Evolutionary Ecology Research, 2014, **16**: 235–248

A test of the fast–slow continuum model of life-history variation in the lizard *Sceloporus grammicus*

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ABSTRACT

Background: The fast–slow continuum hypothesis (Promislow and Harvey, 1990) suggests that mortality rates are a strong selective factor that shapes inter- and intraspecific variation in life-history traits. At the fast end of the continuum, we expect higher mortality rates, faster growth rates, small size and/or early age at maturity, short lifespan, and large litters with smaller offspring. At the slow end, we expect the opposite.

Question: Is intraspecific (spatial) variation in life-history traits associated with spatial differences in mortality rates, as the fast–slow continuum hypothesis suggests?

Organism: The viviparous lizard *Sceloporus grammicus* (Sauria: Phrynosomatidae).

Study system: Eight different populations of *S. grammicus* in central Mexico (latitudinal range: 19°11′N to 20°47′N).

Methods: We used likelihood methods to calculate mortality rates from mark–recapture data. We also measured rates of body growth, size and age at maturity, litter size, offspring size, and offspring body condition from marked animals, preserved specimens, and females kept in captivity. We used a multi-model inference framework to examine inter-population variation in life-history traits and their potential association with mortality. Each model represented a different hypothesis about variation in life-history traits, and the relative fit of each was determined using AICc (adjusted Akaike Information Criterion).

Conclusions: Life-history traits differed widely among populations, but litter size was the only trait that varied with site-specific mortality rates. Larger litters were associated with higher mortality, consistent with the fast–slow continuum hypothesis. Other life-history traits showed no clear evidence of influence of mortality rates.

Keywords: age at maturity, body growth, life-history evolution, litter size, size at maturity, stage-specific mortality.

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INTRODUCTION

Life-history theory attempts to understand the diversity of life cycles in living organisms as well as the role that natural selection has played in the evolution of traits associated with survival, growth, and reproduction (Stearns, 1992; Roff, 2002). To understand the differences within and among species in their life histories, we need to explore the putative causal factors driving the correlated evolution of life-history traits (Roff, 2002). Theoretical models suggest that intra- and interspecific variation in life-history traits is often shaped by several selective factors. Perhaps the most important hypotheses are bet-hedging (Cohen, 1966; Den Boer, 1968; Murphy, 1968; Schaffer, 1974; Slatkin, 1974), r–K selection (MacArthur and Wilson, 1967), and the fast–slow continuum (Promislow and Harvey, 1990).

The fast–slow continuum hypothesis suggests that life-history traits covary with mortality rates. Specifically, higher mortality rates favour fast growth rates, small size and/or early age at maturity, short lifespan, and large litters with small offspring. Low mortality rates should favour the opposite set of traits. According to this model, species and populations occur within a gradient going from the 'fast' end (extremely high mortality and the fastest life cycles) to the 'slow' end (extremely low mortality and the slowest life cycles), depending on the particular regimes of mortality that they experience. Several studies have tested this model by comparing populations of different species and by removing the confounding effects of shared evolutionary history (Promislow and Harvey, 1990; Blackburn, 1991; Franco and Silvertown, 1996; Bauwens and Díaz-Uriarte, 1997; Clobert *et al.*, 1998; Heppell *et al.*, 2000; Rochet *et al.*, 2000; Sæther and Bakke, 2000; Dobson and Oli, 2008). In general, these studies suggest that mortality intensity has indeed had a significant effect on life-history variation among species, as predicted by the fast–slow continuum hypothesis.

However, one can also test the fast–slow continuum hypothesis by comparing isolated populations within a single species (Reznick and Ghalambor, 2001; Rojas-González *et al.*, 2008), where gene flow does not dilute the effects of local adaptation. Such intraspecific comparisons would allow us to explore the recent (microevolutionary) impact of age-specific mortality on life-history traits. Model predictions apply directly: populations experiencing higher mortality will exhibit relatively 'fast' life-history traits, whereas populations experiencing lower mortality will exhibit relatively 'slow' life-history traits. In this study, we tested these predictions by quantifying variation in key life-history traits (body growth rates, size and age at maturity, litter size, offspring size, and offspring body condition) of a viviparous lizard (*Sceloporus grammicus*), and then evaluating potential associations of these traits with site- and stage-specific mortality rates. We used demographic data from eight different populations as well as reproductive traits from both preserved individuals and captive females. Then we used a multi-model inference framework to evaluate life-story patterns.

MATERIALS AND METHODS

Study system

The viviparous lizard *Sceloporus grammicus* occurs in diverse habitats throughout central Mexico (Sites *et al.*, 1992) and has been studied extensively in ecological and evolutionary analyses (Arévalo *et al.*, 1994; Bastiaans *et al.*, 2013a, 2013b). However, the environmental causes that have promoted the observed spatial variation in life-history traits of this lizard remain unknown (Zúñiga-Vega *et al.*, 2008a, 2008b; Ramírez-Bautista *et al.*, 2011; Pérez-Mendoza *et al.*, 2014).

At other sites, males reach sexual maturity between 6 and 7 months of age, whereas females mature between 8 and 9 months (Jiménez-Cruz *et al.*, 2005). Births occur during spring and average-sized females produce about five offspring per litter (Guillette and Bearce, 1986; Ramirez-Bautista *et al.*, 2004, 2011). Litter size increases with female size (Jiménez-Cruz *et al.*, 2005; Ramírez-Bautista *et al.*, 2011).

We focused on eight populations of *S. grammicus* in the Mexican states of Hidalgo, Tlaxcala, and Queretaro (Table 1). We conducted mark–recapture experiments with these populations from July 2009 to November 2011. We visited each population about every two months, marked and recaptured individual lizards, collected live pregnant females (for litter parameters), and preserved specimens for histological examination (for details, see Pérez-Mendoza *et al.*, 2013).

Our studied populations may be genetically distinct because chromosomal races are known in *S. grammicus* (Arévalo *et al.*, 1993). The races of our study populations are not known with certainty (Pérez-Mendoza *et al.*, 2013). However, previous studies have treated known races as conspecific because extensive hybridization and mtDNA introgression occur among races (Arévalo *et al.*, 1993, 1994). Therefore, following the unified concept of species (de Queiroz, 2007), we do not treat chromosomal races of *S. grammicus* as evolutionary independent lineages.

Mortality rates

We used mark–recapture data to estimate site- and stage-specific mortality rates by likelihood methods implemented in the program MARK (White and Burnham, 1999). We used two stage classes: juveniles (individuals smaller than the minimum size at maturity) and adults. Size at maturity differed among populations (see below).

Since some juveniles became adults during our study, we used a multi-state framework (Brownie *et al.*, 1993) to estimate rates of survival (φ), recapture (p), and transition between juveniles and adults (ψ). We built competing models to account for different sources of variation in these parameters. For both φ and p, we tested the effects of stage (juvenile or adult) and site, as well as additive and interactive effects of these two factors. For ψ, we only

Table 1. Locations, sample sizes, and model-averaged annual mortality rates (standard errors are shown in parentheses) of the eight populations of the viviparous lizard, *Sceloporus grammicus*

Study site	Geographic coordinates	Sample sizes		Mortality rates	
		Juveniles	Adults	Juveniles	Adults
1	20°47′N, 99°43′W	19	79	0.64 (0.19)	0.52 (0.14)
2	20°02′N, 98°37′W	84	88	0.77 (0.11)	0.67 (0.06)
3	19°11′N, 97°55′W	45	103	0.79 (0.11)	0.69 (0.07)
4	20°16′N, 99°38′W	97	198	0.85 (0.09)	0.78 (0.07)
5	19°33′N, 98°13′W	100	133	0.86 (0.08)	0.79 (0.05)
6	20°01′N, 98°31′W	147	195	0.90 (0.05)	0.85 (0.03)
7	19°47′N, 98°32′W	83	165	0.92 (0.04)	0.87 (0.03)
8	19°38′N, 98°06′W	72	23	0.95 (0.04)	0.92 (0.05)

Note: Study sites are numbered according to mortality, from lowest to highest.

tested the effect of site (no stage effect because only juveniles become adults and not vice versa). In addition, we fitted null models for the three parameters (constant values with no effects of site or stage).

The fit of each model was evaluated using the adjusted Akaike Information Criterion for small sample sizes [AICc (Akaike, 1973; Hurvich and Tsai, 1993; Burnham and Anderson 2004)]. The AICc is a measure of model likelihood and parsimony, and the smallest value indicates the best-fitting model. A difference in AICc values (ΔAICc) larger than 2 indicates a real difference between models in fit to the data (Burnham and Anderson, 2002). We report ΔAICc for each competing model with respect to the best-fitting model.

To estimate site- and stage-specific annual survival rates, we followed the multi-model inference approach recommended by Burnham and Anderson (2002), which consists of calculating weighted averages of the annual survival rates based on the relative support for each model. These estimates of φ incorporate uncertainty in model selection and, therefore, are more robust than those derived from any single model (Johnson and Omland, 2004; Amstrup *et al.*, 2005). Finally, annual mortality rates were calculated as 1 – model-weighted annual survival rate. Despite the fact that newborns reach maturity before a year, mortality was calculated annually also, as time intervals in models were established annually. Because different stage-specific schedules of mortality can result in different life-history strategies (Promislow and Harvey, 1990; Rochet *et al.*, 2000; Bashey, 2008), we considered juvenile and adult mortality separately.

Body growth rates

Body growth rates were estimated as the difference in individual size [snout–vent length (SVL)] between two captures, divided by the time in days between captures (Zúñiga-Vega *et al.*, 2008a). Thus growth rates were measured as a daily rate (mm SVL per day). When an individual was captured more than twice, we used data from time intervals larger than 30 days and smaller than 100 days to minimize error associated with size measurements (Van Devender, 1978).

Size and age at maturity

We determined size at maturity as the size of the smallest female with enlarged follicles (determined by palpation of free-ranging females and by dissections of preserved specimens), and of the smallest male with mature spermatozoids (histological analysis). Data on size at maturity included information reported by Pérez-Mendoza *et al.* (2013), as well as new data obtained during 2013.

To estimate age at maturity, we constructed growth curves based on theoretical growth models (size vs. age). We fitted three different growth models separately for each study site and sex: Von Bertalanffy (1957), logistic by weight, and logistic by length (Dunham, 1978; Schoener and Schoener, 1978). All three models account for the size-dependence of growth rates (i.e. smaller individuals grow faster than larger ones). These models have two parameters: the asymptotic body length (A) and the characteristic growth (damping) parameter (r). For each model we calculated R^2 as a measure of fit. For detailed descriptions of the growth models, see Dunham (1978).

The Von Bertalanffy model had the best fit in most cases, except for females from site 1 and for males from site 8. All growth models had similar fit for these cases. Therefore, we used the Von Bertalanffy parameters to construct growth curves and to estimate age at maturity for each sex and for each population. We report site- and sex-specific age at maturity in months.

Litter size, offspring size, and offspring body condition

We captured gravid females from the study sites during February, March, and April of 2011. These months correspond to the late phases of pregnancy (Pérez-Mendoza *et al.*, 2014). Captured females were kept in the laboratory in individual terraria and provided with food and water *ad libitum*. Environmental temperature and photoperiod were held as similar as possible to their site-specific natural conditions. Every other day we measured (SVL) and weighed (g) females until parturition. Most females gave birth shortly after capture (most within 15 days). A few females remained in captivity as long as one month. Shortly after parturition, females and their offspring were released in their home population.

For each female, we quantified litter size as the number of newborns produced, regardless if they were born dead or alive; even though those dead individuals cannot be considered as recruitment for the population, they represent a cost for females. We thus ran the litter size analysis with and without (analysis not shown) dead individuals and the results show the same pattern, except the models without dead individuals have weaker support. We measured mass and SVL of every newborn within one day of birth. Offspring body condition was calculated as $\text{mass}^{1/3}/\text{SVL}$ (Stevenson and Woods, 2006; Vervust *et al.*, 2008). To characterize individual litters, we estimated and analysed the average offspring size (SVL) and body condition for each litter (for this analysis, dead born individuals were excluded, as they usually were highly dehydrated; therefore body mass is unreliable).

Statistical tests of the fast–slow continuum hypothesis

To examine variation in life-history traits (body growth rates, size and age at maturity, litter size, offspring SVL and body condition) and their potential association with mortality, we implemented generalized linear models in R (R Development Core Team, 2008). Each model represents a different hypothesis about the life-history traits. To treat each trait individually, we fitted separate sets of models to the data of each life-history trait. For most traits, we used a Gaussian distribution of the error term and an identity link function; for litter size, however, we used a Poisson distribution of the error term and a log link function.

For body growth rates, we tested the effects of initial size for the analysed time period (SVL), site, sex, and of the site-specific estimates of juvenile and adult mortality. We also tested two-way additive and interactive effects of these variables (except between juvenile and adult mortality). Testing the effect of SVL accounts for the fact that in *S. grammicus* body growth rates are size-dependent (Zúñiga-Vega *et al.*, 2008a). The sample sizes reported here are the total number of individuals from which we could estimate growth rates (174 females and 173 males).

For size and age at maturity, we tested the effects of sex, juvenile mortality, adult mortality, as well as additive and interactive effects between sex and juvenile mortality and between sex and adult mortality. Here we did not test the effects of site or individual SVL because only one data point was available for each site and sex (i.e. the average size and age at maturity that we calculated for each site and sex; total $n = 16$).

For litter size, offspring SVL, and offspring body condition, we tested the effects of site, maternal size (SVL), maternal body condition, juvenile mortality, and adult mortality. We also tested additive and interactive effects of these predictor variables (except between juvenile and adult mortality). We tested the effect of maternal body condition because previous studies demonstrated that litter size, offspring size, and offspring body condition depend on the body condition of the mother in addition to the widely recognized effect of maternal size itself (Goodman, 2010; Rosier and Langkilde, 2013). Maternal body condition was also calculated as mass$^{1/3}$/SVL. Here we used the female mass and SVL measurements within one day of parturition. The sample size is the total number of females that gave birth in the laboratory ($n = 73$).

In all cases, models including effects of either juvenile or adult mortality address the fast–slow continuum hypothesis. For each life-history trait, we also fitted null models (i.e. a constant value of the trait with no effects of predictor variables). We evaluated model fit and differences in fit between models by their AICc and ΔAICc, respectively (Burnham and Anderson, 2002).

RESULTS

Mortality rates

Two models had strong support in the mark–recapture data. The best-fitting model indicated that survival (φ) varied by site and by stage (see evolutionary-ecology.com/data/2906Appendix.pdf, Table S1). The combined effect of these two predictors was additive, meaning that the difference in mortality (1 − φ) between juveniles and adults was similar at all sites. Juveniles had consistently higher annual mortality than did adults (Table 1). The second best-fitting model (site only) had similar support (ΔAICc = 0.7). Variation in model-averaged mortality among sites ranged between 0.64 and 0.95 for juveniles and between 0.52 and 0.92 for adults (Table 1). Note that sites with relatively low juvenile mortality also had relatively low adult mortality, and sites with relatively high juvenile mortality also had relatively high adult mortality ($r_p = 0.99$, $t = 38.35$, $P < 0.01$).

In the two best-fitting models, recapture probability (p) was affected by the additive effect of site and stage (variation among sites: 0.01–0.14 for juveniles and 0.11–0.25 for adults), whereas probability of maturing (ψ) was similar across sites (0.26 ± 0.08 s.e.; 2906Appendix.pdf, Table S1). However, model-weighted averages of ψ varied moderately among sites (between 0.21 and 0.33).

Life-history traits and potential associations with mortality

All life-history traits varied among sites (Table 2). Age at maturity had the greatest inter-population variation (between 5.3 and 12.4 months for males, 5.4 and 10.0 months for females), whereas offspring body condition had the least (between 0.030 and 0.032).

Two models for body growth had strong support. Both indicated that variation in growth was explained by size and by site (2906Appendix.pdf, Table S2). The best-fitting model indicated an additive effect, whereas the second best model indicated an interactive effect (ΔAICc = 1.8). As expected, the growth rates declined with SVL (β from the top model = −0.004 ± 0.0002 s.e.). Including either juvenile or adult mortality yielded models with remarkably poor fits (ΔAICc > 64; Table S2).

Table 2. Average estimates of life-history traits for eight populations of the viviparous lizard *Sceloporus grammicus* (standard errors are shown in parentheses)

Study site	Size at maturity (mm SVL)		Age at maturity (months)		Body growth parameter (*r*)		Litter size	Offspring size	Offspring body condition
	Females	Males	Females	Males	Females	Males		(mm SVL)	(mass$^{1/3}$/SVL)
1	41.4	48.8	10.0	9.0	0.002 (0.0013)	0.004 (0.0013)	3.3 (1.8)	21.2 (0.6)	0.030 (0.0006)
2	40.7	42.5	5.4	5.6	0.006 (0.0011)	0.006 (0.0010)	5.3 (0.6)	21.2 (0.1)	0.030 (0.0002)
3	42.9	51.0	5.7	8.1	0.004 (0.0004)	0.003 (0.0012)	4.2 (0.4)	22.2 (0.8)	0.031 (0.0003)
4	41.4	41.6	6.1	5.3	0.006 (0.0017)	0.005 (0.0007)	3.4 (0.3)	21.6 (0.3)	0.030 (0.0004)
5	48.1	47.6	7.0	12.4	0.005 (0.0011)	0.002 (0.0006)	3.9 (0.4)	23.3 (0.3)	0.030 (0.0004)
6	39.4	44.6	8.2	5.9	0.004 (0.0005)	0.007 (0.0010)	4.3 (0.3)	20.5 (0.2)	0.030 (0.0003)
7	41.5	45.6	7.5	10.0	0.004 (0.0010)	0.003 (0.0012)	3.5 (0.3)	18.7 (0.5)	0.032 (0.0003)
8	43.1	44.0	8.2	12.4	0.003 (0.0011)	0.002 (0.0021)	3.5 (1.0)	22.5 (0.5)	0.030 (0.0005)

Note: SVL = snout–vent length.

For size at maturity, the best-fitting model indicated that sex was the best predictor (2906Appendix.pdf, Table S2). Males matured at slightly larger sizes than did females in most populations (not site 5; Table 2). All other models resulted in worse fit (ΔAICc > 2). Support for effects of juvenile or adult mortality on size at maturity was thus weak.

For age at maturity, two models had strong support (2906Appendix.pdf, Table S2). The best-fitting model indicated constant age at maturity across sites and between sexes, whereas the second best model indicated differences between the sexes (ΔAICc = 1.2). In five of eight sites, males matured later than females (Table 2). All other models resulted in worse fits (ΔAICc > 2). Thus, the effects of juvenile or adult mortality on age at maturity were weak.

For litter size, four models had similar fits (2906Appendix.pdf, Table S2). All included a positive effect of maternal SVL (β from the top model = 0.02 ± 0.009 s.e.). The second best-fitting model included an additive effect between maternal SVL and maternal body condition (β for maternal body condition = 26.3 ± 21.9 s.e.; ΔAICc = 0.7). The third and fourth best-fitting models included interactive effects between maternal SVL and juvenile mortality and between maternal SVL and adult mortality, respectively (ΔAICc = 1.7 and 1.8, respectively; Table S2). Both juvenile and adult mortality had positive effects on litter size (β for juvenile mortality = 14.6 ± 9.0 s.e.; β for adult mortality = 10.6 ± 6.6 s.e.).

The interactive effect between maternal SVL and juvenile mortality on litter size is shown in Fig. 1. Larger female size and higher juvenile mortality are both associated with larger litters. However, at the highest mortalities, the relationship between female SVL and litter size is opposite: larger females produce slightly fewer newborns (Fig. 1). Given that sites with low juvenile mortality correspond to sites with low adult mortality, and sites with high juvenile mortality correspond to sites with high adult mortality, the interaction between maternal SVL and adult mortality affecting litter size is virtually identical to that between maternal SVL and juvenile mortality.

For offspring size, two models had strong support (2906Appendix.pdf, Table S2). The best-fitting model only included the effect of site, whereas the second best model also included an additive effect between maternal SVL and site (ΔAICc = 0.4). The effect of maternal SVL was positive (β = 0.04 ± 0.03 s.e.). Models that included effects of either juvenile or adult mortality on offspring SVL had remarkably poor fits (ΔAICc > 23; Table S2).

For offspring body condition, three models had similar fits to the data (2906Appendix.pdf, Table S2). The best-fitting model indicated constant offspring body condition (null model) with no effects of predictor variables. The second and third best-fitting models included effects of maternal SVL and maternal body condition, respectively (ΔAICc = 0.1 and 1.6, respectively). Both effects were positive (β for maternal SVL = 0.00004 ± 0.00003 s.e.; β for maternal body condition = 0.04 ± 0.06 s.e.). All other models resulted in worse fit (ΔAICc > 2). Thus, the effects of juvenile or adult mortality on offspring body condition were weak.

DISCUSSION

Stage-specific mortality rates (Table 1) differed widely among populations of *S. grammicus* (Ortega-Rubio and Arriaga, 1990; Ortega-Rubio *et al.*, 1999; Zúñiga-Vega *et al.*, 2008b). Spatial differences in mortality schedules theoretically can lead to spatial differences in the patterns of co-variation among life-history traits (Gordon *et al.*, 2009; Seiter and Kingsolver, 2013). The fast–slow continuum hypothesis suggests that under intense mortality, populations should evolve

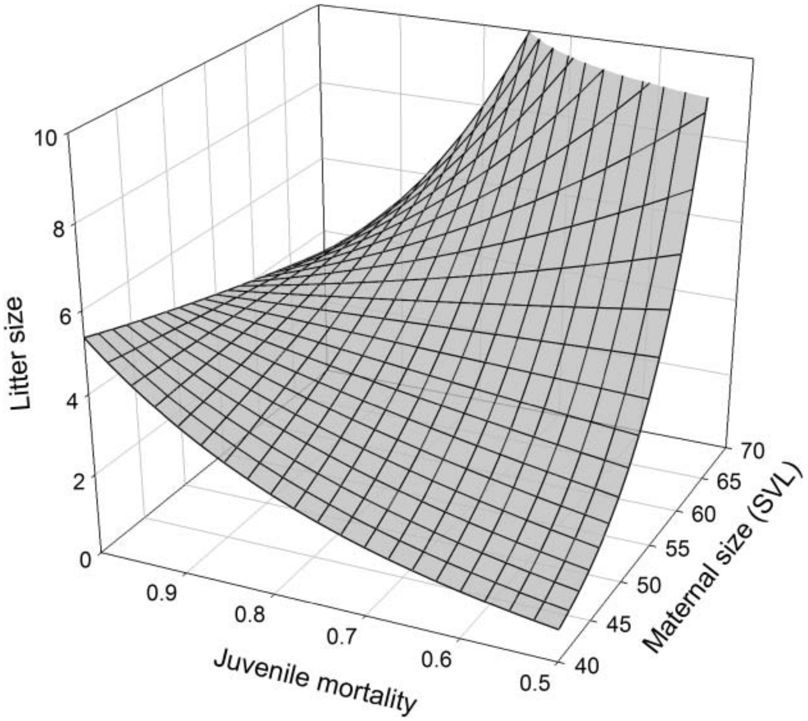

Fig. 1. Interactive effect of maternal size (snout–vent length, SVL) and juvenile mortality on litter size for eight populations of the lizard *Sceloporus grammicus*. The model is $\log_{10}$ (litter size) = −12.3 + 0.2 maternal SVL + 14.6 juvenile mortality – 0.3 maternal SVL × juvenile mortality.

'fast' life cycles (early age at maturity, small size at maturity, fast body growth, and a large number of small offspring). In contrast, under low mortality, populations should evolve 'slow' life cycles (late age at maturity, large size at maturity, slow body growth, and a few but large offspring) (Promislow and Harvey, 1990). The present study is one of the few to have tested this theoretical model by sampling more than two populations of a single species (Nielsen *et al.*, 2009; Moreno-Arias and Urbina-Cardona, 2013).

Our results provide partial support for the fast–slow continuum hypothesis. There was good support for an effect of both juvenile and adult mortality on litter size (2906Appendix.pdf, Table S2). Higher mortality apparently selects for larger litters (Fig. 1). Several studies of different taxa have also demonstrated that high-mortality environments are associated with higher fecundity (Gasser *et al.*, 2000; Reznick *et al.*, 2001). Furthermore, experimentally increased mortality rates for several generations resulted in females producing more offspring (Reznick *et al.*, 1990). Higher mortality selects for larger litters because this increases the probability of at least one offspring surviving to reproduce. This must be particularly true for species without parental care, such as most lizard species (Tinkle *et al.*, 1970; Shine, 2005).

The fast–slow continuum hypothesis also predicts large litters with relatively small young in high-mortality environments because of the potential trade-off between offspring size and number (Promislow and Harvey, 1990; Roff, 2002). This trade-off may result from limitations of available energy or space within the reproductive tract (Warne and Charnov, 2008). However, litter size in our populations was not statistically associated with offspring SVL ($r = -0.04$, $P = 0.75$) or offspring body condition ($r = -0.07$, $P = 0.54$). Hence, in high-mortality environments, females of *S. grammicus* produce more offspring of the same size and body condition than females inhabiting low-mortality environments and thus make a larger reproductive investment.

Furthermore, we observed an interaction between mortality and maternal size that affected litter size (2906Appendix.pdf, Table S2). In general, larger females produce more newborns in numerous taxa (Fox and Czesak, 2000), including lizards (Tinkle *et al.*, 1970; Shine, 2005). However, in high-mortality environments, the litter size of larger *S. grammicus* females is slightly less than that of smaller females (Fig. 1). This is an intriguing pattern that lacks a clear explanation.

The effects of mortality rates on all the other life-history traits (body growth rates, size and age at maturity, offspring size, and offspring body condition) were weak. Neither juvenile nor adult mortality could explain more variation than already explained by sex, site, size, maternal size or maternal body condition (2906Appendix.pdf, Table S2). Because the fast–slow continuum hypothesis was unsupported in these traits, intraspecific variation in annual mortality does not appear to be a strong selective factor that promotes spatial variation. Several other potential selective factors (and their interactions) and/or spatial variation in life-history trade-offs might have promoted the observed inter-population variation in these life-history traits.

For instance, spatial variation in food availability and in the thermal regime might result in spatial variation in the rates of body growth and in the size and age at maturity of ectothermic vertebrates (Sinervo and Adolph, 1994; Adolph and Porter, 1996; Angilletta, 2001). In addition, inter-population differences in the social system might affect patterns for male lizards (Stevenson and Bancroft, 1995; Bastiaans *et al.*, 2013b). Intense territoriality and agonistic interactions between males due to competition for mates promote delayed age at maturity because relatively older males are usually larger and have better territories (Lima and Dill, 1990; Cooper, 1999; Calsbeek and Sinervo, 2002; Cooper and Vitt, 2002).

Spatial differences in food availability and in the thermal environment may also promote inter-population variation in offspring size and body condition. In environments where food or thermal opportunities are restricted, females produce smaller embryos that require less energetic resources (Wapstra, 2000; Lourdais *et al.*, 2004; Du *et al.*, 2005). In addition, spatial variation in population density might also promote differences in offspring size and body condition because high density usually increases intraspecific competition, which in turn selects for newborns with large size or better body condition (Bashey, 2008).

Alternative explanations for the observed inter-population variation in life-history traits focus on historical processes rather than on environmental factors. As noted above, our populations might belong to distinct chromosomal races (Arévalo *et al.*, 1994). Therefore, populations sharing the same chromosomal race may share similar life histories just because of shared ancestry. The phylogeographic history of these populations, along with formal comparative methods that account for shared ancestry are needed to test this hypothesis.

The seminal study on the fast–slow continuum hypothesis (Promislow and Harvey, 1990) found that, among several mammal species, juvenile mortality had a stronger correlation with life-history traits than did adult mortality. However, the intensity of mortality might have differential selective effects on life history, depending on whether high mortality occurs on either juveniles or adults (Roff, 2002). We expected a stronger correlation between adult mortality and body growth rates, age, and size at maturity because, for adults, a high risk of dying entails the consequence of not reproducing at all. Therefore, individuals that reach maturity quickly (i.e. fast-growing individuals) would be more likely to leave offspring. In contrast, we expected a stronger correlation between juvenile mortality and litter size, offspring size, and offspring body condition because, if the risk of dying is higher for young individuals, then large litters or large newborns in better body condition must be favoured (Stearns and Koella, 1986; Stearns, 1992; Roff, 2002). However, we did not find stronger effects of either juvenile or adult mortality on the single life-history trait that was affected by mortality rates (i.e. litter size). The positive effects of juvenile and adult mortality had similar support in our data (i.e. ΔAICc < 2; 2906Appendix.pdf, Table S2). This similar effect can be explained by the fact that our two mortality estimates were strongly related. Populations of *S. grammicus* that experienced high juvenile mortality also experienced high adult mortality.

ACKNOWLEDGEMENTS

This paper is a requisite to fulfil the requirements to obtain a doctorate degree in the Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México. We would like to thank the Consejo Nacional de Ciencia y Tecnología 210458 and the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (project PAPIIT-IN206309-3) from Universidad Nacional Autónoma de México for financial support of this research. We also thank C. Martorell and J. Fornoni for comments that improved the manuscript. Finally, we thank I. Solano-Zavaleta, P. Mendoza-Hernández, A. Hernández-Rosas, A. Molina-Moctezuma, Y. Zurita-Gutiérrez, J. Maceda-Cruz, L. Moyers-Arévalo, M. Romano-García, C. Molina-Zuluaga, C. Olivera-Tlahuel, and F. Rodríguez-Reyes for field assistance.

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