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American Naturalist 172: E80-E98 (2008)

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# Reproductive Allometry and the Size-Number Trade-Off for Lizards

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Submitted March 5, 2007; Accepted March 14, 2008;  
Electronically published August 1, 2008

**ABSTRACT:** Fundamental to life-history theory is the assumed inverse proportionality between the number of offspring and the resource allocation per offspring. Lizards have been model organisms for empirical tests of this theory for decades; however, the expected negative relationship between clutch size and offspring size is often not detected. Here we use the approach developed by Charnov and Ernest to demonstrate that this often concealed trade-off can be made apparent in an interspecific comparison by correcting for size-dependent resource allocation. Our data set also shows a tight allometry for annual production that is consistent with life-history models for indeterminate growers. To account for nonindependence of species data we also compare the fit of nonphylogenetic and phylogenetic regression models to test for phylogenetic signal in these allometry and trade-off patterns. When combined, these results demonstrate that the offspring size/clutch size trade-off is not isolated to a single clutch but is shaped by the resource investment made over an entire year. We conclude that, across diverse lizard species, there is strong evidence for the predicted trade-off between offspring size and the annual number of eggs produced.

**Keywords:** clutch size, offspring size, trade-off, reproductive allometry, life history, lizards.

The trade-off between the number and size of offspring is a central tenet of life-history theory (Lack 1954; Smith and Fretwell 1974; Stearns 1992; Roff 2002). Finite resources (or perhaps body space available for bearing offspring) constrain an individual's reproductive allocation,

resulting in a trade-off between many small offspring versus a few large offspring. This trade-off may be further shaped by selective constraints on the parsing of reproductive investment into single or multiple clutches during a breeding season. Lizards have been a model study organism for the examination of both the proximate and ultimate factors driving this trade-off. Indeed, the clutch size/offspring size trade-off has been shown to be constrained by the maximal space available in a female's abdominal cavity (Vitt and Congdon 1978; Shine 1992; Du et al. 2005) and pelvic opening (Congdon and Gibbons 1987; Sinervo and Licht 1991), and offspring size has been convincingly linked to offspring survival (Ferguson and Fox 1984; Sinervo and Doughty 1996). However, it has been argued that resource availability is a primary driver of reproductive investment and the clutch size/offspring size trade-off (DeMarco 1989; Schwarzkopf 1992; Bonnet et al. 2001; Jordan and Snell 2002; Olsson et al. 2002; Du et al. 2005; Uller and Olsson 2005; Oufiero et al. 2007). Despite the great successes of trade-off research in the herpetological literature, the link between maternal resources and reproductive trade-offs remains somewhat tenuous and the predicted clutch size/offspring size trade-off is not always observed (Doughty and Shine 1997; Zera and Harshman 2001; Jordan and Snell 2002; Bowden et al. 2004; Uller and Olsson 2005).

This lack of evidence does not negate the existence of the offspring size/clutch size trade-off but may be a result of concealment by mitigating factors (van Noordwijk and de Jong 1986; Roff 2002). If a parent has  $R$  resources to invest in offspring and each offspring costs  $I$  units, the clutch size  $C$  must be  $C \propto R/I$  (Smith and Fretwell 1974). If adults are of various sizes within a species (i.e., they experience indeterminate growth, as in lizards, fish, etc.) then  $\bar{C} \propto \bar{R}/I$ , where overbar indicates the adult average of  $R$  and  $C$ . If we plot  $\ln(\bar{C})$  vs.  $\ln(I)$  for a collection of species,  $\ln(\bar{C})$  will have a linear relationship with a slope of  $-1$  if (i) all the species have the same  $\bar{R}$  value or (ii)  $\bar{R}$  does not correlate with  $I$  across species. Unfortunately, for many taxa (including lizards and mammals),  $I$  correlates with  $\bar{R}$  and so the expected  $-1$  slope is not seen

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(Charnov and Ernest 2006). In other words, the trade-off (inverse proportionality) assumed by the classic Smith-Fretwell model is probably masked if resource availability and reproductive allocation vary greatly among individuals or species (van Noordwijk and de Jong 1986; Roff 2002). Clearly, we expect  $\overline{C}/\overline{R} \propto 1/I$ , or a slope of  $-1$  (for  $\ln \overline{C}/\overline{R}$  vs.  $\ln I$ ), if we first remove the effects of  $\overline{R}$  varying among species. Charnov and Ernest (2006) demonstrated (with mammals) that there exists a very general way to correct for variation in  $\overline{R}$  among species. They argued that, across species and within a taxon,  $\overline{R} \propto (m)^{0.75}$  (where  $m$  is body mass) and, thus,  $C/m^{0.25} \propto 1/I$ .

In this study we use a compiled lizard life-history data set to first test a prediction from a recent life-history evolution model where, for indeterminate growers such as lizards,  $\overline{R} \propto m_{\alpha}^{0.75}$  (Charnov et al. 2001). Here,  $m_{\alpha}$  is body mass at first reproduction. We then use this data set of 138 populations of 115 species of lizards and the Charnov and Ernest (2006) approach to examine the relationship between size-dependent resource allocation and the clutch size/offspring size trade-off in lizards. It is important to note that the optimization models of Charnov et al. (2001), as well as those of Lester et al. (2004) and Shuter et al. (2005), have demonstrated that the scaling exponent of 0.75 that describes the relationship between reproductive allocation and  $m_{\alpha}$  incorporates the effects of mortality on size at maturity and reproductive effort. Because their optimization models allowed for the adjustment of age/size at maturity and reproductive allocation in the face of mortality, our use of this scaling in our analysis thus captures the effects of mortality on the clutch size/offspring size trade-off. Using maximum likelihood techniques, we also compare the fit of both conventional comparative and phylogenetic regression models to these allometric and trade-off data. Through these analyses we thus show that average yearly reproductive allocation across the lizards in this data set is indeed proportional to  $m_{\alpha}^{0.75}$ , and we further demonstrate that, by accounting for this size-dependent reproductive allocation, the often obscured offspring size/clutch size trade-off is made apparent and robust, even in lizards exhibiting very diverse life histories.

## Methods

### Data

Life-history data were compiled from the published literature for 138 populations and 115 species of lizards of the following 15 families: Agamidae, Anguidae, Chamaeleonidae, Corytophanidae, Crotaphytidae, Gekkonidae, Gymnophthalmidae, Iguanidae, Lacertidae, Phrynosoma-

tidae, Polychrotidae, Scincidae, Teiidae, Tropiduridae, and Xantusiidae. Values for the parameters of female snout-vent length (SVL) at maturity, average hatchling SVL, average clutch size, and average annual number of clutches were gathered from both primary literature sources and previously published reviews of lizard life histories (see app. A). The SVL at maturity ( $m_{\alpha}$ ) used in our data set is either that reported by the original authors or the SVL recorded for the smallest reproductive female reported in a study. Female SVL at maturity ranged from 28.5 to 378 mm across species. If all of the above data were not available for a single population (or from a single source), then average values for a species were derived from a number of studies.

In our analysis we used the calculation  $(SVL)^3$  (using both maturity SVL and hatchling SVL) as a proxy for body mass. This conversion is supported by a previous study that found body mass scales as SVL raised to an exponent of 2.98 across 47 species of lizard (Pough 1980). Similarly unpublished field data from one of the authors (R.W.W.) suggest an exponent of 3.12 when analyzing 14 species of lizards composed of 436 individuals ranging from hatchling to adult ( $\log(\text{body mass}) = -10.9 + 3.12 \times \log(SVL)$ ; 95% CI of exponent, 2.99–3.23;  $r^2 = .87$ ). We did not use body mass in our analyses for two reasons: SVL is much more commonly reported in the herpetological literature as a measure of size and age, and the body mass of lizards of a given SVL can be highly variable due to relatively large ingested and egested meals.

Annual clutch size  $\overline{C}$  was estimated by multiplying average clutch size by number of clutches per year. We estimated the average yearly body mass given to reproduction by multiplying the average annual clutch size  $\overline{C}$  by hatchling  $(SVL)^3$  (again,  $(SVL)^3$  is used to estimate hatchling body mass).

### Statistical Analysis

Slope estimates for all conventional analyses were calculated using ordinary least squares (OLS) regression and reduced major axis (RMA) estimation. For these analyses we used the line fitting package SMATR (<http://web.maths.unsw.edu.au/~dwarton/programs>) implemented on the R software platform (R Development Core Team 2007). It has been argued that RMA estimation or Type II regression is more appropriate than OLS regression for analyzing allometric data (see LaBarbera 1989). As shown by Warton et al. (2006), however, there is no single correct method for finding a line of best fit to allometric data (see also Ricker 1973). Contrary to claims in the literature, RMA estimation should not be used simply because the

$X$ -axis data are measured with error (Warton et al. 2006). The RMA method is designed to account for error (random and measurement error) along both the  $X$ - and  $Y$ -axes (Warton et al. 2006; O'Connor et al. 2007). An important limitation of RMA, however, is that to account for this error it assumes that variance in the data is partitioned equally between both axes. On the other hand, OLS regression assumes that variance in the  $Y$ -axis is greater than variance in the  $X$ -axis. In their recent review, O'Connor et al. (2007) demonstrated that these regression methods worked well under the conditions for which they were designed (i.e., OLS when  $\sigma_y/\sigma_x$  is large and RMA when  $\sigma_y/\sigma_x = 1$ ).

The data presented in this study are compiled data from field studies that inherently have a degree of measurement error that includes both operator error and sampling error. The degree of this error is not known. In this study, however, our presentation of this data warrants the use of OLS regression because the compounding error in the  $Y$ -axis variables (e.g., clutch size  $\times$  number of clutches  $\times$  hatchling size) swamps any error in the  $X$ -axis variables (e.g., hatchling size or maturity size). We present both OLS and RMA regressions in this study for comparison with phylogenetic regressions (see below) and for discussion.

### *Phylogenetic Analysis*

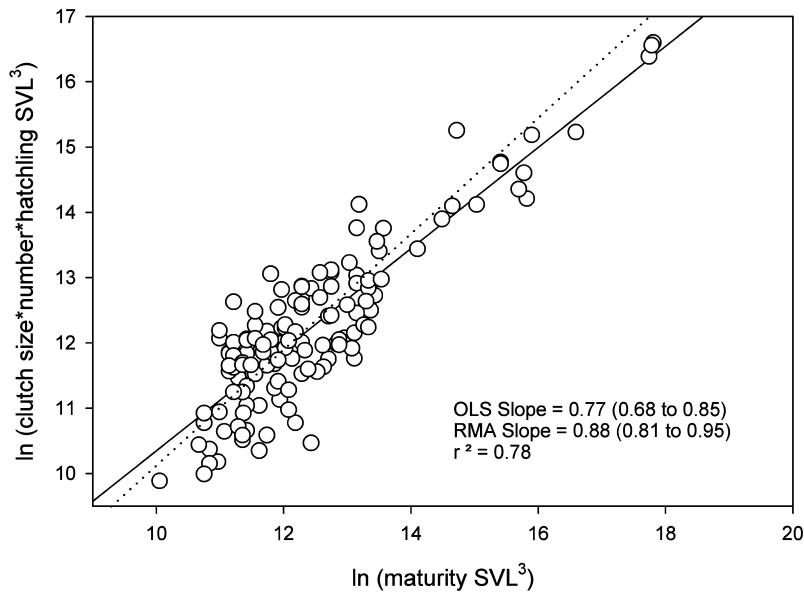
The relationship between size, reproductive effort, and the clutch size/offspring size trade-off across species may be driven not only by resource trade-offs but by phylogenetic inertia between closely related species. To account for a phylogenetic effect among these traits, we developed a composite phylogeny using the most recent comprehensive phylogenies available for all of the lizard species analyzed in this study (see app. B). This tree was drawn using Mesquite (Maddison and Maddison 2006), and species with multiple data points were drawn as polytomies (not shown in fig. B1) with no hierarchical arrangement of populations (Perry and Garland 2002). Initial branch lengths were arbitrarily set to a value of 1, which is appropriate for a speciation model of evolution (Martins and Garland 1991). We then used a new Matlab program *regressionv2.m* (<http://biology.ucr.edu/people/faculty/Garland/physig>) to implement and compare nonphylogenetic OLS and phylogenetic generalized least square (GLS) regressions using the Ornstein-Uhlenbeck (OU) transformation (Blomberg et al. 2003; Lavin et al. 2008). In this article, we refer to this phylogenetic regression model with the OU transformation as PROU. A detailed explanation of this Matlab program and phylogenetic regression methodology (outlined below) can be found in Lavin et al.'s (2008) paper. It is important to note that models resulting

from phylogenetic GLS regressions are equivalent to those resulting from the method of independent contrasts (Freckleton et al. 2002; Blomberg et al. 2003). Analysis using PROU, however, has several advantages that include an estimate of the strength of phylogenetic signal in the data (see below: the  $d$  parameter), as well as the ability to compare the fit of competing OLS and phylogenetic regression models using a maximum-likelihood ratio test (Lavin et al. 2008).

Briefly, regression by OLS assumes that residual variation is independent among species, whereas phylogenetic GLS regression assumes that residual variation is correlated and models these correlations using a Brownian or random evolutionary process along the phylogenetic tree. The *regressionv2.m* program also produces GLS regression models based on stabilizing selection around an optimum given by the OU process along the phylogenetic tree. Note that we do not present our analyses using GLS because the PROU models always outperformed the GLS models. Using restricted maximum likelihood, the program estimates the optimal OU transformation parameter  $d$ , which is an estimate of the optimal branch lengths. The parameter  $d$  can vary between 0 and 1: a value of 0 indicates that the nonphylogenetic OLS regression model best fits the data, whereas a value of 1 indicates that the PROU model best fits the data. If  $d$  is intermediate but significantly greater than 0, then the residual variation in the dependent variable exhibits a statistically significant phylogenetic signal. The model with better fit can be determined by a maximum-likelihood ratio test in which twice the difference in the natural log of the maximum likelihoods of the OLS and PROU models will be distributed approximately as a  $\chi^2$  with degrees of freedom equal to the difference in the number of parameters estimated in the two models (PROU has one more parameter with  $d$ ).

### **Results and Discussion**

The predicted reproductive allometry of  $\bar{R} \propto m_\alpha^{0.75}$  as the annual body mass given to reproduction is strongly supported in the data, with a very tight allometry and an estimated OLS regression slope of 0.77, which is not significantly different from our assumed value of 0.75 (95% CI, 0.70–0.84; RMA = 0.88; 95% CI, 0.8–0.94;  $r^2 = 0.78$ ; fig. 1). Although the RMA analysis does not overlap the predicted 0.75 exponent, the OLS regression slope is the more appropriate model because, as argued above, the error in the  $Y$ -axis is compounded and must swamp any error in the  $X$ -axis data. Phylogenetic regression analysis using the PROU transformation also generally supports this predicted allometry with a 95% CI that overlaps the



**Figure 1:** Annual production allometry as estimated by (clutch size)  $\times$  (number of clutches per year)  $\times$  (hatchling (SVL)<sup>3</sup>) scales with an OLS regression slope of 0.77 (95% CI, 0.68–0.85; RMA regression slope [dotted line], 0.88, 95% CI, 0.81–0.95). Phylogenetic regression analysis similarly supports a 0.75 slope value (see table 1). These results support the predictions of previous optimization models (see text), which indicate that this 0.75 scaling captures the effects of mortality on the trade-off between reproductive effort and size at maturity. These results also support our use of  $m_{\alpha}^{0.75}$  as a correction factor for revealing the offspring size/clutch size trade-off in lizards.

0.75 exponent (table 1). However, the two major clades in this data set exhibit differing slopes, with Iguania strongly supporting the predicted 0.75 value. Scleroglossa, on the other hand, shows wide confidence intervals that overlap the expected 0.75 value using an OLS regression model but not with the PROU model (table 1). Notice that the generally tight allometric relationship  $\bar{R} \propto m_{\alpha}^{0.75}$  is for annual reproduction; fitted allometries for yearly clutch size versus size at maturity (slope, 0.02;  $r^2 = 0$ ) or offspring body mass per clutch versus size at maturity are not very strong or informative (slope, 0.61;  $r^2 = 0.37$ ). Thus, an individual's body size at maturity determines the annual body mass available for reproduction, which can be partitioned among a single or multiple clutches. This result also strongly supports the predicted 0.75 value of Charnov et al. (2001), which reflects the influence of mortality on the growth and reproductive trade-off in lizards.

Next we examine the data set for the expected clutch size/offspring size trade-off by first simply asking whether clutch size or yearly clutch size is inversely correlated with offspring size across lizard species. We find no evidence, however, of a trade-off for either clutch size (fig. 2A) or for yearly clutch size (fig. 2B). Given the tight reproductive allometry of  $\bar{R} \propto m_{\alpha}^{0.75}$  exhibited by these lizards, we can use this estimate of  $\bar{R}$  to control for the size-dependent allocation to annual reproduction by plotting

ln (annual clutch size/ $m_{\alpha}^{0.75}$ ) versus ln (hatchling SVL<sup>3</sup>). As shown in figure 3A, the  $\bar{R}$ -corrected yearly clutch size is now very strongly related to offspring size, with a slope value not significantly different from  $-1$  (OLS slope,  $-0.96$ ; 95% CI,  $-0.87$  to  $-1.05$ ;  $r^2 = 0.78$ ; RMA slope,  $-1.09$ ; 95% CI,  $-1$  to  $-1.18$ ; fig. 3A). Phylogenetic regression analysis also generally supports this result, with a slope for the entire data set that trends toward  $-1$  although the confidence intervals do not overlap the expected slope (PROU slope,  $-0.79$ ; 95% CI,  $-0.69$  to  $-0.92$ ;  $r^2 = 0.63$ ; fig. 3B). However, the two major clades exhibit differing slopes, with Iguania again strongly supporting the predicted slope value of  $-1$  (PROU slope,  $-1.02$ ; 95% CI,  $-0.9$  to  $-1.15$ ;  $r^2 = 0.79$ ; fig. 3B). Scleroglossa, on the other hand, shows a more shallow slope that trends toward, but does not overlap, the expected  $-1$  slope value (PROU slope,  $-0.73$ ; 95% CI,  $-0.61$  to  $-0.88$ ;  $r^2 = 0.67$ ; fig. 3B). The offspring size/clutch size trade-off is thus revealed after controlling for variation in  $\bar{R}$ , as shown by both the comparative OLS slope value of  $-0.96$  and the negative trends near  $-1$  for the phylogenetic regression analysis.

#### Phylogenetic Analysis

The newly developed phylogenetic regression program regressionv2.m by T. Garland Jr. (Lavin et al. 2008) provides

**Table 1:** Regression slopes from nonphylogenetic (OLS regression) and phylogenetic (PROU) analyses for annual reproductive effort in relation to size at maturity

Analysis	<i>N</i>	Slope	95% CI	$r^2$	ln likelihood	AIC	<i>d</i>
Nonphylogenetic OLS regression:							
All lizards	138	.77	.7–.84	.77	–124.6	255.2	...
Iguania	64	.7	.64–.77	.87	–41.1	88.2	...
Scleroglossa	71	.82	.71–.91	.78	–53.1	112.2	...
Phylogenetic GLS regression with OU transformation:							
All lizards	138	.85	.75–.94	.63	–94.9 <sup>a</sup>	197.7	.68
Iguania	64	.74	.71–.91	.77	–37.1 <sup>a</sup>	82.1	.45
Scleroglossa	71	.9	.8–.99	.82	–44.4 <sup>a</sup>	96.8	.66

Note: Values for  $r^2$  obtained from OLS and PROU models are not comparable. The term  $d$  is the restricted maximum-likelihood estimate of the OU transformation parameter. Akaike Information Criterion (AIC; smaller is better) is computed as  $-2(\ln \text{maximum likelihood}) + 2(\text{no. of parameters})$ .<sup>a</sup>

<sup>a</sup> On the basis of likelihood ratio tests, the PROU models are statistically significantly better than the OLS regression models.

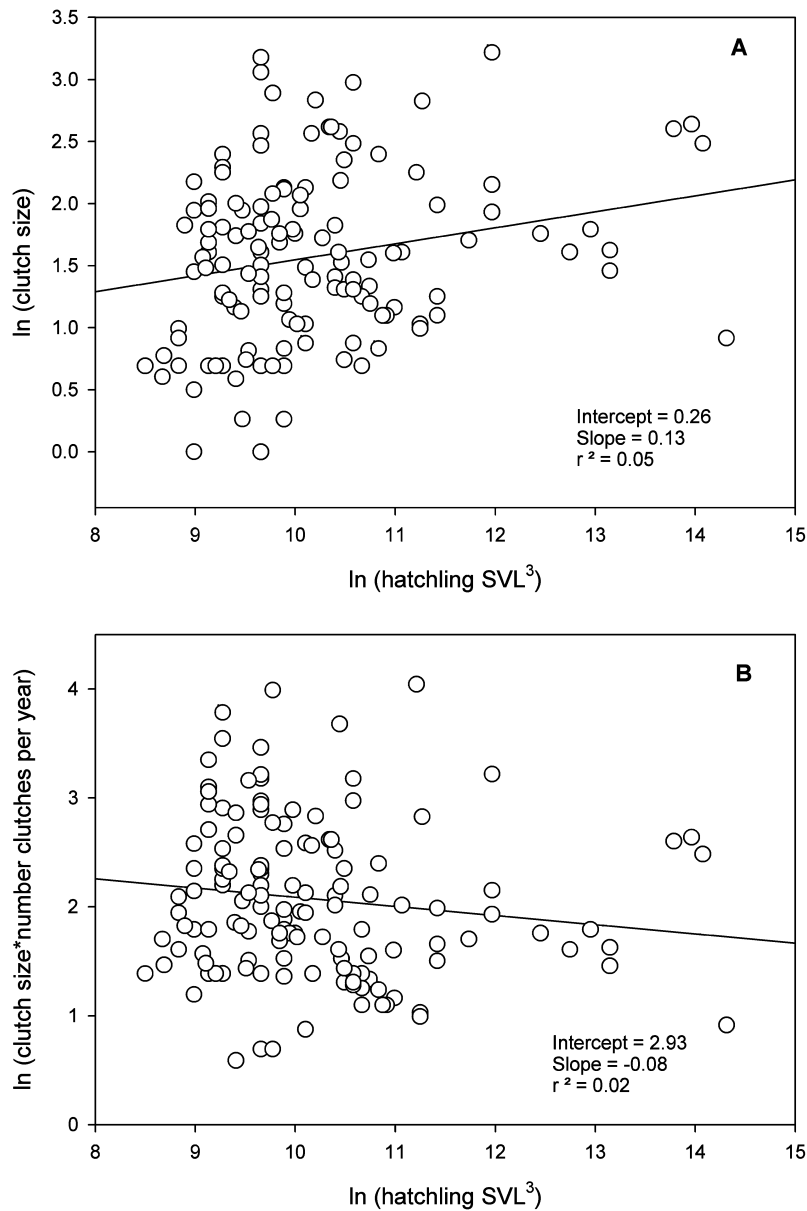
for tests of the strength of phylogenetic signal among traits (Blomberg et al. 2003), as well as maximum-likelihood data for the comparison of fit between models ranging from conventional nonphylogenetic to complex phylogenetic regressions. For both the data for the reproductive allometry (table 1) and the offspring size/clutch size trade-off (table 2), likelihood ratio tests indicate that phylogenetic regressions using the PROU transformation fit significantly better ( $P < .05$ ) than do OLS regression models. For all lizards in the data set and between the two clades, PROU models provided a better fit because they contain an additional parameter  $d$  (Lavin et al. 2008). Note that the all lizard and clade data sets show values that are significantly greater than 0 for the parameter  $d$  (allometry and trade-off analysis average,  $0.61 \pm 0.13$  SD; tables 1, 2). Because this parameter  $d$  gives a measure of how well the branch lengths estimated by the OU transformation fit the data, the residual values for these lizards have a statistically significant phylogenetic signal (Blomberg et al. 2003; Lavin et al. 2008). It must be noted, however, that there is a rather large degree of uncertainty in the topology of our phylogenetic tree, especially within Scleroglossa, as indicated by polytomies (fig. B1). Garland and Diaz-Uriarte (1999) found, however, that phylogenetic analysis provides reliable estimates of trait correlations despite such phylogenetic uncertainty. A separate issue is whether the slopes from the comparative OLS regression models differ from the phylogenetic PROU models, which can be determined by the overlap of their 95% CIs (Lavin et al. 2008). For our reproductive allometry analysis, the confidence intervals of both OLS and PROU models did overlap the predicted 0.75 slope value for all lizards and the Iguania clade, whereas the PROU slope for Scleroglossa did not overlap this value (table 1). For our trade-off analysis, the confidence intervals and slope values from the OLS model were very near the predicted value of  $-1$  for all the lizards and the Iguania clade (table 2). For the

PROU analysis, however, only the Iguania clade exhibited a slope and confidence interval that was indistinguishable from  $-1$ .

These differences in the slope patterns between the two major clades suggest that correlated life-history traits such as body plan and reproductive effort may play a very important role in the reproductive allometry and trade-offs of these lizards (Vitt and Congdon 1978; Shine 1992). Lizards in the Iguania clade generally have rounded body plans and have clutch sizes and an annual number of clutches that are, on average, twofold greater than those of the lizards in Scleroglossa (which are characterized by slender body plans). An examination of the differing ecomorphologies included in this data set may, therefore, be a very informative way to understand how selective forces have shaped the clutch size/offspring size trade-off. Included in this data set are species representing the great diversity of coevolved body plans, foraging modes, and reproductive strategies that are inherent to lizards ranging from the rotund horned lizards (*Phrynosoma* genus) to the sleek whiptails (*Teiidae*) and including both oviparous and viviparous species.

The oviparous and viviparous reproductive modes did not affect our trade-off results; oviparous species had an OLS regression slope value of  $-0.92$  (95% CI,  $-0.82$  to  $-1.02$ ;  $r^2 = 0.77$ ;  $n = 112$ ) and viviparous species had a slope value of  $-0.98$  (95% CI,  $-0.76$  to  $-1.20$ ;  $r^2 = 0.78$ ;  $n = 26$ ). The intercepts are also indistinguishable, with wide overlapping confidence intervals for the oviparous species (intercept, 2.20; 95% CI, 1.20–3.19) and for the viviparous species (intercept, 2.47; 95% CI, 0.14–4.81).

Analysis of the clutch size/offspring size trade-off at the rather coarse taxonomic family level indicates that most of the lizards in this data set (we excluded families with  $<4$  data points) do show the predicted negative relationship between  $\bar{R}$ -corrected annual clutch size and hatchling size (fig. 4). Although the family designation may be a

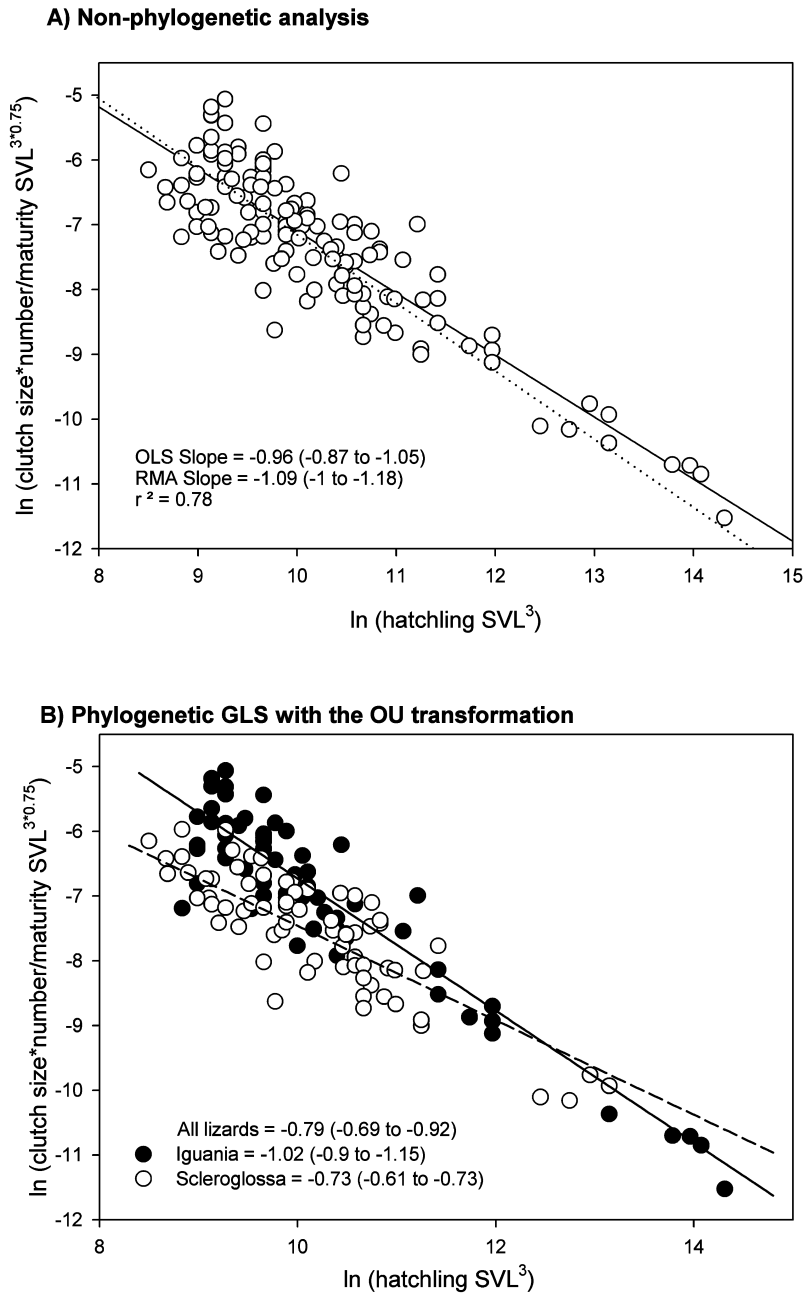


**Figure 2:** A, Counter to theoretical predictions for an offspring size/clutch size trade-off (negative relationship), comparative data for 138 populations and 115 species of lizards show a slightly positive nonsignificant relationship for log-transformed hatchling SVL ( $\text{mm}^3$ ) versus clutch size. B, Similarly annualized data do not support the predicted trade-off, with a slightly negative and nonsignificant relationship between hatchling SVL ( $\text{mm}^3$ ) and annual clutch size (clutch size  $\times$  number of clutches per year).

somewhat arbitrary phylogenetic distinction, we believe that this analysis satisfactorily captures the significant and consistent ecomorphologies represented by different families (e.g., Gekkonidae vs. Iguanidae, etc.). Although generally small sample sizes and limited ranges of hatchling size preclude much precision, all of the 95% CIs for each family include the expected  $-1$  slope value. Indeed, the estimated slope value is indistinguishable from  $-1$  (OLS

slope,  $-0.99$ ;  $r^2 = 0.82$ ) if only those five families with four or more data points (Teiids and horned lizards excluded) are included in the across-species trade-off analysis.

The distinct ecomorphologies characterized by the horned lizards (*Phrynosoma*) and Teiids are possibly the exceptions (fig. 4). These lizards may represent the extremes in differing body plans between the clades of Igua-



**Figure 3:** A, Correcting for size-dependent  $R$  (estimated by  $(\text{mass})^{0.75}$ ) reveals a negative relationship with an OLS regression slope of  $-0.96$  (95% CI,  $-0.87$  to  $-1.05$ ; RMA slope [dotted line]  $-1.09$ , 95% CI,  $-1$  to  $-1.18$ ) indistinguishable from a  $-1$  slope, strongly supporting the theoretically predicted offspring size/clutch size trade-off across lizards. B, Phylogenetic analysis using GLS regression also shows regressions of negative slopes near  $-1$ , with the Iguania clade (solid line) strongly supporting the  $-1$  slope, whereas the Scleroglossa clade (dashed line) does not show a slope overlapping  $-1$ .

nia and Scleroglossa, and their differing slope values may reflect how the correlation between body shape and body mass allocation to a single clutch have shaped the clutch size/offspring size trade-off in these lizards. As argued by

other researchers, body shape is highly correlated with lizard ecology, feeding strategies (active vs. sit-wait predators), and reproductive effort (Vitt and Congdon 1978; Shine 1992). The five horned lizard species, however,



**Table 2:** Regression slopes from nonphylogenetic (OLS) and phylogenetic (PROU) analyses for annual clutch size/maturity body mass<sup>0.75</sup> in relation to hatchling size

Analysis	<i>N</i>	Slope	95% CI	<i>r</i> <sup>2</sup>	ln likelihood	AIC	<i>d</i>
Nonphylogenetic OLS regression:							
All lizards	138	−.96	−.88 to −1.04	.77	−124.4	254.8	...
Iguania	64	−1.07	−.98 to −1.16	.9	−40.1	86.2	...
Scleroglossa	71	−.82	−.7 to −.93	.73	−49	104	...
Phylogenetic GLS regression with OU transformation:							
All lizards	138	−.79	−.69 to −.92	.63	−89.1 <sup>a</sup>	186.2	.76
Iguania	64	−1.02	−.9 to −1.14	.79	−36.1 <sup>a</sup>	80.2	.45
Scleroglossa	71	−.73	−.61 to −.88	.67	−38.7 <sup>a</sup>	85.3	.64

Note: Values for  $r^2$  obtained from OLS regression and PROU models are not comparable. The term  $d$  is the restricted maximum likelihood estimate of the OU transformation parameter. Akaike Information Criterion (AIC; smaller is better) is computed as  $-2(\ln \text{maximum likelihood}) + 2(\text{no. of parameters})$ .

<sup>a</sup> On the basis of likelihood ratio tests, the PROU models are statistically significantly better than the OLS regression models.

show no statistically significant reproductive allometry (slope = 0.16;  $r^2 = 0.18$ ), and the nine Teiids have a weak allometry (slope = 0.65;  $r^2 = 0.31$ ). The exclusion of these two taxa has no affect for either the overall production allometry (OLS slope = 0.78;  $r^2 = 0.79$ ) or the trade-off analysis (OLS slope = −0.96;  $r^2 = 0.78$ ).

### Temperature

Temperature also plays a critical and predictable role in driving life-history patterns in lizards (Shine 2005). Surprisingly, our results include the predicted 0.75 and −1 slope values (figs. 2A, 3) without including an explicit temperature parameter in our model. Charnov and Ernest (2006) suggested that the  $\bar{R} \propto m_\alpha^{0.75}$  correction might be distorted if larger-bodied species always lived at higher average annual temperatures than small-bodied species did (Gillooly et al. 2002). However, this does not appear to be true for these lizards, as  $\bar{R} \propto m_\alpha^{0.75}$  shows a very tight relationship. A lack of a temperature effect is not necessarily that surprising, however, considering that diurnal reptiles can behaviorally adjust their own body temperatures precisely and over a considerable thermal range (Shine 2005). Thus, most reproducing females are likely optimizing their resource allocation to a clutch by behaviorally regulating their body temperature. That is, the life-history traits of a particular species or population have been molded by temperature, and our data therefore include any temperature effects on resource dynamics.

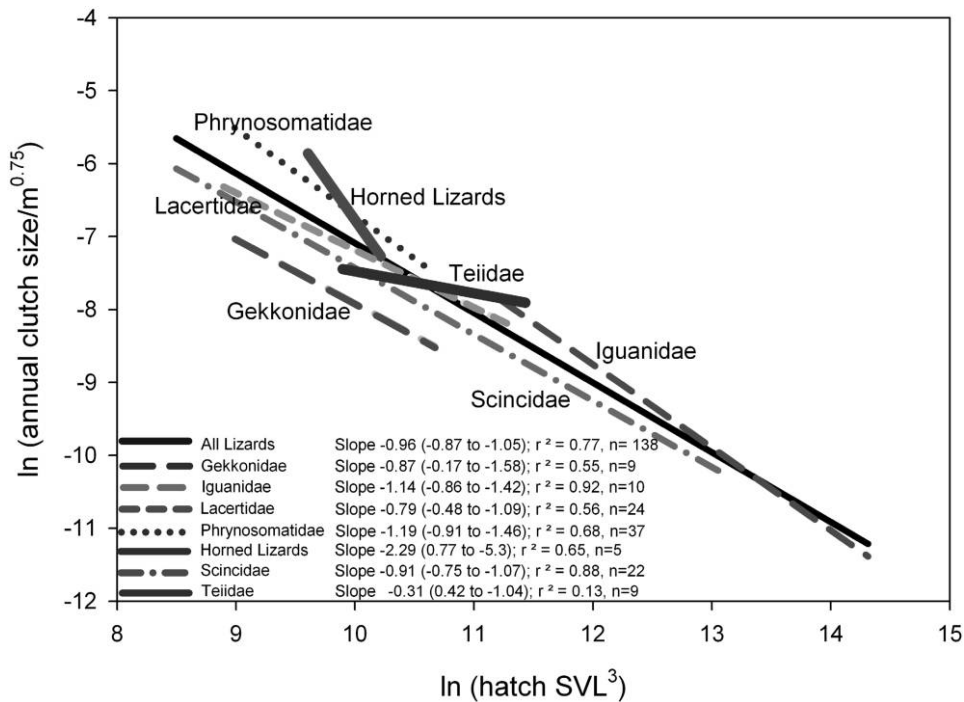
### Mortality

Ontogenetic increases in body size, clutch size, reproductive effort, and survival that are characteristic to most species of lizards must play an extremely important role in shaping the clutch size/offspring size trade-off in a single breeding effort, especially within the context of potential

future reproduction. Our use of yearly average values certainly does not capture these ontogenetic dynamics. To explicitly model such interage class differences, however, would require detailed knowledge of when mortality occurs for each age class (e.g., before or after a first, second, or third clutch). These data simply do not exist, even for well-studied taxa as such lizards; all life-history and demographic data for lizards are average estimates. Despite the coarse nature of such field estimates (and the compiled data in this article) and our admittedly coarse method of estimating resources for reproduction ( $\bar{R} \propto m_\alpha^{0.75}$ ), our results are robust and strongly support the theoretical predictions. We also do not include an extra mortality cost induced by increased reproduction because such a trade-off has rarely been demonstrated in nature (van Noordwijk and de Jong 1986; Charnov 1993; Schwarzkopf 1993; Charnov et al. 2001; Uller and Olsson 2005).

### Allometry Methodology

The primary objective of allometry analysis is often the estimation of slopes. Slopes estimated by regression can provide insight into the functional biology of organisms and ecosystems and have been the fuel for much recent debate (e.g., Calder 1984; White and Seymour 2003; Brown et al. 2004). Critical to the estimation and confidence of allometry slopes is the variance structure within the data. Because variance due to measurement and sampling error is always present (often to an unknown degree) in both comparative and phylogenetic data, the use of Type II RMA regressions has more often been recommended over least squares methods (Sokal and Rohlf 1995; Warton et al. 2006). As demonstrated by O'Connor et al. (2007), however, OLS and RMA regression methods provided accurate slope values only under the conditions for which they were designed (i.e., OLS when  $\sigma_y/\sigma_x$  is large and RMA when  $\sigma_y/\sigma_x = 1$ ). The alternative least squares variance-



**Figure 4:** Six of 15 families with more than four data points have the predicted negative relationship between hatchling size and the  $R$ -corrected annual clutch size, with OLS confidence intervals overlapping the predicted  $-1$  slope. The distinct slopes for Teiids and horned lizards may reflect differences caused by correlated body plans and reproductive patterns. Small sample size and ranges in hatchling size, however, preclude any strong conclusions.

oriented residuals regression method (LSVOR) outlined by O'Connor et al. (2007) would be ideal with the use of more complete life-history data that include variance estimates.

Admittedly our OLS, RMA, and PROU slope estimates are not the most accurate because of unknown variance, but the critical point is that the predicted allometry and trade-off patterns are always supported (figs. 1, 3). The approximate slope values for these lizard data are very near the predicted slopes of  $0.75$  and  $-1$  when the data are analyzed using both comparative and phylogenetic methods. If we had better variance data, both our comparative and phylogenetic slope values would presumably be similar to the LSVOR simulation results reported by O'Connor et al. (2007). Our estimated comparative and phylogenetic slope values would thus lie between the reported OLS, RMA, and PROU estimates, with confidence intervals closely overlapping the predicted  $0.75$  and  $-1$  slope values.

In summary, our results show that, by correcting for size-dependent variation in  $\bar{R}$ , the often-observed inverse proportionality between  $\bar{C}$  and  $I$  is revealed for lizards, despite our rather crude measure of resource investment. These data also demonstrate a very tight allometry for

annual production, a relationship that has been rarely shown for lizards. Phylogenetic GLS models similarly support these results, although they highlight differing trade-off and reproductive patterns between the two major clades of Iguania and Scleroglossa. When combined, these analyses demonstrate the importance of examining the offspring size/clutch size trade-off from the perspective of annual resource investment in reproduction because the offspring size/clutch size trade-off is not isolated to a single clutch but is shaped by resource investment over an entire breeding season. Considering the importance of body size for a spectrum of life-history traits (Calder 1984; Charnov 1993), allometric relationships such as  $\bar{R} \propto m_{\alpha}^{0.75}$  are also invaluable tools for increasing our understanding of the evolution of life-history trade-offs. Indeed, through the use of these tools, we conclude that, across lizard species with a wide diversity of evolved life-history traits, there is strong evidence for the predicted trade-off between offspring size and the annual number of eggs produced.

#### Acknowledgments

We would like to thank the many biologists who diligently collected the life-history data compiled for this article. We

also thank M. Moses, C. Oufiero, S. Poe, and three anonymous reviewers for greatly improving this article through their insightful critiques. R.W.W. was supported by an NSF-UNM Biocomplexity Fellowship (DEB-0083422) and an NSF GK-12 Fellowship (DGE-0538396).

## APPENDIX A

Table A1: Compiled lizard life-history data

Family, species	Female maturity SVL	Female average SVL	Hatchling average SVL	Clutch size (mean)	No. clutches per year (mean)	Reference
Agamidae:						
<i>Amphibolurus fordi</i>	48.0	...	24.0	2.3	2.0	Dunham et al. 1988
<i>Amphibolurus isolepis</i>	51.0	61.0	27.0	3.3	2.0	Dunham et al. 1988
<i>Amphibolurus nuchalis</i>	86.0	88.3	32.0	4.1	2.0	Dunham et al. 1988
<i>Amphibolurus ornatus</i>	69.0	...	32.0	3.8	2.0	Dunham et al. 1988
<i>Japalura swinhonis</i>	53.5	76.1	20.0	4.3	2.0	Lin and Lu 1982
Anguidae:						
<i>Elgaria coerulea principis</i>	72.0	91.4	32.7	4.6	1.0	Dunham et al. 1988
<i>Elgaria coerulea</i>	75.0	87.7	35.9	3.8	1.0	Stewart 1985
<i>Elgaria m. multicarinata</i>	92.0	108.8	34.0	12.0	2.0	Dunham et al. 1988
Chamaeleonidae:						
<i>Chamaeleo namaquensis</i>	81.0	120.4	32.5	13.2	3.0	Dunham et al. 1988
<i>Chamaeleo pumilus</i>	51.0	79.0	22.0	11.0	4.0	Dunham et al. 1988; Clobert et al. 1998
Corytophanidae:						
<i>Basiliscus basiliscus</i>	135.0	168.0	42.0	9.5	6.0	Dunham et al. 1988; Shine and Charnov 1992
Crotaphytidae:						
<i>Crotaphytus collaris</i>	70	85.1	40.0	5.0	1.5	Turner 1977; Ballinger and Hipp 1985; Degenhardt et al. 1996
<i>Gambelia sila</i>	86.0	97.5	45.0	3.0	1.5	Howard 1974
<i>Gambelia wislizenii</i>	90.0	105.0	45.0	7.3	1.0	Tinkle and Hadley 1975; Degenhardt et al. 1996
Gekkonidae:						
<i>Coleonyx variegatus</i>	52.0	62.0	27.0	2.0	3.0	Degenhardt et al. 1996; Clobert et al. 1998
<i>Diplodactylus damaeus</i>	45.0	52.7	22.0	2.0	2.0	Henle 1991
<i>Diplodactylus tessellatus</i>	45.0	50.2	25.0	2.0	2.0	Henle 1991
<i>Gehyra variegata</i>	48.0	53.7	25.0	1.0	2.0	Henle 1990
<i>Gymnodactylus geckoides amarali</i>	38.7	43.8	20.0	1.7	2.0	Kitchener et al. 1988
<i>Heteronotia binoei</i>	44.0	46.7	21.0	2.0	2.0	Henle 1991
<i>Oedura ocellata boulenger</i>	79.0	80.0	35.0	2.0	1.5	Bustard 1971
<i>Oedura reticulata</i>	63.0	66.3	26.0	2.0	1.0	Dunham et al. 1988; Kitchener et al. 1988
<i>Oedura tryoni</i>	73.0	80.0	35.0	2.0	2.0	Dunham et al. 1988
Gymnophthalmidae:						
<i>Gymnophthalmus speciosus</i>	37.0	41.5	18.0	1.8	3.0	Dunham et al. 1988
<i>Leposoma rugiceps</i>	37.0	...	18.1	2.2	2.0	Dunham et al. 1988
<i>Neusticurus ecleopus</i>	50	56.6	21.5	2	2.0	Dunham et al. 1988
Iguanidae:						
<i>Amblyrhynchus cristatus</i>	252.0	279.0	118.0	2.5	1.0	Laurie 1990; Laurie and Brown 1990

Table A1 (Continued)

Family, species	Female maturity SVL	Female average SVL	Hatchling average SVL	Clutch size (mean)	No. clutches per year (mean)	Reference
<i>Conolophus subcristatus</i>	370.0	416.0	99.0	13.5	1.0	Werner 1982; Wiewandt 1982; Clobert et al. 1998
<i>Ctenosaura similis</i>	200.0	276.0	54.0	25.0	1.0	Fitch 1970; Dunham et al. 1988; Clobert et al. 1998
<i>Cyclura carinata</i>	192.0	225.0	80.0	4.3	1.0	Dunham et al. 1988; Shine and Charnov 1992
<i>Cyclura pinguis</i>	378.0	468.0	105.0	14.0	1.0	Wiewandt 1982; Clobert et al. 1998; Iverson et al. 2004
<i>Cyclura stejnegeri</i>	375.0	475.0	109.0	12.0	1.0	Wiewandt 1982; Clobert et al. 1998; Iverson et al. 2004
<i>Dipsosaurus dorsalis</i>	110.0	120.0	50.0	5.5	1.0	Krekorian 1984
<i>Sauromalus ater</i>	125.0	160.0	54.0	6.9	1.0	Abts 1987
<i>S. ater</i>	150.0	170.0	54.0	8.6	1.0	Dunham et al. 1988
Lacertidae:						
<i>Acanthodactylus erythrurus</i>	61.0	71.9	34.0	3.7	1.0	Bauwens and Diaz-Uriarte 1997
<i>Aporosaura anchietae</i>	44.0	44.0	27.0	1.3	3.0	Dunham et al. 1988
<i>Lacerta agilis</i>	62.0	68.4	26.6	5.8	1.0	Bauwens and Diaz-Uriarte 1997
<i>Lacerta lepida</i>	132	168.4	42.8	16.9	1.0	Bauwens and Diaz-Uriarte 1997
<i>Lacerta monticola</i>	67.3	...	25.9	6.5	1.0	Dunham et al. 1988
<i>Lacerta monticola cantabrica</i>	56	66.1	25	7.2	1.5	Bauwens and Diaz-Uriarte 1997
<i>Lacerta monticola cyreni</i>	60	70.1	26.6	5.4	1.0	Bauwens and Diaz-Uriarte 1997
<i>Lacerta schreiberi</i>	91.0	108.5	31.6	13.7	1.0	Bauwens and Diaz-Uriarte 1997
<i>Lacerta viridis</i>	84.0	98.5	32.6	8.9	1.0	Bauwens and Diaz-Uriarte 1997
<i>Lacerta vivipara</i>	44.2	57.6	21.0	6.0	1.0	Sorci et al. 1996; Clobert et al. 1998
<i>L. vivipara</i> (oviparous)	43.0	53.0	19.4	6.2	1.0	Bauwens and Diaz-Uriarte 1997
<i>L. vivipara</i> (viviparous)	44.0	55.5	20.8	4.4	1.0	Bauwens and Diaz-Uriarte 1997
<i>Meroles cuneirostris</i>	44.0	49.0	27.5	2.9	2.0	Dunham et al. 1988
<i>Podarcis atrata</i>	51.0	63.1	29.0	2.8	2.5	Krekorian 1984
<i>Podarcis bocagei</i>	44.0	55.2	24.0	4.2	2.0	Bauwens and Diaz-Uriarte 1997
<i>Podarcis hispanica atrata</i>	53.0	63.1	28.2	2.8	2.0	Bauwens and Diaz-Uriarte 1997
<i>Podarcis hispanica hispanica</i> (Asturias)	39.0	49.6	23.8	2.1	2.0	Bauwens and Diaz-Uriarte 1997
<i>P. hispanica hispanica</i> (Salamanca)	49.0	61.3	27.0	3.6	2.0	Bauwens and Diaz-Uriarte 1997
<i>Podarcis muralis</i>	49.0	58.5	24.8	5.2	2.0	Bauwens and Diaz-Uriarte 1997
<i>Psammodromus algirus</i>	58.0	69.2	27.8	6.0	1.5	Bauwens and Diaz-Uriarte 1997
<i>Psammodromus hispanicus</i>	42.0	48.4	22.9	3.2	2.0	Bauwens and Diaz-Uriarte 1997
<i>Takydromus septentrionalis</i>	56.0	65.0	23.4	3.1	2.0	Bauwens and Diaz-Uriarte 1997
<i>Takydromus tachydromoides</i>	41.0	45.7	22.0	3.6	3.0	Telford 1969
<i>T. tachydromoides</i>	46.0	53.5	22.5	3.4	3.0	Bauwens and Diaz-Uriarte 1997
Phrynosomatidae:						
<i>Phrynosoma cornutum</i>	70	87.0	25	21.3	1.5	Howard 1974; Munger 1986
<i>Phrynosoma douglassi</i>	63	76.0	25	24	1.0	Degenhardt et al. 1996
<i>Phrynosoma modestum</i>	42	57.0	25	13	1.5	Howard 1974; Munger 1986
<i>Phrynosoma platyrhinos</i>	70.0	76.5	27.0	8.4	1.5	Medica et al. 1973; Pianka and Parker 1975
<i>Phrynosoma solare</i>	80	...	30	17	1.0	Parker 1971; Degenhardt et al. 1996
<i>Callisaurus draconoides</i>	60.0	75.5	29.0	4.42	3.0	Pianka and Parker 1972
<i>Cophosaurus texanus</i>	50.0	60.0	22.0	6.1	3	Sugg et al. 1995; Degenhardt et al. 1996
<i>Holbrookia maculata</i>	45	54.0	25	5	2.0	Gennaro 1974

Table A1 (Continued)

Family, species	Female maturity SVL	Female average SVL	Hatchling average SVL	Clutch size (mean)	No. clutches per year (mean)	Reference
<i>H. maculata</i>	41	50.0	25.0	4.5	2	Jones and Ballinger 1987
<i>Sceloporus clarkii</i>	89.0	100.0	34.0	19.6	1.0	Tinkle and Dunham 1986; Degenhardt et al. 1996
<i>Sceloporus cyanogenys</i>	88.0	106.0	29.6	13.0	1.0	Dunham et al. 1988
<i>Sceloporus graciosus</i> (CA)	57	...	25	4.1	2.0	Tinkle et al. 1993
<i>S. graciosus</i> (UT)	50	52.0	25	3.7	2.0	Tinkle et al. 1993
<i>Sceloporus jarrovii</i>	54.0	72.4	28.5	7.07	1.0	Dunham et al. 1988
<i>S. jarrovii</i>	54.0	77.0	29	8.4	1.0	Ballinger 1973
<i>S. jarrovii</i>	54.0	72.0	30.7	5.6	1.0	Dunham et al. 1988
<i>Sceloporus magister</i>	80	89.0	32	6.2	2.0	Vitt and Ohmart 1974; Tinkle 1976
<i>Sceloporus merriami</i>	43.0	50.2	22.0	4.5	2.0	Dunham 1981
<i>Sceloporus olivaceus</i>	80.0	96.0	26.0	18.0	3.0	Blair 1960
<i>Sceloporus poinsettii</i>	85.0	104.0	33.0	10.5	1.0	Ballinger 1973
<i>Sceloporus scalaris</i>	41	52.0	20.0	8.8	1.5	Ballinger and Congdon 1981; Degenhardt et al. 1996
<i>Sceloporus u. consobrinus</i> (NM)	54.0	68.4	22.0	9.9	3.5	Vinegar 1975b
<i>Sceloporus u. tristichus</i> (NM)	53.0	63.3	25.0	7.2	2.5	Vinegar 1975b
<i>Sceloporus undulatus</i> (AZ)	60.0	65.0	27.0	8.3	3.0	Tinkle and Dunham 1986
<i>S. undulatus</i> (CO)	58.0	70.0	28.5	7.9	2.0	Tinkle and Dunham 1986
<i>S. undulatus</i> (KA)	47.0	57.0	24.0	7.0	2.5	Tinkle and Dunham 1986
<i>S. undulatus</i> (NE)	45	60.2	23.0	5.7	2.5	Jones and Ballinger 1987
<i>S. undulatus</i> (NJ)	60.0	73.0	26.0	8.0	2.0	Niewiarowski and Roosenburg 1993; Niewiarowski et al. 2004
<i>S. undulatus</i> (OH)	66.0	75.0	25.0	11.8	2.0	Tinkle and Dunham 1986
<i>S. undulatus</i> (SC)	55.0	63.0	23.0	7.4	3.0	Tinkle and Dunham 1986
<i>S. undulatus</i> (TX)	47.0	57.0	22.0	9.5	3.0	Tinkle and Dunham 1986
<i>S. undulatus</i> (UT)	60.0	69.0	25.0	6.3	3.0	Tinkle and Dunham 1986
<i>Sceloporus virgatus</i>	47	48.2	22	9.5	1	Vinegar 1975a; Rose 1981
<i>Sceloporus woodi</i>	45	...	21	5	3	Jackson and Telford 1974; McCoy et al. 2004
<i>Urosaurus ornatus</i> (AZ)	45.0	...	20.0	7.0	1.5	Smith 1977
<i>U. ornatus</i> (AZ)	39.0	52.0	21.0	7.1	3.0	Tinkle and Dunham 1983
<i>U. ornatus</i> (NM)	41.0	49.0	21.0	7.5	2.0	Ballinger 1977
<i>U. ornatus</i> (TX)	41.0	48.4	21.0	5.0	3.0	Dunham 1981
<i>U. ornatus</i> (TX)	39.0	48.0	21.0	5.4	3.5	Martin 1977
<i>Uta stansburiana</i> (CA)	42.0	49.0	25.0	3.5	3.0	Goldberg 1977
<i>U. stansburiana</i> (NV)	42.0	45.4	22.0	3.5	3.0	Turner et al. 1974
<i>U. stansburiana</i> (TX)	42.0	47.2	22.0	3.6	3.5	Tinkle 1967; Tinkle and Hadley 1975
Polychrotidae:						
<i>Anolis acutus</i>	36.0	42.2	20.0	1.0	6.0	Ruibal et al. 1972; Ruibal and Philibosian 1974
<i>Anolis carolinensis</i>	46.5	50.0	23.5	1.3	6.0	Dunham et al. 1988
Scincidae:						
<i>Ctenotus taeniolatus</i>	52.3	66.4	33.0	3.7	1	Dunham et al. 1988
<i>Egernia coventryi</i>	73.0	115.0	37.5	3.0	1.0	Chapple 2003
<i>Egernia cunninghami</i>	195.0	240.0	63.5	5.8	1.0	Chapple 2003
<i>Egernia kingii</i>	187.0	215.0	70.0	5.0	1.0	Chapple 2003
<i>Egernia kintorei</i>	170.0	195.0	75.0	6.0	1.0	Chapple 2003
<i>Egernia modesta</i>	85.0	105.0	42.5	2.7	1.0	Chapple 2003

Table A1 (Continued)

Family, species	Female maturity SVL	Female average SVL	Hatchling average SVL	Clutch size (mean)	No. clutches per year (mean)	Reference
<i>Egernia stokesii</i>	170.0	172.5	80.0	5.1	1.0	Chapple 2003
<i>Egernia whitii</i>	78.0	80.7	35.0	3.5	1	Dunham et al. 1988
<i>E. whitii</i>	83.0	95.0	42.5	2.8	1.0	Chapple 2003
<i>Emoia atrocostata</i>	80.0	90.0	35.0	2.0	3.0	Alcala and Howard 1967
<i>Eulamprus tympanum</i> (high altitude)	79.0	88.0	39.0	3.2	1.0	Schwarzkopf 1993; Blomberg and Shine 2001
<i>Eumeces egregius</i>	40.0	...	20.6	4.8	1.0	Dunham et al. 1988
<i>Eumeces fasciatus</i>	52.0	63.3	24.0	5.9	1.0	Turner 1977; Dunham et al. 1988
<i>Eumeces laticeps</i>	85.0	103.8	31.4	13.7	1.0	Dunham et al. 1988
<i>Eumeces obsoletus</i>	77.0	120.0	37.0	11.0	1.0	Hall 1971; Degenhardt et al. 1996
<i>Mabuya bistrata</i>	55.0	93.1	35.8	4.7	1.0	Vitt and Blackburn 1991
<i>Mabuya heathi</i>	45.0	70.3	32.4	5.0	1.0	Dunham et al. 1988
<i>Menetia greyii</i>	28.5	34.6	17.0	2.0	2.0	Dunham et al. 1988
<i>Morethia boulengeri</i>	36.0	45.0	19.00	2.7	3.0	Lin and Lu 1982
<i>Niveoscincus ocellatus</i>	65.0	72.9	29.7	4.0	1.0	Wapstra et al. 1999; Wapstra and Swain 2001
<i>N. ocellatus</i>	56.0	62.7	29.0	2.4	1.0	Wapstra et al. 1999; Wapstra and Swain 2001
<i>Scincella lateralis</i>	35.0	42.0	19.0	2.5	2.0	Brooks 1967
Teiidae:						
<i>Aspidoscelis dixonii</i>	67.0	87.7	34.0	4.0	1.0	Walker 1994; Degenhardt et al. 1996
<i>Aspidoscelis hyperythra</i>	53.0	59.7	27.0	2.3	2.0	Dunham et al. 1988
<i>Aspidoscelis inornata</i>	51	57.0	34	2.4	1.5	Christiansen 1971
<i>Aspidoscelis neomexicana</i>	47.0	65.0	37.0	2.3	1.5	Christiansen 1971
<i>Aspidoscelis sexlineata</i>	55.0	73.0	33.0	2.1	2.0	Fitch 1958; Degenhardt et al. 1996
<i>Aspidoscelis tessellata</i>	66.0	83.0	45.0	3.5	1.5	Knopf 1966; Schall 1978; Degenhardt et al. 1996
<i>Aspidoscelis tigris</i>	60	82.3	38	3	1.0	Tinkle and Hadley 1975; Degenhardt et al. 1996
<i>Aspidoscelis uniparens</i>	60	66.0	36	3.3	2.5	Hulse 1981; Degenhardt et al. 1996
<i>Teius teyou</i>	76.1	103.1	38.9	5.0	1.0	Cruz et al. 1999
Tropiduridae:						
<i>Liolaemus multiformis</i>	69	80.6	28	5.8	1	Dunham et al. 1988
<i>Tropidurus semitaeniatus</i>	58	70.5	19	2	3.5	Dunham et al. 1988
<i>Tropidurus torquatus</i>	70	88.5	27.8	6	3	Dunham et al. 1988
Xantusiidae:						
<i>Xantusia vigilis</i>	36.0	40.0	23.0	1.8	1.0	Zweifel and Lowe 1966

Note: Compiled data for female snout-vent length (SVL) at maturity, average adult female SVL, average hatchling SVL, average clutch size, and average annual number of clutches gathered from both primary literature sources and previously published reviews of lizard life histories.

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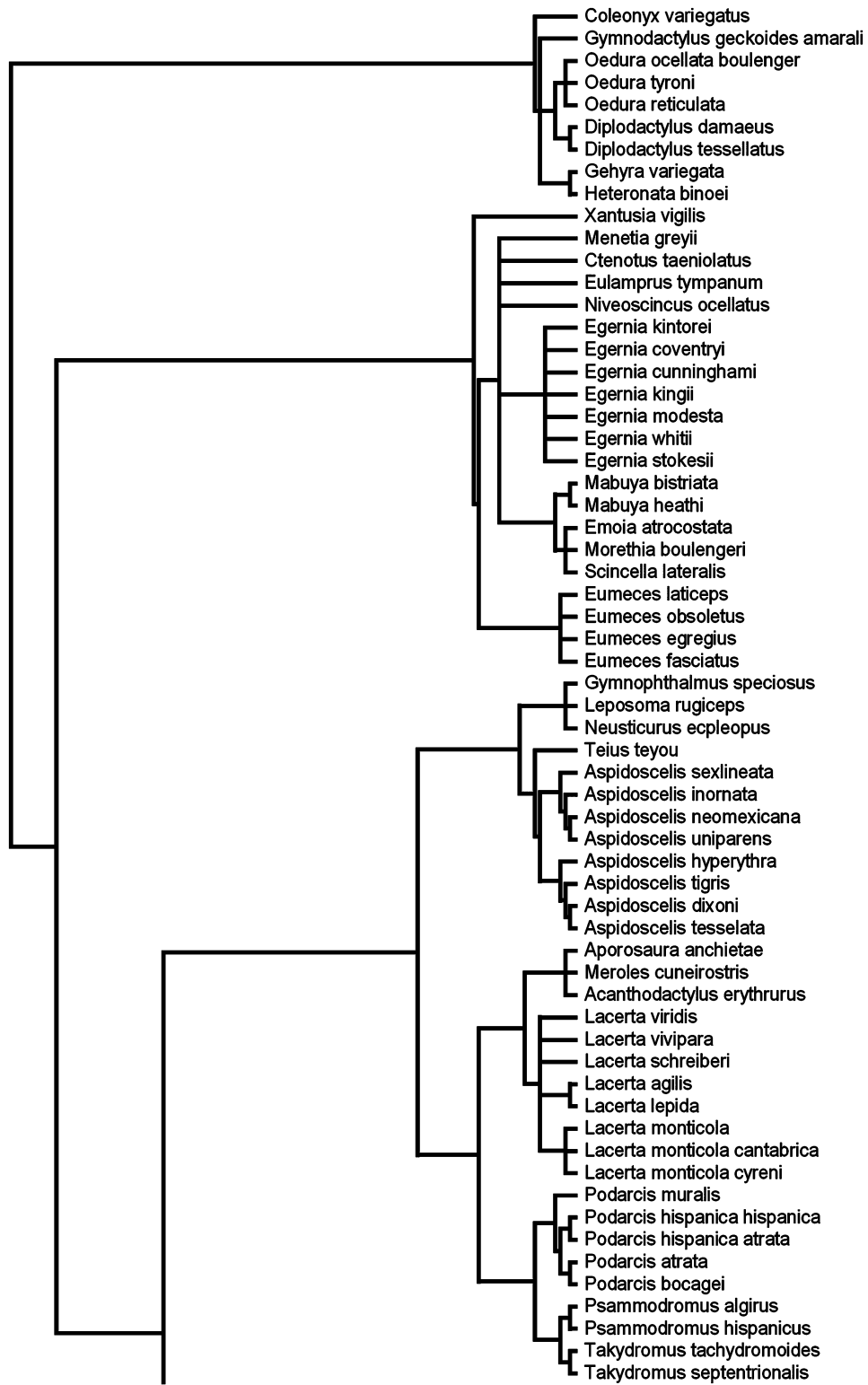
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## APPENDIX B

### Sources for Figure B1

This tree was drawn using the *Treeview* program (Page 1996). The broad topology for Squamata follows Townsend et al. (2004). Phylogenies at the family level were drawn from Kluge (1987) for Gekkonidae, Schmitz et al. (2005) for Scincidae, Reeder et al. (2002) for Teiidae, and Carranza et al. (2004) for Lacertidae. Relationships for the lizards of Phrynosomatidae were drawn from Reeder and Wiens (1996), whereas for the *Sceloporus* group we relied on Wiens and Reeder (1997) and Miles et al. (2002). The Agamidae phylogeny follows the topology drawn by Macey et al. (2000). Relationships within Iguanidae were drawn from Etheridge and de Queiroz (1988) and Sites et al. (1996). The phylogenies for Crotaphytidae are from McGuire (1996), Tropicuridae from Harvey and Gutberlet (2000), and Polychrotidae from Jackman (1999).





**Figure B1:** Compiled lizard phylogeny. This composite tree was drawn from the most recent or comprehensive phylogenies available for all of the lizard species analyzed in this study. This tree is rooted in Gekkonidae with “Scleroglossa” presented here as a paraphyletic outgroup to Iguania. Species with multiple populations (see table A1) were drawn as polytomies (not shown in this figure) with no hierarchical arrangement of populations.

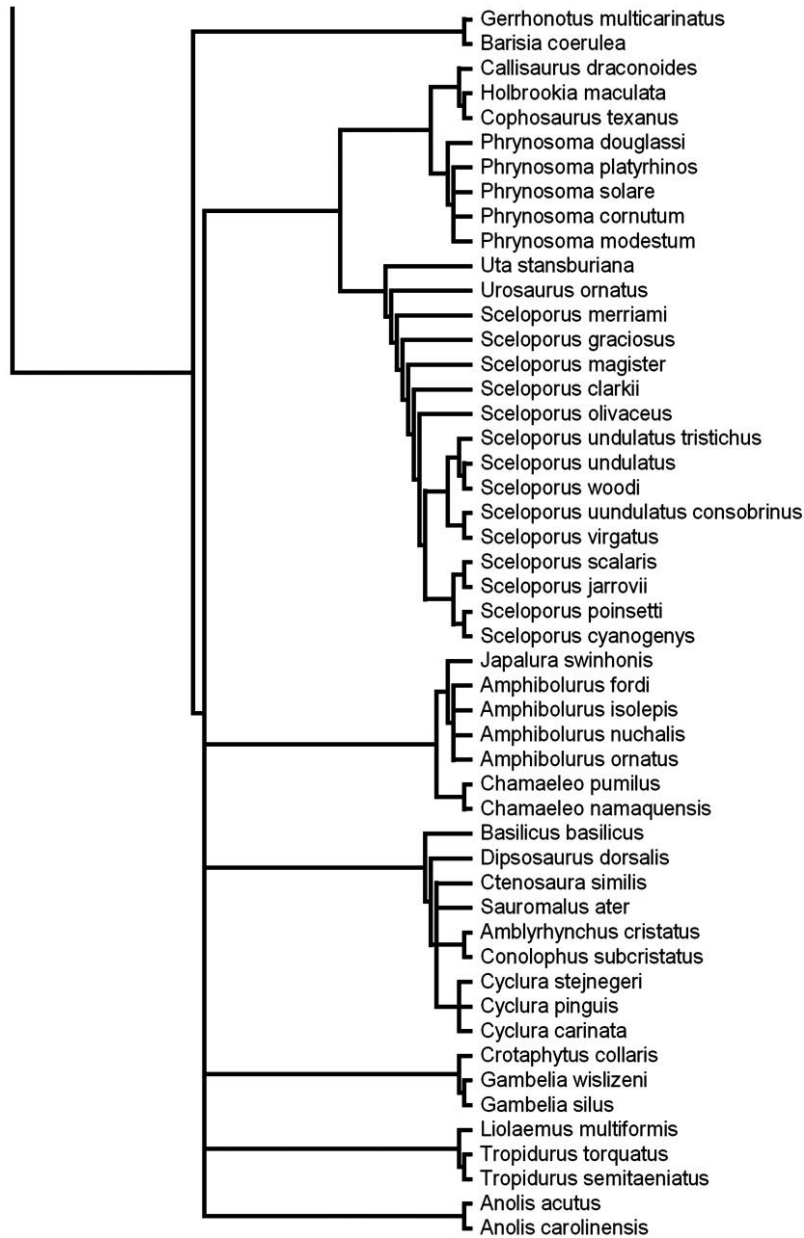


Figure B1 (Continued)

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