COVARIATION OF LIFE-HISTORY TRAITS IN LACERTID LIZARDS: A COMPARATIVE STUDY

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Abstract.—We analyzed patterns of life-history covariation within a clade of lacertid lizards, using the method of phylogenetically independent contrasts. Examination of allometric relations and correlations among life-history traits showed that species within this clade can be arranged along a single, multivariate axis. At one end of this continuum are small-sized species that mature early, have small clutches of relatively large young, may have multiple broods per year, and have short adult lives. At the other extreme are the larger lacertids with the opposite suite of traits. Much of this pattern can be deduced from two relations: the increase of adult life span with adult body size and the negative allometry of offspring size. After the effects of body size were statistically removed, residuals of adult life span and age at sexual maturity were positively correlated, whereas residuals of the number and size of offspring were negatively correlated. The detection of these size-free relations supports an interpretation of coadaptive adjustments among life-history variables. The pattern of life-history covariation in lacertid lizards differs fundamentally from the "fast-slow" continuum. This gradient reflects a negative association between adult life span and fecundity, whereas both variables are positively correlated among species of lacertid lizards.

If populations are to persist over time, natality must balance mortality. Such a balance can be achieved in various ways. For example, species that experience high mortality as adults could compensate either by starting to reproduce early, by increasing the number of offspring, or by increasing the size of each offspring (which typically reduces juvenile mortality). Comparative studies indicate that organisms subject to high adult mortality exhibit high values not for single characteristics but rather for suites of traits that promote increased reproductive output. The presence of such patterns of covariation among life-history traits has led to the description of the "fast-slow" (Stearns 1983) or "*r-K*" gradient (Pianka 1970). Species at the "fast" end are small, short-lived, early maturing, and produce many small young, whereas species with the opposite suite of traits are positioned at the "slow" end (Stearns 1983; Sæther 1988; Gaillard et al. 1989; Harvey et al. 1989; Promislow and Harvey 1990; Blackburn 1991). Patterns of covariation are considered as representing coadaptations of reproductive traits to each other and to mortality rates (Read and Harvey 1989; Promislow and Harvey 1990).

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Stearns (1980, 1983, 1984) questioned to what extent the pattern was induced by differences in body size, taxonomic diversity, or both rather than being the outcome of coadaptational processes. Variation in most, if not all, life-history traits is often tightly related to variation in body size (e.g., Blueweiss et al. 1978; Calder 1984). It is therefore not surprising that correlations among life-history variables are often substantially reduced after statistical removal of the effect of body size (Stearns 1983; Dunham and Miles 1985; Dunham et al. 1988). Nevertheless, patterns of covariation analogous to the fast-slow gradient persist when the effects of body size are removed (Stearns 1983; Sæther 1988; Gaillard et al. 1989; Read and Harvey 1989; Promislow and Harvey 1990), which supports a coadaptational interpretation. However, these studies compare higher taxonomic levels (i.e., they use mean values for families or orders as data points), and it is unclear whether the observed pattern is indicative for correlated evolution that is induced by microevolutionary processes (Harvey and Pagel 1991; Stearns 1992). The observed relations among life-history traits may instead reflect, at least in part, major differences among taxonomic groups in morphology, physiology, and lifestyle. This interpretation is supported by the observation that patterns of life-history covariation vary from family to family in mammals and lizards (Stearns 1983; Dunham and Miles 1985; Dunham et al. 1988).

Moreover, theories of life-history evolution are explicitly microevolutionary (Roff 1992; Stearns 1992), whereas patterns of life-history covariation are most evident when comparisons are made among higher taxonomic levels. The link between these broad macroevolutionary patterns and the mechanistic models of life-history evolution is remote. Studies that compare lower taxonomic units (i.e., populations or species) within small, monophyletic groups could help bridge this gap (Emerson and Arnold 1989), by exploring the existence of subtle patterns and by documenting the phenotypic manifestation of trade-off functions. Such analyses have rarely been undertaken, so that the question, Does covariation among life-history traits exist at the species level? (Stearns 1983) has remained largely unanswered.

Here we examine patterns of covariation among life-history traits within a group of species from the lizard family Lacertidae. Our study differs from prior investigations of life-history covariation in several important aspects. First, we compare closely related species and employ phylogenetically based statistical analyses. Thus, we use character differences between closely related species, not mean values for higher-level taxa, as independent evolutionary events. Second, the species studied form a relatively homogeneous group with respect to many aspects of their general biology. Most lacertid lizards treated here are highly similar in body shape, active-searching foraging mode, arthropod-based diet, diurnal activity patterns, and thermoregulatory behavior (Arnold 1987; Bauwens et al. 1995). This point is important, because body shape and foraging mode affect the life-history variation of lizards (Dunham et al. 1988). Thus, our choice of species should reduce the risk that patterns of covariation are masked, confounded, or induced by differences in morphological and ecological traits that were not included in the analyses (Huey and Bennett 1986; Losos 1990; Harvey and Pagel 1991).

Our study has three main objectives. First, we document, using phylogenetically based statistical procedures, the scaling of reproductive traits with body size and explore patterns of covariation among reproductive traits and an index of adult survival rate. Specifically, our phenomenological approach aims at identifying the key relations that govern most of the pattern. This allows the formulation of mechanistic hypotheses for the evolution of the observed character relationships. Second, we examine covariation of life-history characteristics when the effect of adult body size is removed statistically. These analyses should allow the identification of evolutionary correlations and trade-offs that exist independently of body size. Third, we compare the relations observed in lacertid lizards with those in other groups of vertebrates. We demonstrate that the lacertid pattern differs fundamentally from the fast-slow gradient.

MATERIAL AND METHODS

Species and Data

The lizard family Lacertidae comprises over 230 species, presently assigned to about 30 genera, that are distributed over Europe, Africa, and large parts of Asia (Arnold 1973, 1989). Our analyses are restricted to 16 species or subspecies, representing eight monophyletic species groups. Most species treated here inhabit the Palearctic and Mediterranean regions of Europe; information on the biology of African and Asian lacertids is absent or fragmentary. Thus, we study here a taxonomically and geographically biased subsample of the whole family. Our results therefore only apply to the clade of species studied, and at present we cannot judge whether they are representative for the Lacertidae as a whole.

Our analyses are largely based on recently published or original data for Old World temperate lizards, a group of species that was poorly represented in previous studies (Tinkle et al. 1970; Dunham and Miles 1985; Dunham et al. 1988; Shine and Charnov 1992). We extracted data from the literature and collected supplementary information for some populations. We only retained information pertaining to single populations or to a restricted geographical area in which no life-history differences among populations could be detected. Life-history differences may reflect, at least in part, proximal responses to variation in environmental factors such as temperature and food availability (Ballinger 1983; Adolph and Porter 1993). We explicitly assume that the among-species variation studied here reflects mainly genetic differences, not environmentally induced plasticity. As virtually nothing is known about the genetic basis of lizard life-history traits, we cannot directly test this assumption.

Sixteen species or subspecies and a total of 18 populations were included in the analyses (table 1). We only incorporated populations or species for which we obtained data on at least the following six traits: mean adult female length, female length at maturity, age at maturity, hatchling size, mean clutch size, and clutch frequency. Data for additional traits (egg mass, adult life span) were retained when available. The oviparous and live-bearing forms of *Lacerta vivipara* were considered separately because of the difference in the mode of reproduction (note

TABLE 1

MEAN VALUES FOR LIFE-HISTORY VARIABLES IN POPULATIONS OF LACERTID LIZARDS

Species	Mean Length (mm)	Length Maturity (mm)	Maximum Length (mm)	Age at Maturity (mo)	Adult Life Span (mo)	Clutch Size	Clutch Frequency	Egg Mass (g)	Hatchling Length (mm)	Hatchling Mass (g)	Locality
Psammodromus algirus	69.2	58	82	13	...	6.0	1.5	.441	27.8	.572	Salamanca (Spain)
Psammodromus hispanicus	48.4	42	56	5	11	3.2	2.0	.256	22.9	.310	Salamanca (Spain)
Lacerta lepida	168.4	132	190	19	59	16.9	1.0	...	42.8	2.235*	Ciudad Real, Cáceres (Spain)
Lacerta monticola cantabrica	66.1	56	72	11	...	7.2	1.5	.330	25.0	.441	Asturias, La Coruña (Spain)
Lacerta monticola cyreni	70.1	60	81	10	...	5.4	1.0	.450	26.6	.550	Avila, Segovia (Spain)
Podarcis h. hispanica (Asturias)	49.6	39	57	8	19	2.1	2.0	.274	23.8	.310	Asturias (Spain)
P. h. hispanica (Salamanca)	61.3	49	67	8	...	3.6	2.0	.340	27.0	.421	Salamanca (Spain)
Podarcis h. atrata	63.1	53	71	7	...	2.8	2.0	.352	28.2	.513	Columbretes Islands (Spain)
Podarcis bocagei	55.2	44	64	8	28	4.2	2.0	.259	24.0	.304	La Coruña (Spain)
Podarcis muralis	58.5	49	65	12	38	5.2	2.0	.284	24.8	.353	Asturias (Spain)
Acanthodactylus erythrurus	71.9	61	84	10	...	3.7	1.0	.820	34.0	1.051	Madrid (Spain)
Takydromus septentrionalis	65.0	56	76	13	...	3.1	2.0	.268	23.4*	.316	Xinshau Island (China)
Takydromus tachydromoides	53.5	46	64	7	25	3.4	3.0	.218	22.5	.214	Honsu (Japan)
Lacerta vivipara (oviparous)	53.0	43	63	11	...	6.2	1.0	.220	19.4	.210	Asturias (Spain)
L. vivipara (livebearing)	55.5	44	70	11	32	4.4	1.0	.364†	20.8	.177	Antwerpen (Belgium)
Lacerta agilis	68.4	62	82	15	51	5.8	1.0	.470	26.6	.540	Limburg (The Netherlands)
Lacerta schreiberi	108.5	91	124	16	44	13.7	1.0	.716	31.6	.767	Salamanca (Spain)
Lacerta viridis	98.5	84	123	12	38	8.9	1.0	.757	32.6	.886	Loire-Atlantique, la Vendée (France)

NOTE.—Age at maturity and maximum adult life span (age of the oldest adult female in the population minus age at maturity) were expressed in number of months of activity (thus excluding the hibernation period), which is more equivalent to physiological time than are measures in total number of months and are therefore more relevant for life-history patterns (Roff 1992; Adolph and Porter 1993). Maximum adult life span was estimated through recaptures of individuals of known age or by skeletochronology (age estimation by counting the annually deposited rest lines in bone tissue). For clutch frequency (number of clutches produced per year), the following categories were retained: 1, species in which all or virtually all females produce only a single clutch per year; 1.5, species for which many females lay one clutch, whereas a considerable fraction (20%–50%) produces two clutches; 2, species with most females (>50%) laying two clutches per year, although females that produce one and others that lay three annual clutches are also present; 3, species for which most females (>50%) produce three clutches per year. A detailed list of literature sources can be obtained from the authors on request.

* We used the independent contrast regressions between log hatchling length and log hatchling mass to estimate the length of hatchling *Takydromus septentrionalis* from the data on hatchling mass and the mass of hatchling *Lacerta lepida* from data on hatchling length.

† Calculated as clutch mass divided by clutch size; clutch mass was measured as the difference between female mass before and after parturition (Bauwens and Verheyen 1987).

that with the exception of the live-bearing form of *L. vivipara,* all species considered are oviparous).

The life-history variables are (1) mean adult female length (snout-vent length, or SVL), (2) female length at maturity, (3) maximum length of adult females, (4) age at maturity, (5) maximum adult life span, (6) clutch size, (7) clutch frequency, (8) egg mass, (9) hatchling length, and (10) hatchling mass (see table 1 for details).

To obtain estimates of traits 1–7, we considered only those studies that sampled individuals of all sizes and that obtained a sample of at least 20 mature females. For variables 8–10, we only retained measurements made within 24 h after oviposition or hatching, with a minimum sample size of 10 eggs or hatchlings, from at least four different females. We explicitly discarded all estimates of egg size based on measurements of oviductal eggs and data on juvenile size obtained in uncontrolled field conditions (i.e., exact birth dates unknown).

From these 10 variables, we derived the following composite traits: (11) clutch mass (the product of clutch size [6] and egg mass [8]); (12) total neonate mass (the product of clutch size and hatchling mass [10]); (13) eggs (young) per year (the product of clutch size and clutch frequency); (14) clutch mass per year (clutch mass [11] times clutch frequency [7]); (15) total neonate mass per year (the product of total neonate mass [12] and clutch frequency); and (16) immature growth rate (relative growth rate during the immature period, calculated as [log (female SVL at maturity/hatchling SVL)]/age at sexual maturity).

Phylogenetic Analyses

We used the method of phylogenetically independent contrasts (Felsenstein 1985) for testing hypotheses and estimating relationships among variables. This method uses information on the putative phylogenetic relations of the N species considered to obtain $N - 1$ statistically independent contrasts. From these contrasts, both correlation and regression coefficients can be computed. If contrasts are appropriately standardized, then the correlation coefficients can be compared with conventional critical values (Martins and Garland 1991; Garland et al. 1992; Díaz-Uriarte and Garland 1996).

Within the Lacertidae, phylogenetic reconstructions based on either immunological (Mayer and Benyr 1994) or morphological (Arnold 1989) information are not completely equivalent (fig. 1). Given this uncertainty, we analyzed our data using both putative phylogenies. Estimates of divergence times between species are based on immunological distances and were also applied to the phylogeny constructed from morphological data. This implied that several arbitrary choices had to be made. Because of this uncertainty in the assignment of branch lengths, we conducted additional analyses on both phylogenetic trees with all branches set to unit lengths. These procedures allow us to evaluate the robustness of our results with respect to both the topology of the phylogeny and the branch lengths.

The original branch lengths of the phylogenies were in units of estimated divergence time. Adequate standardization of the independent contrasts (i.e., no correlation between absolute value of contrasts and their standard deviation; Garland et al. 1992) was obtained by log_{10} transformation of the branch lengths. After transformation, scatterplots of all reported relationships did not show patterns of nonlinearity or heteroscedasticity.
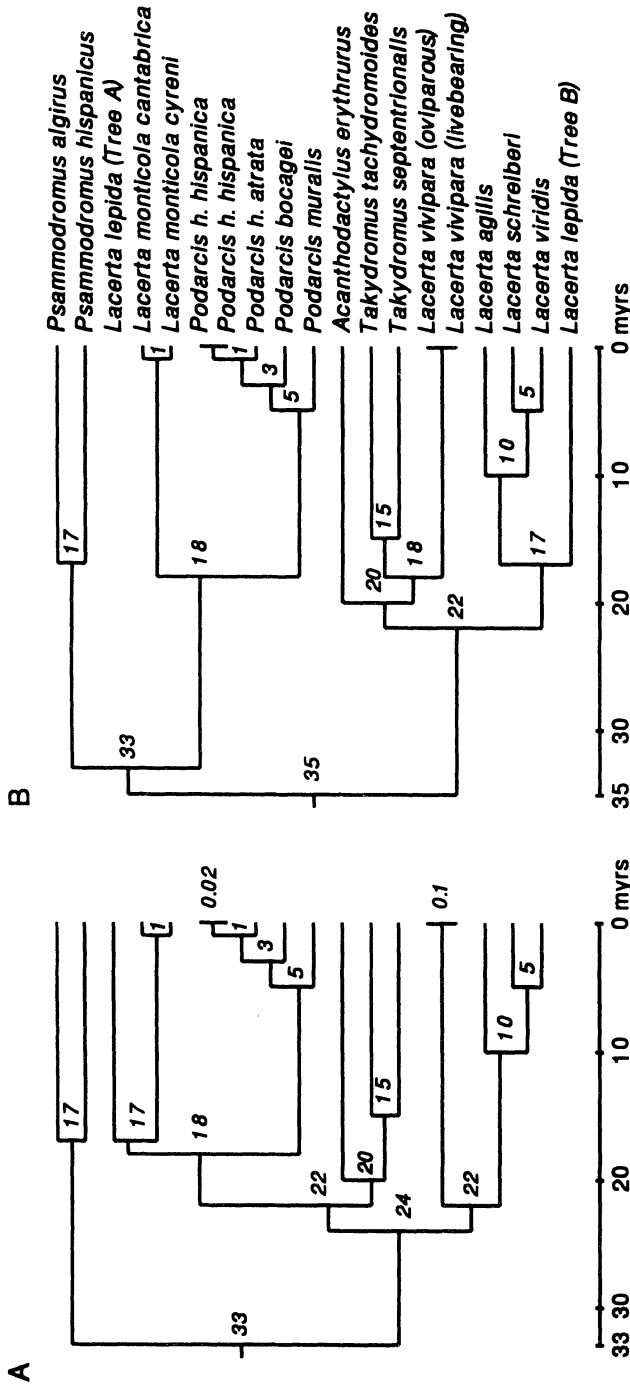
FIG. 1.—Hypothesized phylogenetic relationships and estimated divergence times (numbers at nodes, in millions of years) for the species or subspecies considered. Branching patterns are based on (A) immunological distances (microcomplement fixation of albumins) and (B) external and internal morphological characteristics. Divergence times for main branching patterns are based on immunological distances and were used for both phylogenetic trees. Details on the reconstructions of both phylogenies for part of the species studied are given elsewhere (Bauwens et al. 1995); a full account can be obtained from the authors on request.

Correlation and Regression Coefficients

To test for the correlated evolution of pairs of traits, all correlation coefficients were calculated from standardized phylogenetically independent contrasts. Because of the largely exploratory nature of this study, we used individual tests to judge the statistical significance of correlations within a matrix of coefficients. As this procedure may overestimate the number of significant coefficients, we also denote the correlations that are considered significant by the sequential Bonferroni method (Chandler 1995). As recommended by Chandler (1995), we used an experiment-wise (or table-wide) error rate of $\alpha = 0.10$. This level is more appropriate for multiple tests than the conventional single test error rate (i.e., $\alpha = 0.05$) (Chandler 1995).

To examine how variation in life-history variables scales to body size, we calculated regression slopes from standardized independent contrasts. This method provides good estimates for the evolutionary regression coefficient (Pagel 1993). We estimated slopes using both ordinary least squares (OLS) regression and reduced major axis (RMA) regression. In our case, the OLS regression will underestimate the true slope, as it assumes that the independent variable has no associated error variance (LaBarbera 1989). We therefore based our interpretations on the RMA regression slopes, which were computed only when the correlation coefficient was significant at $P < .05$.

Estimates of regression slopes relating each trait to mean adult female length were compared to the values expected under a model of geometric similarity among the species. Expected values are one for length variables, three for mass traits, and zero for clutch size (the expected value is three for both clutch mass and egg mass, and clutch size equals clutch mass/egg mass). The significance of the difference between the estimated RMA regression slope and the expected value was assessed with a t-test, using the standard error of the corresponding OLS regression slope (McArdle 1988).

To statistically remove the effect of body size on other traits, we computed residuals from the OLS regression between the contrasts for a variable and the body length contrasts (a detailed description of the procedure appears in Garland et al. 1992). When the objective is to remove the effect of one variable on others, OLS regression should be employed instead of RMA regression (Harvey and Pagel 1991).

Principal component analysis (PCA) was used as a means to examine the multivariate structure of the pattern of life-history covariation. The analyses were based on the matrix of independent contrasts' correlation coefficients and were performed both before and after statistically removing the effects of adult female body length. The number of components to retain in each analysis was determined using the broken-stick model (Jackson 1993).

All variables were $\log_{10}$ transformed before contrasts were obtained. Reported correlation coefficients (r) and P values are those obtained using phylogenetically independent contrasts. Slopes (b) are those obtained with RMA regression using independent contrasts. Independent contrast analyses were carried out with the programs PDTREE (Garland et al. 1993) and CMSINGLE (Martins and Garland 1991). Additional statistical analyses were done with SPSS/PC+, version 5.0 (Norusis 1992).

THE AMERICAN NATURALIST

TABLE 2

SUMMARY STATISTICS OF RELATIONS BETWEEN LIFE-HISTORY TRAITS AND MEAN ADULT FEMALE
LENGTH, BASED ON STANDARDIZED INDEPENDENT CONTRASTS

Dependent Variable	r	P_r	b_{exp}	b_{OLS}	SE b	P_b	b_{RMA}	P_{RMA}
Egg mass	.763	***	3	1.679	.367	**	2.201	*
Hatchling mass	.875	***	3	1.804	.249	***	2.061	**
Hatchling SVL	.900	***	1	.572	.069	***	.636	***
SVL at maturity	.993	***	1	.953	.029	NS	.960	NS
Maximal SVL	.991	***	1	.981	.032	NS	.990	NS
Age at maturity	.648	**	· · ·	.746	.219	· · ·	1.151	· · ·
Immature growth rate	− .334	NS	· · ·	− .296	.209	· · ·	· · ·	· · ·
Clutch mass	.904	***	3	2.942	.358	NS	3.254	NS
Total neonate mass	.943	***	3	3.040	.268	NS	3.224	NS
Clutch size	.802	***	0	1.236	.230	***	1.541	***
Clutch frequency	− .505	*	· · ·	− .493	.211	· · ·	− .976	· · ·
Clutch mass/year	.825	***	3	2.216	.392	NS	2.686	NS
Total neonate mass/year	.908	***	3	2.547	.293	NS	2.804	NS
Eggs/year	.478	*	0	.743	.342	*	1.555	***
Maximum adult life span	.681	*	· · ·	.756	.288	· · ·	1.110	· · ·

NOTE.—Definitions are as follows: SVL, snout-vent length; r, correlation coefficient; P_r, significance of correlation coefficient (H_0: $r = 0$); b_{exp}, expected value of the regression slope under a model of geometric similarity (see Material and Methods); b_{OLS}, slope of ordinary least squares (OLS) regression; SE b, standard error of the OLS regression slope; P_b, P value for the difference between b_{exp} and b_{OLS}; b_{RMA}, slope of reduced major axis (RMA) regression (only computed when the correlation was significant at $P < .05$); P_{RMA}, P value of the difference between b_{exp} and b_{RMA}. Standardized independent contrasts were obtained for the immunological tree with variable branch lengths (tree A of fig. 1). Estimates are based on data for 18 species (17 contrasts), except for egg mass, clutch mass, and clutch mass per year (17 species, 16 contrasts) and maximum adult life span (10 species, nine contrasts).
 * $P < .05$.
 ** $P < .01$.
 *** $P < .001$.

RESULTS

Alternative Phylogenies and Regression Models

We first explored the sensitivity of our main results to the various modes of analysis. Estimates of RMA regression slopes and correlation coefficients obtained with standardized independent contrasts using the two alternative phylogenetic trees were very similar and led to identical biological interpretations (i.e., the null hypothesis was either accepted or rejected in both data sets, and if rejected, it was rejected in the same direction). Also, correlation coefficients and RMA regression slopes obtained from analyses using phylogenies with variable branch lengths (i.e., those depicted in fig. 1) were virtually identical to those calculated using phylogenies with unit branch lengths. Because of this similarity among data sets, we only present the results that were obtained using the immunological tree with variable branch lengths (tree A in fig. 1).

Tests of the difference between estimated and expected slope values generally yielded similar results for OLS and RMA regression slopes (table 2). In addition,

the RMA regression slopes calculated using standardized independent contrasts were very similar to those obtained with two other methods that account for phylogenetic relations, namely, unstandardized independent contrasts and inferred minimum evolutionary changes (procedures FL2G and ME1G, respectively, of Martins and Garland 1991), and to those calculated with nonphylogenetic analyses.

In summary, our estimates of correlation and regression coefficients, and hence interpretations, are robust to variations in the hypothesized phylogenetic relationships, phylogenetic methods, and regression models used.

Correlations and Allometric Relationships with Body Size

Most of the life-history traits examined, with the exception of clutch frequency and immature growth rate, were strongly and positively correlated with mean adult female length (table 2). However, a more subtle view emerges after we consider the scaling relations with body length.

Egg mass, hatchling mass, and hatchling length, which index the reproductive investment per individual offspring, scale with negative allometry to mean adult female length (table 2). Thus, eggs and neonates of the larger-sized species are absolutely larger but proportionately smaller than those of the smaller-bodied species. For example, the three smallest species hatch at an SVL that is, on the average, 44.0% of mean adult female length, whereas this figure is only 29.2% for the three biggest species.

Length at sexual maturity and maximum length of adult females increase with mean female length. The regressions have scaling exponents close to one and account for >95% of the variation in both traits (table 2). The relation between maximum length and length at sexual maturity is almost perfectly isometric (b_{RMA} [± 1 SE] = 1.031 ± 0.050, r = 0.981, P < .001). These results indicate that species of lacertid lizards tend to mature at a constant proportion of their maximum body length and that the relative increase in size between maturation and maximum length is independent of mean adult SVL.

Because the scaling exponent to mean adult female length is lower for hatchling length than for length at maturity (table 2; fig. 2), size at birth is a smaller proportion of mature size in the larger species. Consequently, the ratio of hatchling length to SVL at maturity is negatively correlated to mean female size (r = −0.778, P < .001). Thus, hatchling length is, on the average, 53.6% of mature size in the three smallest species, but only 35.3% for the three largest (fig. 2). Therefore, the length increase between birth and maturation is both absolutely and proportionately larger in the bigger species (fig. 2).

Age at sexual maturity is strongly and positively related to mean adult female length, whereas relative growth rate during the immature period is independent of mean adult size (table 2). The correlation between age at maturity and the size-specific length increase between birth and maturity (the ratio of length at maturity to hatchling length) is positive (r = 0.670, P < .01). This suggests a simple mechanistic cause for the relation between age at first reproduction and body size: larger species take longer to mature because they must increase more
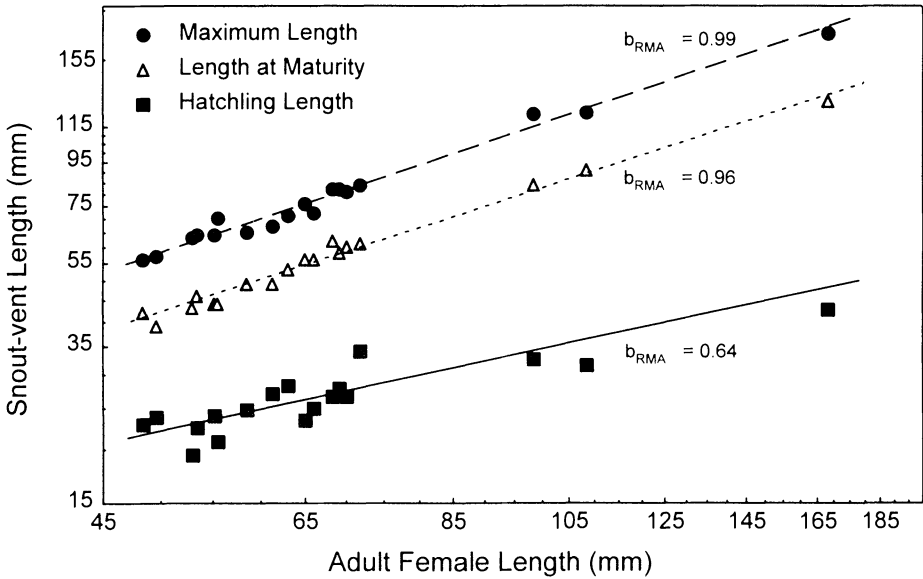
FIG. 2.—Relation of body length (SVL) at hatching, SVL at maturity, and maximum length with mean adult female body length. Data represented are original species' mean values; the reduced major axis regression lines are those obtained with independent contrasts calculated using the immunological tree with variable branch lengths (tree A of fig. 1).

in size after birth. They attain sexual maturity at proportionately the same length but hatch at a disproportionately small size, and their immature growth rate is not faster than that of smaller species.

Clutch mass and total neonate mass, estimates of the absolute amount of energy invested per bout of reproduction, increase isometrically with adult female SVL (table 2). Because of this proportional relationship, and because relative hatchling size decreases with body size (see earlier discussion), the number of offspring per clutch must increase disproportionately with mean adult female size. Accordingly, the slope for the relation between clutch size and adult female SVL is significantly greater than zero, the expected slope value under a model of geometric similarity among the species (table 2; fig. 3).

Clutch frequency declines with female size (table 2). Both clutch mass per year and total neonate mass per year, estimates of the reproductive investment per year, increase proportionately with female size. The number of eggs produced per year, an estimate of annual fecundity, increases with adult female length with approximately the same slope as does clutch size (table 2). Hence, the incorporation of the variation in clutch frequency does not appreciably alter the patterns found for reproductive expenditure per clutch.

Adult longevity increases with mean adult female length (table 2).

Removal of the Correlations with Body Size

Here we examine to what extent the statistical removal of the effect of body size alters the patterns of covariation among life-history traits. We first compare
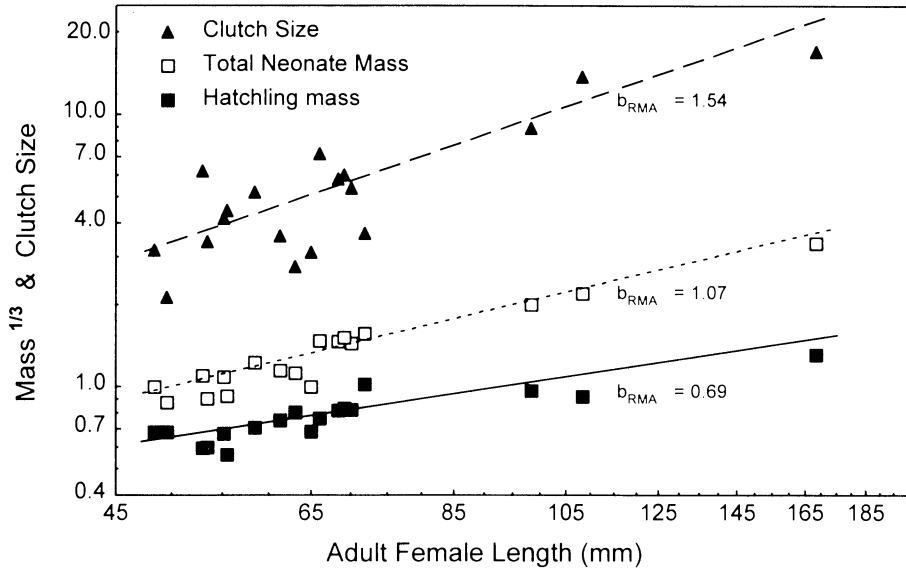
FIG. 3.—Relation of clutch size, hatchling mass, and total neonate mass with mean adult female body length. Data represented are original species' mean values; the reduced major axis regression lines are those obtained with independent contrasts calculated using the immunological tree with variable branch lengths (tree A of fig. 1).

the matrices of correlation coefficients calculated before and after removing the effects of female length (table 3; to avoid spurious correlations, no derived variables were included).

As expected from the tight bivariate relations of most traits to mean female length, correlations among life-history characteristics are generally high and positive (table 3), with the exception of correlations with clutch frequency, which are negative.

When the effects of body size were controlled, few of these correlations remain significant (table 3). Residuals of age at maturity are positively correlated with the residuals of maximum adult life span. Thus, species that mature relatively late for their body size have longer adult lives.

Correlations between residual egg mass, hatchling mass, and hatchling length are positive, which indicates, unsurprisingly, that species with relatively heavy eggs will also have relatively large and heavy offspring. More interestingly, residuals of all three estimates of offspring size (egg mass, hatchling mass, hatchling length) are negatively correlated with residual clutch size (table 3). Note that these correlations are significant when considered on an individual basis but not when adjustment is made for multiple tests. We tentatively conclude that species with relatively large offspring tend to produce a relatively small number of eggs per clutch.

Principal component analysis (PCA) was performed on the correlation matrix of independent contrasts, both before and after removing the effects of mean

TABLE 3
PAIRWISE CORRELATIONS BETWEEN LIFE-HISTORY TRAITS CALCULATED BEFORE AND AFTER STATISTICALLY REMOVING THE EFFECTS OF MEAN ADULT FEMALE LENGTH

	SVL at Maturity	Hatchling Mass	Hatchling SVL	Egg Mass	Clutch Size	Age at Maturity	Clutch Frequency	Maximum Adult Life Span
SVL at maturity	...	**.894*****	**.910*****	**.748*****	**.785*****	**.638****	-.501*	.696*
Hatchling mass	.430†	...	**.972*****	**.855*****	**.593****	.512*	-.639**	.570†
Hatchling SVL	.307	**.872*****	...	**.926*****	**.597****	.474*	-.565*	.593†
Egg mass	-.023	**.640****	**.813*****	...	.209	.325	-**.682****	.386
Clutch size	-.158	-.376	-.481*	-.558*	...	**.634****	-.302	**.766****
Age of maturity	-.058	-.150	-.330	-.168	.251	...	-.483*	**.918*****
Clutch frequency	.007	-**.472***	-.294	-.550*	.200	-.237	...	-.628†
Maximum adult life span	.234	-.254	-.352	-.031	.493	**.844****	-.287	...

NOTE.—SVL, snout-vent length. All correlations are based on standardized independent contrasts obtained for the immunological tree with variable branch lengths (tree A of fig. 1). Elements above the diagonal are correlations between the original variables; elements below the diagonal are correlations for residuals from relations with mean adult female length. Estimates are based on data for 18 species (17 contrasts), except for egg mass (17 species, 16 contrasts), maximum adult life span (10 species, nine contrasts), and the pairwise correlation between egg mass and maximum adult life span (nine species, eight contrasts). Bold type indicates correlations with table-wide $P < .10$, as judged from the sequential Bonferroni method.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

† $.10 > P > .05$.

TABLE 4

SUMMARY OF RESULTS OF PRINCIPAL COMPONENTS ANALYSES USING
STANDARDIZED INDEPENDENT CONTRASTS, OBTAINED FOR THE
IMMUNOLOGICAL TREE WITH VARIABLE BRANCH LENGTHS (TREE A OF
FIG. I), BEFORE AND AFTER REMOVAL OF THE EFFECTS OF BODY SIZE

	RAW CONTRASTS		RESIDUAL CONTRASTS	
	PC1	PC2	PC1	PC2
Eigenvalue	5.16	.80	2.64	1.28
Percentage variance	73.7	11.4	43.9	21.4
Extracted	+	−	−	−
Female SVL	.971	.118	· · ·	· · ·
Hatchling SVL	.923	− .190	.915	− .080
Hatchling mass	.929	− .244	.922	.164
SVL at maturity	.971	.099	.485	− .117
Clutch size	.792	.493	− .633	.172
Clutch frequency	− .644	.604	− .460	− .746
Age at maturity	.716	.263	− .317	.806

NOTE.—SVL is snout-vent length. For each analysis, we indicate
for the first two principal components the eigenvalue, the percentage
of the total variance explained, whether (+) or not (−) the axis
was extracted by the broken-stick model, and correlation coeffi-
cients with original variables.

adult female length. We included only seven variables (table 4)—six in the case
of residuals—to have a ratio of observations to variables not too far from 3:1
(see Grossman et al. 1991). As a stopping rule for the extraction of factors, we
employed the broken-stick model (Jackson 1993). The results of this stopping
rule were coincident with the patterns revealed by scree plots (Jackson 1993),
and in most cases the axes that were not extracted had eigenvalues less than one.

The PCA performed before removing the effect of mean adult female length
extracted only one factor, which explained about 74% of the total variation (table
4). All variables have high positive correlations with this axis, except clutch
frequency, which exhibits a negative correlation. This axis explains much of the
variation that is associated with body size. The fact that no further axes were
extracted suggests that no clear-cut pattern of life-history covariation exists inde-
pendently of body size.

We subsequently analyzed the residuals of the relations with female length.
Using scree plots and the broken-stick model as stopping rules, no axes could be
extracted. Nevertheless, the first principal component had fairly high eigenvalues
(table 4), explaining 44% of the total variation. It was positively related to esti-
mates of offspring size and negatively to clutch size (table 4), and it can therefore
be interpreted as a representation of a trade-off between the size and the number
of offspring.

DISCUSSION

This work is the first comparative study that explores relations between a suite
of reproductive traits and an estimate of adult survival rate within a clade of

closely related vertebrate species. Unlike comparative analyses that cut across major lineages, our study addresses subtle patterns of trait covariation. Several of our findings are likely to be of general interest. First, we show that a clear-cut pattern of life-history covariation, which is tightly related to variation in body size, can be perceived at the species level. Much of the pattern can be deduced from the negative allometry of offspring size. Second, the strength of the pattern is reduced after statistical removal of the influence of body size. However, evolutionary correlations independent of body size persist between age at maturity and adult life span and between offspring size and number. Finally, the pattern of life-history covariation in lacertid lizards differs fundamentally from the fast-slow continuum: the latter is based on a negative relationship between adult life span and clutch size, whereas this relation is positive in the lacertids.

Covariation of Body Size and Life-History Traits

Our analyses demonstrate covariation among reproductive characteristics and between reproductive traits and maximum adult life span within a clade of lacertid lizards. Body size is a major correlate of this pattern. Thus, the lacertid lizards studied here can be arranged along a single axis that describes most of the variation in life-history characteristics. On one end of this axis are small-sized species that mature early, have small clutches of relatively large young, may have multiple broods per year, and have short adult lives. At the other extreme are the larger lacertids; they mature at a later age, produce a single annual clutch composed of a disproportionately high number of relatively small young, and have a long adult life span. The main features of this pattern can be summarized by the following relations, which can be considered mechanistically independent.

The first is the relation of maximum adult life span with adult female length. Adult life span is an inverse index of adult mortality rate, which indicates that larger lacertids experience lower mortality as adults than do the smaller species.

A second series of important relations are those that link reproductive investment and offspring size with adult female size. All estimates of parental investment (clutch mass and total neonate mass, calculated either per clutch or per year) increase in direct proportion to female size. Hence, smaller species do not invest relatively more in reproduction, neither per clutch nor per year, than do the larger species. Measures of offspring size (egg mass and hatchling mass and length) also increase with adult size but less rapidly than does clutch mass. As a consequence, the number of eggs increases disproportionately with adult length. Thus, the fundamental change with body size is in the partitioning of reproductive investment into either few, relatively large young (small species) or many, relatively small hatchlings (large species). Because length at sexual maturity was a constant proportion of adult female size, the larger species must cover a greater length increment, both absolutely and proportionately, between birth and maturation. These differences are not balanced by variation in immature growth rates, which is not related to adult female length. It follows that larger species mature at a more advanced age than the smaller-sized lacertids. Thus, differences in age at maturity can be considered, at least in part, to be a consequence of the negative allometric relation between hatchling size and adult female size.

The large-sized lacertids live absolutely longer adult lives and have a higher annual fecundity than do the smaller species. Thus, the lifetime production of offspring by individuals that survive to adulthood will be much higher in the larger species. Given that birth and mortality schedules must be balanced in natural populations, mortality during the nonadult life stages (i.e., eggs and immatures) must be highest in the biggest species. This predicted higher mortality over the nonadult period may, at least in part, be a simple consequence of the longer time required for the larger species to reach sexual maturity. Data on death rates of eggs and immatures are too scarce for a comparative test of this idea. Nevertheless, available information (Bauwens 1985; Strijbosch and Creemers 1988; Galán 1994) indicates that in some lacertids mortality is independent of age (i.e., a Type II survivorship curve; Krebs 1985), which suggests that the finite mortality rate over the nonadult period is proportional to the duration of this period.

In short, we can reframe much of the observed pattern of life-history covariation into the increase of adult life span with adult female length and the negative allometry of offspring size. Variation of other traits is conditioned by these relations and by the proportionality of reproductive investment and size at maturity and the constancy of immature growth rates in relation to adult size.

The Allometry of Offspring Size and Number

The negative allometry of egg and offspring size among lacertid lizards is associated with a size-related change in the partitioning of reproductive investment: small lacertids produce few, relatively large young, whereas the bigger species have a disproportionately large number of relatively small offspring. This differential partitioning reveals a macroevolutionary trade-off (sensu Stearns 1992) between the size and the number of offspring in this clade of lizards.

What factors could explain the negative allometry of offspring to female size in lacertid lizards? Although our study was not designed to answer this question, we can suggest some testable hypotheses. First, hatchling size in the smaller species may be close to the lower limit for absolute size imposed by physiological processes or ecological interactions. Above this size, offspring survival is supposed to increase rapidly with size but at a diminishing rate (Lloyd 1987). Hence, it should pay more for larger species of lizards to invest in additional young, rather than in increasing the size of each offspring, as this would result in only marginal fitness increments. The basis of a second hypothesis is that morphological characteristics, such as the width of the pelvic girdle, pose upper limits to egg size (Congdon and Gibbons 1987; Sinervo and Licht 1991). This hypothesis then assumes a negative allometric relation between the diameter of the pelvic opening and body length, so that large lizards are constrained to produce eggs that are proportionately smaller than those of the smaller-sized species. We know of no mechanistic evidence to support this idea. A third hypothesis considers development time of eggs as a constraining factor. At a given temperature, duration of external incubation increases with absolute egg size (Sinervo 1990; Birchard et al. 1995). Any benefits associated with an increment of egg size may then be counterbalanced by the costs incurred by late-born juveniles, including

failure of egg hatching before the end of the activity season. Thus, the interaction between environmental factors and the rate of embryo development may place an upper limit on the absolute size of eggs. This may impede the larger species from laying eggs that are proportionately as big as those of the smaller species.

We note that the negative allometry for egg or offspring size, and associated increments in clutch size with adult female size, have been documented for a variety of ectotherms, including lizards (Andrews 1982), turtles (Andrews 1982; Elgar and Heaphy 1989), fish (Blueweiss et al. 1978), insects (Berrigan 1991), and spiders (Marshall and Gittleman 1994). The constancy of this pattern across such a wide range of taxa is remarkable and suggests that the underlying mechanism is a fundamental feature of ectotherm biology.

Life-History Covariation Independent of Body Size

Given the strong relations between life-history traits and body size, some authors consider variation in life histories as an inescapable result of the evolution of body size (Western and Ssemakula 1982). However, it could equally be argued that differences in body size are correlates of selection for particular life histories or that both size and life histories exhibit parallel evolutionary responses to the same selective regimes (Dunham and Miles 1985; Millar and Hickling 1991). An approach to assess the importance of body size in shaping character correlation consists of examining the pattern of covariation once the effects of body size are removed statistically. If the relations among life-history traits remain unaltered, this state implies that evolutionary correlations between life-history traits exist independently of body size (Harvey et al. 1989; Read and Harvey 1989).

When we statistically removed the important effect of body size, much of the pattern of life-history covariation vanished. However, the following important relations were detected, despite the low variation in the residuals of most traits. First, residuals of maximum adult life span and age at sexual maturity were positively correlated. Thus, at a given body size, species that mature late also tend to live longer as adults. Interestingly, several optimality models of life-history evolution predict that increased adult survival will result in delaying age at maturity (Roff 1984; Stearns and Koella 1986). This is precisely the correlation that we find.

Second, the size-free data provide evidence for a negative correlation between offspring size and number and hence for a macroevolutionary trade-off between both traits. The view that increments in offspring size are accompanied by decreases in clutch size is a central tenet of life-history theories (e.g., Lack 1967; Smith and Fretwell 1974; Lloyd 1987; Stearns 1992). The existence of this physiological trade-off is intuitively obvious in individual organisms, given morphological and/or energetic restrictions on total clutch mass (Roff 1992). We suggest that the macroevolutionary compromise observed in lacertid lizards is ultimately induced by the physiological trade-off function.

Thus, the relations that we considered as governing the whole organism pattern (i.e., the increase of adult life span with body size, and hence with age at maturity, and the trade-off between the relative size and the number of offspring) were

also evident in the size-free data. This supports an interpretation of coadaptive adjustments among life-history variables.

Apart from these two relations, correlations among other life-history traits are much lower for the size-free residuals than for the raw data. We suggest three mutually nonexclusive hypotheses for the lack of a strong multivariate pattern in the size-free data. First, the observed association between residual age at maturity and residual adult life span may provide sufficient adjustments between the schedules of fecundity and mortality. Thus, this hypothesis proposes that selection in response to varying levels of mortality would act mainly on the age at maturity rather than on other reproductive characteristics. Several theoretical studies show that, under some conditions, the age at maturity has a larger impact on fitness than other reproductive traits (Lewontin 1965; Caswell and Hastings 1980; Roff 1992; Stearns 1992).

A second hypothesis suggests that no strong size-free pattern of life-history covariation exists because adjustments of the residual reproductive traits to varying mortality schedules are species specific. Thus, some species may adjust age at maturity, others may respond by changes in clutch size, and still others may alter clutch frequency. The type of response will probably depend on the exact nature of the selective force (e.g., immature vs. adult mortality, extrinsic vs. intrinsic mortality) and may be constrained by environmental factors (e.g., an increase in the number of clutches produced per year is only feasible in climates with prolonged reproductive seasons; Adolph and Porter 1993).

Finally, a pattern of trait covariation may exist, but we were unable to detect it. Life-history data are subject to considerable sampling and estimation errors. In addition, some of our variables are very tightly related to adult female length (e.g., length at sexual maturity, $R^2 > 0.95$), so residuals from this relation will have low variation. Consequently, the sample size and/or the strength of the relationship between residuals of two variables should be very large to make that relation detectable. Therefore, the moderate sample size of this study may impede the statistical detection of some relations among the size-free variables.

Lacertid Life Histories and the Fast-Slow Continuum

Does the fast-slow gradient (discussed earlier) adequately describe life-history covariation in lacertid lizards? No. The pattern observed in this clade of lacertids differs from the fast-slow continuum because of a radically opposite association between adult mortality rates and the way in which reproductive investment is partitioned. Species at the fast end of the gradient are short-lived and have many, small young. By contrast, lacertid lizards with short adult lives produce few young, which are relatively large-sized. Organisms at the slow end are long-lived and have few, large young, whereas lacertids with long adult life spans produce a disproportionately large number of young, of a relatively small size. We anticipate that the association between immature and adult mortality rates will reveal a second important difference. Both mortality rates are positively correlated in mammals (Promislow and Harvey 1990), whereas the observed association between adult life span and fecundity predicts that the relation should be negative in

lacertid lizards (see *Covariation of Body Size and Life-History Traits*). Empirical verification of this prediction must await further data on age-specific mortality rates. Future studies should also examine whether the pattern of life-history covariation in the lacertids studied here is shared by other lizard groups.

In summary, the relation between fecundity and adult life span in lacertid lizards differs fundamentally from the relationship underlying the fast-slow gradient. Charnov and Berrigan (1990) and Charnov (1993) report differences among fish, reptiles, mammals, and birds in the values of the slopes of the relationship between adult life span and age at maturity. Our findings extend these fundamental differences: slopes of the relations between clutch size and adult life span, and between clutch size and age at maturity, are negative in mammals and birds (e.g., Harvey et al. 1989; figs. 1.2 and 1.3 in Charnov 1993), whereas they are positive in lacertid lizards (table 3). Thus, endotherms and lacertids differ in the *direction* of these relationships. A major challenge for evolutionary biologists is to link these basic differences to general aspects of the biology of these groups (Charnov and Berrigan 1990).

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