



## Evolutionary patterns in life-history traits of lizards of the genus *Xenosaurus*

J. Jaime Zúñiga-Vega<sup>1</sup>, Jesualdo A. Fuentes-G.<sup>2</sup>, J. Gastón Zamora-Abrego<sup>3</sup>, Uri O. García-Vázquez<sup>4</sup>, Adrián Nieto-Montes de Oca<sup>5</sup> & Emília P. Martins<sup>2,6</sup>

<sup>1</sup>Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México. Ciudad Universitaria, Distrito Federal, 04510, México.

<sup>2</sup>Department of Biology, Indiana University. Bloomington, Indiana, 47405, United States.

<sup>3</sup>Departamento de Ciencias Forestales, Facultad de Ciencias Agrarias, Universidad Nacional de Colombia. Medellín, Antioquia, 050034, Colombia.

<sup>4</sup>Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México. Batalla 5 de Mayo s/n, Ejercito de Oriente, Iztapalapa, Distrito Federal, 09230, México.

<sup>5</sup>Laboratorio de Herpetología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México. Ciudad Universitaria, Distrito Federal, 04510, México.

<sup>6</sup>School of Life Sciences, Arizona State University, Tempe, Arizona, 85287, United States.

Life histories are directly related to fitness and, hence, are the focus of strong selective pressures. However, different life-history traits may evolve at different paces and may respond differentially to particular selective pressures. We examined patterns of evolutionary change in the following life-history traits of xenosaurid lizards: size at maturity, average size of adult females, litter size, neonate size, and relative litter mass. We used a phylogenetic hypothesis of the genus *Xenosaurus* and different phylogenetic comparative methods to search for evolutionary relationships between traits as well as to estimate ancestral states, rates of evolution, and the amount of phylogenetic signal on each trait. In addition, we searched for differences in these life-history traits among the different environments where these lizards inhabit (cloud forest, tropical forest, oak-pine forest, and xeric scrub). We found an evolutionary relationship between size at maturity and average adult size, with larger species maturing at larger sizes. We also found an evolutionary trade-off between litter size and neonate size. Ancestral state reconstructions revealed differences among traits in the relative timing of diversification. Litter size and neonate size began diversification early in the history of the genus. In contrast, size at maturity and relative litter mass remained phenotypically invariant for a long time period before diverging into distinct phenotypic values. Litter size exhibited significant phylogenetic signal because the diversification history of this trait has tracked the phylogeny closely. The observed variation among species in neonate size also showed some trace of the phylogenetic relationships. The remaining three traits diverged throughout time without a clear phylogenetic pattern. In addition, litter size and relative litter mass exhibited the highest evolutionary rates whereas average adult size and neonate size exhibited the lowest rates. Litter size was the only trait that differed significantly among environments, with largest litters in cloud forests. We discuss potential hypotheses to explain the observed differences among life-history traits in the tempo and mode of evolution.

*Key words:* ancestral state reconstructions, evolutionary rates, life histories, phylogenetic signal, trade-offs, xenosaurid lizards.

### INTRODUCTION

Life-history traits are strongly linked to individual fitness (Roff, 2002). The particular combination of age and size at maturity, body growth rates, adult size, number and size of offspring, and lifespan directly determines the total reproductive output of all living organisms. Hence, natural selection is usually strong on these phenotypic traits and changes in the local conditions may promote adaptive responses that quickly lead to new phenotypic optima (Lande, 1982; Crozier et al., 2008; Zhu et al., 2014). Life-history traits may also vary among different environments as a result of phenotypic plasticity (e.g., Karjalainen et al., 2016; Osorio et al., 2017). However, within particular lineages, the evolution of life-history traits might also be driven by random processes such as genetic drift, which promote gradual changes that accumulate throughout time. In this case, variation

among species and populations in life-history traits may be better explained by their phylogenetic relationships, with closely related species or populations being more similar to each other compared to distant species or populations (i.e. phylogenetic signal; Blomberg & Garland, 2002; Revell et al., 2008). However, similarity between closely related species might also occur when they inhabit similar environments. In this case, resemblance in their life histories might be explained by parallel adaptations to the same ecological conditions rather than by shared ancestry (Losos, 2008). Several studies focused on the evolution of life-history traits have attempted to understand how much of the phenotypic variation is accounted for by the ancestor-descendant relationships within the focal lineage and how much can be associated with selection operating in local environments (e.g., Staggemeier et al., 2010; Brandt & Navas, 2011; Vukov et al., 2014; Salguero-Gómez et al., 2016).

*Correspondence:* J. Jaime Zúñiga-Vega (jzuniga@ciencias.unam.mx)

However, we can expect differences among life-history traits in how much of the variation among taxa can be explained by local adaptation versus phylogenetic history, as well as in the timing and amount of evolutionary change (Gittleman et al., 1996; Ackerly, 2009; Adams, 2013). Such differences in how these traits evolve can arise from several causes, such as constraints caused by particular trade-offs with other traits (Poos et al., 2011), differences among traits in both the amount of genetic variability and degree of phenotypic plasticity (Houle, 1992; Osorio et al., 2017), specific selective pressures arising from the local conditions that affect one particular trait but not others (Kingsolver et al., 2001), and differences in their relative impact on the fitness of individuals (Stearns, 1992; Burns et al., 2010). For example, age and size at maturity usually have the strongest impacts on fitness such that, under a set of particular conditions, minimal differences in these traits from the optima are rapidly selected against (Stearns & Koella, 1986; Oli & Dobson, 1999; Crozier et al., 2008). Both theoretical and empirical studies have demonstrated that individual fitness is strongly correlated with age and size at maturity, such that slight changes in these life-history traits may have profound impacts on the lifetime reproductive output (Heino & Kaitala, 1997; Oli et al., 2002; Verdú, 2002; Kinnison et al., 2011). In this way, changes in the selective environment should quickly promote changes in these two traits (assuming sufficient genetic variability and no constraints). Therefore, we expect lower phylogenetic signal in age and size at maturity compared to other life-history traits such as litter size, size at birth, adult body size, or longevity. However, if closely related species experience similar selective pressures affecting age and size at maturity, we would observe high phylogenetic signal in the ecological conditions and, in consequence, high phylogenetic signal in age and size at maturity (Losos, 2008; Revell et al., 2008).

Trade-offs might also account for differences among life-history traits in the tempo and mode of evolution. For example, numerous studies have documented a physiological trade-off between number and size of offspring (e.g., Kolm et al., 2006; Walker et al., 2008; Warne & Charnov, 2008). Producing a large number of offspring usually comes at the cost of decreasing their individual size because energy and resources are limited. Similarly, producing large individual offspring usually causes a reduction in their number. In viviparous organisms, this trade-off between litter size and size at birth can also result from space restrictions within the female reproductive tract (Bleu et al., 2013; Ford & Seigel, 2015). In many oviparous species, the total number of offspring may also be constrained by the size of each individual egg, which in turn is apparently constrained to an optimal volume (larger eggs cannot pass undamaged through the pelvic girdle and smaller eggs may not contain enough nutrients to support embryo development; Congdon & Gibbons, 1987; Rollinson & Brooks, 2008). Even when there is strong directional selection for changing the number or size of offspring, the tight link between these two traits may restrict their response to selection, leading to a negative evolutionary

correlation between number and size of offspring.

Evidence for different evolutionary patterns and trade-offs between life-history traits can be found in diverse taxa such as fishes (Rochet et al., 2000), amphibians (Gomez-Mestre et al., 2012), birds (Ricklefs, 2000), and mammals (De Magalhães et al., 2007). However, the tempo and mode of life-history evolution have not been examined in several lineages of reptiles, including several snakes and lizards which are under-represented in the literature on this topic (Bauwens & Díaz-Uriarte, 1997; Clobert et al., 1998; Shine, 2005; Scharf et al., 2015; Mesquita et al., 2016). In this study, we used different phylogenetic comparative methods to estimate and compare evolutionary patterns in life-history traits of lizards in the Neotropical genus *Xenosaurus*. Xenosaurid, or knob-scaled, lizards are small, live-bearing, and crevice-dwelling animals, closely related to the anguillid alligator and legless lizards. Xenosaurid lizards are only found in restricted habitats of Mexico and Guatemala (Lemos-Espinal et al., 2012). We focused on: (1) searching for evolutionary relationships (e.g., trade-offs) between traits, (2) reconstructing life-history traits for the common ancestor of the genus, and estimating (3) the amount of phenotypic change throughout time (i.e. evolutionary rates) as well as (4) the amount of phylogenetic signal in each trait and in the different environments that these lizards inhabit.

In addition, given that similar environmental conditions may have promoted convergent evolutionary changes in the life histories of these lizards, we examined if different types of environment (i.e. cloud forest, tropical forest, oak-pine forest, and xeric scrub) have had different evolutionary impacts on the life-history traits. We addressed this additional question also using a phylogenetically-informed approach.

## MATERIALS AND METHODS

### Study species, life-history data, and phylogeny

Lizards of the genus *Xenosaurus* are members of the monotypic family Xenosauridae and are viviparous, crevice-dwelling lizards found only in restricted areas of eastern and southern Mexico and western and central Guatemala (Lemos-Espinal et al., 2012). Currently, eight species have been formally described. One of them, *X. grandis*, has five subspecies, some of which have been treated as species in other studies (Niето-Montes de Oca et al., 2013). In addition, other populations of uncertain taxonomic status may also represent undescribed species (Zamora-Abrego, 2009; Niето-Montes de Oca et al., 2017). We conducted an extensive literature search from which we gathered life-history data for nine recognised taxa (six species and three subspecies of *X. grandis*) and five populations whose taxonomic status is still uncertain (Table 1). We analysed the following five life-history traits: female minimum size at sexual maturity (mm snout-vent length, SVL), average adult female size (mm SVL), litter size (number of newborns), average size of the neonates (mm SVL), and relative litter mass (RLM, which is the proportion of the female mass that is devoted to reproduction) (Table 1). In those cases

where data was available from two different localities, we calculated a weighted average using the sample size of each locality as the weighting factor. Only in one case (*X. tzacualtipantecus*) data was not available for all five life-history traits (Table 1; Fig. 1). We log-transformed these variables before analyses to place them on a common scale and to homogenise variances (this is particularly important for estimating evolutionary rates; Adams, 2013).

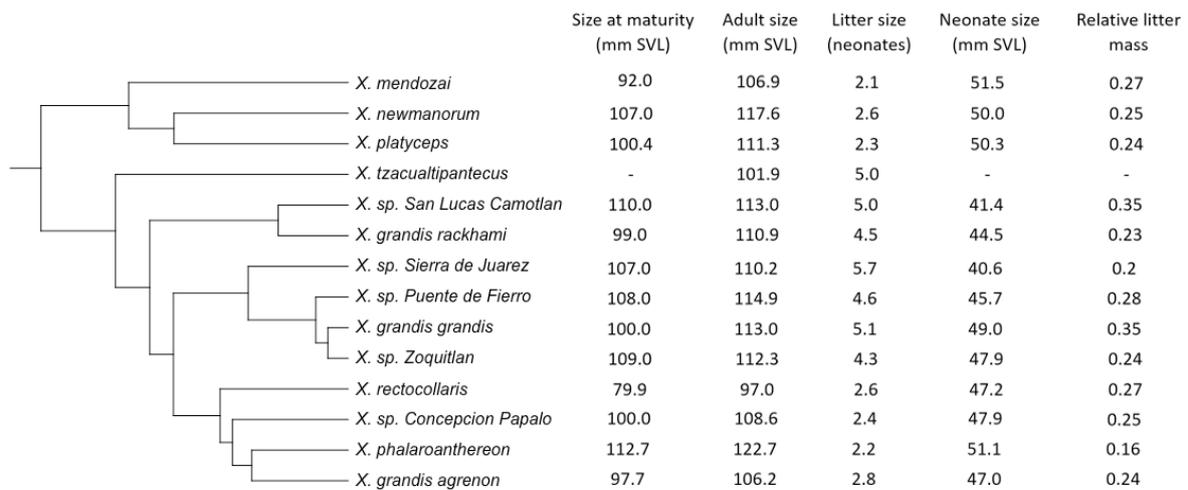
We based our comparative analyses on the phylogenetic hypothesis for the genus *Xenosaurus* recently inferred from RADseq data with maximum likelihood methods by Nieto-Montes de Oca et al. (2017). Branch lengths were estimated as the number of expected substitutions per site. We trimmed the phylogeny to the 14 taxa for which life-history data were available (Table 1), and created an ultrametric tree (Fig. 1) by using a semi-parametric smoothing method based on penalised likelihood (Sanderson, 2002) implemented in the R package ‘ape’ (Paradis et al., 2004; R Development Core Team, 2008). We used a smoothing parameter equal to 0.1, which is a conservative value (Revell & Reynolds, 2012). For our study we did not differentiate between recognised species (or subspecies) and populations of uncertain taxonomic status. Instead, we treated them all as evolutionary independent units because all the known populations of these lizards are geographically isolated and because xenosaurid lizards are highly phylopatric and exhibit remarkably restricted movement (Zamora-Abrego, 2009; Lemos-Espinal et al., 2012). Hence, gene flow among populations is likely negligible (Nieto-Montes de Oca et al., 2017). We used information on the topology and branch lengths from the ultrametric tree as estimates of expected evolutionary divergence (Fig. 1).

**Evolutionary relationships**

We followed two approaches to search for evolutionary relationships between pairs of life-history traits. First, we

estimated correlation coefficients using phylogenetically independent contrasts (Felsenstein, 1985) calculated with the R package ‘ape’ (Paradis et al., 2004). Felsenstein’s (1985) method assumes that traits evolve along a phylogeny with random fluctuations occurring at a constant rate, such as when phenotypes diverge predominantly under random genetic drift. This mode of evolution can be described by a Brownian motion model in which the expected phenotypic difference between sister species grows in direct proportion to the time of divergence from a common ancestor. Using Felsenstein’s independent contrasts (FIC), we calculated a phylogenetically-corrected correlation coefficient (*r*) to describe the magnitude of the evolutionary relationship between each pair of traits (forced through the origin as per Martins & Garland, 1991). We also calculated a non-phylogenetic correlation coefficient for each pair of life-history traits using the observed data. This non-phylogenetic correlation assumes a ‘star’ phylogeny, with phenotypes evolving without any trace of the phylogenetic relationships between taxa.

Second, we used phylogenetic generalised least squares (PGLS; Martins & Hansen, 1997) to search for potential evolutionary relationships between life-history traits. PGLS explicitly incorporates the phylogenetic information as part of the error term of the regression model. We implemented this procedure using different microevolutionary assumptions. First, we assumed that traits coevolve in a way that is well-described by a Brownian motion model (PGLS-BM), such that changes accumulate steadily through time, leaving substantial phylogenetic signal. Hence, PGLS-BM provides the exact same result as would fitting a least-squares regression using Felsenstein (1985) contrasts as input variables (Rohlf, 2001). Second, we assumed that phenotypic evolution is better described by an Ornstein-Uhlenbeck model of evolution, as would, for example, phenotypes experiencing random genetic drift with some stabilising



**Figure 1.** Phylogenetic hypothesis for 14 distinct taxa of the lizard genus *Xenosaurus*. Populations of uncertain taxonomic status are identified by the name of the type locality. We used this phylogeny to implement all phylogenetic comparative methods. Branch lengths represent relative time. We show for each taxon the five life-history traits that we analysed. In those cases where data was available from two different localities (see Table 1), the values that we show correspond to weighted averages across localities.

**Table 1.** Minimum female size at maturity, average adult female size, litter size, neonate size, and relative litter mass for 14 distinct taxa of lizards of the genus *Xenosaurus*. These data represent six species, three subspecies, and five populations of uncertain taxonomic status (identified by the name of the type locality within parentheses). Relative litter mass is the proportion of female mass devoted to reproduction. The type of ecosystem and altitude (m above sea level) are also shown. The codes are used in figures to identify each taxon. For some taxa and some traits data was available from two different localities. Standard errors can be found in the original sources, and are not shown here because they were not included in the phylogenetic comparative analyses. SVL = snout-vent length.

Taxon	Code	Locality and Mexican state	Size at maturity (mm SVL)	Adult size (mm SVL)	Litter size (neonates)	Neonate size (mm SVL)	Relative litter mass	Altitude (m)	Type of environment	References
<i>X. sp.</i> (Zoquitlán)	Xzoq	Zoquitlán, Puebla	109	112.3	4.3	47.9	0.24	2000	Cloud forest	Zamora-Abrego et al. 2007
<i>X. grandis grandis</i>	Xgra	Cuatlan, Veracruz	100	113.0	5.1	49.0	0.35	1100	Tropical forest	Ballinger et al. 2000
<i>X. sp.</i> (Puente de Fierro)	Xpfi	Puente de Fierro, Oaxaca	108	114.9	4.6	45.7	0.28	1108	Tropical forest	Zamora-Abrego et al. 2007
<i>X. sp.</i> (Sierra de Juárez)	Xsju	Sierra de Juárez, Oaxaca	107	110.2	5.7	40.6	0.20	1750	Cloud forest	Zamora-Abrego et al. 2007
<i>X. sp.</i> (Concepción Pápalo)	Xcpa	Concepción Pápalo, Oaxaca	100	108.6	2.4	47.9	0.25	2097	Oak-pine forest	Zamora-Abrego et al. 2007
<i>X. phalaroanthereon</i>	Xpha	San Juan Acaltepec, Oaxaca	109	119.2	2.3	51.1	0.16	2130	Oak-pine forest	Zamora-Abrego et al. 2007
		Santa María Ecatepec, Oaxaca	117	125.0	2.0	—	—	2185	Oak-pine forest	Lemos-Espinal & Smith 2005; Sheetz et al. 2010
<i>X. grandis agrenon</i>	Xagr	San Gabriel Mixtepec, Oaxaca	98	107.0	2.7	47.0	0.24	724	Tropical forest	Zamora-Abrego et al. 2007
		San Juan Lachao, Oaxaca	97	105.0	3.2	46.3	—	1000-1470	Tropical forest	Lemos-Espinal et al. 2003
<i>X. rectocollaris</i>	Xrec	Zapotitlán de las Salinas, Puebla	93	102.9	2.6	47.2	0.27	2200	Xeric scrub	Zamora-Abrego et al. 2007
		Tehuacán Valley, Puebla	69	92.1	2.6	—	—	2100-2400	Xeric scrub	Lemos-Espinal et al. 2012; Woolrich-Piña et al. 2012, 2014
<i>X. sp.</i> (San Lucas Camotlán)	Xslc	San Lucas Camotlán, Oaxaca	110	113.0	5.0	41.4	0.35	1800	Cloud forest	Zamora-Abrego et al. 2007
<i>X. grandis rackhami</i>	Xrac	Ocozucua, Chiapas	99	110.9	4.5	44.5	0.23	838	Tropical forest	Zamora-Abrego et al. 2007
<i>X. newmanorum</i>	Xnew	Xilitla, San Luis Potosí	107	117.6	2.6	50.0	0.25	780	Tropical forest	Ballinger et al. 2000
<i>X. platyceps</i>	Xpla	El Madroño, Tamaulipas	101	110.7	2.5	50.9	0.26	1210	Oak forest	Ballinger et al. 2000; Rojas-González et al. 2008a, 2008b
		Gómez Farías, Tamaulipas	100	111.7	2.1	49.6	0.21	420	Tropical forest	Rojas-González et al. 2008a, 2008b
<i>X. mendozai</i>	Xmen	Tilaco, Querétaro	92	106.9	2.1	51.6	0.27	1184	Oak forest	Lemos-Espinal et al. 2004; Zamora-Abrego et al. 2007
		El Pinalito, Hidalgo	—	108.0	4.0	48.5	—	1600	Oak forest	Reaño-Hernández et al. 2016
<i>X. tzacualtipantecus</i>	Xtza	La Mojonera, Hidalgo	—	101.9	5.0	—	—	1900	Cloud forest	Woolrich-Piña & Smith 2012; García-Rico et al. 2015

selection towards a fixed optimum (PGLS-OU). This second regression model includes an additional parameter ( $\alpha$ ) that could be interpreted as a measure of the strength of selection acting on the phenotypes. When  $\alpha$  is small (close to zero), the model depicts a situation similar to Brownian motion evolution, with weak selection and phenotypic change accumulating as a function of time. In this case, closely-related species would be more similar to each other than they would be to more distantly-related species. When  $\alpha$  is large (close to 20 for ultrametric trees scaled to a total length of 1), the PGLS-OU model describes a situation in which selection is strong and phenotypes adapt quickly to the local environment, leaving behind no trace of the phylogenetic relationships. Third, we conducted an ordinary least squares regression (OLS) that does not account for the phylogenetic relationships and, hence, assumes a 'star' phylogeny.

We fit these three regression models (PGLS-BM, PGLS-OU, and OLS) to each pair of life-history traits and compared their fit to the data using the Akaike Information Criterion adjusted for small sample sizes (AICc). The lowest value of the AICc indicates the best-fitting model and a difference between two models in AICc values ( $\Delta$ AICc) larger than two indicates a clear difference in their fit to the data (Burnham & Anderson, 2002). These regression models are explicitly directional. Thus, we conducted each analysis twice, using one variable as explanatory (X) and the other as response (Y) in the first analysis, and then repeating with reversed variables because we had no *a priori* hypotheses about potential causality. In all cases, reversing the order of the explanatory and response variables yielded qualitatively similar results, so we report only one set of results below.

### Ancestral state reconstructions

We reconstructed ancestral states of the five life-history traits using maximum likelihood (Schluter et al., 1997), as implemented by the R package 'phytools' (Revell, 2012). We focused on estimating the ancestral value at the root of the phylogeny. However, we also estimated ancestral states for all the internal nodes. Again here, we assumed and tested two different evolutionary processes: Brownian motion (BM) and Ornstein-Uhlenbeck (OU). As explained in Martins (1999) and Rohlf (2001), ancestral states estimated using maximum likelihood and assuming a BM model are identical to those resulting from least-squares parsimony (Maddison, 1991), PGLS (Martins, 1999) and Felsenstein's (1985) independent contrasts on the root node. We used AICc to compare the fit of BM and OU versions, and report ancestral estimates derived from the best-fitting model.

### Rates of evolution

To estimate the rates of evolutionary change for the studied life-history traits, we used maximum likelihood procedures (O'Meara et al., 2006) implemented in the R package 'mvMORPH' (Clavel et al., 2015). In particular, we used multivariate approaches for estimating evolutionary rates simultaneously for a set of continuous characters, applying both BM and OU models of

evolution, as described above (Bartoszek et al., 2012; Adams, 2013). Again, we used AICc to compare the fit of these two evolutionary models to our data. We report here evolutionary rates derived from the best-fitting model. To compare these rates among life-history traits, we used a Monte Carlo simulation procedure, generating 100 data sets based on the original conditions (i.e. the estimated rates, 13 or 14 taxa depending on the particular life-history trait, and our topology and branch lengths), and calculating evolutionary rates for each simulated data set. We then used a Kruskal-Wallis test and post-hoc pairwise comparisons (as per Siegel and Castellan, 1988) to determine which life-history traits exhibited the fastest and slowest rates of evolution.

### Phylogenetic signal

We estimated the amount of phylogenetic signal (i.e. the amount of resemblance among species due to their shared evolutionary history) for each of the five life-history traits using two different methods implemented in the R package 'phytools' (Revell, 2012). First, we calculated  $\lambda$  (Pagel, 1999), which is a scaling parameter that weights the influence of the phylogeny in explaining the observed phenotypic data. Second, we calculated  $K$  (Blomberg et al., 2003), which measures the strength of phylogenetic signal as the ratio between the mean squared error of the observed data and the mean squared error based on the variance-covariance matrix derived from the given phylogeny. For both  $\lambda$  and  $K$ , values close to zero indicate independence from the phylogeny, values equal to one indicate that the phylogeny explains substantial variation among species, and values larger than one indicate a stronger similarity between related species than that expected under BM. To assess whether  $\lambda$  was significantly different than zero (i.e. significant phylogenetic signal), we used a likelihood ratio test that compares the model that accounts for the observed  $\lambda$  against a model in which  $\lambda$  is set equal to zero. For  $K$ , we used a randomisation test that permutes several times the observed phenotypic values across the tips of the tree, calculates new values of  $K$ , and compares the observed  $K$  against the distribution of  $K$  values obtained under random trait variation (Münkemüller et al., 2012).

In addition, we estimated the amount of phylogenetic signal in the type of environment where these lizards inhabit (Table 1). We used the R package 'geiger' (Harmon et al., 2008) to implement continuous-time Markov models of trait evolution, from which a maximum likelihood estimate of  $\lambda$  can be obtained for discrete characters. Before estimating  $\lambda$ , we compared the fit of three different Markov models. First, an 'equal-rates' model, where all transition rates between types of environment share the same value. Second, a 'symmetric' model, in which forward and reverse transition rates between two particular environments share the same value. Third, an 'all-rates-different' model, where each particular transition has a different value. We compared the fit of these models using AICc and then used the best-supported model to calculate  $\lambda$ . To assess whether  $\lambda$  was significantly different than zero, we used a likelihood ratio test to compare a model that accounts for the

estimated  $\lambda$  against a model that does not incorporate the phylogenetic information (i.e.  $\lambda = 0$ ).

### Differences among environments

To compare the life-histories of xenosaurid lizards among different environments (i.e. cloud forest, tropical forest, oak-pine forest, and xeric scrub), we used the adaptation-inertia model as implemented in the R package 'slouch' (Hansen, 1997; Hansen et al., 2008). This comparative method fits an explicit evolutionary model that accounts for phylogenetic relatedness and time spent in different selective contexts using an Ornstein-Uhlenbeck model of evolution. This model envisions several competing selective forces, some of which may have stronger impacts on phenotypic evolution than others. We implemented this method by treating each type of environment as a different selective scenario that may promote convergent adaptive evolution in the life histories of xenosaurid lizards. We used the adaptation-inertia method to fit two different models for each life-history trait. First, we fit a model that estimates a different optimal value for each type of environment and, second, we fit a model that estimates a single optimum for all taxa across all environments. We used AICc to compare the fit of these two models.

This comparative method also estimates the strength of phylogenetic inertia by means of the phylogenetic half-life ( $t_{1/2}$ ), which is the time taken for a trait to evolve halfway towards its adaptive optimum (Hansen et al., 2008). If  $t_{1/2}$  is small (close to zero), adaptation to the optimum is fast and the trait does not exhibit phylogenetic inertia. As  $t_{1/2}$  increases and approaches infinity, traits retain the influence of their ancestral values and the evolutionary process corresponds to a Brownian-motion model.

To apply the adaptation-inertia method, we assumed previous knowledge about the evolutionary history of the putative selective agent across the phylogeny (Hansen, 1997; Hansen et al., 2008). Thus, we inferred the relative amount of time that each species spent evolving in each type of environment, using an ancestral reconstruction based on maximum likelihood implemented in the program MESQUITE 3.04 (Maddison & Maddison, 2015).

## RESULTS

### Evolutionary correlations

Using the raw data (non-phylogenetic correlation), average adult size and minimum size at sexual maturity were positively correlated ( $r = 0.90$ ; Fig. 2a). When using FIC, the positive correlation coefficient between these two traits was smaller ( $r = 0.78$ ; Fig. 2a), although still significant as compared to the critical value of  $r_{0.05} = 0.55$  for  $n = 13$ . In contrast, we found a negative relationship between litter size and neonate size as indicated by both non-phylogenetic and phylogenetic (FIC) correlations ( $r = -0.77$  and  $-0.58$ , respectively; Fig. 2b). All other pairwise correlations using both the raw data and FIC were not significant ( $-0.55 < r < 0.55$  in all cases).

### Evolutionary regressions

We found a significant, positive relationship between adult size and size at maturity using both OLS and PGLS-BM models (Table 2; Fig. 2a). The OLS model provided a better fit to the data than did the PGLS-BM model ( $\Delta\text{AICc} = 8.3$ ), indicating little or no phylogenetic signal in the residuals of this bivariate relationship. We were unable to obtain estimates of this relationship using the PGLS-OU model because the optimisation algorithm failed to converge.

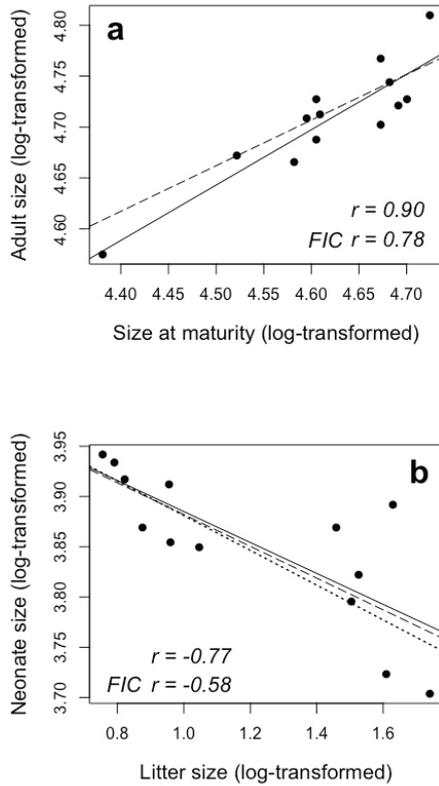
We also found a significant, negative relationship between litter size and neonate size using all three regression models (OLS, PGLS-BM, and PGLS-OU; Table 2; Fig. 2b). Again in this case, the OLS model provided the best fit, although both PGLS-OU and PGLS-BM models resulted in similar fit compared to the top model ( $\Delta\text{AICc} = 1.9$  and  $2.0$ , respectively). We found no other significant relationships between life-history traits, regardless of the evolutionary model being used (Table 2).

### Ancestral state reconstructions

We estimated the following states for the common ancestor of xenosaurid lizards at the root of the phylogeny ( $\pm$  SE):  $100.2 \pm 7.06$  mm SVL for minimum size at maturity,  $109.5 \pm 4.36$  mm SVL for average adult size,  $3.2 \pm 0.47$  neonates for litter size,  $47.8 \pm 2.30$  mm SVL for neonate size, and  $0.25 \pm 0.044$  for relative litter mass (Fig. 3). Two clades (including *X. grandis grandis*, *X. g. rackhami*, and four of the undescribed taxa), as well as *X. tzacualtipantecus*, evolved litter sizes that are substantially larger than that of the root ancestor (Fig. 3c). Some of these taxa with larger litters (*X. g. rackhami*, *X. sp.* San Lucas Camotlán, and *X. sp.* Sierra de Juárez) also evolved much smaller neonates than were present in the root ancestor (Fig. 3d). In contrast, two clades retained relatively small litters (Fig. 3c), and one of these clades (including *X. newmanorum*, *X. platyceps*, *X. mendozai*) along with *X. phalaroanthereon* evolved large offspring (Fig. 3d). These patterns also suggest a possible evolutionary trade-off between number and size of offspring.

Our ancestral reconstructions also find that the relative timing of diversification varied among life-history traits. Litter size (Fig. 3c) and neonate size (Fig. 3d) began to diverge early in the history of the genus, whereas size at maturity (Fig. 3a) and relative litter mass (Fig. 3e) apparently remained relatively constant for a long time period and began divergence quite a bit later. The history of litter size appears to have tracked the phylogeny closely (Fig. 3c). In the case of neonate size, the clade including *X. mendozai*, *X. platyceps*, and *X. newmanorum*, as well as their common ancestor, evolved relatively large neonate sizes early in the history of the genus (Fig. 3d). All other traits diverged throughout time without a clear phylogenetic pattern.

For all five traits, the log likelihood of the BM and OU models was quite similar. Given that OU models have one additional parameter ( $\alpha$ ), AICc penalised these models and indicated that BM provided a better fit when estimating ancestral states. Moreover, in size at maturity, litter size, and neonate size the estimated  $\alpha$  was quite



**Figure 2.** Relationships between (log-transformed) size at maturity and adult size (a) and between litter size and neonate size (b) for distinct taxa of the lizard genus *Xenosaurus*. The continuous line corresponds to an ordinary (non-phylogenetic) least squares regression. The dashed line corresponds to a phylogenetic generalised least squares regression (PGLS) assuming a Brownian motion model of evolution. In (b) the additional dotted line corresponds to a PGLS assuming an Ornstein-Uhlenbeck model of evolution. In both (a) and (b)  $r$  is the non-phylogenetic correlation coefficient and FIC  $r$  is the correlation coefficient between phylogenetically independent contrasts.

small ( $< 0.001$ ), indicating that a BM model sufficiently explained variation in these three traits. Given such small  $\alpha$  values, the ancestral estimates from OU models were similar to those obtained from BM models. In adult size and relative litter mass the estimated  $\alpha$  values were somewhat larger (1.4 and 1.8, respectively), but still small enough to result in similar BM and OU ancestral reconstructions.

### Rates of evolution

The BM model provided a substantially better fit than the OU model when estimating evolutionary rates ( $\Delta\text{AICc} = 9.0$ ). We show the estimated rates in Table 3. According to simulations and a Kruskal-Wallis test, these evolutionary rates differed significantly among life-history traits ( $\chi^2 = 420.1$ ,  $df = 4$ ,  $P < 0.001$ ). The highest rate was observed in relative litter mass (0.170) and the lowest in adult size (0.007). Post-hoc comparisons revealed significant differences among most traits (Table 3), excepting between neonate size (0.009) and adult size (0.007) and between litter size (0.126) and relative litter mass (0.170).

### Phylogenetic signal

Size at maturity, adult size, and relative litter mass did not exhibit significant phylogenetic signal according to both  $\lambda$  and  $K$  (Table 3). In fact, the estimated  $\lambda$  values for these three life-history traits were quite close to zero. In contrast, litter size exhibited strong phylogenetic signal according to  $\lambda$  (1.01,  $P = 0.003$ ). Furthermore, according to  $K$  (1.35,  $P = 0.004$ ), the litter sizes of these lizards exhibit stronger resemblance between related species than expected from their phylogenetic relationships. The estimated  $\lambda$  value for neonate size was considerably high (0.83), but not statistically different than zero ( $P = 0.34$ ). However, according to  $K$  (0.74) neonate size exhibits marginally significant phylogenetic signal ( $P = 0.06$ ; Table 3).

The ‘equal-rates’ model provided substantially better fit to the observed changes among taxa in the type of environment, compared to both ‘symmetric’ ( $\Delta\text{AICc} = 17.7$ ) and ‘all-rates-different’ ( $\Delta\text{AICc} = 328.8$ ) models. The estimate of phylogenetic signal for type of environment was remarkably low ( $\lambda < 0.001$ ) and not significantly different than zero ( $P = 0.64$ ).

### Differences among environments

The model that estimated differences among environments in the optimal value of litter size provided a better fit compared to the model that estimated a single optimum for all environments ( $\Delta\text{AICc} = 6.5$ ). According to 95% confidence intervals around the estimated optimal values of this trait (Fig. 4), lizards that have evolved in cloud forests produce more neonates per litter (back-transformed estimates to the original scale: 5.2 neonates) compared to those evolving in all other environments. In addition, the optimal litter size for lizards evolving in tropical forests (3.1 neonates) was larger than that for lizards evolving in oak-pine forests (2.1 neonates; Fig. 4). The phylogenetic half-life revealed a relatively fast adaptation to these optimal values ( $t_{1/2} = 0.19$ ).

In contrast, the single-optimum model provided substantially better fit than the model that estimated differences among environments for adult size, neonate size, and relative litter mass ( $\Delta\text{AICc} = 7.1$ , 2.8, and 15.3, respectively). For size at maturity, the single-optimum model also provided the best fit, but the different-optima model differed in less than two AICc units from this top model ( $\Delta\text{AICc} = 1.6$ ). However, regardless of the similar fit between these two alternative models, we considered stronger evidence for a single optimum because estimating a different optimal size at maturity for each type of environment did not substantially improve the model fit.

## DISCUSSION

Our results clearly demonstrate several important differences among life-history traits in the way they have evolved in xenosaurid lizards. Larger species mature at larger body sizes and there is strong evidence for an evolutionary trade-off between the number and size of offspring. Adult size and neonate size have both evolved slowly in *Xenosaurus*. In contrast, relative litter mass and litter size have evolved quickly. However, despite

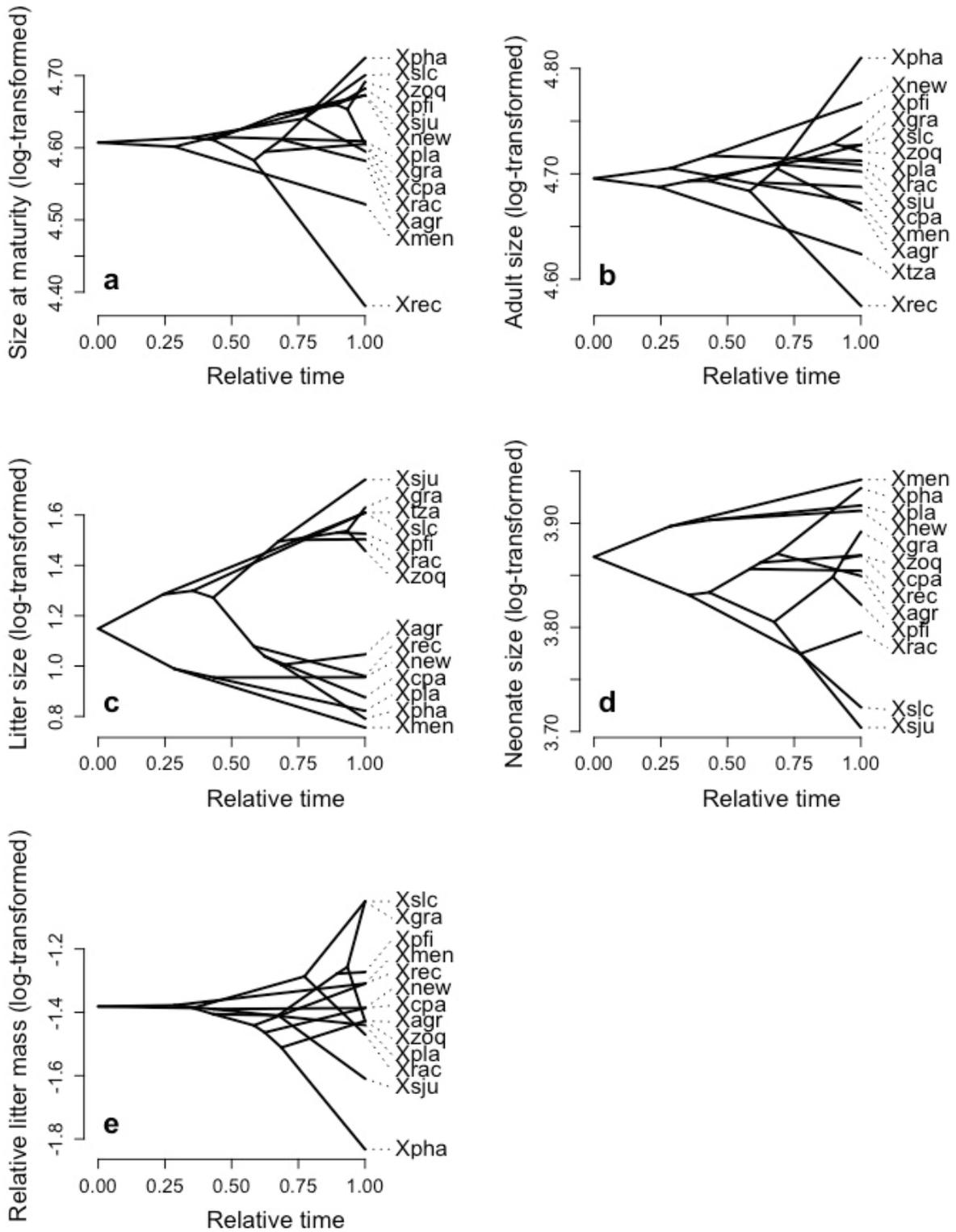
**Table 2.** Results from phylogenetic generalised least squares (PGLS-BM and PGLS-OU) and ordinary least squares (OLS) regression models fitted to life-history traits of lizards of the genus *Xenosaurus*. PGLS was implemented using two evolutionary models: Brownian motion (BM) and Ornstein-Uhlenbeck (OU). The fit of each model to the data was evaluated using the Akaike Information Criterion (AICc), with the smallest value indicating the best-fitting model. Differences in AICc values between each model and the best-fitting model ( $\Delta$ AICc) are also shown. For each pair of life-history traits, models are listed according to their AICc values (from lowest to highest, from best to worst). Standard errors of the regression slopes are shown within parentheses. PGLS-OU estimates an additional parameter,  $\alpha$ , which measures the strength of stabilising selection. In two cases (regressions between size at maturity and adult size, and between litter size and adult size) the PGLS-OU model did not provide parameter estimates because the optimisation algorithm failed to converge.

Life-history traits	Model	AICc	$\Delta$ AICc	Regression slope	P	$\alpha$
Adult size (Y) ~ Size at maturity (X)	OLS	-40.3	0	0.5 (0.08)	<0.001	
	PGLS-BM	-32.0	8.3	0.4 (0.11)	0.002	
Litter size (Y) ~ Size at maturity (X)	PGLS-BM	10.3	0	-0.002 (0.73)	0.99	
	PGLS-OU	14.7	4.4	-0.002 (0.73)	0.99	1x10 <sup>8</sup>
Neonate size (Y) ~ Size at maturity (X)	OLS	17.9	7.6	1.4 (1.14)	0.23	
	PGLS-BM	-18.6	0	-0.1 (0.20)	0.51	
	OLS	-16.3	2.3	-0.2 (0.24)	0.51	
Relative litter mass (Y) ~ Size at maturity (X)	PGLS-OU	-14.5	4.1	-0.1 (0.20)	0.52	0.6
	OLS	5.8	0	-0.5 (0.66)	0.44	
	PGLS-OU	10.0	4.2	-0.7 (0.66)	0.34	8.4
Litter size (Y) ~ Adult size (X)	PGLS-BM	11.2	5.4	-1.3 (0.76)	0.11	
	OLS	19.3	9.3	-0.01 (1.85)	0.99	
	PGLS-BM	10.0	0	-0.4 (1.24)	0.75	
Neonate size (Y) ~ Adult size (X)	OLS	19.3	9.3	-0.01 (1.85)	0.99	
	PGLS-BM	-19.6	0	0.2 (0.35)	0.54	
	OLS	-17.1	2.5	0.2 (0.40)	0.67	
Relative litter mass (Y) ~ Adult size (X)	PGLS-OU	-15.5	4.1	0.2 (0.35)	0.56	0.5
	OLS	4.5	0	-1.0 (1.07)	0.35	
	PGLS-OU	8.8	4.3	-1.1 (1.08)	0.34	13.7
Neonate size (Y) ~ Litter size (X)	PGLS-BM	12.1	7.6	-1.3 (1.46)	0.39	
	OLS	-22.8	0	-0.2 (0.04)	0.002	
	PGLS-OU	-20.9	1.9	-0.2 (0.04)	0.001	4.4
Litter size (Y) ~ Relative litter mass(X)	PGLS-BM	-20.8	2.0	-0.2 (0.07)	0.04	
	OLS	10.4	0	0.3 (0.23)	0.16	
	PGLS-OU	14.7	4.3	0.3 (0.23)	0.16	1x10 <sup>-10</sup>
Neonate size (Y) ~ Relative litter mass (X)	OLS	19.6	9.2	0.6 (0.51)	0.25	
	PGLS-BM	-16.0	0	0.002 (0.07)	0.98	
	OLS	-14.5	1.5	-0.1 (0.11)	0.61	
	PGLS-OU	-12.0	4.0	-0.01 (0.08)	0.94	0.8

of the high evolutionary rate in litter size, this trait has retained strong phylogenetic signal. We also found some resemblance between closely related species in neonate size, whereas all other traits diverged throughout time without a clear phylogenetic pattern. Additional studies are needed to determine the causes of these differences in the tempo and mode of evolution among life-history traits, and below are some hypotheses that could guide future research.

The first evolutionary relationship that we detected was between average body size and minimum size at maturity. This relationship was positive: larger species mature at larger sizes. This pattern was clear in the raw data (in both a significant non-phylogenetic correlation and a significant slope from the OLS regression) and when taking into account the phylogeny (a significant correlation between FIC and a significant slope from the PGLS-BM regression). The non-phylogenetic approach

provided a better fit which indicated that phylogenetic relationships add little to our understanding of the correlated evolution between mean body size and size at maturity. The evolution of larger sizes both as adults and at sexual maturity may be the result of local responses to selective pressures. For example, larger body sizes could be the result of predation on smaller lizards (i.e. low extrinsic adult mortality; Day et al., 2002). If the chances of death are low, delaying maturity can provide an additional advantage because larger females would produce more or larger offspring (Olsson et al., 2002). In fact, Ballinger et al. (2000) and Rojas-González et al. (2008a) demonstrated that larger females produce more newborns per litter in both *X. grandis grandis* and *X. platyceps*, respectively. Further increases in adult size are then favoured because even greater reproductive output can be attained and the risk of mortality may decrease further as body size increases. In addition, both



**Figure 3.** Phenograms depicting ancestral states for (a) size at maturity, (b) adult size, (c) litter size, (d) neonate size, and (e) relative litter mass of lizards of the genus *Xenosaurus*. Taxon codes are as given in Table 1.

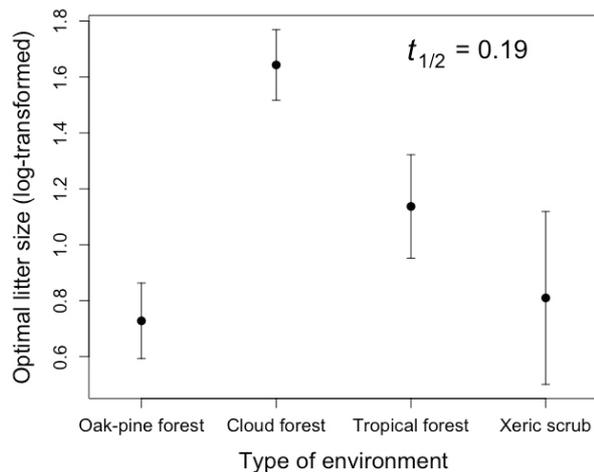
adult size and size at maturity may be positively affected by factors that promote fast body growth, such as warm temperatures and high food availability (Adolph & Porter, 1993; 1996; Zúñiga-Vega et al., 2005). In fact, body growth rates and, consequently, adult size and size at maturity may exhibit plastic responses to temporal and spatial variation in both temperature and food availability (Madsen & Shine, 2000; Angilletta, 2001). Also, selection on age at first reproduction indirectly affects adult

size and size at maturity, such that environments that promote early reproduction, indirectly promote small size at maturity and small adult size (Beckerman et al., 2010). Several taxa exhibit a similar pattern in which the evolution of delayed maturity is also associated with the evolution of a larger body size (Blueweiss et al., 1978; Kozłowski, 1996; Morand, 1996).

The second clear pattern that we detected was an evolutionary trade-off between number and size

**Table 3.** Rates of evolution and estimates of phylogenetic signal ( $\lambda$  and  $K$ ) for life-history traits of lizards of the genus *Xenosaurus*. We also show post-hoc pairwise comparisons from a Kruskal-Wallis analysis of variance. NS indicates non-significant differences; \* indicates  $P < 0.001$ .

Life-history trait	Evolutionary rate	Adult size	Litter size	Neonate size	Relative litter mass	$\lambda$	$P$ -value	$K$	$P$ -value
Size at maturity	0.021	*	*	*	*	$7 \times 10^{-5}$	0.99	0.48	0.39
Adult size	0.007	-	*	NS	*	$7 \times 10^{-5}$	0.99	0.59	0.23
Litter size	0.126		-	*	NS	1.01	0.003	1.35	0.004
Neonate size	0.009			-	*	0.83	0.34	0.74	0.06
Relative litter mass	0.170				-	$7 \times 10^{-5}$	0.99	0.29	0.77



**Figure 4.** Estimated optimal litter sizes of xenosaurid lizards for different environments according to the adaptation-inertia method. Error bars represent 95% confidence intervals. We also show the estimated phylogenetic half-life ( $t_{1/2}$ ) for litter size.

of offspring. Regardless of the assumed evolutionary model, a negative relationship between these two traits was always evident. This trade-off between number and size of offspring was also evident from our ancestral state reconstructions because some of the clades (including some hypothesised ancestors) that evolved large litters also evolved small offspring and vice versa. Thus, when selection favoured the evolution of more offspring in a particular species, a likely consequence was the evolution of a reduction in the size of each individual offspring (or vice versa). This trade-off is likely the result of a limited space within the reproductive tract (i.e. a biomechanical trade-off). All the lizard species from this genus are strict crevice dwellers, which means that they rarely go out of their crevices (Lemos-Espinal et al., 1998; 2004). These crevices are usually narrow, and the space within is barely enough to fit the body of these lizards. This has resulted in a flattened morphology that clearly restricts the space that these viviparous females can devote to offspring production (Lemos-Espinal et al., 2012). Similar constraints on reproductive allocation imposed by a flattened morphology have been observed in other crevice-dwelling lizards (e.g., *Dalmatolacerta oxycephala* and *Tropidurus semitaeniatus*; Vitt, 1981; Bejakovic et al., 1996; Ribeiro et al., 2012). Other viviparous reptiles

also exhibit this trade-off between number and size of offspring (King, 1993; Doughty & Shine, 1997; Gignac & Gregory, 2005; Uller & Olsson, 2005). A similar evolutionary trade-off has been documented in diverse taxa such as butterflies (García-Barros, 2000), fishes (Elgar, 1990), turtles (Elgar & Heaphy, 1989), and birds (Figuerola & Green, 2006).

In addition to providing estimates of the phenotypes of the common ancestor of the genus, our ancestral reconstructions also revealed an interesting difference among traits in the relative timing of diversification. Litter size and neonate size began diversification early in the history of the genus. In contrast, size at maturity and relative litter mass remained phenotypically invariant for a long time period before diverging into distinct phenotypic values. These differences might be related to how the selective environment differentially affected these life-history traits during the early diversification of the genus. A biogeographic hypothesis would suggest that in the initial geographic distribution of the oldest ancestors, the environment was relatively constant, exerting stabilising selection on size at maturity and relative litter mass. However, litter size and offspring size were relatively more sensitive to slight changes in the environment. Then, as these xenosaurid lizards colonised new regions, they experienced a wider array of selective environments, which in turn began promoting changes in size at maturity and relative litter mass in parallel to further changes in litter size, neonate size, and average adult size. Interestingly, the genus *Xenosaurus* is apparently of Nearctic origin (Gauthier, 1982), whereas most extant taxa have a Neotropical distribution (Zamora-Abrego, 2009; Lemos-Espinal et al., 2012; Nieto-Montes de Oca et al., 2017). The late diversification of size at maturity and relative litter mass could have coincided with the colonisation of more tropical regions. Interestingly, we found no phylogenetic signal in the types of environments that these lizards currently inhabit. This result indicates that closely related species were able to colonise drastically different ecological conditions (Losos, 2008), which is now reflected in the relatively wide diversity of environments where these 14 taxa of xenosaurid lizards can be found (cloud forests, tropical forests, oak-pine forests, and xeric scrubs).

The rates of evolution differed drastically among life-history traits. Adult size and neonate size have evolved at a slower pace, as indicated by the slowest observed rates. This is also evident in the relatively small amount

of interspecific variation observed in both traits (less than 0.24 in the log scale between the largest and smallest observed values; Figs. 3b and 3d). In contrast, relative litter mass and litter size exhibited the fastest evolutionary rates, which is also consistent with greater amount of interspecific variation (1 and 0.8 in the log scale between the largest and smallest observed values of litter size and relative litter mass, respectively; Figs. 3c and 3e). The difference in the rate of evolution between relative litter mass (fastest rate) and adult size (slowest rate) is about 24-fold (relative litter mass: 0.170, adult size: 0.007). Therefore, in this genus both adult size and neonate size are relatively conserved life-history traits, likely as a result of strong stabilising selection, whereas relative litter mass and litter size are labile traits. However, even though adult size has evolved at a slow rate, the changes that have occurred throughout the history of the genus have not retained trace of the phylogeny as indicated by negligible phylogenetic signal in this trait. Hence, such moderate and slow phenotypic changes in adult size likely occurred as particular responses to local conditions. These changes may represent either local adaptations or plastic responses. In contrast, neonate size, which also has evolved at a relatively slow rate, has retained some trace of the phylogenetic relationships, a pattern that is partially consistent with gradual evolution through genetic drift rather than with adaptive or plastic responses to particular ecological conditions.

Notably, the relatively large evolutionary changes observed in litter size have closely tracked the phylogeny and related species have similar litter sizes. This high phylogenetic signal in litter size was evidenced by the high and significant estimates of  $\lambda$  and  $K$  as well as by the reconstruction of ancestral states (Fig. 3c). However, despite this high phylogenetic signal, an environmental effect on litter size could be possible if some of the species and common ancestors that share either large or small litters (see these two clearly distinct groups in Fig. 3c), also shared a common feature of the environment with a selective effect on this life-history trait. Our results of the adaptation-inertia method indicate that this is in fact the case. We found an evident effect of the type of environment that these lizards inhabit on litter size: the largest optimal value of this trait corresponded to cloud forests. All the four taxa that inhabit this type of environment (*X. tzacualtipantecus*, *X. sp.* [Zoquitlán], *X. sp.* [Sierra de Juárez], and *X. sp.* [San Lucas Camotlán]) have evolved relatively large litters (Fig. 3c). In contrast, all four taxa that inhabit oak-pine forests (*X. phalaroanthereon*, *X. platyceps*, *X. mendozai*, and *X. sp.* [Concepción Pápalo]) have evolved relatively small litters (Fig. 3c). In fact, the smallest optimal value of litter size corresponded to oak-pine forests (Fig. 4).

What is the potential benefit of large litters in cloud forests? Cloud forests represent a unique ecosystem that receives large amounts of humidity from rain, clouds, and fog and which contains a mixture of tropical and temperate flora and fauna (Sánchez-González et al., 2008). In Mexico, cloud forests have the highest biodiversity per unit area, harbouring approximately 10% of all Mexican flora and 12% of the terrestrial vertebrates (Pineda &

Halffter, 2004; Ornelas et al., 2013). Thus, the diversity and abundance of potential predators of xenosaurid lizards (e.g., birds and snakes) might be higher in cloud forests compared to other environments. Therefore, a potential selective factor that could promote large litters is a high mortality risk in these environments (Pérez-Mendoza & Zúñiga-Vega, 2014). High mortality selects for larger litters because this increases the probability of at least one offspring surviving to reproduce (Promislow & Harvey, 1990; Roff, 2002). Testing this hypothesis would require mortality estimates for all these species and, until present, mortality data are only available for *X. g. grandis*, *X. platyceps*, and *X. mendozai* (Zúñiga-Vega et al., 2007; Rojas-González et al., 2008b; Zamora-Abrego et al., 2010; Zúñiga-Vega, 2011; Molina-Zuluaga et al., 2013). In contrast, temperate environments such as oak-pine forests (usually located at higher elevations; Table 1) may constrain reproductive output. In this type of forest, temperatures are generally colder and food availability (diversity and abundance of arthropods) may be relatively low. Thus, lizards could not afford to produce larger litters and, hence, the smallest litters that we observed in oak-pine forests may represent a plastic response to restrictive conditions (Rohr, 1997; Zeng et al., 2013). A common garden experiment would help to understand whether the observed differences among taxa in litter size represent adaptive genetic differentiation or plastic responses.

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