The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution

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Abstract

We analyze, with an augmented data base, patterns of covariation of the three primary demographic parameters (age at maturity, fecundity, adult survival, all measured in the same unit of time) in lizards. This also constitutes a first attempt to use all three of these parameters for this group of species. We attempt to place these analyses in the framework of recent theories on life history evolution (Ferrière and Clobert, 1992; Charnov, 1993). Life history data were collected from the literature and from our original work, and a composite phylogeny was assembled, based on a variety of published sources. Using a phylogenetically based statistical method (independent contrasts), the allometric (log-log) relationship of fecundity (and of clutch size) in relation to snout-vent length was found to differ significantly between the two major clades of extant lizards, Iguania (43 species in our data set) and Scleroglossa (47 species). We therefore emphasize analyses done separately for the two clades. Without removing correlations with body size, the relationships between fecundity and survival, and between fecundity and age at maturity, were also found to differ between clades, which differs from Charnov's (1993) predictions. When correlations with body size were removed statistically, however, the two clades did not differ significantly in these relationships. In a principal components analysis (PCA) of the three demographic variables plus snout-vent length, the first axis explained the majority (53–57%) of variation in both clades, while the second axis explained 27–31% of the variation and loaded mainly on fecundity. In a PCA of size-adjusted demographic variables residuals (from log-log regressions on snout-vent length), the first axis explained 66–68% of the variation and was clearly interpretable as the classical "slow-fast" continuum, which has been described in birds and mammals. The PCA of residuals did not provide clear evidence of additional significant patterns of covariation. However, the rate of evolution of

mortality (size-corrected), but not of fecundity or age at maturity, differed significantly between clades. Furthermore, fecundity and age at maturity, both corrected for variation in adult mortality (in addition to body size), were still significantly related, indicating the existence of other patterns of variation in these life history traits. In other words, the ratios between age at maturity and adult mortality, or between fecundity and adult mortality, were not found to be invariant, because the variation not accounted for by these ratios was significantly associated with variation in another variable. This result contradicts the prediction of Charnov (1993), and suggests the existence of other directions of evolution in these life history traits.

Introduction

Potentially many combinations of the three basic demographic parameters (age at first reproduction, age-specific survival and age-specific fecundity) could allow the persistence of a population, even restricted to those leading to a stable population size. Attempts to identify those combinations of parameters which are optimal within a given set of internal and external constraints have generated considerable theoretical work (reviewed in Roff, 1992; Stearns, 1992). Although many of these theoretical studies considered only subsets or even sub-components (e.g., clutch size) of the three primary demographic parameters (i.e., those parameters measured in the same unit of time), they led to the concept of the so called r-K gradient (Cody, 1966; McArthur and Wilson, 1967; Pianka, 1970). Along this gradient, species range from those which mature early, produce many offspring, and have a short adult lifespan, to those which mature late, produce very few offspring, and have a longer lifespan. Thus, age at maturity and survival covary positively, while both covary negatively with fecundity (number of offspring produced per unit of time, Allainé et al., 1987). The existence of this "slow-fast" gradient has been only partially documented among species in a variety of organisms (Stearns, 1983, 1984; Dunham and Miles, 1985; Harvey and Zammuto, 1985; Dunham et al., 1988a; Saether, 1988; Gaillard et al., 1989; Harvey et al., 1989), because most studies only considered a subset of demographic components, generally not expressed in the same unit of time, and have not used phylogenetically based statistical methods. The existence of patterns of variation in addition to the slow-fast continuum has been debated several times (Stearns, 1976, 1977; Western, 1979; Wittenberg, 1981; Promislow and Harvey, 1990, 1991; Stearns, 1992), but was rarely searched for in empirical studies (Gaillard et al., 1989).

More recently, Charnov and colleagues developed life history models incorporating all three demographic parameters, and used these models to search for those combinations of parameters which lead to evolutionarily stable strategies (Charnov, 1990, 1991, 1993; Charnov and Berrigan, 1990, 1991a). These models predict that the evolutionarily stable relationships link age at maturity, adult lifespan, and fecundity such that they covary two-by-two in only one direction. In other words, the relation between adult lifespan and age at maturity, or between fecundity and

adult life span, has a slope equal to unity. The model of Charnov and colleagues was based on the assumptions that populations are stationary (unchanging in size, and stable equilibrium) and that competition affects all age classes (except juveniles) in an equal way. Relaxing these assumptions can yield different results. In particular, in addition to the expected positive correlation between age at maturity and survival, two other patterns of association were found (Ferrière and Clobert, 1992): one in which survival probability increases independently of age at maturity, but with age at maturity kept to low values (iteroparity gradient); the other in which age at maturity increases, with adult survival probability kept to low values (semelparity gradient).

Predictions of Charnov et al.'s models were tested by interspecific comparisons for several groups of vertebrates (Charnov, 1990; Charnov and Berrigan, 1991b; Berrigan et al., 1993; Purvis and Harvey, 1995) and the intensity of covariation of demographic variables was found to vary among taxonomic groups (Charnov, 1990, 1993). The proposed reason for these differences was based on the fact that every demographic parameter is related to body size allometrically, i.e., as a power function $y = a(\text{size})^b$ (Peters, 1983; Calder, 1984). Thus, the slope of log of age at maturity with respect to log of adult life span will depend on the respective value of a and b for the two demographic parameters, and the way these coefficients vary among groups (Charnov and Berrigan, 1990; Charnov, 1993). The intensity of the interspecific covariation was not examined after statistically removing correlations with body size. Also, Charnov (1993) pointed out the considerable scatter around the regression lines for pairs of the three primary demographic parameters. The extent to which this scatter is attributable to imprecision and bias in the data (Lebreton et al., 1987; Krementz et al., 1989; Charnov, 1993; Gaillard et al., 1995; Martin et al., 1995) or something else is unclear. It may well be that this scatter indicates the existence of other patterns of variation in the data, patterns which remains to be found, as suggested theoretically by Ferrière and Clobert (1992) and empirically by Gaillard et al. (1989).

Lizards have often been used as a model in ecological and evolutionary studies (Huey et al., 1983; Vitt and Pianka, 1994), including many studies of life history evolution (Tinkle et al., 1970; Dunham and Miles, 1985; Huey, 1987; Dunham et al., 1988a; Stearns, 1984; Shine and Charnov, 1992; Miles and Dunham, 1992; Bauwens and Diaz-Uriarte, 1997). Indeed, the group is often considered to be relatively homogenous in terms of morphology and behavior, as compared with other groups of vertebrates that have been considered in comparative studies of life history (e.g., Osteichthyes, Aves, Mammalia), and the method used for estimating life history parameters in natural populations of lizards are more comparable across species (Dunham et al., 1988b) than in other taxa (Lebreton et al., 1987; Krementz et al., 1989; Gaillard et al., 1994). The existence of the slow-fast continum in lizards was looked for several times with various results (Tinkle et al., 1970; Stearns, 1984; Dunham et al., 1988a). The only study which both used phylogenetically based statistical methods and demographic parameters which included survival failed to find the slow-fast turn-over (Bauwens and Diaz-Uriarte, 1997). Two studies of lizards found evidence for Charnov's invariant numbers (Shine and Charnov, 1992;

Bauwens and Diaz-Uriarte, 1997). However, these studies involved a very restricted sample of lizard species (fewer than 20), which obviously reduces the chance of finding additional patterns of variation. Finally, none of the studies employed the primary demographic parameters measured in the same time units (per year or generation), as recommended by standard demographical considerations (Caswell, 1989; Gaillard et al., 1989).

The goals of this paper are, therefore, to: 1) verify the existence of the slow-fast turn-over gradient, using phylogenetically based statistical methods; 2) verify that the same gradient is found when correlations with body size are removed statistically, while also examining the role of size in the diversification of demographic strategies in lizards (i.e., allometry); 3) investigate the existence of other axes of correlated demographic variation; 4) estimate the two-by-two relationships between demographic parameters (age at maturity, fecundity, mortality); and 5) analyze whether 1)–4) vary between the two major clades of lizards. We used a recently augmented body of information on the three demographic parameters (90 species, Promislow et al., 1992). Although it is probable that such factors as reproductive mode, foraging behavior, and habitat usage (Tinkle et al., 1970; Stearns, 1984; Dunham et al., 1988a; de Fraipont et al., 1996) are coadapted with demographic patterns, a consideration of the selective processes which have resulted in the organization of life history patterns is beyond the scope of this paper.

Methods

The data

We extracted data from the literature for 90 species of lizards. Available phylogenetic information suggests that snakes constitute a (probably monophyletic) group that evolved from within scleroglossan lizards (Estes and Pregill, 1988; Heise et al., 1995). However, we excluded snakes from our analyses because relatively few demographic data are available (e.g., Shine and Charnov, 1992), their typical ecology and behaviour is rather different from that of most lizards, and their phylogenetic relationships are relatively poorly known as compared with lizards (e.g., see Estes and Pregill, 1988; Heise et al., 1995).

The variables analyzed are mean adult female snout-vent length (hereafter, often referred to as body size), clutch size (number of eggs or offspring per clutch), brood frequency (per year), annual fecundity (clutch size ∗ brood frequency), age at maturity (in years), and adult mortality rate (per year; computed as $-\log[\text{adult survival rate}]$). For species which rarely survive more than one year, we assigned arbitrarily the value of 0.01 (Barbault, 1976) for mathematical convenience. For long-lived species, we sometimes back-calculated the mean annual survival rate from average lifespan, because only the latter data were available. In some cases, we restimated some parameters with more appropriate methods (Lebreton et al., 1992) when raw data were available. In lizards, both brood frequency and the mean clutch size for different reproductive episodes within a breeding season

may not be accurately described in all cases. Although we did calculate average clutch size for the entire breeding season when data were available, quite often the average clutch size was given only for the first reproductive episode while it is known that the value of this variable tends to decrease as the breeding season progresses. This may, therefore, lead to an overestimation of the annual reproductive output if only the mean clutch size of the first reproductive output is used. In the same way, brood frequency is ill-estimated, because it was not looked for in some species, or, because, as fewer and fewer individuals are participating in a reproductive episode as the breeding season proceeds, the probability of detecting a reproductive episode becomes smaller and smaller (Dunham et al., 1988b). This leads to an underestimation of brood frequency. The extent to which the overestimation of the annual reproductive output caused by using the clutch size of the first reproductive episode is balanced by the chronic overestimation of brood frequency is unknown. For a given species, the magnitude of the biases are likely to go in parallel because if a species is not well studied we usually have poor information on both clutch sizes at different reproductive episodes and brood frequencies. In turn, this is likely to increase the scatter around the relationship rather than to cause systematic biases (spurious relationships), because poorly described species are present throughout the phylogeny.

To maximize the number of species represented in this work, we included the species with small and invariant clutch sizes. Indeed, this phenotype has arisen independently several times throughout lizard phylogeny (at least three times in our composite phylogeny, Appendix II), so that we can consider this as a strategy (responding to ecological conditions) rather than as a phylogenetic constraint. Furthermore, brood frequency is higher for species with a fixed clutch size than for species with a non-fixed clutch size, which results in there being no difference in their annual reproductive output (nonphylogenetic ANOVA on fecundity with clade, clutch mode as factor effect and size as a covariate: clutch mode effect $F_{1,86} = 0.31$, $p = 0.58$). Discarding these species would reduce arbitrarily the diversity of life history strategies without good reason, and would also raise the question of why not discard species with a fixed brood frequency, age at maturity, etc. However, we investigated the role at fixed-clutch size species by performing an additional analysis with these species removed. We also removed large iguanas to examine the influence of the difference in size variance among clades. The species removed are indicated by a + in Appendix I.

Also, we sometimes pooled data for different populations of the same species. For each variable and for each species, the datum analyzed was the mean of the characters for all of the populations. This procedure was necessary because in many cases not all variables were available for a single population. The way we gathered the data and the particularities of the studied populations as well as the methods used to estimate some of the parameters (in particular, survival and age at maturity; see Dunham et al., 1988b, Martin et al., 1995), may have induced some imprecisions in the description of species life history. In all cases, we verified that the parameter estimates for each species led to a more or less stable population (growth rate around unity) using matrix projection (Caswell, 1989) when enough

details on the life cycle of the species were given. The data are presented in Appendix I.

Statistical analysis

We used Felsenstein's (1985) comparative method of phylogenetically independent contrasts for estimation and statistical hypothesis testing of relationships among variables. The statistical properties of this method have been checked via computer simulation by Grafen (1989), Martins and Garland (1991), Purvis et al. (1994), Diaz-Uriarte and Garland (1996), and Martins (1996). The method seems relatively robust and is the best understood and most widely used of available phylogenetically based statistical methods (Harvey and Pagel, 1991; Garland et al., 1992, 1993; Pagel, 1993; Garland, 1994; Garland and Adolph, 1994; Pianka, 1995). Moreover, independent contrasts are applicable to a wide range of questions including correlation, principal components analysis (PCA), regression, multiple regression, analysis of variance (ANOVA), and analysis of covariance (ANCOVA).

The topology used for analyses is shown and discussed in Appendix II. Because it includes soft polytomies, reflecting current uncertainty about relationships, degrees of freedom for hypothesis testing with independent contrasts can only be bounded (Purvis and Garland, 1993; empirical example in Christian and Garland, 1996). Following their recommendations, we computed all $N - 1$ contrasts at each polytomy for use in estimation, and bounded degrees of freedom for hypothesis testing between the maximum of (total number of contrasts -1, i.e., 88 for the full 90 species) and the minimum of (total number of nodes -1, i.e., 68 for the partially unresolved topology we used).

All variables were $\log_{10}$ transformed prior to computation of independent contrasts, because this typically improved linearity and homoscedasticity in regressions on snout-vent length and because log-log relationships are needed for comparisons with various theoretical predictions. Independent contrasts were computed with Version 2.0 of the PDTREE program, which includes a module for independent contrasts (Version 1.0 was first discussed by Garland et al., 1993).

Estimates of phylogenetic branch lengths in terms of divergence times, genetic distances, or some other common metric are not available for all of the 90 species included herein. Therefore, we tried three different sets of arbitrary branch lengths. The statistical adequacy of each of the three sets was checked independently for all variables as described in Garland et al. (1992). For all log-transformed characters, plots of the absolute values of the standardized independent contrasts versus their standard deviations (see Garland et al., 1992; Diaz-Uriarte and Garland, 1996) showed no statistically significant linear trends when using branch lengths all set equal to one (Pearson correlations ranged from -0.195 to 0.064, all $P > 0.05$). When either Pagel's (1992) arbitrary branch lengths (as shown in Appendix II) or Grafen's (1989) arbitrary branch lengths were used, however, plots for all characters showed negative linear correlations ($r = -0.371$ to -0.240 and -0.385 to -0.171, respectively), some of which were statistically significant at $P < 0.05$

(2-tailed tests). Because the branch lengths of unity seemed to work adequately (i.e., none of the diagnostic linear correlations is statistically significant at $P < 0.05$ with either 68 or 88 d.f.), we did not try the alternative of various transformations of the other two types of arbitrary branch lengths (see Garland et al., 1992; Diaz-Uriarte and Garland, 1996). We therefore used branch lengths of unity for all characters, which is consistent with a speciational model of evolutionary change (and assuming that all speciation events are represented in the phylogeny [Martins and Garland, 1991], which is not true in the present case, because many extant species [as well as extinct species] are not included).

Depending on the question being addressed, we used Pearson product-moment correlations, regression, multiple regression, and principal components analysis (PCA) on the phylogenetically independent contrasts. We used the heuristic broken stick method to determine how many principal components to interpret (Jackson, 1993). These analyses were performed using SPSS/PC+ Version 5.0. In all cases, no intercept term was included in the model, as is required for independent contrasts (Felsenstein, 1985; Grafen, 1989; Garland et al., 1992). To compare bivariate correlations between pairs of life history traits in the two suborders, we used multiple regression with a dummy variable coding for clade, and tested for significance of the crossproducts term. For PCA, we first used the REGRESSION procedure of SPSS with the no intercept option to produce a centered correlation matrix (see Garland et al., 1992, p. 27), and then input this to the FACTOR procedure. The correlation matrix, as opposed to the covariance matrix, was chosen in order to compare with previous published results (Bauwens and Diaz-Uriarte, 1997).

In general, all analyses with independent contrasts were performed twice: first with the data not corrected for body size (snout-vent length) and second with data corrected for size by computing residuals from log-log least-squares regressions (on snout-vent length) through the origin using standardized independent contrasts (Garland et al., 1992). Differences between these two analyses were used to determine whether selection may have altered life histories mainly through their correlation with body size.

Extant squamates consist of two major clades, Iguania and Scleroglossa, which diverged in the early Jurassic (approximately 178–208 million years ago). This is a considerably longer time than for the earliest divergences within extant Mammalia (about 110 millions years ago; J. A. W. Kirsch, pers. comm.) or Aves (possibly only about 65 million years ago; Feduccia, 1995), two other vertebrate clades which have often been analyzed in terms of life history variation. As well, the two major lizard clades differ, on average, in a number of respects, especially with regard to typical mode of foraging and prey acquisition (see Estes and Pregill, 1988; Vitt and Pianka, 1994). Finally, our initial allometric analyses revealed statistically significant differences in the scaling relationships within these two clades. Therefore, although we present analyses for all 90 species combined, our emphasis is on the analyses performed within each clade.

In preliminary analyses, we also searched for heterogenetity in allometric relationships among subclades within the Iguania and within the Scleroglossa. We did

indeed find statistically significant differences. For example, using independent contrasts and the topology shown in Appendix II, the allometry (slope) of both clutch size and fecundity differs significantly ($P = 0.0472$ and $P = 0.0129$, respectively) among Gekkota ($N = 9$ species), Scincidae ($N = 18$ species), and (Lacertidae + Teiidae + *Xantusia vigilis* ($N = 20$ species) in a three-group comparison. However, the sample sizes within these clades are rather small for multivariate statistical analyses, and we wished to avoid overanalysis of the data set. Therefore, we do not present analyses of smaller clades within the Iguania or Scleroglossa.

Results

Rates of evolution in Iguania versus Scleroglossa

We compared the two major clades with respect to the central tendency (median) of the distribution of the absolute values of standardized independent contrasts, using Mann-Whitney tests. A difference in central tendency indicates a difference in average (minimum) rate of evolution (Garland, 1992; Martins, 1994; see also Pianka, 1995). Because arbitrary branch lengths were used, these analyses may not be interpretable in any real biological sense as comparisons of "rates of evolution" between clades. For example, if all traits showed a difference between clades, then this result might be attributable to the arbitrary branch lengths being differentially "wrong" for the two clades (i.e., relatively too long for one clade with respect to the other). On the other hand, if some traits show differences between clades whereas others do not, then a real biological difference between clades would seem to exist.

The two clades showed a significant difference only for mortality (Mann-Whitney $U = 643.0$, $Z [88] = -2.698$, 2-tailed $P = 0.0070$; for the other traits, all $P \geq 0.1356$). We also performed these comparisons after computing residuals from regressions on snout-vent length (using all 89 contrasts). Again, only mortality showed a significant difference ($U = 637.0$, $Z [88] = -2.749$, 2-tailed $P = 0.0060$: for the other traits, all $P \geq 0.4622$). Thus, the two clades differ in average minimum rate of evolution either for mortality or for one or more of the other five traits (snout-vent length, clutch size, brood frequency, fecundity, age at maturity).

Allometry

Table 1 presents allometric slopes based on independent contrasts analyses of log-transformed data. Separate estimates are presented for all 90 species (89 contrasts) and for the two halves of the phylogeny, corresponding to Iguania (43 species) and Scleroglossa ([Gekkota plus Autarchoglossa] = 47 species in our data set) (see Appendix II).

Both age at maturity (slope about 0.9) and mortality (slope about -0.7) scale similarly in the two clades (Tab. 1). Brood frequency also scales with a similar exponent in the two clades (-0.500 for Iguania vs. -0.715). The allometry of

clutch size, however, differs significantly between the two clades, with the slope being much higher in Iguania (1.161 vs. 0.233). As a consequence, fecundity, which is computed as the product of brood frequency and clutch size, also scales significantly differently in the two clades (slopes = 0.661 for Iguania vs. −0.482; as noted at the end of the Methods section, statistically significant differences in allometric slopes among subclades within Scleroglossa can also be found).

We redid the allometric analyses with fixed-clutch species removed (see Appendix I). In this analysis of the reduced data set, we obtained qualitatively very similar results. In particular, the allometric slopes for clutch size changed to 0.649 (95% CI 0.312–0.980), 0.915 (0.423–1.407) and 0.233 (−0.142–0.773), respectively for all species, the Iguania, and the Scleroglossa. The comparison of slopes between the two clades yielded $p = 0.0754$, versus $p = 0.0023$ for the full data set. For fecundity, allometric slopes in the reduced data set were, respectively 0.229 (−0.229–0.686), 0.730 (0.100–1.360), and −0.406 (−1.054–0.243) for all the data, the Iguania and the Scleroglossa. For this character, the comparison of allometric slopes between the two clades yielded $p = 0.0129$ versus $p = 0.0057$ for the full data set. Thus, the analyses of the reduced data set support the conclusion that the two clades differ significantly in the allometry of certain life history traits. Consequently, we did not remove those species from our data set in the following analyses.

Table 1. Allometric equations based on phylogenetically independent contrasts (independent variable is snout-vent length). All variables were $\log_{10}$ transformed prior to computation of contrasts, using topology shown in Appendix II and all branch lengths set equal to one.

Variable	Slope	95% Conf.	Interval	r^2	F	P	Clade P
89 Contrasts for all 90 species of lizards							
Clutch size	0.736	0.4320	1.0400	0.208	23.15	<0.0001	0.0023
Brood frequency	−0.588	−0.9488	−0.2273	0.107	10.50	0.0017	0.5618
Fecundity	0.148	−0.2645	0.5604	0.006	0.51	0.4778	0.0057
Age at maturity	0.880	0.5865	1.1735	0.287	35.50	<0.0001	0.9342
Mortality	−0.674	−0.9323	−0.4153	0.234	26.83	<0.0001	0.1857
42 Contrasts for Iguania							
Clutch size	1.161	0.7135	1.6076	0.401	27.48	<0.0001	
Brood frequency	−0.500	−0.9855	−0.0135	0.095	4.31	0.0442	
Fecundity	0.661	0.1054	1.2166	0.123	5.77	0.0209	
Age at maturity	0.879	0.4515	1.3055	0.296	17.26	0.0002	
Mortality	−0.516	−0.7570	−0.2754	0.314	18.74	0.0001	
46 Contrasts for Scleroglossa							
Clutch size	0.233	−0.1596	0.6256	0.031	1.43	0.2383	
Brood frequency	−0.715	−1.2802	−0.1496	0.126	6.46	0.0144	
Fecundity	−0.482	−1.0742	0.1104	0.056	2.69	0.1082	
Age at maturity	0.903	0.4704	1.3365	0.282	17.66	0.0001	
Mortality	−0.867	−1.3381	−0.3955	0.234	13.72	0.0006	

95% confidence intervals are computed using the maximum of 88, 41 or 45 degrees of freedom.
''Clade P'' refers to significance level for comparison of slopes between the two clades, omitting the basal contrast.

Differences in mean values between Iguania and Scleroglossa

Mean values for traits of species in two sister clades can be compared using independent contrasts (i.e., the equivalent of an analysis of variance), as described in Garland et al. (1993). In brief, if the value of the basal contrast is an "outlier" in magnitude, then a difference in mean value between the two clades is indicated. For a single trait, the absolute values of the standardized independent contrasts can simply be ranked and the rank of the basal contrast determined (Garland et al., 1993, p. 283; see pp. 277–278 for a parametric *t*-test equivalent). For snout-vent length, the basal contrast is ranked 18 of 89 and so is not unusual; thus, the two clades do not differ in average body size.

To compare mean values of a trait after controlling for body size (i.e., the equivalent of an analysis of covariance), we use regression (through the origin) with standardized independent contrasts. Garland et al. (1993, pp. 278–279, their Fig. 5) used the approach of fitting a regression line and associated 95% prediction interval for a new observation to the set of all contrasts except the basal one; the basal contrast was then compared to the prediction interval. We have employed an equivalent test: we regressed standardized independent contrasts in a life history trait on contrasts in snout-vent length plus a 0–1 dummy variable coded as 1 for the single basal contrast and 0 for all other contrasts. The partial regression coefficient for this dummy variable and its associated partial F statistic and P value test for the significance of the basal contrast as an outlier from the overall relationship; this is effectively a test for a mean difference between the two clades, after controlling for the correlation of the life history trait with snout-vent length.

The foregoing test assumes that the slopes of the relationship between the life history trait and snout-vent length is the same for the two clades. As shown in Table 2, however, the slopes of the relationships for clutch size and for fecundity differ significantly between Iguania and Scleroglossa. Therefore, for these traits, an additional crossproducts term needs to be added to the regression model. This crossproducts term is computed as the standardized independent contrasts in snout-vent length multiplied by a second 0–1 dummy variable, which is coded as 0 for one clade and 1 for the other (for this dummy variable, the code for the basal contrast is irrelevant once all three independent variables are forced into the model).

Considering all of the foregoing analyses, for none of the life history traits was the basal contrast a statistically significant outlier (all $P \geq 0.42$). This, we find no evidence for statistically significant between-clade differences in mean value for any of the life history traits examined herein, once correlations with snout-vent length have been controlled.

Principal components analysis

Table 2 presents correlation matrices and the results of PCA for all lizards and for the two major clades separately, including body size (snout-vent length) as a variable. Separate analyses are presented which use either clutch size and brood

frequency or their product, fecundity. Thus, for completeness, a total of six PCAs is shown. However, because we have already documented statistically significant differences in allometric relationships between the two major clades (Tab. 1), our emphasis is on the separate analyses rather than those which include all 90 species

Table 2. Principal components analysis based on correlation matrix (computed through origin) of standardized phylogenetically independent contrasts. All variables were $\log_{10}$ transformed prior to computation of contrasts.

89 contrasts for all 90 species of lizards
Correlation matrix:

	S-V length	Clutch size	Brood freq.	Age at mat.
Clutch size	0.456			
Brood frequency	−0.326	−0.350		
Age at maturity	0.536	0.090	−0.498	
Mortality	−0.483	−0.029	0.474	−0.663

Determinant of correlation matrix = 0.168
Factor matrix (component correlations):

	1	2	3	4	5
S-V length	0.775	0.246	0.501	0.012	−0.297
Clutch size	0.435	0.862	−0.035	−0.057	0.251
Brood frequency	−0.732	−0.075	0.643	−0.027	0.211
Age at maturity	0.825	−0.342	0.074	0.394	0.204
Mortality	−0.788	0.429	0.047	0.418	−0.136
Eigenvalue	2.63	1.11	0.67	0.33	0.26
% of variance	52.5	22.2	13.5	6.7	5.1
Cumulative %	52.5	74.7	88.2	94.9	100.0

Correlation matrix:

	S-V length	Fecundity	Age at mat.
Fecundity	0.076		
Age at maturity	0.536	−0.386	
Mortality	−0.483	0.413	−0.663

Determinant of correlation matrix = 0.252
Factor matrix (component correlations):

	1	2	3	4
S-V length	0.674	0.649	0.122	−0.332
Fecundity	−0.512	0.807	−0.138	0.260
Age at maturity	0.891	0.025	0.293	0.348
Mortality	−0.880	0.052	−0.470	−0.054
Eigenvalue	2.28	1.08	0.34	0.30
% of variance	57.1	26.9	8.5	7.5
Cumulative %	57.1	83.9	92.5	100.0

Table 2. (continued)

42 Contrasts for Iguania
Correlation matrix:

	S-V length	Clutch size	Brood freq.	Age at mat.
Clutch size	0.634			
Brood frequency	−0.308	−0.411		
Age at maturity	0.544	0.148	−0.367	
Mortality	−0.560	−0.366	0.570	−0.595

Determinant of correlation matrix = 0.123
Factor matrix (component correlations):

	1	2	3	4	5
S-V length	0.822	0.220	0.434	0.010	−0.296
Clutch size	0.670	0.701	−0.003	0.059	0.238
Brood frequency	−0.696	0.054	0.675	−0.198	0.132
Age at maturity	0.714	−0.549	0.287	0.280	0.165
Mortality	−0.838	0.263	0.107	0.460	−0.068
Eigenvalue	2.82	0.91	0.74	0.33	0.19
% of variance	56.4	18.3	14.8	6.7	3.9
Cumulative %	56.4	74.7	89.5	96.1	100.0

Correlation matrix:

	S-V length	Fecundity	Age at mat.
Fecundity	0.351		
Age at maturity	0.544	−0.171	
Mortality	−0.560	0.134	−0.595

Determinant of correlation matrix = 0.252
Factor matrix (component correlations):

	1	2	3	4
S-V length	0.835	0.420	0.022	0.355
Fecundity	0.031	0.972	0.011	−0.233
Age at maturity	0.843	−0.251	0.440	−0.180
Mortality	−0.851	0.199	0.458	0.161
Eigenvalue	2.13	1.22	0.40	0.24
% of variance	53.3	30.6	10.1	6.0
Cumulative %	53.3	83.9	94.0	100.0

46 Contrasts for Scleroglossa
Correlation matrix:

	S-V length	Clutch size	Brood freq.	Age at mat.
Clutch size	0.175			
Brood frequency	−0.355	−0.317		
Age at maturity	0.531	0.001	−0.612	
Mortality	−0.483	0.229	0.446	−0.743

Table 2. (continued)

Determinant of correlation matrix = 0.130
Factor matrix (component correlations):

	1	2	3	4	5
S-V length	0.725	0.115	0.651	−0.194	0.000
Clutch size	0.110	0.956	0.056	0.260	−0.061
Brood frequency	−0.754	−0.352	0.450	0.315	0.070
Age at maturity	0.906	−0.124	−0.118	0.180	0.342
Mortality	−0.828	0.414	0.039	−0.225	0.303
Eigenvalue	2.61	1.24	0.65	0.29	0.22
% of variance	52.3	24.7	12.9	5.8	4.3
Cumulative %	52.3	77.0	89.9	95.7	100.0

Correlation matrix:

	S-V length	Fecundity	Age at mat.
Fecundity	−0.237		
Age at maturity	0.531	−0.606	
Mortality	−0.483	0.593	−0.743

Determinant of correlation matrix = 0.179
Factor matrix (component correlations):

	1	2	3	4
S-V length	−0.669	0.695	0.254	−0.066
Fecundity	0.757	0.531	−0.376	0.059
Age at maturity	−0.905	−0.010	−0.165	0.392
Mortality	0.887	0.061	0.345	0.300
Eigenvalue	2.63	0.77	0.35	0.25
% of variance	65.7	19.2	8.8	6.3
Cumulative %	65.7	84.9	93.7	100.0

(89 contrasts). In addition, we emphasize the analyses using fecundity, because it along with age at maturity and mortality constitute the three basic demographic parameters.

PCA yields different results for the two major clades. For Iguania, the first PC accounts for 53% of the total variance and loads heavily on snout-vent length, age at maturity, and mortality; the second PC accounts for 31% of the variance and loads heavily only on fecundity. Thus, interspecific variation in fecundity is almost completely independent of variation in the other three variables. Therefore, for this clade, the PCA does not yield a single factor that can be interpreted as the classic "fast-slow" continuum (see Introduction).

For Scleroglossa, the first principal component accounts for more of the total variance (66%) and loads most heavily on age at maturity and mortality, with weaker (but still substantial) loadings on both snout-vent length and fecundity. This

factor does, therefore, suggest the fast-slow continuum. The second PC loads moderately on both snout-vent length and fecundity, but accounts for only 19% of the variance (barely more than twice that accounted for by PC 3) and has an eigenvalue of only 0.8. Thus, it is not clear that biologically important variation in fecundity exists independently of variation in the other three variables.

Do the foregoing patterns of association of the three demographic variables persist after removing statistically the correlations of each with body size? Table 3 presents correlation matrices and PCAs of size-corrected demographic variables. For both clades, only the first principal component seems interpretable, as it accounts for about 2/3 of the total variance. Also for both clades, PC 1 demonstrates clearly the "fast-slow" continuum, one end of which represents early maturation, high fecundity, and high adult mortality.

Comparisons of pairwise relationships with theoretical predictions

We tested for differences between clades in the slopes of the three pairwise relationships between the three basic life history variables (using independent contrasts), because these have been discussed as "invariants" by Charnov and colleagues. Considering the whole-organism values, we found significant differences in the relationships between age at maturity and fecundity ($P < 0.0001$) and between fecundity and mortality ($P < 0.0001$). After computing residuals from log-log regressions on snout-vent length (using all 89 contrasts for all 90 species), however, none of the three pairwise relationships differed significantly between clades (all $P \geq 0.3577$). We also computed residuals from regressions separately for each of the two major clades (omitting the basal contrast altogether). Using these residuals, we also found no statistically significant differences between Iguania and Scleroglossa with respect to the slopes of the pairwise relationships (all $P \geq 0.4352$).

Reduced major axis slopes of the pairwise relationships for residuals were as follows (with $\pm 95\%$ confidence interval calculated from formula in McArdle, 1988):

$$\text{Age at Maturity on Mortality} = -1.15 \pm 0.196, \, r = -0.550$$

$$\text{Fecundity on Mortality} = 1.53 \pm 0.241, \, r = 0.498$$

$$\text{Age at Maturity on Fecundity} = -0.75 \pm 0.146, \, r = -0.525.$$

Finally, we repeated these pairwise slope computations using double residuals. That is, we regressed residual contrasts for two of the demographic variables on residual contrasts for the third, computed residuals, and then correlated these double residuals. (Alternatively, we could have used multiple regression or partial correlation analyses, but the present procedure allows us to compare directly with the foregoing results.) Indeed, according to Charnov (1993), no pattern should be found in residuals of the above relationships. These double residuals (controlling for snout-vent length plus the third demographic variable) showed the following

Table 3. Principal components analysis based on correlation matrix (computed through origin) of standardized phylogenetically independent contrasts, using residuals (denoted as R_) from regressions on average female adult snout-vent length. All variables were $\log_{10}$ transformed prior to computation of contrasts.

89 contrasts for all 90 species of lizards
Correlation matrix:

	RClutch size	RBrood freq.	RAge mat.
RBrood frequency	−0.239		
RAge at maturity	−0.206	−0.405	
RMortality	0.245	0.383	−0.547

Determinant of correlation matrix = 0.435
Factor matrix (component correlations):

	1	2	3	4
RClutch size	0.243	0.905	0.014	0.349
RBrood frequency	0.660	−0.610	0.062	0.435
RAge at maturity	−0.846	−0.076	0.498	0.174
RMortality	0.842	0.140	0.447	−0.266
Eigenvalue	1.92	1.22	0.45	0.41
% of variance	48.0	30.4	11.3	10.3
Cumulative %	48.0	78.4	89.7	100.0

Correlation matrix:

	RFecundity	RAge mat.
RAge at maturity	−0.506	
RMortality	0.516	−0.547

Determinant of correlation matrix = 0.464
Factor matrix (component correlations):

	1	2	3
RFecundity	0.813	0.579	−0.061
RAge at maturity	−0.803	0.338	0.444
RMortality	0.834	−0.228	0.502
Eigenvalue	2.05	0.50	0.45
% of variance	68.2	16.7	15.1
Cumulative %	68.2	84.9	100.0

42 Contrasts for Iguania
Correlation matrix:

	RClutch size	RBrood freq.	RAge mat.
RBrood frequency	−0.293		
RAge at maturity	−0.303	−0.249	
RMortality	−0.018	0.504	−0.417

Table 3. (continued)

Determinant of correlation matrix = 0.469
Factor matrix (component correlations):

	1	2	3	4
RClutch size	−0.048	−0.916	0.250	0.310
RBrood freqeuncy	0.776	0.420	−0.063	0.467
RAge at maturity	−0.677	0.547	0.466	0.161
RMortality	0.853	0.000	0.440	−0.279
Eigenvalue	1.79	1.32	0.48	0.42
% of variance	44.8	32.9	11.9	10.5
Cumulative %	44.8	77.6	89.5	100.0

Correlation matrix:

	RFecundity	RAge mat.
RAge at maturity	−0.461	
RMortality	0.426	−0.417

Determinant of correlation matrix = 0.595
Factor matrix (component correlations):

	1	2	3
RFecundity	0.800	−0.253	0.544
RAge at maturity	−0.795	0.359	0.489
RMortality	0.773	0.631	−0.060
Eigenvalue	1.87	0.59	−0.54
% of variance	62.3	19.7	17.9
Cumulative %	62.3	82.1	100.0

46 Contrasts for Scleroglossa
Correlation matrix:

	RClutch size	RBrood freq.	RAge mat.
RBrood frequency	−0.277		
RAge at maturity	−0.110	−0.535	
RMortality	0.364	0.336	−0.655

Determinant of correlation matrix = 0.280
Factor matrix (component correlations):

	1	2	3	4
RClutch size	0.212	0.915	0.327	−0.105
RBrood frequency	0.678	−0.602	0.418	0.066
RAge at maturity	−0.902	0.058	0.208	0.374
RMortality	0.855	0.311	−0.193	0.368
Eigenvalue	2.05	1.30	0.36	0.29
% of variance	51.2	32.5	9.0	7.3
Cumulative %	51.2	83.7	92.7	100.0

Table 3. (continued)

Correlation matrix:

	RFecundity	RAge mat.
RAge at maturity	−0.583	
RMortality	0.562	−0.655

Determinant of correlation matrix = 0.344
Factor matrix (component correlations):

	1	2	3
RFecundity	0.829	0.556	0.055
RAge at maturity	−0.875	0.213	0.436
RMortality	0.865	−0.318	0.388
Eigenvalue	2.20	0.46	0.34
% of variance	73.4	15.2	11.4
Cumulative %	73.4	88.6	100.0

RMA slopes ($\pm$95% confidence interval):

Age at Maturity on Mortality $= -1.12 \pm 0.213$, $r = -0.219$

Fecundity on Mortality $= 1.56 \pm 0.289$, $r = 0.295$

Age at Maturity on Fecundity $= -0.72 \pm 0.153$, $r = -0.347$.

Discussion

Role of body size

The strong relationship between body size and the slow-fast continuum of life history variation was pointed out very early (MacArthur and Wilson, 1967; Pianka, 1970). The strength of this correlation led some researchers to suggest that body size at maturity, with which most of the primary demographic parameters were found to correlate, could have been the primary or even sole target of natural selection (Western and Ssemakula, 1982). Indeed, a majority of studies (Stearns, 1983, 1984; Harvey et al., 1991) found that body size alone explained a large part of the variation in life history components and that the three primary demographic parameters (age at maturity, adult survival, fecundity) were allometrically related to body mass with a slope of about 0.25 in many taxa (Peters, 1983; Calder, 1984; Allainé et al., 1987; Gaillard et al., 1989; Reiss, 1989). However, a number of these comparisons involved a very wide range of body size (and a corresponding diversity in terms of phylogenetic relationships, e.g., all Mammalia) and so the role of size may have been overemphasized. Indeed, when comparing families within birds and within mammals, Allainé et al. (1987) found (although not using phylogenetically

based statistical methods) that slopes of the relationships between primary demographic parameters and body size were sometimes significantly different from 0.25 (see also Dunham et al., 1988a), and that some families differed from one another in slopes. Allainé et al. (1987) interpreted their results as indicating that parameters for some families were poorly estimated, or that some specific methods of estimation that may induce biases in the estimates were used more often in some families than in others (Lebreton et al., 1987; Krementz et al., 1989); therefore, they did not reconsider the role of body size.

Our PCA analyses (Tab. 2) indicated that body size was more strongly correlated to the slow-fast continuum in one clade (Iguania) than in the other (Scleroglossa). Allometric relationships between size and the three primary demographic parameters showed significant differences between the two clades (Tab. 1), as was suggested in a previous study (Promislow et al., 1992). Fecundity was positively associated with size in Iguania but negatively associated (although not significantly so) in Scleroglossa. One of the main differences between the two clades involves foraging mode (Dunham et al., 1989a; Cooper, 1994). Iguania is dominated by species with a sit-and-wait strategy, or which are large herbivores, whereas Scleroglossa is dominated by widely-foraging species. This difference may have entailed different evolutionary pathways for fecundity and size, as life history traits seem to vary in relation to foraging mode (Dunham et al., 1988a).

The differences in allometric relationships could also be attributable to sampling problems, but we think this is unlikely to be the sole explanation. The sampling of Scleroglossa in our data set may seem relatively incomplete with respect to body size, because of the absence of Varanidae, many of which are relatively large-bodied (Green and King, 1993; Pianka, 1995; Christian and Garland, 1996). However, our samples of Iguania and Scleroglossa did not differ significantly with respect to mean body size, using a test with independent contrasts as described in Garland et al. (1993, pp. 277–278, 283; the basal contrast for log snout-vent length is only the 18th most extreme of 89 total contrasts). Moreover, after controlling for snout-vent length, the two clades did not differ significantly in mean values for any other variable (see Results). The proportion of species with a small and invariant clutch size (*Anolis* in Iguania, some geckos in Scleroglossa) was also similar between clades for our samples. Finally, an analysis with these species removed yielded very similar results. Thus, we believe that the observed difference in the allometric slope of clutch size and fecundity is unlikely to result solely from sampling inadequacies. In any case, the addition of large varanids to the data set would be an obvious improvement for future studies.

Differences in allometry between clades cause differences in the way the three demographic parameters scale to one another. The relationship between fecundity and survival, and between fecundity and age at maturity, was significantly different between clades, indicating that the ratio of these variables is not constant throughout lizards. This finding contradicts what Shine and Charnov (1992) found on a restricted sample of lizard ($N = 19$) plus snake ($N = 16$) species. If our analyses were stopped at this stage, they would be in opposition with Charnov's (1993) predictions. It is worth nothing that, in most of the tests of Charnov's model predictions on life history trade-offs, the demographic parameters were not corrected for size

(Charnov, 1990; Charnov and Berrigan, 1990; Charnov and Berrigan, 1991a; Shine and Charnov, 1992; Charnov, 1993). One may, therefore, wonder how much and in which direction the intensity of correlations is modified after statistically subtracting the effect of body size.

The slow-fast continuum

After removing correlations with body size by computing residuals from allometric regressions (using independent contrasts), the first axis of a principal components analysis explained most (62–73%) of the remaining variation, in a similar way for both clades (Tab. 3). The three demographic parameters load in almost an equal way on this first axis for the two clades. So, after removing correlations with body size, adult mortality was correlated negatively with age at maturity and positively with fecundity, clearly indicating the "slow-fast" continuum. This result agrees with other studies done on sub-components of these life history traits (Stearns, 1984; Dunham et al., 1988a; Shine and Charnov, 1992 for lizards) and/or which did not use phylogenetically based statistical methods (Stearns, 1984; Gaillard et al., 1989 for birds and mammals). However, it contradicts the results of the only similar analysis which was done on a single family of lizards (Lacertidae, Bauwens and Diaz-Uriarte, 1997). These authors used as a measure of survival the maximum lifespan which is critically dependent on sample size. They also used several measures of size, even in their residual analysis. Finally, they used a single family that is clearly more morphologically and ecologically homogeneous than our sample of 47 Scleroglossa.

The slopes of the relationships between the three basic demographic parameters when taken two-by-two are all significantly different from zero (see end of Results). The second two relations differ significantly from unity, whereas the first one probably does not. The two major clades did not differ significantly with respect to these relationships. Although the signs of the relationships agreed with the predicted ones (Charnov, 1991; Charnov and Berrigan, 1991a), comparing the values of the slopes was difficult for two reasons. First, in previous studies, the effect of size was not removed so it is not possible to compare directly with our values. Second, quantitative predictions are not available for several combinations of demographic parameters (Charnov and Berrigan, 1991a). Even when quantitative predictions exists, it is not clear to which value our results should be compared. For example, the relation between age at maturity and mortality for lizards was predicted and tested with respect to unity in Shine and Charnov (1992), but was expected to be different from unity (around 0.7) in Charnov and Berrigan (1991a). Some reconciliation of these discrepancies may emerge from searching for the existence of other life history patterns in addition to the slow-fast continuum.

Other patterns of variation and covariation

Even corrected for body size, mortality showed a different average rate of evolution in the two clades, whereas the rate of evolution of age at maturity and fecundity did not differ statistically (see first section of Results). This result may

suggest that indeed the primary association between the three demographic parameters (the slow-fast continuum) does not explain all of the variation in the life history variables, despite the fact that the PCA did not give any convincing indication of a second direction of variation in the data (Tab. 3). Indeed, if the ratio between age at maturity and adult mortality, or the ratio between fecundity and adult mortality, are to be constant values (Charnov, 1990, 1993), then it follows that residuals of these relations should not show any pattern, i.e., that the residuals must represent random noise related to imprecisions in parameters estimates and/or peculiarities of the studied populations. In particular, no significant association should be found between residuals of the two relationships. However, residuals from the regression of age at maturity on mortality were in fact significantly related to residuals of the regression of fecundity on mortality (RMA slope = -0.72 ± 0.144; see last section of Results).

Biological interpretation of the foregoing correlation depends on the assumption that no sampling correlation exists between the estimation of fecundity and age at maturity. In lizards, age at maturity is usually estimated by looking for the appearance of any secondary sexual characters or by dissecting individuals to assess the maturity of the gonads (without necessarily involving egg formation, Dunham et al., 1988b). Most of the estimates of clutch size that we have used are tertiary (Dunham et al., 1988b), i.e., based on the number of eggs layed, most of the time from clutches found in the field, i.e., without knowing the female. The number of broods was most often deduced from the number of peaks in the number of clutches that are layed within a year. So, although we cannot dismiss the possibility of a sampling correlation (as for any other correlations between the three demographic parameters), this one is likely to be small, as it usually does not involve the same individuals or even the same populations. Therefore, the scatter observed around the relation between, for example, age at maturity and mortality, can be explained at least partly by variation in fecundity, which means that this cannot be attributed entirely to random "noise" in the data.

As noted by Charnov (1993, p. 5), "How constant is constant enough to be considered invariant is worthy of much thought . . . " We believe that our analyses indicate that various ratios are actually not constant enough to be considered invariant across all lizard species. Most probably, therefore, other patterns of variation besides the slow-fast continuum exist in lizards and in other groups of vertebrates as well. This suggestion is not at all revolutionary when one remembers the variation of lifestyle in semelparous species, such as salmon or dragonflies (i.e., much variation in age at maturity but no variation in the mortality of adult reproductive females). This suggestion is also consistent with the findings of Gaillard et al. (1989) for mammals and birds.

If other patterns of life history variation do indeed exist, then one of the assumptions of Charnov (1993)'s model – that a stationary population is a general characteristics of all species – may not hold. Deviation from a stationary population may be particularly common for annual species, such as some *Anolis* or *Mabuya*, which are good candidates for displaying cyclic or chaotic population dynamics (Ferrière and Clobert, 1992, potential examples in Barbault, 1974b, and

Andrews, 1991). It also may mean that life history invariants have to be found at lower taxonomic levels (Bauwens and Diaz-Uriarte, 1997), where no significant variation in body organization is expected to be found (strict allometry prevails, Calder, 1984), or that life history invariants have to be derived from more complex adaptive programmes of development (Vollestad et al., 1993; Mangel, 1996).

The difficulty of finding a third-order axis of variation in life histories (first-order being the effect of body size [relatively weak in our analyses], second-order being the slow-fast continuum; see Western, 1979; Gaillard et al., 1989) is probably related to the small proportion of the total variation among species that this source may represent (Schoener, 1985). A small contribution to the total amount of variation may be explained by the rareness of semelparous lizards (like *Mabuya butnerii*, for example) which display delayed age at maturity. At present, claiming the existence of this third-order source of variation seems premature. Also, comparison with the results of Gaillard et al. (1989) is a bit difficult because we did not use the same statistical approach. In particular, inferring explanations or processes based on the second axis of the PCA is problematic, because, in this statistical framework, alternative "strategies" must be orthogonal to the slow-fast continuum. For example, if a PCA was done on the points which represent evolutionary stable strategies uncovered by Ferrière and Clobert's (1992, their figure 2) model, then the second axis of the PCA, although also opposing semelparous to iteroparous species (in relative terms), would suggest quite a different evolutionary pathway than the one reported in the present paper.

Furthermore, we only considered the three primary demographic parameters, and excluded those which were sub-components of one of these parameters (i.e., clutch size and number of broods as the components of fecundity) or for which virtually no data were available (juvenile survival). Including these variables might reveal additional patterns (Dunham et al., 1988a; Bauwens and Diaz-Uriarte, 1997). However, we presently lack a general theory of life history evolution which embodies all of these variables. Thus, both the acquisition of more data and additional modeling are still badly needed in order to allow deeper insight regarding the correlated evolution of life history traits in lizards.

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Appendix I: Life history data

S = mean proportion surviving per year
SVLA (mm) = mean snout-vent length of adults (females)
SVLM (mm) = mean snout-vent length at maturity (females) – not used
AGEMAT (months) = mean age at sexual maturity
CS = mean clutch size (number of offspring per clutch)
BF = mean brood frequency (# /year)
+ is species which were removed for a complementary analysis

Genus and species	S	SVLA	SVLM	AGEMAT	CS	BF	Reference
Polychrus acutirostris	0.61	125	96	9	17.9	1	16, 121
Anolis acutus+	0.37	42	36	12	1	6	89, 90
Anolis cupreus+	0.01	39	35	4	1	18	6, 47, 51
Anolis intermedius+	0.01	47	38	4	1	11	6, 47
Anolis limifrons+	0.01	44	39	4	1	18	5, 6, 7, 47
Anolis roquet+	0.12	52.3	46	10.6	1	23.6	71
Anolis tropidolepis+	0.04	52	42	9	1	12	4, 6, 47
Dipsosaurus dorsalis	0.66	120	110	32	5.5	1	79
Amblyrhynchus cristatus	0.85	279	252	41	2.5	1	69, 70
Conolophus subcristatus	0.90	416	−9	84	13.5	1	123, 124
Ctenosaura similis	0.78	275	191	22	43.4	1	16, 50, 116
Sauromalus obesus	0.80	148	137.5	48	7.35	1	1, 19
Cyclura carinata	0.90	225	190	72	4.3	1	65
Cyclura pinguis	0.90	468	375	96	14	1	28, 36
Cyclura stejnegeri	0.90	475	375	72	12	1	36, 126
Gambelia wislizenii	0.51	107	88.6	21.5	5.9	1	75, 85, 99, 113
Crotaphytus collaris	0.48	96	92	10	7.55	2	46, 110
Uta stansburiana	0.25	44.7	38.5	9.2	3.62	3	84, 102, 109, 114
Urosaurus ornatus	0.32	49	41.2	10.2	7.5	2	11, 39
Scleoporus variabilis	0.01	63	44	4	3	5	16, 48
Sceloporus merriami	0.32	50	44	11	4.5	2	37, 38
Sceloporus graciosus	0.53	57.8	51	25	5	1.33	25, 91, 94, 95, 104
Sceloporus clarki	0.50	101	90	22	19.1	1	107
Sceloporus grammicus	0.30	55	40	5	6.17	1	80, *
Sceloporus jarrovi	0.36	68	53	5	6.3	1	9, 10, 46, 88, 108
Sceloporus poinsetti	0.53	104	86	17	10.4	1	8, 9
Sceloporus scalaris	0.25	54	40.5	7	8.65	1.2	12, 80, *
Sceloporus magister	0.51	92	80.5	22	6.6	1.5	82, 105, 122, 125
Sceloporus occidentalis	0.70	84	70	22	11.2	1	53, 91
Sceloporus undulatus	0.27	63.7	55	14	8.5	2.7	41, 42, 67, 103, 106, 120
Sceloporus virgatus	0.50	57	47	10	9.5	1	109, 119
Sceloporus olivaceus	0.16	96	80	10	16.5	3	20
Cophosaurus texanus	0.25	58	45	10	4.25	3	63, 41, 78
Holbrookia maculata	0.29	55	49.7	10.3	5.21	2.5	52, 67
Holbrookia propinqua	0.08	50	44	10	3.1	3	68
Phrynosoma platyrhinos	0.50	77	72	22	6.7	2	15, 76
Basiliscus basiliscus	0.40	160	135	20	10	6	115
Ctenophorus ornatus	0.50	75	69	9	3.75	2	21
Ctenophorus fordi	0.13	55.9	48	9	2.2	3	33
Japalura swinhornis	0.17	70	54	12	4.27	2	72, 73
Draco volans	0.20	85	76	7	7	1	2, 110
Chameleo pumilis	0.65	75	50	5	11	4	26
Uromastix acanthinurus	0.65	215	195	48	13	1	54, **
Coleonyx variegatus+	0.06	62	52	10	2	3	81, 83
Diplodactylus damaeus+	0.33	57	51	5.7	2	2	58, 61
Diplodactylus tessellatus+	0.18	58	52	7.5	2	2	58, 61
Oedura ocellata+	0.88	80	−9	25	2	2	27

(continued)

Genus and species	S	SVLA	SVLM	AGEMAT	CS	BF	Reference
Oedura reticulata+	0.82	64.4	60.9	56	2	1	62
Gonatodes aldogularis+	0.01	42	35	5	2	12	16, 48, 49
Gehyra variegata+	0.76	53.7	48.9	28.7	1	2	58, 60
Heteronotia binoei+	0.28	52	48	9	2	2	58, 60
Lygodactylus conraui+	0.01	32	28	4	2	12	16
Eumeces fasciatus	0.45	72	64	22	9.1	1	43
Eumeces obsoletus	0.50	120	105	32	11.5	1	44, 55
Eumeces okadae	0.73	79	72	24	7.6	0.5	56
Dasia smaragdina	0.50	93	82	11	2.2	1	2
Panapsis kitsoni	0.10	46	42	6	1.9	8	16,*
Panapsis nimbaensis	0.10	45	41	6	2.5	5	13
Lerista punctatovittata+	0.96	90.5	84	24	1	2.7	58
Lerista xanthura+	0.82	46	50	12	1	2	58
Eremiascincus richardsoni+	0.87	94.6	75	24	1	4	58
Mabuya affinis	0.10	64	56	6	2.7	8	16,*
Mabuya buettneri	0.01	83	76	7	8.4	1.6	14
Mabuya fasciata	0.50	121	112	9	7	1	2
Mabuya maculilabris	0.10	65	58	6	5.5	5.53	13,*
Mabuya varia	0.10	64	50	8	9.1	1	66
Tiliqua rugosus	0.80	230	−9	36	2.2	1	23, 58
Morethia boulengeri	0.16	51	44	6.5	2.7	3	58, 59
Emoia atrocostata	0.30	90	80	9	2	3	3, 58, 90
Scincella lateralis	0.41	45	35	9	2.5	2	22
Takydromus tachydromoides	0.36	49	43	10	3.6	2.5	64, 98, 100
Lacerta vivipara	0.52	56.6	44.2	26.8	6	1	18, 74, 97
Acanthodactylus dumerili	0.01	47	40	7	1.5	5	30
Acanthodactylus pardalis	0.41	56	53	22	2.5	1	77, ***
Eremias olivieri	0.24	37	33	8	1.9	2	77
Ichnotropis capensis	0.01	55	48	7	6	2	66
Lacerta lepida	0.83	165.6	150	30	11.2	1	86, 118
Lacerta viridis	0.60	92.2	86.1	27	5.14	1.19	92
Lacerta agilis	0.57	68.4	62	33	6.2	1	97, 117
Podarcis bocagei	0.75	57.4	50	19	2.01	2	118
Podarcis muralis	0.26	63.5	54	22	5.75	2.5	17
Podarcis sicula	0.19	64.7	50	10	5	3	57
Podarcis taurica	0.80	58	54	22	4.8	1	29, 34, 35
Cnemidophorus tigris	0.52	82.3	71.5	18	3.06	3	93, 109, 112
Cnemidophorus inornatus	0.20	57	50	10	2.9	3	32, 96
Cnemidophorus sexlineatus	0.41	73	55	10	2.1	2	31, 45
Cnemidophorus scalaris	0.37	77	61	10	3.32	3	12, *
Cnemidophorus deppei	0.01	70	59	5	2.8	6	16, 48, 49
Gymnophthalmus speciosus	0.01	42	37	7	1.9	3	101
Xantusia vigilis	0.80	44	39	33	1.9	1	127

* Barbault, pers. data; ** Grenot, pers. data; *** Nouira, pers. data.
(1) Abts, 1987. (2) Alcala, 1966. (3) Alcala and Howard, 1967. (4) Andrews, 1976. (5) Andrews, 1979a. (6) Andrews, 1979b. (7) Andrews and Nichols, 1990. (8) Ballinger, 1971. (9) Ballinger, 1973. (10) Ballinger, 1979. (11) Ballinger, 1984. (12) Ballinger and Congdon, 1981. (13) Barbault, 1974a. (14) Barbault, 1974b. (15) Barbault, 1976. (16) Barbault, 1987. (17) Barbault and Mou, 1988. (18) Bauwens,

Heulin and Pilorge, 1987. (19) Berry, 1974. (20) Blair, 1960. (21) Bradshaw, 1971. (22) Brooks, 1967. (23) Bull, 1987. (24) Burghardt and Rand, 1982. (25) Burkholder and Tanner, 1974. (26) Burrage, 1973. (27) Bustard, 1971. (28) Carey, 1975. (29) Chondropoulos and Lykakis, 1983. (20) Cissé and Karns, 1977. (31) Clark, 1976. (32) Christiansen, 1971. (33) Cogger, 1969. (34) Cruce, 1977. (35) Cruce and Leonte, 1973. (36) Dugan and Wiewandt, 1982. (37) Dunham, 1980. (38) Dunham, 1981. (39) Dunham, 1982. (40) Dunham, Miles and Reznick, 1988a. (41) Ferguson and Bohlen, 1978. (42) Ferguson, Bohlen and Wooley, 1980. (43) Fitch, 1954. (44) Fitch, 1955. (45) Fitch, 1958. (46) Fitch, 1970. (47) Fitch, 1973a. (48) Fitch, 1973b. (49) Fitch, 1982. (50) Fitch and Henderson, 1978. (51) Fleming and Hooker, 1975. (52) Gennaro, 1974. (53) Goldberg, 1974. (54) Grenot, 1976. (55) Hall, 1971. (56) Hasegawa, 1984. (57) Henlé, 1988a. (58) Henlé, 1988b. (59) Henlé, 1989. (60) Henlé, 1990a. (61) Henlé, 1990b. (62) How and Kitchener, 1983. (63) Howland, 1992. (64) Ishihara, 1971. (65) Iverson, 1979. (66) Jacobsen, 1982. (67) Jones and Ballinger, 1987. (68) Judd, 1976. (69) Laurie, 1990. (70) Laurie and Brown, 1990. (71) Leclair, 1980. (72) Lin and Cheng, 1986. (73) Lin and Lu, 1982. (74) Massot, Clobert, Pilorge, Lecomte and Barbault, 1992. (75) McCoy, 1967. (76) Medica, Turner and Smith, 1973. (77) Nouira, 1982. (78) Nouira, Maury, Castanet and Barbault, 1982. (79) Krekorian, 1984. (80) Ortega, 1986. (81) Parker, 1972. (82) Parker and Pianka, 1973. (83) Parker and Pianka, 1974. (84) Parker and Pianka, 1975. (85) Parker and Pianka, 1976. (86) Paulo, 1988. (87) Rhodin and Miyata, 1983. (88) Ruby and Dunham, 1984. (89) Ruibal and Philibosian, 1974. (90) Ruibal, Philibosian and Adkins, 1972. (91) Ruth, 1977. (92) Saint Girons, Castanet, Bradshaw and Baron, 1989. (93) Shine and Schwarzkopf, 1992. (94) Stebbins, 1948. (95) Stebbins and Robinson, 1946. (96) Stevens, 1983. (97) Strijbosch and Creemers, 1988. (98) Takenaka, 1981. (99) Tanner and Krogh, 1974. (100) Telford, 1969. (101) Telford, 1971. (102) Tinkle, 1967. (103) Tinkle, 1972. (104) Tinkle, 1973. (105) Tinkle, 1976. (106) Tinkle and Ballinger, 1972. (107) Tinkle and Dunham, 1986. (108) Tinkle and Hadley, 1973. (109) Tinkle and Hadley, 1975. (110) Turner, 1977. (111) Turner, Hoddenbach, Medica and Lannom, 1970. (112) Turner, Medica, Lannom and Hoddenbach, 1969a. (113) Turner, Medica, Lannom and Hoddenbach, 1969b. (114) Turner, Medica and Smith, 1974. (115) Van Devender, 1982a. (116) Van Devender, 1982b. (117) Van Nuland and Strijbosch, 1981. (118) Vicente, 1989. (119) Vinegar, 1975a. (120) Vinegar, 1975b. (121) Vitt and Lacher, 1981. (122) Vitt and Ohmart, 1974. (123) Werner, 1982. (124) Werner, 1983. (125) Whitford and Creuserie, 1977. (126) Wiewandt, 1977. (127) Zweifel and Lowe, 1966.
Note. Some general information about size and reproduction was also taken from the following general references: Fitch, 1970, 1973b; Burghardt and Rand, 1982; Rhodin and Miyat, 1983; Barbault, 1987; Dunham et al., 1988.

Appendix II: Phylogenetic information

Information on phylogenetic relationships (see Fig. 1) was compiled from a variety of sources. Estimates of divergence times are available for some lizard groups (e.g., see Estes' (1983a, b), but are not complete. Therefore, as explained in the Methods, we used arbitrary branch lengths for computation of phylogenetically independent contrasts. Branch lengths in the figure are also arbitrary, and correspond with those suggested by Pagel (1992; see Methods). Higher-order taxonomic names are based on Estes et al. (1988), Frost and Etheridge (1989), and Zug (1993).

The topology for the families studied herein is based on Estes et al. (1988; see also Estes, 1983a). The tree depicted in their figure 6 includes all of the extant lizard families, plus the Amphisbaenidae and Serpentes, and represents the authors' ''conservative evaluation of relationships among squamates''.

The earliest split among the lizard families occurred during the early Jurassic (178–208 million years ago) between the infraorders Iguania (Chamaeleonidae, Opluridae, Tropiduridae, Hoplocercidae, Polychrotidae [Polychridae], Iguanidae,
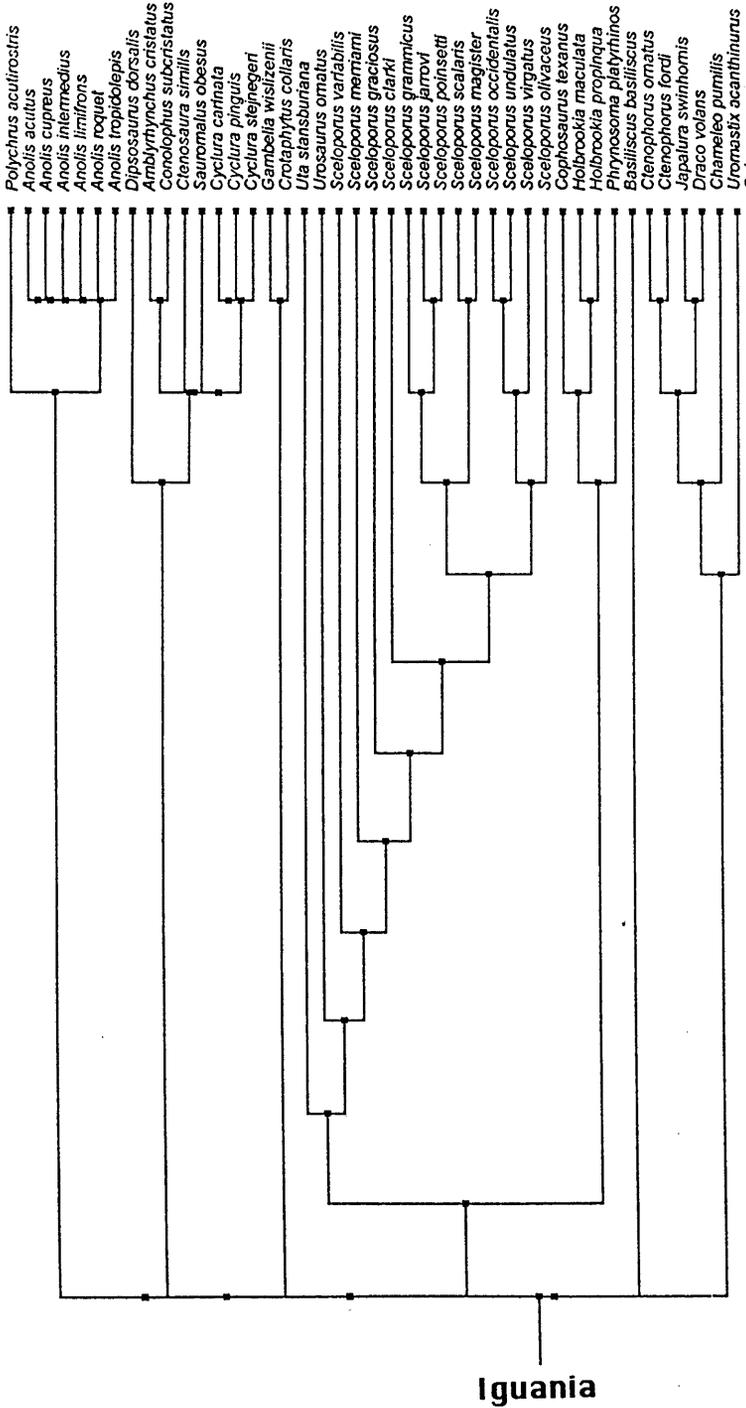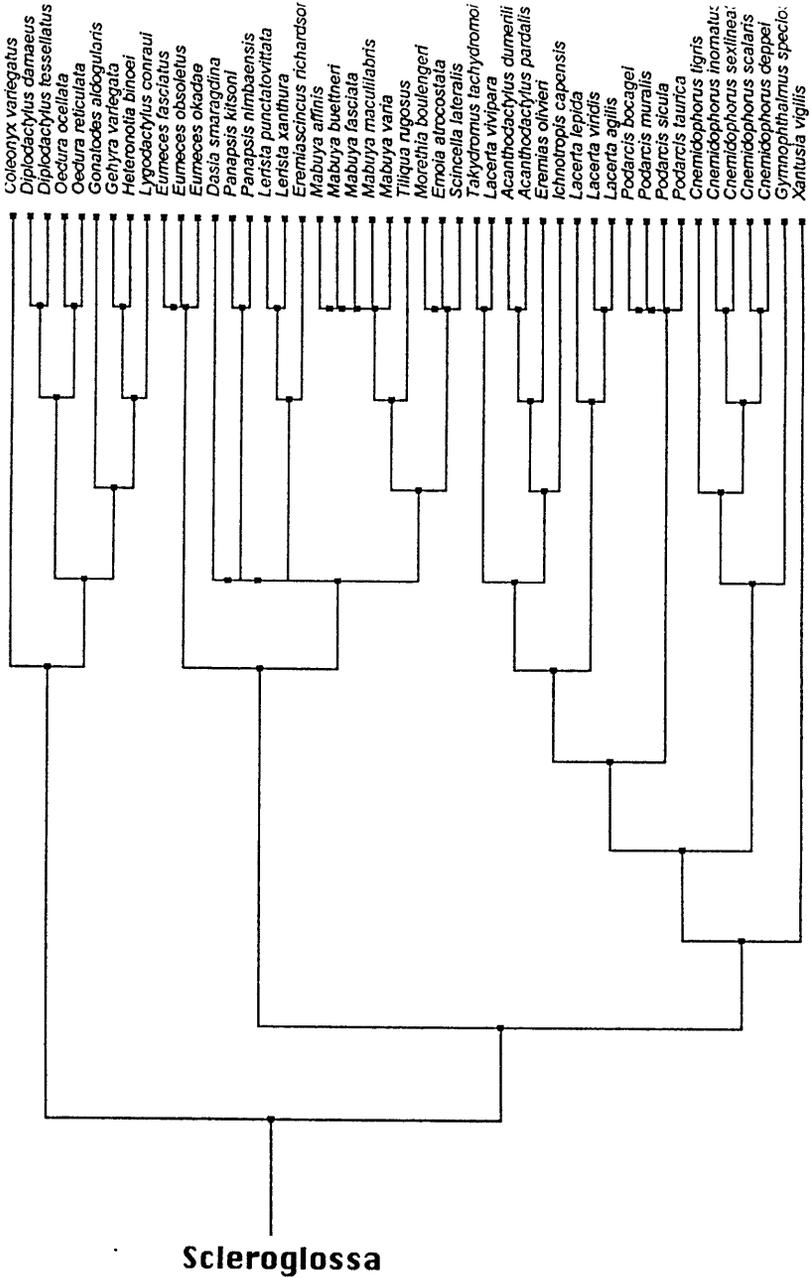
Iguania

Fig. 1.

Fig. 1.

Crotaphytidae, Phrynosomatidae, Corytophanidae) (upper main branch Fig. 1) and Scleroglossa (all other lizards: Estes et al., 1988; Frost and Etheridge, 1989). Following Frost and Etheridge (1989), we have represented the relationships among iguanian families as a polytomy (Polychrotidae, Iguanidae, Crotaphytidae, Phryno-somatidae, Corytophanidae, and Chamaeleonidae in our data set). Within the Scleroglossa (bottom of tree shown in figure), the major divergence is between the Gekkota (including Eublepharinae [represented here only by *Coleonyx variegatus*] and Gekkonidae; see Kluge, 1987) and the Autarchoglossa (including Scincidae, Lacertidae, Teiidae, Gymophthalmidae, Xanthusidae, Anguidae, Varanidae and Helodermatidae).

Within the Iguanidae, Etheridge and de Queiroz (1988, Fig. 13) represent *Amblyrhynchus-Sauromalus-Cyclura* as an unresolved polytomy; they also suggest that *Conolophus* is the sister group of *Amblyrhynchus*.

The topology for Phrynosomatidae is derived from Wiens and Reeder (1995) and Reeder and Wiens (1996), who include all of the species studied herein.

The new family Chamaeleonidae, defined by Frost and Etheridge (1989), gathers together the usual "Agamidae" and "Chamaeleonidae" because their analysis indicated little evidence that these two families are monophyletic. We have used the topology 1 of Fig. 10 in their paper, in which *Uromastix* is the outgroup of chameleons and agamas. The relationships between the species *Japalura swinhornis*, *Draco volans*, and the genus *Ctenophorus* (formerly *Amphibolurus*) are taken from Moody (1980).

The Gekkota (including Gekkonidae and Eublepharidae) topology is based on Kluge (1987). We had no information concerning the relationships between *Gehyra*, *Heteronotia*, and *Lygodactylus*, but as *Lygodactylus* is an African genus and the other two are from Australia, we made the assumption that *Gehyra* and *Heteronotia* were sister groups.

The Australian scincid topology was derived from Baverstock and Donnellan (1990), supplemented by information presented in Greer (1989). We had no information on the phylogenetic position of the genus *Dasia*, and so placed it at the root of the subfamily Lygosominae (which includes all Australian skinks, repre-sented in our data set by the genera *Lerista*, *Fremiascincus*, *Mabuya*, *Tiliqua*, *Morethia*, and *Emoia*), creating a polytomy, because the only information we had was its distribution in New Guinea and the fact that most skinks from that part of the world are in the Lygosominae (Greer, 1989).

All relationships for the lacertid species studied herein are from Arnold (1989, fig. 23).

Within the Teiidae, the topology for *Cnemidophorus* was taken from Dessauer and Cole (1989), particularly their Figure 14.

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