can also have a profound ultimate effect on lizard performance, such as jumping and sprinting ability (Arnold, 1983; Irschick & Garland, 2001). Large trees dominate the habitat of our central California populations, whereas the southern habitats have more bushes and stumps (C. Buckley, pers. observ.). Animals in the more open, southern habitats might sprint faster to escape from predators, whereas the central populations rely more on the close availability of hiding places, making fast sprinting speeds less important. However, animals of this species from warmer populations have been

shown to perch higher in trees than those in cool populations (Adolph, 1990a; Adolph, 1990b), and ecomorphological models predict that lizards that perch on narrow perches (i.e. in trees) have shorter limbs than those that perch on wider perches (i.e. rocks and stumps). These conflicting selection pressures might result in the maintenance of short hindlimbs to increase maneuverability on narrow perches in southern populations at the same time as also selecting for fast sprint speeds in response to the more open habitat. Indeed, animals in the south displayed shorter forelimbs and longer tails than their central counterparts, both of which are characteristic of animals that live in open spaces and display fast sprint speeds. Additionally, animals at Table Mountain, the southern mountain site, were the fastest sprinters relative to their hindlimb lengths. Lizards at this site tend to perch on rocks, shrubs, and stumps (Buckley, 2008), which might expose lizards to more open habitat and increase selection pressure for fast speeds. Further studies on the muscular physiology of animals from these populations could determine if the ability to sprint fast despite relatively short limbs lies at the level of individual muscles.

PHENOTYPES OVER TIME: ONTOGENETIC EFFECTS

Many studies have recognized that the developmental environment can change resultant phenotypes of hatchling ectotherms. The few studies that have examined whether these traits endure throughout the animals' lifetime provide conflicting results. Despite this lack of consistency, there are several possible mechanisms that could contribute to our observed patterns of phenotypic variation. First, basic changes at the physiological level might have caused the persistence of incubation-induced variation that we observed in some traits. As mentioned above, the relationships among traits that we observed to exhibit lasting developmental effects (e.g. relative forelimb length, inter-limb length, tail length) remain unclear, as do the relationships of these traits with sprinting performance at hatching. Susceptibility to plasticity in these traits may therefore confer no disadvantage (or advantage) to these animals.

Second, the concept of countergradient variation, in which the effects of selection counteract the proximate effects of temperature, could explain our observations. Animals incubated in a warmer environment had consistently larger values for mass and relative forelimb length and inter-limb length, despite the fact that animals from the central (cooler) latitude also had larger values for these traits. It is possible that, within the central California populations, although the direct physiological effect of temperature is smaller morphological trait values, selection is strong

for larger trait values, which counteracts the temperature effect. When released from that selection pressure and raised in a common environment, we would expect animals that develop in a warm environment to be larger (Berven, Gill & Smith-Gill, 1979; Conover & Present, 1990; Arendt & Wilson, 1999; Alvarez, Cano & Nicieza, 2006), as we observed for some traits. Indeed, the animals in the present study were raised purposefully under conditions that allowed them to thermoregulate freely; these conditions provided an opportunity to compensate for negative effects associated with the restrictive incubation environment.

The results obtained in the present study also showed, however, that the traits that differed only by population of origin (SVL, hindlimb length) were canalized in their body shape differences over time, such that the 'rank' order of phenotypes was preserved through ontogeny (across 5 weeks; Fig. 1); suggesting that compensatory growth is not occurring for these traits. Furthermore, the variation in these traits was consistent with adults from their source populations. Natural selection might thus be strong for canalization in the traits that contribute the most over time to organismal survival, such as body size and tail length (Berven *et al.*, 1979).

It is interesting to note that this explanation does not fit for head shape because head shape traits varied over time by incubation temperature and population of origin. In many lizards, maximum bite performance has been shown to be far greater than necessary for consuming invertebrate prey (Herrel *et al.*, 1999), and large bite forces instead has been implicated as the result of sexual selection for large head size and bite force in aggressive lizards (Lappin *et al.*, 2006; Herrel *et al.*, 2007). In this case, although we found no overall differences in head shape among sexes, it is possible that head shape is more susceptible to environmental differences as sexual selection begins to act on male lizards over ontogeny.

Irrespective of population of origin, hatchlings from the warm incubation treatments gained mass more quickly and had a higher BMI after the first week than did those from the cool incubation treatment. Although animals from cool climates tend to gain mass more slowly, they have a longer growth period within their lifetime and attain a larger adult body size. Because the present study was limited to 5 weeks, we could not determine whether cool-incubated lizards would overtake their warm-incubated counterparts over a longer time period. However, we found that body size differences among adults in these populations were consistent with Bergmann's rule, which is often cited as a cause of variation in body size along latitudinal and eleva-

tional gradients for populations within a species (Mayr, 1956). Phylogenetic analyses have shown that squamates tend to reverse Bergmann's rule (Arnett & Gotelli, 1999; Ashton & Feldman, 2003); however, the results obtained in the present study were consistent with Bergmann's rule along a latitudinal gradient. We found no differences in body size between the desert and mountain populations in southern California, but mountain lizards were larger than desert lizards in central California. Significant historical levels of gene flow have been shown between the two southern California sites (S. Adolph & C. McFadden, unpubl. data), which may explain the lack of size differences between the sites. Because the sites within each latitude are similar distances from each other (12–15 km), other factors, such as mountainous terrain, may prevent gene flow between the central California sites. Future studies should further investigate relationships among hatchlings and adults by including performance metrics such as sprinting and bite force in adult lizards.

Local adaptation and phenotypic plasticity are two factors that can contribute to an organism's phenotype, although the relative importance of each factor across ontogeny is poorly understood. In the present study, we found that, in *S. occidentalis*, some hatchling traits showed environmentally induced phenotypic variation, and that this variation persisted for 5 weeks into the animals' lifetime. Other hatchling traits, however, only differed among populations, suggesting that these traits are less plastic. The phenotypic differences we observed therefore appear to be a mosaic of plastic traits that are highly sensitive to the environment and canalized traits that are less sensitive. Future studies should measure specific traits' level of phenotypic plasticity in addition to their relative importance to organismal survival across a wide geographic range.

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