Life-History Patterns of Lizards of the World

Daniel O. Mesquita,[1],[*],[†] **Gabriel C. Costa,**[2],[†] **Guarino R. Colli,**[3] **Taís B. Costa,**[1] **Donald B. Shepard,**[4] **Laurie J. Vitt,**[5] **and Eric R. Pianka**[6]

1. Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, Avenida Castelo Branco, s/n, João Pessoa, Paraíba, 58000-000, Brazil;   2. Departamento de Ecologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Lagoa Nova, Natal, Rio Grande do Norte, 59072-970, Brazil;   3. Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade de Brasília, Brasília, Distrito Federal, 70910-900, Brazil;   4. Department of Biology, University of Central Arkansas, Conway, Arkansas 72035;   5. Sam Noble Museum and Department of Biology, University of Oklahoma, Norman, Oklahoma 73072;   6. Department of Integrative Biology, University of Texas, Austin, Texas 78712

abstract: Identification of mechanisms that promote variation in life-history traits is critical to understand the evolution of divergent reproductive strategies. Here we compiled a large life-history data set (674 lizard populations, representing 297 species from 263 sites globally) to test a number of hypotheses regarding the evolution of life-history traits in lizards. We found significant phylogenetic signal in most life-history traits, although phylogenetic signal was not particularly high. Climatic variables influenced the evolution of many traits, with clutch frequency being positively related to precipitation and clutches of tropical lizards being smaller than those of temperate species. This result supports the hypothesis that in tropical and less seasonal climates, many lizards tend to reproduce repeatedly throughout the season, producing smaller clutches during each reproductive episode. Our analysis also supported the hypothesis that viviparity has evolved in lizards as a response to cooler climates. Finally, we also found that variation in trait values explained by clade membership is unevenly distributed among lizard clades, with basal clades and a few younger clades showing the most variation. Our global analyses are largely consistent with life-history theory and previous results based on smaller and scattered data sets, suggesting that these patterns are remarkably consistent across geographic and taxonomic scales.

Keywords: Squamata, life history, reproduction, historical factors, climatic factors, phylogenetic analysis.

Introduction

Life-history traits are fundamentally constrained by trade-offs among survival, growth, and reproduction (Stearns 1992). Considering that resources may be limited, differential allocation of energy to one of these life functions reduces investment in others. As a consequence, individu-

als cannot simultaneously optimize all life-history traits. Therefore, traits are shaped by a complex natural selection landscape that is influenced by a variety of factors, such as physical condition of individuals, climate, food supply, bauplan, and evolutionary history, which are often correlated and difficult to tease apart (Dunham and Miles 1985; Miles and Dunham 1992). Identification of mechanisms that generate variation in life-history traits is critical for understanding evolution of divergent reproductive strategies. The timing and magnitude of reproductive investment, size and number of offspring, growth patterns, age at maturity, reproductive life span, and age-specific mortality schedules are examples of life-history traits that have traditionally been considered as key variables in life-history studies (Mesquita et al. 2016b; Roff 1992; Roff 2002; Stearns 1992). Here, we use a new global data set on lizard life-history traits (Mesquita et al. 2015), with high geographic and taxonomic coverage, to explore patterns of covariation in life-history traits. We use this new and extended data set to test general hypotheses derived from life-history theory. In addition, we attempt to unravel whether observed life-history patterns are shaped by climate, foraging mode, tropical versus temperate distribution, and/or habitat specialization.

The evolution of phenotypic characteristics such as life-history traits is a complex phenomenon, influenced by many different processes affecting rates and mode of evolution (Ackerly 2009; Mahler et al. 2010; Revell et al. 2012). The interaction of different phenotypic rates (e.g., slow or fast evolution) with different evolutionary modes (e.g., stabilizing and/or directional selection, genetic drift) will result in a range of patterns regarding the phenotypic similarity among related species (Revell et al. 2008). At one end of the range, closely related species may show similar life-history traits. Many underlying mechanisms—such as stabilizing selection, genetic constraints, and/or gene flow—may contribute to this pattern (i.e., niche conservatism; Losos

* Corresponding author; e-mail: danmesq@dse.ufpb.br.

† These authors contributed equally to this work.

2011; Pyron et al. 2015; Wiens and Graham 2005). For instance, if life-history traits show adaptive responses to climatic conditions and related species continue to occupy similar climates, then natural selection will prevent species divergence in those traits. In this scenario, the predicted outcome is a strong pattern of phylogeny predicting life-history traits. At the other end of the range, phenotypic similarity may be largely independent of phylogenetic relationships, and in some cases, even closely related species can be very dissimilar in some ecological attributes (e.g., in adaptive radiations). This can be caused by rapid rates of phenotypic evolution or stabilizing selection on a single optimum (Ornstein-Uhlenbeck model; Revell et al. 2008). Previous studies found strong evidence for niche conservatism of reproductive traits in squamates. For instance, some clades of tropical South American lizards show high phylogenetic conservatism in body and clutch size (Mesquita and Colli 2010). Conversely, other studies showed high lability in life-history traits. For example, viviparity in squamate reptiles is a well-known case of multiple convergences evolving as a response to cooler climates (Fraipont et al. 1996; Shine 2005; Pyron and Burbrink 2014). Therefore, understanding how traits evolve is essential to quantify life-history variation and test hypotheses about what factors affect life-history traits.

Many hypotheses have been proposed to explain variation in life-history traits in lizards. For instance, some studies suggest that body size and relative clutch mass (RCM) have coevolved with foraging mode (see Vitt and Congdon 1978; Huey and Pianka 1981). By virtue of their streamlined bodies, active foragers tend to have clutches representing a small proportion of total body mass. Conversely, sit-and-wait ambush foragers tend to have stockier bodies and higher RCM (Vitt and Congdon 1978). Therefore, this hypothesis predicts that RCM will be higher in sit-and-wait foragers. Other hypotheses suggest that reproductive mode is influenced by thermal regimes associated with development: in tropical regions, ectotherms can rely on warm temperatures for egg development, whereas in cold climates, as in temperate regions, maternal thermoregulation (i.e., viviparity) can yield more efficient embryo protection and more rapid development (Huey 1977; Blackburn 1982; Shine 2005). Therefore, this hypothesis predicts that viviparity should be more common in colder climates. Also, many studies suggest different hypotheses about the relationship of climate and life-history traits. For instance, as a result of increased competition, higher predation on hatchlings, energetic advantages of frequent oviposition, and/or lower clutch mass due to maternal mobility in tropical lizards (e.g., Inger and Greenberg 1966; Tinkle et al. 1970; Andrews and Rand 1974), larger clutches are expected in more seasonal climates (James and Shine 1988). Previous studies have also suggested that habitat specialization can constrain life-history traits. For example, use of rock crevices as shelter strongly influences body shape,

suggesting morphological constraints on the evolution of life-history traits, including clutch/litter size, size at birth, and RCM (see Vitt 1981; Zamora-Abrego et al. 2007). Therefore, this hypothesis predicts differences in life-history traits among different habitat use specialization categories, such as arboreal, fossorial, and saxicolous (Losos 2011).

Herein we apply modern phylogenetic comparative methods to analyze the data set mentioned above (Mesquita et al. 2015). With these new data and tools, we aim to effectively account for evolutionary history while testing the following specific ecological hypotheses: (1) Foraging mode constrains RCM. Prediction: active foragers will have lower RCM. (2) Temperature affects reproductive mode. Prediction: viviparity will be more conspicuous in temperate species and those found at higher elevations. (3) Habitat specialization constrains life-history traits. Prediction: lizards with different habitat specializations will show differences in traits, such as clutch/litter size, size at birth, and/or RCM. (4) Evolutionary history explains trait characteristics but in varying degrees across clades (see Vitt and Pianka 2005). Prediction: variation in trait values explained by clade membership will be unevenly distributed among lizard clades.

Methods

Lizard Life-History Data Set

Our data set consists of life-history data for 674 lizard populations, representing 297 species in 33 families, from 263 study sites including all continents except Antarctica (fig. 1). About 65% of these data were collected directly by the authors, and remaining data were obtained from the literature (fig. 1). All data collected are described in a data paper and deposited in Ecological Archives, http://dx.doi.org/10.1890/14-1453.1 (Mesquita et al. 2015), and in the Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.55610 (Mesquita et al. 2016a), and a summary is presented in the supplemental material, table S1 (available online).

Regarding data collected by authors, lizards were sexed by dissection and direct examination of gonads. Females were considered reproductive if vitellogenic follicles or oviductal eggs were present. We regarded the simultaneous presence of enlarged vitellogenic follicles and either oviductal eggs or corpora lutea as evidence for the sequential production of more than one clutch of eggs per year. Two different and possibly valid ways to determine clutch size exist. One is based on the number of oviductal eggs or enlarged vitellogenic follicles. The other is based on the number of eggs an individual would place in a nest (number of eggs actually deposited). Since we do not have data on lizard nests, we used the first estimate. For each lizard, we measured snout-vent length (SVL) with calipers or rulers to the nearest millimeter.
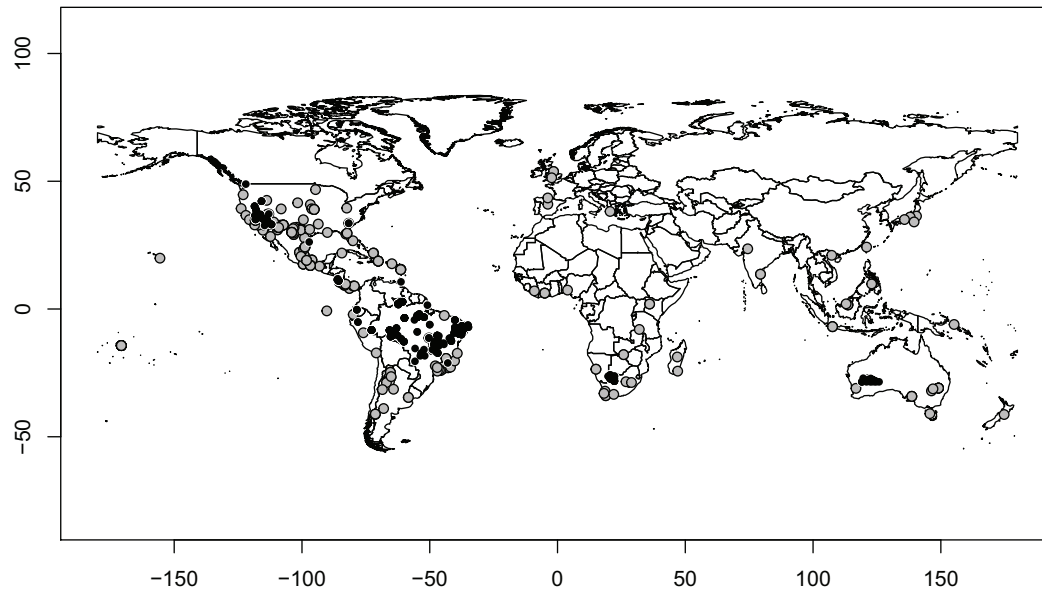
Figure 1: Localities from which lizard life-history data were collected. Black symbols, data collected by authors. Gray symbols, data from literature. Names of all study localities and their sources are given in the study by Mesquita et al. (2015).

For each population, we recorded the following variables: adult female mass (g), adult female SVL (mm), female SVL at maturity (based on SVL of smallest reproductive female), offspring SVL (based on hatchling size or smallest individual in the population), clutch or litter size (mean number of offspring per clutch or litter for all reproductive females in the population), number of broods per year, clutch frequency (single or multiple brooded), relative clutch or litter mass − RCM (total volume or weight of eggs or embryos [cm³] divided by adult female mass [g]), reproductive mode (oviparous or viviparous), foraging mode (sit-and-wait or active), distribution (tropical or temperate), and preferred habitat type (semiaquatic, arboreal, bromelicolous, fossorial, psammophilous, saxicolous, semiarboreal, or terrestrial). We use the word clutch to include both eggs and embryos (litters). To determine the distribution (tropical or temperate), we used the latitude where each study was conducted. We considered as tropical the zone between the Tropic of Cancer (23.5° north latitude) and the Tropic of Capricorn (23.5° south latitude). Remaining localities at higher latitudes were considered temperate.

For each lizard population, we obtained climatic data (altitude and bioclimatic variables) from the WorldClim project database (Hijmans et al. 2005; www.worldclim.org). The 19 climatic variables (BIO 1–BIO 19) used in our analyses were derived from monthly temperature and rainfall data over a 50-year period (1950–2000). For details, see Hijmans et al. (2005).

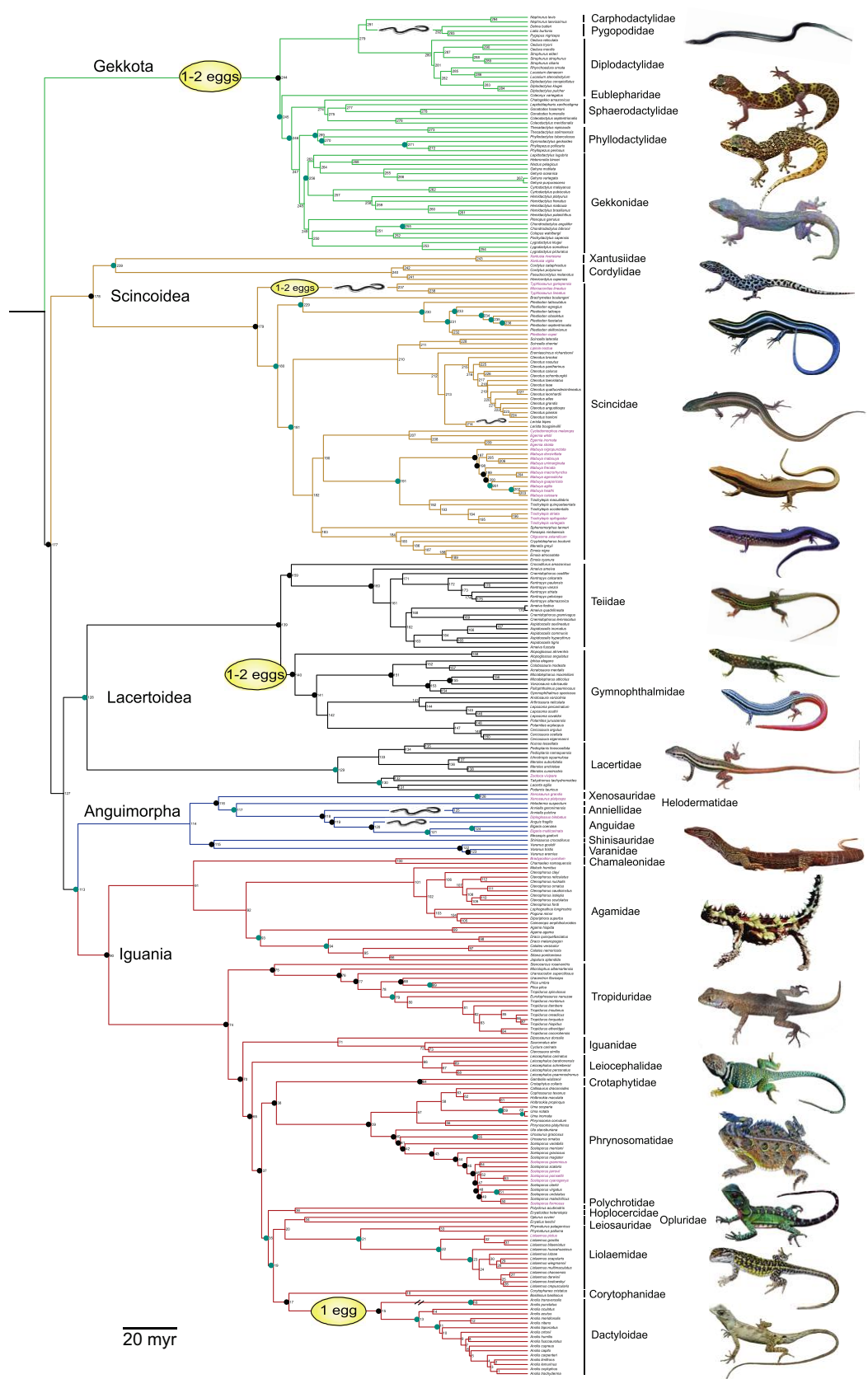We performed most analyses at the species level, meaning that each species was represented by one tip in the phylogeny and by a single value for each trait and climatic variable. In species for which we had data on multiple populations, we averaged across populations to derive a single value for each trait and climatic variable. Because variation among populations within species occurs and may provide additional insight into how climatic factors influence life history, we also performed an analysis (described below) using population-level data.

Phylogeny

Analysis of species-level data requires phylogenetic comparative methods that account for nonindependence due to shared ancestry (Felsenstein 1984; Felsenstein 1985; Brooks and McLennan 1991; Harvey and Pagel 1991). We used the time-calibrated tree from Pyron and Burbrink (2014) and pruned the phylogeny to include only those taxa represented in our data set.

Statistical Analyses

Phylogenetic Signal. We tested for phylogenetic signal in binary life-history variables (reproductive mode) with the statistic D of Fritz and Purvis (2010), using the phylo.d function in the caper R package (Orme et al. 2013). For continuous life-history and climatic variables, we used the statistics λ (Pagel 1997; Pagel 1999) and K (Blomberg et al. 2003) with the phylosig function in package phytools (Revell 2012). For both λ and K, values near 0 indicate phylogenetic independence, whereas values near 1 indicate that species' traits fol-

Gekkota
1-2 eggs

Carphodactylidae
Pygopodidae
Diplodactylidae
Eublepharidae
Sphaerodactylidae
Phyllodactylidae
Gekkonidae

Scincoidea
1-2 eggs

Xantusiidae
Cordylidae

Scincidae

Lacertoidea
1-2 eggs

Teiidae

Gymnophthalmidae

Lacertidae

Anguimorpha

Xenosauridae   Helodermatidae
Anniellidae
Anguidae
Shinisauridae
Varanidae
Chamaeleonidae

Iguania

Agamidae

Tropiduridae

Iguanidae
Leiocephalidae
Crotaphytidae

Phrynosomatidae

Polychrotidae
Hoplocercidae
Leiosauridae   Opluridae

Liolaemidae

Corytophanidae

1 egg

Dactyloidae

20 myr

low a Brownian motion model of trait evolution (Pagel 1999; Freckleton et al. 2002; Blomberg et al. 2003; Losos 2008). Additionally, $K > 1$ implies that close relatives are more similar than expected under a Brownian motion model of trait evolution (i.e., niche conservatism; Blomberg et al. 2003; Münkemüller et al. 2012). We tested for significance in the phylogenetic signal (null hypothesis of λ and K near 0) given by K using 1,000 randomizations of species names in the phylogeny (Blomberg et al. 2003). The significance of λ was assessed with a likelihood ratio test (Pagel 1999). The likelihood ratio test compares the likelihood of λ calculated from the true tree to the likelihood of $\lambda = 1$.

Relationship between Climate and Life-History Traits. To assess the influence of climate on life-history traits, we built ordinary least squares models for continuous traits (adult female mass and SVL, female SVL at maturity, offspring SVL, clutch size, and RCM), general linear models with Poisson error structure for count traits (broods per year, clutch frequency), and binomial error structure for binary traits (reproductive mode). We also built phylogenetic regression models for each trait against abiotic climatic variables. The phylogenetic models comprised the phylogenetic logistic regression (Ives and Garland 2010) for binary traits, phylogenetic Poisson regression (Paradis and Claude 2002) for count traits, and phylogenetic generalized least squares (Grafen 1989) for continuous traits. We checked the assumptions of normality and homoscedasticity of phylogenetic generalized least squares residuals by examining residual plots and with Shapiro and Bartlett tests, respectively (Quinn and Keough 2002). Whenever such assumptions were not met, we employed the Box-Cox transformation (Box and Cox 1964) of the response variable using R package MASS (Venables and Ripley 2002). To generate climatic predictors in these models, we reduced the 19 bioclimatic variables using two principal component analyses (PCAs), one with temperature variables (BIO1–BIO11) and another with precipitation variables (BIO12–BIO19). The first (61.9%) and second (25.9%) axes of the temperature PCA captured 87.8% of the total variation. The first axis was positively correlated with BIO1, BIO3, BIO6, BIO9, and BIO11 (mean and minimum temperatures) and negatively correlated with BIO7 and BIO4 (temperature seasonality), representing a gradient of climate with colder temperatures and high seasonality to warmer temperatures and low seasonality. The second axis was positively correlated with BIO5 and BIO10 (maximum temperatures). The first (67.6%) and second (20.9%) axes of the pre-

cipitation PCA summarized 88.4% of the total variation. The first axis was positively correlated with BIO12, BIO13, BIO14, BIO16, BIO17, BIO18, and BIO19 (overall precipitation), representing a gradient of drier to wetter climates. The second axis was positively correlated with BIO15 (precipitation seasonality), representing a gradient of low to high rainfall seasonality. We retained the first two axes of each PCA and saved factor scores for each species (TempPC1, TempPC2, PrecipPC1, PrecipPC2) for use in analyses. We implemented phylogenetic logistic and phylogenetic Poisson regressions with package phylolm of R (Ho and Ane 2014). To implement phylogenetic generalized least squares models, we built expected covariance matrices under the Brownian motion and the Ornstein-Uhlenbeck models of trait evolution with R package ape (Paradis et al. 2004) and used them in a generalized least squares framework with package nlme (Pinheiro et al. 2015). While trait variance accrues linearly with time in the Brownian motion model (Cavalli-Sforza and Edwards 1967), in the Ornstein-Uhlenbeck model (Lande 1976) trait variance tends to be constant with time, because trait values tend to return to a long-term mean if they evolve away. Thus, the Brownian motion model describes the evolution of continuous traits under random drift or adaptive evolution tracking randomly wandering adaptive optima for each lineage, whereas the Ornstein-Uhlenbeck model describes the evolution of continuous traits around an adaptive optimum toward which they are pulled or the evolution of the adaptive optimum itself (O'Meara and Beaulieu 2014). By using these two different models, we account for differences in modes of trait evolution, and we used the Akaike information criterion (AIC) to determine which model loses the least amount of information.

To test whether phylogenetic conservatism or convergence is more conspicuous in our data set, we used canonical phylogenetic ordination (CPO; Giannini 2003). CPO is a modification of canonical correspondence analysis (CCA; Ter Braak 1986), a constrained ordination method that promotes ordination of a set of variables so that its association with a second set of variables is maximized. The significance of the association is tested via null model randomizations of one or both data sets. In our CPO, one matrix ($\mathbf{Y}$) contained life-history data measured for lizard populations (adult female mass, adult female SVL, female SVL at maturity, offspring SVL, mean clutch size, reproduction mode, number of broods per year, clutch frequency, and RCM), whereas the second matrix ($\mathbf{X}$) consisted of a tree matrix that contained all monophyletic groups of species and populations (fig. 2), each coded sepa-

Figure 2: Individual groups used in canonical phylogenetic ordination (CPO) with life-history data. Phylogeny based on Pyron et al. (2013). Black circles represent a very significant historical effect ($P < .01$) and green circles a moderate effect ($.01 < P < .05$), on the basis of a complete CPO. Viviparous species represented in purple. Limb-reduced and fixed-clutch species are indicated on tree. All lizard photos are by Laurie J. Vitt and Eric. R. Pianka except *Liolaemus multicolor*, which is by Robert E. Espinoza.

rately as a binary variable (0 if population/species is not a member of the group, 1 if the population/species is a group member), and climatic variables (altitude, TempPC1, TempPC2, PrecipPC1, PrecipPC2, foraging mode, distribution, and preferred habitat type). This analysis thus consisted of finding the subset of **X** that best captured variation in **Y**, using CCA coupled with Monte Carlo permutations. One advantage of CPO is that it can tease apart specific clades that are highly correlated with life-history variation, showing whether or not variation in trait values explained by clade membership is clustered in specific areas of the tree (Vitt and Pianka 2005; Colston et al. 2010). The CPO analysis is designed to rank the clades that maximize explanation of the variance in the trait data set; therefore, clades that explain more variation in the trait data set are ranked higher. Much like an ANOVA, a significant CPO analysis indicates differences in trait values between the focal clade and the remaining clades, based on the ratio of the between- and the within-group variance. In the CPO, the variance is represented by χ^2 values (inertia or mean squared contingency coefficient). We implemented the CPO in CANOCO 4.5 for Windows, using the following parameters: symmetric scaling, biplot scaling, manual selection of climatic variables (monophyletic groups and climatic parameters), 9,999 permutations, and unrestricted permutations. After determining the significance of the full model—that is, including all predictors—we used an information theory approach based on the AIC to identify the best predictors and build a reduced model (Burnham and Anderson 2002), with vegan (Oksanen et al. 2007). We used a stepwise approach, starting with an intercept-only model and sequen-

tially adding and trying to drop predictors on the basis of model significance and AIC values (Oksanen et al. 2013). Model significance was assessed with 1,000 Monte Carlo simulations. We conducted other statistical analyses using SYSTAT 13.0 for Windows and R (R Development Core Team 2015), with a significance level of 5% to reject null hypotheses. Means are presented ± 1 SE.

Relationship of Life-History Traits with Foraging Mode, Tropical versus Temperate Distribution, and Habitat Specialization. To determine whether and how life-history traits vary between sit-and-wait and active foragers, between temperate and tropical regions, and with habitat specialization use, we used nonphylogenetic and phylogenetic regression models as described above. To test the hypothesis that viviparity evolved as an adaptation to cold climates, we tested for differences in altitude and mean temperature (BIO1) between reproductive modes using the same procedures.

Results

Relationship between Climate and Life-History Traits

We collected life-history data for 297 lizard species from 33 families (out of a total of 36) distributed on all continents except Antarctica (fig. 1). Phylogenetic signal was significant in all life-history traits examined (table 1). In most of our phylogenetic models, regressions with Brownian motion structure were superior to Ornstein-Uhlenbeck, as assessed by AIC values (table 2). The phylogenetic generalized least squares models showed significant influence of

Table 1: Estimates of phylogenetic signal in life-history traits of lizards of the world and climatic data

Variable	Pagel's λ/D	P	Blomberg's K	P
Life history:				
Adult female mass	.886	<.001	.484	.004
Adult female SVL	.989	<.001	.658	.001
Female SVL at maturity	.966	<.001	.585	.001
Offspring SVL	.976	<.001	.481	.001
Clutch size	1.003	<.001	.383	.001
Broods per year	.966	.002	.292	.004
Clutch frequency	.614	<.001	.234	.001
Relative clutch mass	.756	<.001	.334	.001
Reproductive mode	−.23	0	…	…
Climatic data:				
Altitude	.323	<.001	.229	.002
Temp_PC1	.977	<.001	.605	.001
Temp_PC2	.683	<.001	.285	.001
Prec_PC1	.964	<.001	.439	.001
Prec_PC2	.805	<.001	.277	.001

Note: For reproductive mode, phylogenetic signal was estimated with the D statistic (Fritz and Purvis 2010). Values of D closer to 0 indicate phylogenetically conserved traits as expected under a Brownian threshold model, whereas values of 1 indicate traits evolving at random. The value of D can be both <0 (highly conserved) and >1 (overdispersed). Phylogenetic signals for all variables are strongly significant statistically. PC, principal component; SVL, snout-vent length.

Table 2: Regression results between life-history traits and climatic variables (first two principal component [PC] axes from temperature and precipitation Bioclim variables)

Response variable and model	Regression summaries				β (explanatory variables)					
	Adjusted r^2	F/χ^2	df	P	Intercept	$PC1_{temp}$	$PC2_{temp}$	$PC1_{prec}$	$PC2_{prec}$	AIC
Adult female mass:										
OLS	.039	2.62	4, 155	.04	1.83***	−.22*	.07	.15	.07	…
PGLS$_{BM}$	−.022	9.35	4	.002	1.79**	−.06	.13	.03	.08	451.4
PGLS$_{OU}$	−.004	2.30	4	.128	1.83***	−.23*	.06	.15	.07	528.28
Adult female SVL:										
OLS	.009	1.64	4, 264	.162	1.85***	−.004*	.002	.002	.002	…
PGLS$_{BM}$	.04	37.8	4	<.001	1.86***	.002	.02	<.001	.003	−861
PGLS$_{OU}$	.04	35.17	4	<.001	1.85***	−.004*	.002	.002	.002	−728.3
Female SVL at maturity:										
OLS	.036	3.52	4, 268	.008	1.72***	−.006**	.002	.003	.002	…
PGLS$_{BM}$	.036	33.52	4	<.001	1.74***	<−.001	<−.001	−.001	.005	−877.2
PGLS$_{OU}$	.035	29.05	4	<.001	1.72***	−.006***	.002	.003	.002	−794.5
Offspring SVL:										
OLS	<.001	.64	4, 226	.63	1.90***	<.001	−.001	−.004	.008	…
PGLS$_{BM}$	.06	29.59	4	<.001	1.92***	−.002	.009*	.004	.008	−421.1
PGLS$_{OU}$	.08	33.12	4	<.001	1.91***	<.001	−.001	−.004	.008	−332.1
Clutch size:										
OLS	.16	14.8	4, 284	<.001	.94***	−.11***	.009	.05*	.08**	…
PGLS$_{BM}$	−.05	11.03	4	<.001	.96***	−.02†	.02	.006	.06***	219.75
PGLS$_{OU}$	.07	28.93	4	<.001	.94***	−.11***	.009	.045**	.07**	403.52
Broods per year:										
GLM$_{Poisson}$	<.01	3.81	4	.43	.41***	.009	.06	−.006	−.07	…
Phylo$_{Poisson}$	…	…	…	…	.38*	.03*	.05**	.02	−.12***	…
Clutch frequency:										
GLM$_{Poisson}$	<.01	2.48	4	.65	.269***	−.02	.009	.05	.02	…
Phylo$_{Poisson}$	…	…	…	…	.218†	−.04***	.01	.04***	.02	…
RCM:										
OLS	.21	11.69	4, 152	<.001	1.52***	−.06***	−.04*	.014	−.006	…
PGLS$_{BM}$	−.01	.82	4	.36	−1.46***	−.04**	−.05**	.05**	.02	78.62
PGLS$_{OU}$	.25	15.98	4	<.001	−1.52***	−.06**	−.04*	.01	−.006	60.41
Reproductive mode:										
GLM$_{binomial}$	.10	25.9	4	<.001	−1.87***	−.02	−.42***	−.23	.16	…
Phylo$_{logistic}$	.07	11.65	4	<.001	−1.87*	.01	−.28*	−.12	.01	…

Note: For continuous traits, we used ordinary least squares (OLS) and phylogenetic general least squares (PGLS) models with Brownian movement (BM) and Ornstein-Uhlenbeck (OU) process correlation structures (PGLS$_{BM}$, PGLS$_{OU}$). For count traits, we used general linear models (GLMs) with Poisson error structure and phylogenetic Poisson regression. For binary traits, we used GLMs with binomial error structure and phylogenetic logistic regression. For GLMs and phylogenetic models, adjusted r^2 is calculated as McFadden's pseudo r^2 (McFadden 1973). Akaike information criterion (AIC) is used to compare PGLS models with Brownian or Ornstein-Uhlenbeck structures. Phylogenetic Poisson regression is a non-likelihood-based method; therefore, regression summaries cannot be calculated.

  * $P < .05$.
  ** $P < .01$.
  *** $P < .001$.
  † Marginally significant.

climatic parameters on adult female mass, adult female SVL, female SVL at maturity, clutch size, offspring SVL, and RCM (table 2; fig. 3). However, in general, all regressions showed very low effect sizes, indicating extensive unexplained variation in the data. Number of broods per year is positively related to temperature and negatively re-

lated to seasonality in precipitation (table 2; fig. 3). Clutch frequency is positively related to precipitation and negatively related to minimum and mean temperatures, whereas clutch size is negatively related to mean and minimum temperatures and positively related to precipitation and precipitation seasonality (table 2; fig. 3). Offspring SVL is positively
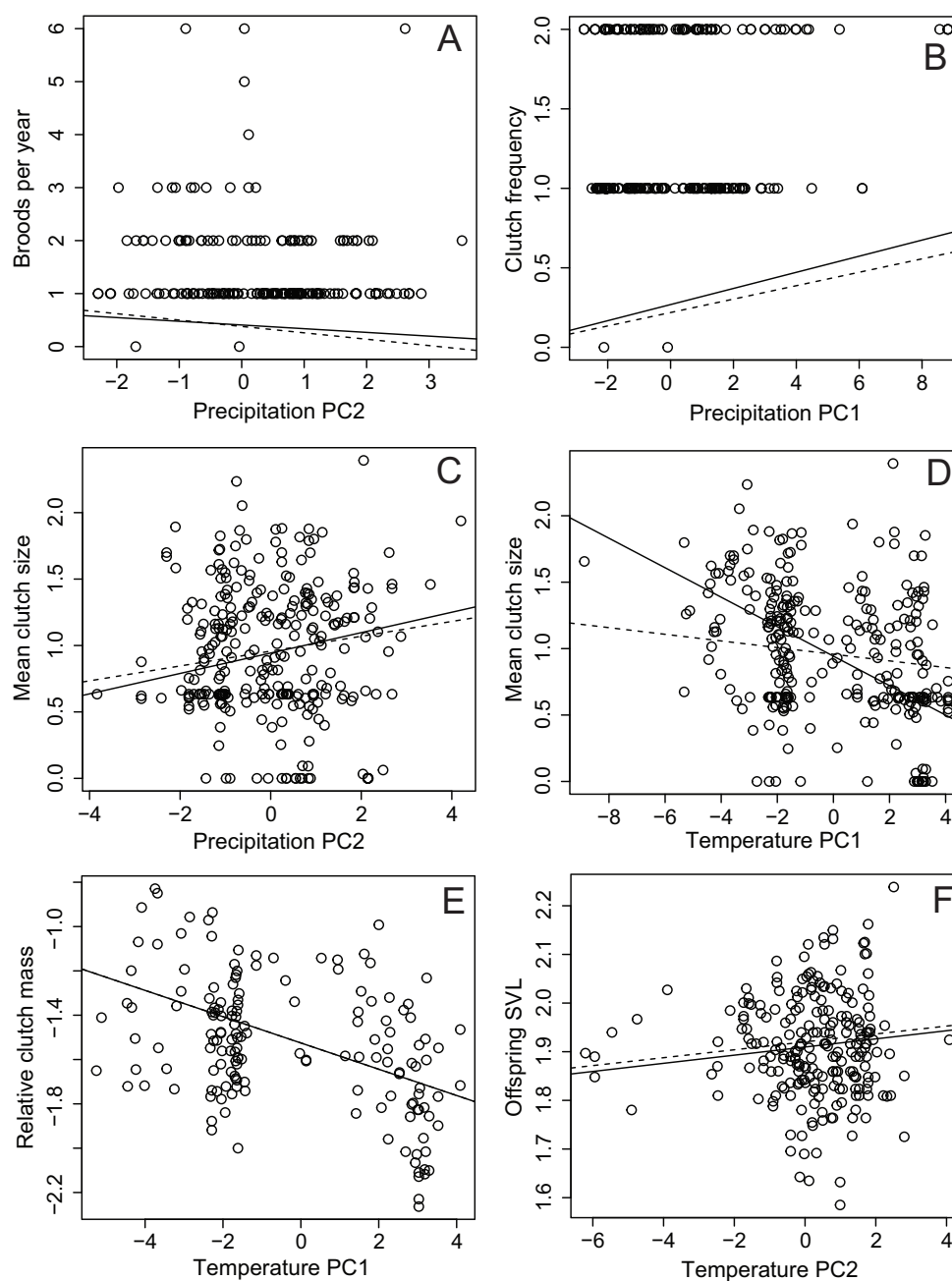
Figure 3: Bivariate scatterplots of the relationships between number of broods per year, mean clutch size, and precipitation principal component 2 (PC2; *A*, *C*), clutch frequency and precipitation PC1 (*B*), mean clutch size and temperature PC1 (*D*), offspring SVL and temperature PC2 (*F*), and relative clutch mass and temperature PC1 (*E*). PCs are scores from two principal component analyses, one with temperature variables and another with precipitation variables from Bioclim (Hijmans et al. 2005; see "Methods"). Solid lines represent partial regression coefficients (intercept and slope) from phylogenetic regression models (phylogenetic generalized least squares), and dashed lines represent conventional (ordinary least squares) regression models. All relations were statistically significant (see table 2).

related to maximum temperature, whereas RCM is negatively related to mean and minimum temperatures and seasonality in temperature (table 2; fig. 3).

The stepwise CPO revealed that variation in trait values explained by clade membership is unevenly distributed among lizard clades. Results show that basal clades tend to explain more of the variation in trait values, but also some specific clades—such as Teiidae, Gymnophthalmidae, and Lacertoidea—were shown to explain significant variation in the trait values (table 3; fig. 4). On the basis of the

Table 3: Results of stepwise canonical phylogenetic ordination analysis

Group(s)	AIC	*F*	*P*
159 (Teiidae)	335.97	40.2820	.005
Foraging mode	357.64	14.3833	.005
139 (Teiidae + Gymnophthalmidae)	358.94	12.9698	.005
160 (Teiidae clade within)	360.24	11.5645	.010
140 (Gymnophthalmidae)	361.21	10.5305	.025
141 (Gymnophthalmidae clade within)	361.71	9.9966	.070
128 (Lacertoidea)	361.97	9.7148	.010
15 (*Anolis* clade within)	362.07	9.6068	.070
17 (Dactyloidea + Corytophanidae)	362.07	9.6068	.040
Distribution (tropical vs. temperate)[a]	362.90	8.7386	.035
TempPC1[a]	363.29	8.3235	.070
PrecipPC1[a]	363.60	8.0004	.025
177/244 (Gekkota vs. everything else)	363.92	7.6640	.055
245 (Gekkota clade within)	363.92	7.6640	.055

Note: Group(s) shows the rank order of phylogenetic clades, climate, and ecological attributes explaining variation in trait values. Results of Monte Carlo permutation tests of individual groups (defined in fig. 2) and climatic variables for the **Y** matrix of life-history data. Akaike information criterion (AIC), *F*, and *P* values for each variable based on 1,000 permutations.

[a] Climatic variables (principal component analysis [PCA] scores; for details about meaning of PCA scores of climatic variables, see "Methods").

complete CPO (available in the supplemental material, table S2), results were very similar, with most trait variation being explained by basal clades and specific clades—such as Crotaphytidae, Varanidae, Phynosomatidae, Anguimorpha, Scincoidea, Iguania, Tropiduridae, Gymnophthalmidae, Teiidae, Anguidae, Scincidae, and Liolaemidae—and no variation being explained by *Anolis* and Gekkota, with the exception of Phyllodactylidae (fig. 2; table S2). CPO results also show that life-history traits were also explained by climate variables, including precipitation seasonality, precipitation of warmest quarter, mean temperature of driest quarter, maximum temperature of warmest month, temperature seasonality, isothermality, mean temperature of coldest quarter, temperature annual range, minimum temperature of coldest month, distribution (tropical vs. temperate), and annual mean temperature (table S2).

Relationship of Life-History Traits with Foraging Mode, Tropical versus Temperate Distribution, and Habitat Specialization

For the nonphylogenetic analysis, among the life-history traits examined, clutch size was larger in temperate and semiarboreal species and smaller in aquatic species (tables 4, 5). Adult female mass was greater in temperate and in aquatic species and smaller in fossorial species (tables 4, 5). Adult female SVL was bigger in temperate species, similar to female SVL at maturity (tables 4, 5). Clutch frequency was larger in tropical species (tables 4, 5). RCM was bigger in temperate and semiarboreal species and smaller in aquatic species (tables 4, 5). Surprisingly, we did not find significant

differences in RCM between foraging modes (table 4). Reproductive mode proportions differ between foraging mode and habitat type (table 4). Taking phylogenetic relationships into account, the fit of models of almost all life-history variables based on Brownian motion was far superior to Ornstein-Uhlenbeck process, as assessed by AIC values (table 4). Adult female mass was greater in aquatic species and smaller in fossorial species (tables 4, 5). Adult female SVL was also larger in aquatic species but smaller in terrestrial species (tables 4, 5).

Eighty-five percent of tropical lizard populations that we analyzed are oviparous, and 15% are viviparous. In temperate lizard populations, 79% are oviparous, and 21% are viviparous. Viviparous lizard species occur at higher elevations (571.84 ± 75.52) than oviparous species (451.30 ± 27.73). The difference is significant when taking phylogenetic relationships into account and marginal in nonphylogenetic analysis (ANOVA; $F_{1,289} = 3.60$, $P = .059$; $F_{1,289\,phylo} = 4.23$, $P_{phylo} = .04$). Mean temperature (BIO1) differs between reproductive modes (ANOVA; $F_{1,289} = 13.37$, $P < .001$), with viviparous species occurring in locations with lower temperatures (oviparous $= 21.71° \pm 3.06°$C, viviparous $= 19.51° \pm 7.84°$C). This difference is marginally significant when considering phylogenetic relationships among species (ANOVA; $F_{1,289\,phylo} = 3.63$, $P_{phylo} = .057$).

Discussion

Relationship between Climate and Life-History Traits

The phylogenetic generalized least squares and ordinary least squares models showed a significant influence of cli-
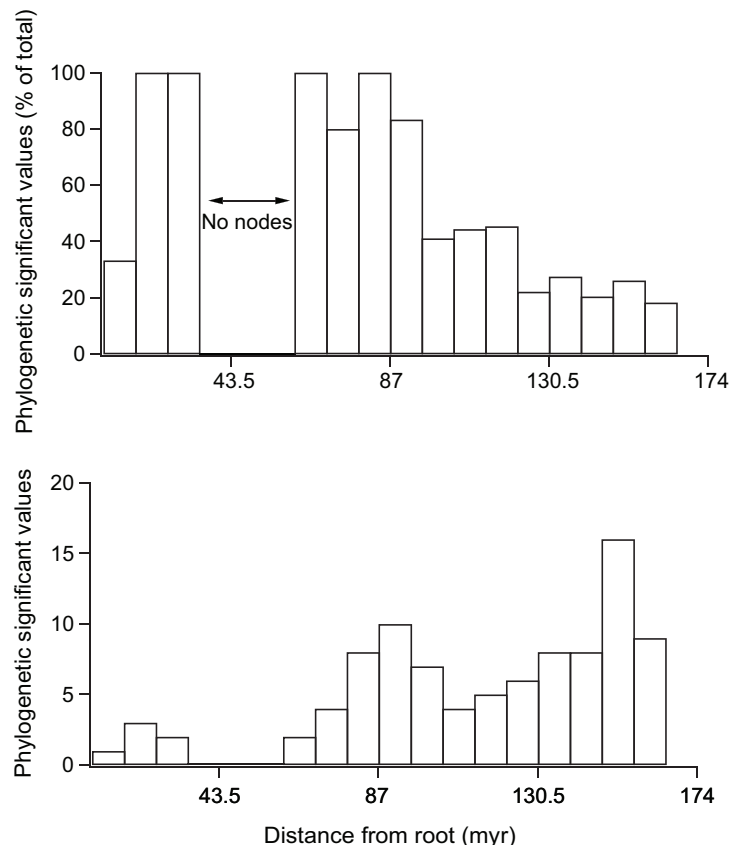
Figure 4: Distribution of statistically significant nodes according to distance of nodes from root of tree, on the basis of a canonical phylogenetic ordination analysis relating nine life-history traits of lizard species and populations worldwide to phylogenetic tree structure and climatic parameters. *Bottom*, raw number of nodes with significant effects. *Top*, percentage of total nodes.

mate variables on broods per year, clutch frequency, clutch size, offspring SVL, and RCM. Although our analysis identified significant effects, most regressions had very low effect sizes. This result indicates that much of the variation in life-history traits remains unexplained. Our data set consists of many species from many regions of the world. A data set of this magnitude is expected to have lots of noise (e.g., sampling error). Large amounts of unexplained variation are not uncommon in ecological studies with large data sets (Ter Braak 1986; Ter Braak and Van Tongeren 1995; Guisan and Zimmermann 2000; Gilbert and Bennett 2010). In addition, life-history traits can be affected by multiple factors in different ways, therefore resulting in weak relationships.

Number of broods per year is positively related to maximum temperature and negatively related to seasonality in precipitation. Clutch frequency varies positively with precipitation. We also found that lizard clutch size is negatively related to mean and minimum temperatures, positively related to seasonality in temperature, and positively related to precipitation seasonality. These results suggest

that lizards from aseasonal, warm and wet regions tend to reproduce more frequently during the year. Also, lizards from colder and seasonal climates tend to produce clutches at lower frequency but with larger sizes. As a result, lizards from colder regions also tend to have a higher RCM. In temperate regions, reproduction is usually seasonal and follows temperature and day length patterns, with the rigorous winter being a limiting factor for reproduction (Duvall et al. 1982; Fitch 1970). In tropical regions, lizards tend to exhibit greater variation in clutch frequency/broods per year (Vitt 1992; Clerke and Alford 1993; Mesquita and Colli 2010). Many species tend to reproduce continuously with several small clutches (Vitt and Colli 1994; Mesquita and Colli 2003*b*, 2010). Some of these results have been shown before in other studies looking at intraspecific variation (Vitt 1986; Colli 1991; Vitt and Colli 1994; Colli et al. 2003; Mesquita and Colli 2003*a*, 2003*b*; Menezes et al. 2011) as well as in interspecific comparisons among tropical lizards (Mesquita and Colli 2010). Our results—using powerful methods to account for evolutionary relationships

Table 4: Nonphylogenetic and phylogenetic regression models relating variation in life-history traits to foraging mode (sit-and-wait, active), distribution (temperate, tropical), and preferred habitat type (aquatic, arboreal, bromelicolous, fossorial, saxicolous, semiarboreal, terrestrial)

Life-history trait and predictor	OLS			$PGLS_{BM}$			$PGLS_{OU}$		
	F	df	P	F	P	AIC	F	P	AIC
Adult female mass:									
Foraging mode	1.61	1, 158	.207	.07	.785	434.2	1.61	.206	519.8
Distribution	7.30	1, 158	**.008**	1.58	.210	434.8	7.34	**.008**	514.3
Habitat	3.11	6, 153	**.007**	3.50	**.003**	426.4	3.11	**.007**	509.1
Adult female SVL:									
Foraging mode	.05	1, 267	.831	.84	.360	−809.4	.05	.823	−670.0
Distribution	5.19	1, 267	**.023**	.08	.775	−806.7	5.10	**.025**	−674.9
Habitat	1.54	6, 262	.167	2.46	**.025**	−780.2	1.56	.160	−642.2
Female SVL at maturity:									
Foraging mode	.01	1, 271	.947	.59	.443	−822.6	.01	.943	−731.9
Distribution	9.93	1, 271	**.002**	.01	.914	−820.0	9.75	**.002**	−741.4
Habitat	1.41	6, 266	.211	.83	.544	−784.3	1.40	.215	−702.2
Offspring SVL:									
Foraging mode	.49	1, 229	.483	1.81	.180	−519.1	.49	.485	−430.2
Distribution	.16	1, 229	.694	.51	.474	−516.0	.13	.718	−429.8
Habitat	1.20	6, 224	.310	.49	.813	−481.7	1.19	.311	−403.4
Clutch size:									
Foraging mode	.33	1, 287	.564	.79	.376	175.1	.33	.566	403.3
Distribution	29.9	1, 287	**<.001**	3.72	.055	174.1	30.1	**<.001**	375.1
Habitat	2.16	6, 282	**.047**	1.32	.250	192.9	2.14	**.049**	408.7
Broods per year:									
Foraging mode	.34	1, 189	.563	.62	.433	55.1	.36	.547	67.6
Distribution	2.54	1, 189	.112	.03	.860	57.7	2.57	.110	65.5
Habitat	1.78	5, 185	.120	.86	.506	73.5	1.73	.130	77.7
Clutch frequency:									
Foraging mode	2.96	1, 271	.086	.27	.602	58.6	3.04	.083	23.0
Distribution	8.74	1, 271	**.003**	.74	.391	60.1	8.70	**.004**	17.5
Habitat	1.57	6, 266	.156	.49	.814	82.5	1.58	.153	40.8
Relative clutch mass:									
Foraging mode	2.68	1, 155	.103	.26	.614	73.2	2.67	.104	71.9
Distribution	25.0	1, 155	**<.001**	.18	.672	74.2	24.8	**<.001**	51.7
Habitat	3.49	5, 151	**.005**	.52	.760	89.5	3.45	**.006**	74.1

	GLM			Phylologistic	
	χ^2	df	P	Z	P
Reproductive mode:					
Foraging mode	8.21	1	**.004**	−.15	.883
Distribution	2.76	1	.097	~0	~1
Habitat	16.25	6	**.012**	2	.157

Note: Nonphylogenetic regression models consisted of generalized linear model (GLM) for reproductive mode and ordinary least squares (OLS) for the other life-history traits. Phylogenetic regression models consisted of phylogenetic logistic regression (phylologistic) for reproductive mode and phylogenetic generalized least squares (PGLS) for the remainder. PGLS was performed under two models of trait evolution: Brownian motion (BM) and Ornstein-Uhlenbeck process (OU). Significant results are in bold.

and a global database—suggest that these patterns are remarkably consistent across geographic and taxonomic scales.

In addition to climatic effects, our global analysis based both on species and on populations revealed some interesting evolutionary patterns. In the species level analysis, most life-history traits showed significant phylogenetic signal (Pagel's λ, Blomberg's K). At the population level, the CPO showed that variation in trait values explained by clade membership is unevenly spaced in the tree, with basal lizard clades and a few younger clades explaining most of the variation in life-history traits. These results suggest not only that life-history traits tend to be con-

Table 5: Means ± SEs of life-history traits associated with foraging mode (sit-and-wait, active), distribution (temperate, tropical), and preferred habitat type (aquatic, arboreal, bromelicolous, fossorial, saxicolous, semiarboreal, terrestrial)

Life-history trait	Adult female mass	Adult female SVL	Female SVL at maturity	Offspring SVL	Clutch size	Broods per year	Clutch frequency	Relative clutch mass
Foraging mode:								
Sit-and-wait	22.612 ± 8.130 (62)	76.511 ± 3.189 (138)	67.070 ± 2.707 (142)	33.990 ± 1.167 (144)	4.550 ± .433 (104)	1.480 ± .092 (99)	1.270 ± .036 (139)	.156 ± .007 (93)
Active	15.721 ± 2.180 (89)	80.487 ± 5.736 (79)	69.680 ± 4.837 (85)	35.670 ± 2.186 (86)	3.520 ± .247 (85)	1.280 ± .063 (55)	1.180 ± .034 (81)	.172 ± .008 (53)
Distribution:								
Temperate	21.710 ± 6.029 (76)	81.782 ± 3.873 (122)	72.540 ± 3.496 (122)	34.620 ± 1.600 (125)	4.67 ± .349 (125)	1.520 ± .091 (66)	1.200 ± .035 (124)	.180 ± .007 (90)
Tropical	15.348 ± 3.803 (75)	73.047 ± 4.370 (95)	62.830 ± 3.429 (105)	34.620 ± 1.465 (105)	3.56 ± .472 (104)	1.330 ± .087 (88)	1.280 ± .039 (96)	.133 ± .008 (56)
Habitat:								
Aquatic	86.310 ± 81.854 (3)	105.986 ± 32.883 (5)	99.600 ± 32.525 (5)	37.710 ± 10.763 (5)	3.390 ± 1.078 (5)	1.200 ± .200 (5)	1.400 ± .187 (5)	.095 ± .037 (2)
Arboreal	25.296 ± 6.703 (35)	80.855 ± 5.625 (45)	67.720 ± 4.903 (49)	34.280 ± 2.244 (49)	3.990 ± .566 (49)	1.460 ± .179 (33)	1.280 ± .063 (46)	.144 ± .014 (29)
Bromelicolous	4.702 ± .132 (2)	65.008 ± 2.105 (2)	60.020 ± 1.523 (2)	41.680 ± 8.395 (2)	3.620 ± .713 (2)	1.000 ± .000 (2)	1.170 ± .167 (2)	…
Fossorial	1.618 ± .560 (4)	96.871 ± 17.249 (7)	89.850 ± 14.721 (8)	33.680 ± 5.791 (9)	3.620 ± 1.060 (9)	1.000 ± .000 (6)	1.000 ± .000 (9)	.167 ± .013 (4)
Saxicolous	13.571 ± 2.698 (11)	83.387 ± 8.171 (34)	71.840 ± 6.327 (34)	39.690 ± 2.634 (34)	5.440 ± 1.235 (34)	1.390 ± .118 (30)	1.310 ± .082 (34)	.202 ± .019 (16)
Semiarboreal	31.700 ± 16.381 (3)	88.225 ± 8.171 (4)	75.000 ± 10.855 (4)	31.250 ± 3.326 (4)	8.840 ± 2.585 (4)	…	1.000 ± .000 (4)	.226 ± .040 (3)
Terrestrial	15.017 ± 4.510 (93)	72.937 ± 3.834 (120)	64.390 ± 3.279 (125)	33.340 ± 1.524 (127)	3.820 ± .312 (126)	1.450 ± .088 (78)	1.220 ± .033 (120)	.159 ± .007 (92)

Note: Significant differences are in bold in table 4.

served in the evolutionary tree but also that variation in life-history traits is mainly explained by a few shifts that occurred early in the evolutionary history of the group. These interesting results may explain different broad patterns observed in lizard ecology. For instance, almost every known lizard reproductive strategy can be seen in a single assemblage in Neotropical lizards from the Caatinga biome in Brazil (see Vitt 1992). All this variation among species exposed to the same climatic conditions suggests that a strong phylogenetic component must influence life-history patterns (Vitt 1990; Vitt 1992). Also, many clades present remarkably similar life-history traits, despite the climatic context they occupy (Mesquita and Colli 2010). For example, clutch size and egg volume were not significantly different between major clades of *Kentropyx* occupying different ecosystems (savannah vs. forest; Werneck et al. 2009). More broadly, our results mirror analysis based on diet composition for 184 lizard species from four continents (Vitt et al. 2003; Vitt and Pianka 2005). These authors found that most variation in lizard diets is explained by a few shifts in early diversification of the group. Interestingly, the clades in which we found most of explained variance in life-history traits were nearly the same ones that Vitt and Pianka (2005) identified using diet data. These parallel results suggest that diets and life histories are evolutionarily linked. Moreover, distinct lizard traits can be largely independent of the ecological context they inhabit.

Another interesting result is the lack of variation being explained by the *Anolis* clade. Anoles are one of most ecologically diverse clades among squamates and apparently were heavily influenced by environment and by presence of competitors (Losos et al. 1993; Losos and de Queiroz 1997; Losos 2009). Some species—depending on the density and/or diversity of potential competitors—evolved rapidly, and changes in habitat use and morphology were perceived in less than a decade (Losos et al. 1993). However, some studies have also reported evidence of evolutionary relatedness within these events of rapid morphological evolution (Revell et al. 2007; Pennell et al. 2014). Anoles have long been a model system for the study of community ecology (Losos 1994, 2009), and the influential work done in this system has affected how ecologists think generally about how communities are structured (Losos 1995, 2009; Losos et al. 2003). Our results suggest that the ecological lability presented by anoles is in fact an exception when analyzed in the context of a larger taxonomic scope.

Relationship of Life-History Traits with Foraging Mode, Tropical versus Temperate Distribution, and Habitat Specialization

We found no relationship between foraging mode and any of the life-history traits. Our results of no difference in RCM among foraging modes require a more in-depth discussion. RCM, body shape, and foraging mode have been hypothesized to be coevolved in lizards (Vitt and Congdon 1978; Vitt and Price 1982). Active foraging lizards have streamlined bodies, allowing an increase in speed; this trade-off may limit reproductive investment. Their clutches typically comprise a relatively low proportion of total body mass (Vitt and Congdon 1978; Huey and Pianka 1981; Vitt and Price 1982; Shine and Schwarzkopf 1992; Warne and Charnov 2008). Conversely, sit-and-wait lizards have a stocky body shape, which could enhance reproductive effort and RCM (Vitt and Congdon 1978; Huey and Pianka 1981; Vitt and Price 1982; Shine and Schwarzkopf 1992; Warne and Charnov 2008). Surprisingly, our results do not support this hypothesis, since we found no difference in RCM among foraging modes. Our results suggest that the expected relationship between body size and RCM may not be as conspicuous as previous work suggests. However, because of problems with RCM estimates, interpretation of analyses of this variable must be performed with caution (Dunham et al. 1988). RCM has been estimated in several different ways, and some authors do not always clearly state what method they used (Vitt and Price 1982; Cuellar 1984; Dunham et al. 1988; Greer 1989). Sources of variation could be related to the freshness of material (preserved or fresh), ratios based on wet or dry mass, or female mass based on total or somatic mass only (Vitt and Price 1982; Cuellar 1984; Dunham et al. 1988). In addition, RCM estimates could be confounded by body mass estimates (Vitt and Price 1982; Seigel and Fitch 1984; Dunham and Miles 1985; Dunham et al. 1988). Although we collected a good proportion of our data, part of our data set came from other sources; thus, our results could be influenced by different methods used to estimate RCM. In addition, our study, like most others, considered single reproductive episodes, whereas the trade-offs of reproductive allocation over a prolonged period (e.g., lifetime) cannot be incorporated. Future studies with more standardized measures of RCM should help to elucidate this question.

We found differences in clutch size, clutch frequency, and RCM among tropical and temperate species. These results are largely related to what was discussed in "Relationship between Climate and Life-History Traits." We found no difference in reproductive mode between tropical and temperate species. However, viviparity is associated with colder temperatures and higher altitudes. These results suggest that viviparous species within tropical regions tend to occupy regions with colder climates and/or higher altitudes. Reproductive mode evolution is complex in squamate reptiles, with both major modes (oviparity and viviparity) occurring within the same family (Shine 2004; Blackburn 2006; Pyron and Burbrink 2014) and even within different populations of the same species (Howard 1974;

Tinkle and Gibbons 1977). The main hypothesis is that viviparity evolved from oviparity via egg retention as an adaptation to colder climates because it facilitates egg protection and more rapid development via maternal thermoregulation (Huey 1977; Blackburn 1982; Shine 2005). Our results support this hypothesis because we found that viviparous lizards tend to occur in colder temperatures and at higher elevations.

We found differences among habitat specializations in female size (SVL and mass) and RCM, with females being larger and having higher RCM in semiarboreal and saxicolous habitats. Previous work suggested that the use of crevices by saxicolous lizards to avoid predators limits evolution of bauplan and clutch mass (Vitt 1981). Our results do not support this hypothesis; females of saxicolous lizards in fact tend to have large bodies and higher RCM when compared with species that are specialized in other habitats. Our result may reflect variation among the ecology of saxicolous lizards—not all saxicolous species rely on use of crevices to avoid predation. Our data set did not have enough resolution to compare different lizard species within the saxicolous habitat specialization. Future studies with more detailed ecological information may help to further test this hypothesis.

Conclusions

Complex interactions of factors that are often correlated and difficult to tease apart can potentially influence the evolution of life-history traits (Dunham and Miles 1985; Miles and Dunham 1992). In our work, we assembled the largest life-history data set on lizards to date, with data covering most of the group's evolutionary history from many different geographical locations representing very distinct climatic regions. On the basis of our global analysis, we found some consistent patterns regarding the association of life-history traits and climatic variables. Our results show that in warmer tropical and less seasonal climates, lizards tend to reproduce more continuously, producing smaller clutches over the course of a year. These results are largely consistent with life-history theory and previous results based on smaller and scattered data sets (e.g., Colli 1991; Vitt and Colli 1994; Mesquita and Colli 2010). We also revealed some interesting evolutionary patterns where variation in trait values explained by clade membership is unevenly distributed among lizard clades, with traits from basal clades and a few specific younger clades concentrating most of the explained variance. These results mirror other large-scale analysis of lizard ecological traits (Vitt and Pianka 2005), suggesting that our results may be general to different ecological traits. Finally, we found significant differences in average temperature between reproductive modes, with viviparous species occurring in cooler climates

and/or higher altitudes. Therefore, our analysis supports the hypothesis that viviparity evolved as a response to cooler climates (Fraipont et al. 1996; Shine 2005; Pyron and Burbrink 2014). One caveat of our analysis is that the variance explained in the data was low (low r^2 values for all analysis). This highlights the complexity regarding life-history trait evolution, especially when many species from divergent evolutionary lineages are analyzed together. Future studies with more focused data sets (e.g., detailed samples within lineages) may help understanding whether our low effect size results are general on life-history traits or whether it is a particular result due to the high variation in our global data set.

Literature Cited

Ackerly, D. 2009. Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. Proceedings of the National Academy of Sciences of the USA 106:19699–19706.

Andrews, R., and A. S. Rand. 1974. Reproductive effort in anoline lizards. Ecology 55:1317–1327.

Blackburn, D. G. 1982. Evolutionary origins of viviparity in the Reptilia. I. Sauria. Amphibia-Reptilia 3:185–205.

———. 2006. Squamate reptiles as model organisms for the evolution of viviparity. Herpetological Monographs 20:131–146.

Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745.

Box, G. E. P., and D. R. Cox. 1964. An analysis of transformations. Journal of the Royal Society of Western Australia 26:211–252.

Brooks, D. R., and D. A. McLennan. 1991. Phylogeny, ecology, and behavior: a research program in comparative biology. University of Chicago Press, Chicago.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Cavalli-Sforza, L. L., and A. W. F. Edwards. 1967. Phylogenetic analysis: models and estimation procedures. Evolution 21:550–570.

Clerke, R. B., and R. A. Alford. 1993. Reproductive biology of four species of tropical Australian lizards and comments on the factors regulating lizard reproductive cycles. Journal of Herpetology 27:400–406.

Colli, G. R. 1991. Reproductive ecology of *Ameiva ameiva* (Sauria: Teiidae) in the cerrado of central Brazil. Copeia 1991:1002–1012.

Colli, G. R., D. O. Mesquita, P. V. V. Rodrigues, and K. Kitayama. 2003. The ecology of the gecko *Gymnodactylus geckoides amarali* in a Neotropical savanna. Journal of Herpetology 37:694–706.

Colston, T. J., G. C. Costa, and L. J. Vitt. 2010. Snake diets and the deep history hypothesis. Biological Journal of the Linnean Society 101:476–486.

Cuellar, O. 1984. Reproduction in a parthenogenetic lizard: with a discussion of optimal clutch size and a critique of the clutch weight/body weight ratio. American Midland Naturalist 111:242–258.

Dunham, A. E., and D. B. Miles. 1985. Patterns of covariation in life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. American Naturalist 126:231–257.

Dunham, A. E., D. B. Miles, and D. N. Reznick. 1988. Life history patterns in squamate reptiles. Pages 441–522 *in* C. Gans and R. B. Huey, eds. Biology of the Reptilia. Vol. 16: Ecology B. Defense and life history. Liss, New York.

Duvall, D., L. J. Guillette Jr., and R. E. Jones. 1982. Environmental control of reptilian reproductive cycles. Pages 201–231 *in* C. Gans and H. Pough, eds. Biology of the Reptilia. Academic Press, New York.

Felsenstein, J. 1984. Distance methods for inferring phylogenies: a justification. Evolution 38:16–24.

———. 1985. Phylogenies and the comparative method. American Naturalist 125:1–15.

Fitch, H. S. 1970. Reproductive cycles of lizards and snakes. University of Kansas Museum of Natural History Miscellaneous Publication 52:1–247.

Fraipont, M., J. Clobert, and R. Barbault. 1996. The evolution of oviparity with egg guarding and viviparity in lizards and snakes: a phylogenetic analysis. Evolution 50:391–400.

Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. American Naturalist 160:712–726.

Fritz, S. A., and A. Purvis. 2010. Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. Conservation Biology 24:1042–1051.

Giannini, N. P. 2003. Canonical phylogenetic ordination. Systematic Biology 52:684–695.

Gilbert, B., and J. R. Bennett. 2010. Partitioning variation in ecological communities: do the numbers add up? Journal of Applied Ecology 47:1071–1082.

Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society B: Biological Sciences 326:119–157.

Greer, A. E. 1989. The biology and evolution of Australian lizards. Surrey Beatty, Chipping Norton.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 35:147–186.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford Series in Ecology and Evolution. Oxford University Press, New York.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

Ho, L. S. T., and C. Ane. 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. Systematic Biology 63:397–408.

Howard, C. W. 1974. Comparative reproductive ecology of horned lizards (genus *Phrynosoma*) in southwestern United States and northern Mexico. Journal of the Arizona Academy of Science 9:108–116.

Huey, R. B. 1977. Egg retention in some high-altitude *Anolis* lizards. Copeia 1977:373–375.

Huey, R. B., and E. R. Pianka. 1981. Ecological consequences of foraging mode. Ecology 62:991–999.

Inger, R. F., and B. Greenberg. 1966. Annual reproductive patterns of lizards from a Bornean rain forest. Ecology 47:1007–1021.

Ives, A. R., and T. Garland. 2010. Phylogenetic logistic regression for binary dependent variables. Systematic Biology 59:9–26.

James, C., and R. Shine. 1988. Life history strategies of Australian lizards: a comparison between the tropics and the temperate zone. Oecologia (Berlin) 75:307–316.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314–334.

Losos, J. B. 1994. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. Annual Review of Ecology and Systematics 25:467–493.

———. 1995. Community evolution in greater antillean *Anolis* lizards: phylogenetic patterns and experimental tests. Philosophical Transactions of the Royal Society B: Biological Sciences 349:69–75.

———. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters 11:995–1003.

———. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. University of California Press, Berkeley.

———. 2011. Seeing the forest for the trees: the limitations of phylogenies in comparative biology. American Naturalist 177:709–727.

Losos, J. B., and K. de Queiroz. 1997. Evolutionary consequences of ecological release in Caribbean *Anolis* lizards. Biological Journal of the Linnean Society 61:459–483.

Losos, J. B., M. Leal, R. E. Glor, K. de Queiroz, P. E. Hertz, L. R. Schettino, A. C. Lara, et al. 2003. Niche lability in the evolution of a Caribbean lizard community. Nature 424:542–545.

Losos, J. B., J. C. Marks, and T. W. Schoener. 1993. Habitat use and ecological interactions of an introduced and a native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes of anole introductions. Oecologia (Berlin) 95:525–532.

Mahler, D. L., L. J. Revell, R. E. Glor, and J. B. Losos. 2010. Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. Evolution 64:2731–2745.

McFadden, D. 1973. Conditional logit analysis of qualitative choice behavior. Pages 105–142 *in* P. Zarembka, ed. Frontiers in econometrics. Academic Press, New York.

Menezes, V. A., M. Van Sluys, A. F. Fontes, and C. F. D. Rocha. 2011. Living in a caatinga-rocky field transitional habitat: ecological aspects of the whiptail lizard *Cnemidophorus ocellifer* (Teiidae) in northeastern Brazil. Zoologia 28:8–16.

Mesquita, D. O., and G. R. Colli. 2003*a*. The ecology of *Cnemidophorus ocellifer* (Squamata, Teiidae) in a Neotropical savanna. Journal of Herpetology 37:498–509.

———. 2003*b*. Geographical variation in the ecology of populations of some Brazilian species of *Cnemidophorus* (Squamata, Teiidae). Copeia 2003:285–298.

———. 2010. Life history patterns in South American tropical lizards. Pages 45–71 *in* O. H. Gallegos, F. R. M. Cruz, and J. F. M. Sánchez,

eds. Reproducción en reptiles: morfología, ecología y evolución. Universidad Autónoma del Estado de México, México.

Mesquita, D. O., G. C. Costa, G. R. Colli, T. B. Costa, D. B. Shepard, L. J. Vitt, and E. R. Pianka. 2016*a*. Data from: Life-history patterns of lizards of the world. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.55610.

Mesquita, D. O., R. G. Faria, G. R. Colli, L. J. Vitt, and E. R. Pianka. 2016*b*. Lizard life-history strategies. Austral Ecology 41:1–5.

Mesquita, D. O., L. J. Vitt, G. R. Colli, D. B. Shepard, G. C. Costa, T. B. Costa, and E. R. Pianka. 2015. Life history data of lizards of the world. Ecology 96:594–594. http://dx.doi.org/10.1890/14 -1453.1.

Miles, D. B., and A. E. Dunham. 1992. Comparative analyses of phylogenetic effects in the life-history patterns of iguanid reptiles. American Naturalist 139:848–869.

Münkemüller, T., S. Lavergne, B. Bzeznik, S. Dray, T. Jombart, K. Schiffers, and W. Thuiller. 2012. How to measure and test phylogenetic signal. Methods in Ecology and Evolution 3:743–756.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, et al. 2013. vegan: community ecology package. R package, version 2.0–10.

Oksanen, J. R., P. Kindt, and P. Legendre. 2007. The vegan package. Community ecology package.

O'Meara, B. C., and J. M. Beaulieu. 2014. Modelling stabilizing selection: the attraction of Ornstein-Uhlenbeck models. Pages 381–393 *in* L. Z. Garamszegi, ed. Modern phylogenetic comparative methods and their application in evolutionary biology. Springer, Berlin.

Orme, D., R. Freckleton, G. Thomas, T. Petzoldt, S. Fritz, N. Isaac, and W. Pearse. 2013. caper: comparative analyses of phylogenetics and evolution in R. R package, version 0.5.2. http://CRAN.R-project .org/package=caper.

Pagel, M. 1997. Inferring evolutionary processes from phylogenies. Zoologica Scripta 26:331–348.

———. 1999. Inferring the historical patterns of biological evolution. Nature 401:877–884.

Paradis, E., and J. Claude. 2002. Analysis of comparative data using generalized estimating equations. Journal of Theoretical Biology 218:175–185.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Pennell, M. W., L. J. Harmon, and J. C. Uyeda. 2014. Speciation is unlikely to drive divergence rates. Trends in Ecology and Evolution 29:72–73.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team. 2015. nlme: linear and nonlinear mixed effects models. R package, version 3.1–120. http://CRAN.R-project.org/package=nlme.

Pyron, R. A., and F. T. Burbrink. 2014. Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. Ecology Letters 17:13–21.

Pyron, R. A., F. T. Burbrink, and J. J. Wiens. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology 13:1–53.

Pyron, R. A., G. C. Costa, M. A. Patten, and F. T. Burbrink. 2015. Phylogenetic niche conservatism and the evolutionary basis of ecological speciation. Biological Reviews 90:1248–1262.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Revell, L. J., L. J. Harmon, and D. C. Collar. 2008. Phylogenetic signal, evolutionary process, and rate. Systematic Biology 57:591–601.

Revell, L. J., L. J. Harmon, R. B. Langerhans, and J. J. Kolbe. 2007. A phylogenetic approach to determining the importance of constraint on phenotypic evolution in the Neotropical lizard *Anolis cristatellus*. Evolutionary Ecology Research 9:261–282.

Revell, L. J., D. L. Mahler, P. R. Peres-Neto, and B. D. Redelings. 2012. A new phylogenetic method for identifying exceptional phenotypic diversification. Evolution 66:135–146.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, London.

———. 2002. Life history evolution. Sinauer, Sunderland, MA.

Seigel, R. A., and H. S. Fitch. 1984. Ecological patterns of relative clutch mass in snakes. Oecologia (Berlin) 61:293–301.

Shine, R. 2004. Does viviparity evolve in cold climate reptiles because pregnant females maintain stable (not high) body temperatures? Evolution 58:1809–1818.

———. 2005. Life-history evolution in reptiles. Annual Review of Ecology, Evolution, and Systematics 36:23–46.

Shine, R., and L. Schwarzkopf. 1992. The evolution of reproductive effort in lizards and snakes. Evolution 46:62–75.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179.

Ter Braak, C. J. F., and O. F. R. Van Tongeren. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge.

Tinkle, D. W., and J. W. Gibbons. 1977. The distribution and evolution of viviparity in reptiles. Miscellaneous Publications, Museum of Zoology, University of Michigan 154:1–47.

Tinkle, D. W., H. M. Wilbur, and S. G. Tilley. 1970. Evolutionary strategies in lizard reproduction. Evolution 24:55–74.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Springer, New York.

Vitt, L. J. 1981. Lizard reproduction: habitat specificity and constraints on relative clutch mass. American Naturalist 117:506–514.

———. 1986. Reproductive tactics of sympatric gekkonid lizards with a comment on the evolutionary and ecological consequences of invariant clutch size. Copeia 1986:773–786.

———. 1990. The influence of foraging mode and phylogeny on seasonality of tropical lizard reproduction. Papéis Avulsos de Zoologia, São Paulo 37:107–123.

———. 1992. Diversity of reproductive strategies among Brazilian lizards and snakes: the significance of lineage and adaptation. Pages 135–149 *in* W. C. Hamlett, ed. Reproductive biology of South American vertebrates. Springer, New York.

Vitt, L. J., and G. R. Colli. 1994. Geographical ecology of a Neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. Canadian Journal of Zoology 72:1986–2008.

Vitt, L. J., and J. D. Congdon. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. American Naturalist 112:595–608.

Vitt, L. J., and E. R. Pianka. 2005. Deep history impacts present-day ecology and biodiversity. Proceedings of the National Academy of Sciences of the USA 102:7877–7881.

Vitt, L. J., E. R. Pianka, W. E. Cooper Jr., and K. Schwenk. 2003. History and the global ecology of squamate reptiles. American Naturalist 162:44–60.

Vitt, L. J., and H. J. Price. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. Herpetologica 38:237–255.

Warne, R. W., and E. L. Charnov. 2008. Reproductive allometry and the size-number trade-off for lizards. American Naturalist 172:E80–E98.

Werneck, F. D., L. G. Giugliano, R. G. Collevatti, and G. R. Colli. 2009. Phylogeny, biogeography and evolution of clutch size in South American lizards of the genus *Kentropyx* (Squamata: Teiidae). Molecular Ecology 18:262–278.

Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics 36:519–539.

Zamora-Abrego, J. G., J. J. Zuniga-Vega, and A. N. M. De Oca. 2007. Variation in reproductive traits within the lizard genus *Xenosaurus*. Journal of Herpetology 41:630–637.

Associate Editor: David D. Ackerly
Editor: Judith L. Bronstein
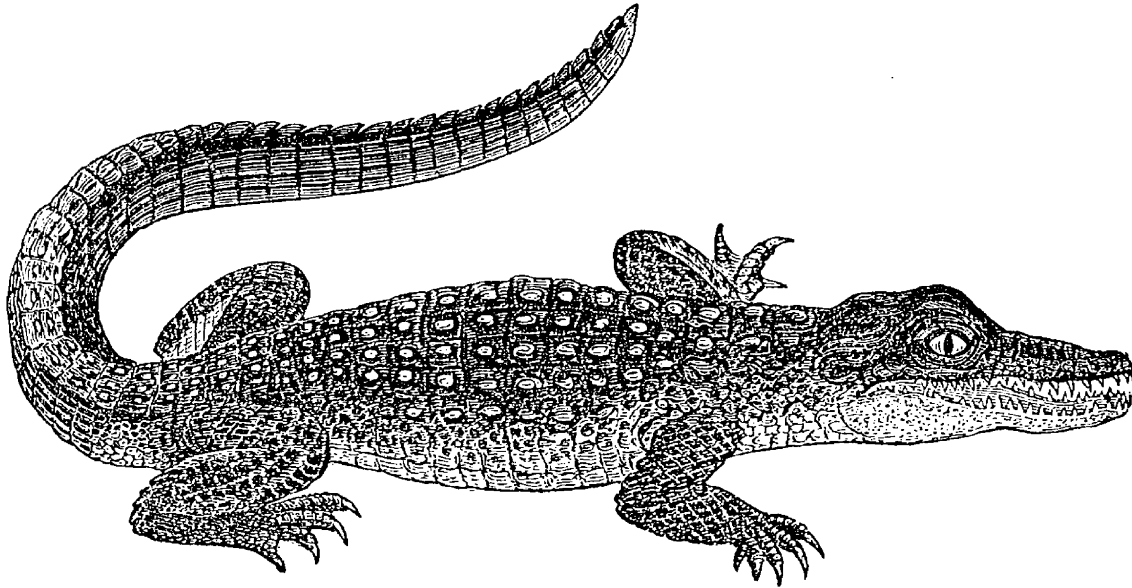
"Although many turtles, and the alligators [illustrated], crocodiles, and gavials, are exceedingly rapacious, they are also among the prominent scavengers, eagerly feeding upon the dead animals which they find in the streams which they inhabit." From "A Few Words About Scavengers" by Sanborn Tenney (*The American Naturalist*, 1877, 11:129–135).