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THE EFFECTS OF SIZE AND PHYLOGENY ON PATTERNS OF COVARIATION IN THE LIFE HISTORY TRAITS OF LIZARDS AND SNAKES

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Early in the development of life history theory, MacArthur and Wilson (1967) and Pianka (1970) emphasized an influential generalization previously noticed by Dobzhansky (1950), Schmalhausen (1949), Skutch (1949), and Darwin (1859, chap. 3). They called attention to a strong trend, among many different types of organisms, for life history traits to covary along a single axis, ranging from organisms that matured early, made large reproductive efforts, had many small young and a short life, to organisms that matured late, made smaller reproductive efforts, and had a few, large young and a long life. They explained this pattern as caused by the mode of population regulation acting to cause local adaptation within species. Density-independent regulation, *r*-selection, was supposed to lead to short-lived organisms with high fecundity; density-dependent regulation, *K*-selection, was supposed to lead to long-lived organisms with low fecundity. Further, the terms were used in a variety of contexts, and came to have at least four different meanings corresponding to contrasts of crowded versus uncrowded conditions, density-dependent versus density-independent regulation, ephemeral versus stable habitats, and large versus small reproductive efforts (Parry 1981).

For at least three reasons, *r*- and *K*-selection is no longer accepted as an explanation for patterns of covariation in life history traits. The patterns are there, but differences in mode of population regulation do not account for them. First, the patterns are not strong in comparisons of organisms within populations, populations within species, or species within genera (Wilbur et al. 1974; Stearns 1977, 1980). Second, *r*- and *K*-selection has been tested seven times in selection experiments. In four cases, the results were not consistent with the predictions of *r*- and *K*-selection, but were roughly consistent with models (see Schaffer 1974; Michod 1979; Charlesworth 1980) based on age-specific mortality rates and the cost of reproduction (Mertz 1975; Taylor and Condra 1980; Barclay and Gregory 1981, 1982). Mueller and Ayala (1981) and Luckinbill (1978, 1979) found no evidence that populations selected for rapid growth necessarily have lower carrying capacities. Lines that grew well at one density also grew well at other

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densities, thus showing that within species a trade-off between rapid population growth and good performance at high densities is not necessary. Third, both Schaffer (1979) and Charlesworth (1980) have shown that there are several different sorts of age-specific selection pressures contained within the category "density dependent," and several others within the category "density independent." Those differences are crucial to accurate predictions.

Thus far all explanations of this pattern of covariation, and all of the tests of *r*- and *K*-selection, have been placed in the framework of selection acting within species to adapt populations to local conditions. However, the perception of the pattern appears to have been a function of the taxonomic units used (Stearns 1980). Broad taxonomic surveys report a strong pattern (e.g., Pianka 1970; Cody 1971); studies of intraspecific variation and response to selection do not (e.g., Birch et al. 1963; Dobzhansky et al. 1964; Dawson 1977; Stearns 1983*a*, 1983*c*). This observation suggests that some of the strength of the pattern called "*r*- and *K*-selection" may be influenced by the taxonomic units used in the analysis. Some of the strength of the pattern may also be influenced by the size of the organisms, independent of phylogenetic position.

Therefore, I have undertaken a survey of patterns of covariation of life history traits in the vertebrates. This paper, the second in a series, reports the results for the reptiles. The first (Stearns 1983*b*) dealt with the mammals. They all aim to answer the same questions. What is the impact of the classwide correlations with size on patterns of covariation in life history traits? What are the statistical effects of removing order, family, and genus means for each trait once the correlations with size have been removed? Are patterns of covariation lineage-dependent and thus correlated with patterns of covariation in morphological traits? Positive answers would explain why workers making comparisons across higher taxonomic levels found strong and suggestive patterns of covariation, whereas studies within species indicate that patterns are weaker and vary from lineage to lineage.

METHODS

The Data

I compiled a list of 307 reptile species in five orders and 22 families. From these, I selected those for which there were values reported for at least five traits: average snout-vent length of adult females, clutch size, age at maturity, mode of reproduction (viviparous or oviparous), and frequency of broods per year. These five traits were the most frequently reported. I then selected only those orders containing two or more families, and only those families containing two or more species. This eliminated turtles, crocodilians, and the tuatara, and left a sample of 61 lizards (6 families) and 10 snakes (3 families). The species and populations used in the analysis are listed in the Appendix. The families that were well represented in the analysis included the Iguanidae, Teiidae, Scincidae, and Elapidae (table 1). Less well represented but included were the Agamidae, Anguidae, Lacertidae, Colubridae, and Viperidae.

TABLE 1

AVERAGE VALUES FOR EACH OF FIVE TRAITS IN TWO ORDERS AND NINE FAMILIES OF REPTILES ANALYZED

TAXON	*n*	TRAITS				
		Length (mm)	Clutch	Age at Maturity (mo)	Mode	Broods/yr
Lizards						
Iguanidae	36	73.2	7.1	15.7	1.1	2.2
Agamidae	4	91.7	6.4	12.0	1.0	2.6
Anguidae	3	130.2	8.6	33.1	1.3	1.3
Lacertidae ...	2	48.3	3.3	7.7	1.0	4.5
Teiidae	9	69.3	3.5	12.3	1.0	2.4
Scincidae	7	62.1	4.5	17.7	1.1	2.1
Snakes						
Elapidae	6	312.3	7.2	25.4	1.0	.9
Colubridae ...	2	424.1	6.3	33.4	1.0	1.0
Viperidae	2	176.4	13.8	48.0	2.0	.7
Lizards	61	73.4	5.9	15.3	1.1	2.3
Snakes	10	307.5	8.3	31.5	1.2	.9

Univariate Statistics

Length, clutch size, and age at maturity were log-transformed before all analyses. Mode of reproduction (1 = oviparous, 2 = viviparous) and number of broods per year were not. I calculated the classwide correlation and regression of each trait on average length of adult female. Then I did a two-level nested ANOVA for unequal sample sizes (Sokal and Rohlf 1981, pp. 294–299), where the two levels were order and family. After removing the classwide effects of adult female length by subtracting $b_i \times$ length (b_i = slope of the regression of the ith trait on length) from the ith trait in each record, I repeated the ANOVA on the residuals.

Principal Components Analysis

Principal components analysis is a method for defining the independent dimensions along which species differ given the patterns of covariation in the data. The percentage of variation explained by each principal component estimates the relative strength of that component. The loadings of the individual traits on each component provide an interpretation of what that component means. Since the correlation matrix of all traits is used in calculating the principal components, I have listed the correlation matrices for each step of the analysis to aid in the interpretation of the results. The algorithm used was BMDP program P4M (Dixon and Brown 1977).

Plan of Analysis

I first did a principal components analysis on all 71 species without removing the classwide correlations with length. Then I removed the length effects and repeated the analysis. After calculating the mean value of each trait for each order, I subtracted the order means from the records for the species within each order and repeated the principal components analysis. This means that the value of each trait for each species was expressed as a deviation of the mean value for that trait for all species in that order. I then reiterated this procedure for family and genus means. In doing the analysis on genera, I restricted the sample to only those genera containing two or more species or populations. This reduced the sample to 51 species or populations. This procedure is intended to reveal, by contrast with preceding cases, the impact of length, order, family, and genus effects on patterns of covariation in life history traits. In order to bring out the effects of length alone, I did the analysis once after removing the correlations with length, and again without removing the correlations with length.

Within one family, the Iguanidae, there were enough genera represented to examine the residual effects of genus after the correlations with length, order, and family had been removed. This was done with one-way analysis of variance.

Within four families, the Elapidae, Iguanidae, Scincidae, and Teiidae, there were enough species and populations represented to justify separate principal components analysis on each family. I took this step to see if the patterns of covariation within families were the same as the patterns among families and orders, and thus to answer the question, Are patterns of life history covariation lineage-dependent?

RESULTS

Univariate Analysis

The summary of average values for each family (table 1) shows considerable variation among families in all traits, with ranges of 48–424 mm for female length, 3.3–13.8 for clutch size, 8–48 mo for age at maturity, all oviparous (1.0) to all viviparous (2.0) for mode of reproduction, and 0.7 to 4.5 broods per yr. The regression of each trait on length shows (table 2) that age at maturity ($r^2 = 0.48$) and brood frequency ($r^2 = 0.27$) are strongly correlated with length, but in opposite ways. Neither clutch size ($r^2 = 0.09$) nor mode of reproduction ($r^2 = 0.03$) varies much with length.

The trait-by-trait analysis with nested ANOVAs (table 3) suggests that order effects are important for length ($P < .001$), age at maturity ($P < .05$), and brood frequency ($P < .025$), but that the order effects on age at maturity and brood frequency are mediated by size, because their significance vanishes when the classwide correlations with size are removed. Thus the distinction between the life histories of lizards and snakes results mostly from their different average sizes; once the effects of size are removed, the life histories of lizards and snakes no longer differ. On the other hand, there are significant family effects on clutch

TABLE 2

Impact of Average Length of Adult Females on Four Traits in 71 Species of Reptiles

Trait	Mean	r	r^2	Slope	Intercept
1. Clutch size	6.5	.30	.09	.22	.86
2. Age at maturity	16.8	.69	.48	.57	.22
3. Mode	1.2	.19	.03	.09	.77
4. Broods per year	2.0	−.52	.27	−.76	5.49

Note.—Length, clutch size, and age at maturity were log-transformed. Mode of reproduction (1 = oviparous, 2 = viviparous) and broods per year were not transformed.

TABLE 3

Two-Level, Nested, Unbalanced ANOVAs for Individual Traits

	Order		Family		% Variance Explained by		
Trait	F	p	F	p	Order	Family	Residual
A. Effects of length left in							
1. Length	69.39	<.001	1.61	NS	85	1	14
2. Clutch	.95	NS	2.87	<.025	0	23	77
3. Age at maturity	8.04	<.05	2.03	NS	41	8	51
4. Mode	1.09	NS	5.39	<.001	1	40	59
5. Broods/yr	9.40	<.025	1.79	NS	42	6	52
B. Effects of length removed							
1. Clutch	.09	NS	2.82	<.025	0	22	78
2. Age at maturity	1.51	NS	1.64	NS	4	9	87
3. Mode	.17	NS	4.83	<.001	0	38	62
4. Broods/yr	.13	NS	1.49	NS	0	7	93

size ($P < .025$) and mode of reproduction ($P < .001$), and their significance is not affected by the removal of length effects. Family effects account for about 20% of the variation in clutch size and 40% of the variation in mode of reproduction.

Principal Components Analysis

The first principal component explains about half the variation in these data before the removal of length effects, and about 40% once length effects are removed. The subsequent reduction in variance explained by the first principal component when order, family, and genus effects are removed is not very striking (table 4). However, the interpretation of the first principal component does change when family and genus effects are removed (table 5). Before length effects are removed, the first principal component represents an axis at one end of which are found small, oviparous, early maturing species with small clutches and many broods per year, and at the other end of which are found large, viviparous, late maturing species with large clutches and few broods per year. This pattern remains when length and order effects are removed, but the loadings reverse sign for each trait when family and genus effects are removed. Some insight into this

TABLE 4

PRINCIPAL COMPONENT ANALYSIS

CASE	% VARIANCE EXPLAINED BY 1	2	3	COMPONENT TOTAL
A. Length effects removed in step 2				
1. 71 species	55.6	16.2	13.4	85.2
2. 71 species-length effects	41.5	23.5	19.3	85.3
3. 71 species-length and order	41.4	24.9	19.2	85.5
4. 71 species-length and family	37.3	24.6	23.0	84.9
5. 51 species-length and genus	37.7	25.7	22.3	85.7
B. Length effects not removed				
1. 71 species	55.6	16.2	13.4	85.2
2. 71 species-order effects	50.0	17.8	14.8	82.6
3. 71 species-family effects	47.6	18.6	16.5	82.7
4. 51 species-genus effects	31.0	23.2	22.2	76.4

TABLE 5

UNROTATED FACTOR LOADINGS FOR PRINCIPAL COMPONENT 1

Case	Length	Clutch	Age at Maturity	Mode	Broods/yr
A. Length effects removed in step 2					
1. 71 species	.83	.66	.81	.57	−.82
2. 71 species-length	...	.56	.61	.60	−.78
3. 71 species-order	...	.56	.60	.61	−.79
4. 71 species-family	...	−.59	−.49	−.50	.81
5. 51 species-genus	...	−.38	−.41	−.72	.83
B. Length effects not removed					
1. 71 species	.83	.66	.81	.57	−.82
2. 71 species-order	.78	.70	.77	.50	−.75
3. 71 species-family	.82	.58	.76	.41	−.80
4. 51 species-genus	.65	.22	.58	.54	−.67

switch in the interpretation of the first principal component can be gained from an inspection of the correlation matrices (table 6). Removing the correlations with length also removes the correlation of clutch size with age at maturity and mode of reproduction, but it leaves the other correlations relatively untouched. Removal of order effects does nothing significant to the correlation matrix, but removal of family effects also removes the correlation of age at maturity with mode of reproduction, and removal of genus effects reduces the negative correlation of brood frequency with clutch size and restores the negative correlation of brood frequency and mode of reproduction to its original level. These changes in the correlation matrix account for the reversal of polarization in the first principal component when family and genus effects are removed. However, throughout this analysis the general interpretation of the first principal component remains the same. The only thing that changes is the direction in which species are ranked; their absolute ordering does not change direction.

TABLE 6

CHANGES IN CORRELATION MATRICES AS EFFECTS OF LENGTH AND TAXON ARE REMOVED

	MATRIX		
CASE	Clutch	Agemat	Mode
A. Untransformed data			
Agemat	.36		
Mode	.21	.37	
Brdfrq	−.50	−.54	−.39
B. Effects of length removed			
Agemat	.09		
Mode	.08	.23	
Brdfrq	−.34	−.27	−.27
C. Effects of order removed			
Agemat	.07		
Mode	.08	.23	
Brdfrq	−.34	−.27	−.27
D. Effects of family removed			
Agemat	.05		
Mode	.04	.08	
Brdfrq	−.31	−.21	−.23
E. Effects of genus removed			
Agemat	−.03		
Mode	.07	.07	
Brdfrq	−.19	−.20	−.37

NOTE.—Abbreviations: Agemat = age at maturity; Brdfrq = brood frequency.

TABLE 7

ONEWAY ANOVAS FOR FOUR TRAITS AFTER EFFECTS OF LENGTH, ORDER, AND FAMILY HAVE BEEN REMOVED: THE RESIDUAL EFFECTS OF GENUS WITHIN ONE FAMILY, THE IGUANIDAE

A. Trait	*F*	*p*	% Variance Explained
1. Clutch size	15.61	<.001	78
2. Age at maturity	1.16	NS	4
3. Mode of reproduction	.67	NS	0
4. Broods per year	1.59	NS	13

B. Residual clutch size

	Anolis	*Dipsosaurus*	*Holbrookia*	*Sceloporus**	*Uma*	*Urosaurus**
n	4	2	3	12	2	5
$\bar{x}$	−.31	.31	.84	1.33	.83	1.30

* Contains some intraspecific variation, from either population or subspecies.

Analysis Within Families

Within one family, the Iguanidae, there were enough genera to permit an analysis of the effects of genus after the removal of the correlations with length, order, and family (table 7). In the residuals, there were significant effects of genus only on clutch size ($P < .001$). Differences among genera explained 78% of the residual variance in clutch size, with *Scleroporus* and *Urosaurus* having relatively large clutches, and *Anolis* small ones.

TABLE 8

Analysis within Families, Length Effects Removed

A. Variance explained by first two Principal Components

Family	*n*	PC 1	PC 2
Elapidae	6	79.7	14.3
Iguanidae	36	36.2	28.2
Scincidae	7	63.4	31.6
Teiidae	9	47.3	17.9

B. Loadings on First Principal Component

	Clutch	Agemat	Mode	Brdfrq
Elapidae	.91	.73	.94	−.98
Iguanidae	−.57	−.13	−.60	.87
Scincidae	.55	.98	.60	−.96
Teiidae	−.63	−.52	−.90	.65

C. Correlations

	Clutch *x*			Agemat *x*		Mode *x*
	Agemat	Mode	Brdfrq	Mode	Brdfrq	Brdfrq
Elapidae	.56	.80	−.85	.51	−.63	−.97
Iguanidae	−.13	−.02	−.33	.02	−.14	−.32
Scincidae	.40	−.21	−.62	.67	−.91	−.40
Teiidae	.09	−.36	−.30	−.50	.06	.48

Note.—Abbreviations: Agemat = age at maturity; Brdfrq = brood frequency.

There were four families, the Elapidae, the Iguanidae, the Scincidae, and the Teiidae, with enough observations (6 or more) to permit an analysis of how patterns of covariation differed among families (table 8). The first principal component accounted for widely differing amounts of the variation in the data within each family (36%–80%, Table 8*A*). Moreover, the interpretation of the first principal component varied strikingly among families, as can be seen from the loadings of each trait (table 8*B*). In the Elapidae and Scincidae, the loadings reflect those seen in the reptiles in general. In the Iguanidae, the interpretation of the axis is the same but the polarity is reversed. In the Teiidae there is an apparent reversal in the loadings of mode of reproduction and brood frequency. This is an artifact of removing the correlations with length on mode of reproduction, because in the original untransformed data there was no variation at all in mode of reproduction within the Teiidae.

The changes from family to family in the pairwise correlations of traits explain the large differences among families in the amount of variability explained by the first principal component and in the changes in polarity of that component. In particular, age at maturity is positively and strongly correlated with clutch size in the Elapidae and the Scincidae, but negatively or weakly correlated with clutch size in the Iguanidae and Teiidae. Age at maturity is negatively and strongly correlated with brood frequency in the Elapidae and Scincidae, but weakly or positively correlated with brood frequency in the Iguanidae and the Teiidae (table 8*C*). Thus patterns of covariation in life history traits do change significantly from family to family.

Summary of Results

In this sample of reptiles, classwide correlations with size explain about half the variation in age at maturity and a quarter of the variation in brood frequency, but have little impact on clutch size and mode of reproduction. There are apparently significant differences between lizards and snakes in age at maturity and brood frequency, but these vanish when the effects of size are removed, and there are no other significant effects of order on life history traits. However, family effects on clutch size and mode of reproduction are significant and are not affected by the removal of length effects.

The single pattern of covariation that explains most of the variability in the data remained throughout an axis that ranked species from small, oviparous, early maturing organisms with many broods per year and small clutches to large, viviparous, late maturing organisms with few broods per year and large clutches. Thus, in this data set two components of reproductive effort—clutch size and brood frequency—appear to compensate in a manner which would reduce the strength of any covariation of reproductive effort itself with other life history traits.

Several lines of evidence suggest that patterns of life history covariation are lineage-dependent in the reptiles. First, removal of family and genus effects, after length and order effects had already been removed, had significant impact on the polarity of the first principal component and on the structure of the correlation matrices of life history traits. Second, even after the removal of length, order, and family effects, there remained significant genus effects on residual clutch sizes in the Iguanidae. However, within the Iguanidae there were no residual effects of genus on age at maturity, mode of reproduction, or brood frequency. Thus most of the covariation among those traits within the Iguanidae arose from differences that can be traced to classwide correlations with length. Third, the amount of variation explained by the first principal component varied from family to family, as did loadings of traits on that component and pairwise correlations of traits within families.

Discussion

In the introduction I posed the questions that this analysis was intended to answer. Does size alone effect patterns of covariation in the life history traits of reptiles? It does. Removing the correlations with size reduced the amount of variance explained by the first principal component more (14%) than did the removal of order, family, or genus effects (0%–4%). Most of the correlation of clutch size with age at maturity and mode of reproduction in the reptiles seems to result from shared correlations with size. Does the removal of order, family, and genus effects change patterns of covariation? All of the impact of order effects on covariation in life history traits is size mediated; there appear to be no residual effects of order that can be traced to differences in morphology per se independent of size. However, family and genus effects were both significant; removal of family and genus effects from the residuals left by the removal of length and order effects had greatest impact on the correlations of clutch size with age at maturity and mode of reproduction and on the correlation of age at maturity with mode of reproduction. Thus there are effects of phylogenetic position on patterns of covariation in life history traits, and the removal of those effects weakens the pattern originally perceived as r- and K-selection. Are patterns of covariation lineage-dependent? At least three lines of evidence, arising mostly from the analysis within families, indicate that patterns of covariation in life history traits are lineage-dependent, varying from family to family.

Comparison with Mammals

In mammals (Stearns 1983*b*), classwide correlations with size had strong impact on all life history traits, accounting on average for about half the variation in a trait, whereas in reptiles size only had strong correlations with half the traits and accounted, on average, for less than a quarter of the variation in a trait. Order effects were important in the mammals, where the sample included 22 orders, but not in the reptiles, where the sample included two orders. This difference probably stems not so much from any fundamental difference in the meaning of the taxonomic unit in the two classes, but from the fact that most mammalian orders are still extant, whereas important sources of variability among reptiles were lost when several orders became extinct by the end of the Cretaceous. In both mammals and reptiles, family effects were important, but they were more important in mammals. In both classes, the within-family analysis revealed patterns of covariation in life history traits that varied from family to family in a lineage-dependent fashion that suggests strong covariation between morphology and life history. Most often, the strongest effects result from the fixation of a trait within a family, e.g., all the Teiids are oviparous, all the Phocids have a single offspring, all the Viperids are viviparous. That sort of difference often arises at the level of the family. In sum, the impact of length and phylogeny on patterns of covariation in life history traits is stronger in the mammals than in the reptiles, but remains significant in the reptiles and leads to similar conclusions.

Relevance to Other Work

Lauder (1982) has clearly laid out the contrast between historical and equilibrium analyses in functional morphology. His framework for explanation neatly anticipates the one developed here. Lauder claims that history plays an important role in shaping the properties that organisms exhibit today. My analysis substantiates his claim for the life history traits of snakes and lizards. I cannot weigh the relative importance of history and local adaptation in this data set because so little intraspecific variability is present. However, I can conclude that history, as seen in lineage-specific patterns of covariation, has played an important role in shaping suprageneric differences in the life histories of reptiles. The research program that Lauder outlines for functional morphology would nicely complement the research program suggested by these results, in that it might identify those aspects of morphology that produce lineage-specific constraints on life history evolution.

Wanntorp (1983) makes a point similar to Lauder's: "In adaptational studies it is not enough to know the taxon investigated, however thoroughly . . . one should have at least some idea about relationship. Otherwise one might . . . discuss the vestigial ancestral condition . . . when its reversion . . . is the specialization. This is like discussing the uses of the vermiform appendix in humans. In both cases the most parsimonious hypothesis is a non-adaptational null hypothesis derived from our knowledge of character distribution in related species. . . . My proposition is not that ecologists should start making detailed phylogenetic analyses of the taxa they study, but some systematic considerations are necessary."

Brown (1983) has recently performed a somewhat different analysis aimed at answering the same general questions for several families of freshwater snails. Although he used discriminant function analysis rather than principal components analysis, and worked on snails rather than reptiles, he too found that much of the pattern of covariation in the data could be explained by lineage-specific effects. His data set was somewhat richer, and he was also able to detect habitat-specific effects, but it was not clear how much of the effect of habitat could be attributed to the fact that different families tend to live in different habitats. He did conclude that contrasts in life history tactics are more evident at higher taxonomic levels, as is the case in the reptiles.

SUMMARY

Explanations of patterns of covariation in life history traits have been couched in terms of processes acting within species to produce adaptations to local habitats and mortality schedules. Analysis of the impact of size and lineage on patterns of covariation in the life history traits of reptiles suggests that microevolutionary explanations, while perhaps necessary, are not sufficient to account for the patterns in the data. Patterns of covariation are strongly influenced by classwide correlations with a single trait, average adult female length; they are further influenced by the effects of family and genus, but the differences between the two orders of reptiles analyzed are entirely accounted for by the correlations with size. Thus much of the tendency for traits to covary in the pattern originally thought to have been produced by *r*- and *K*-selection can be explained by selection on size alone followed by coadaptive shifts in life history traits. However, the pattern described here is also consistent with an adaptationist interpretation that would assert that both size and life history traits have been shaped by the same environmental conditions. Causation cannot be inferred from correlations based on a static description.

In the residual variation, following the removal of correlations with size, there are significant effects of higher taxonomic levels, suggesting that lineage-specific differences in life histories, either constrained by or coadapted with morphological differences, can explain some of the tendency for life histories to be found in certain patterns. These observations do not rule out a role for microevolution operating on local populations through differences in age-specific mortality schedules. They do suggest that such microevolution occurs within a framework of relatively ancient constraints that set limits on the types of covariation of life history traits that occur within a given lineage.

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APPENDIX

Taxon	Length	Clutch	Age	Mode	Frequency	Source
Lizards						
Iguanidae						
Anolis acutus	42.2	1.0	12.0	1.0	3.0	68
Anolis carolinensis	50.0	1.3	12.0	1.0	3.0	29,32
Anolis limifrons	44.0	1.0	8.0	1.0	3.0	71
Anolis tropidolepsis	50.0	2.0	8.5	1.0	6.0	21
Callisaurus draconoides	75.0	4.4	12.0	1.0	3.0	60
Ctenosaura similis	305.0	25.0	36.0	1.0	1.0	2,20
Dipsosaurus dorsalis	100.0	5.5	12.0	1.0	1.0	59
Dipsosaurus dorsalis	120.0	4.0	66.0	1.0	1.0	50
Holbrookia maculata	54.0	6.1	12.0	1.0	3.0	86
Holbrookia maculata	49.8	3.5	12.0	1.0	2.0	14
Holbrookia maculata	53.0	7.0	12.0	1.0	2.0	25
Iguana iguana	340.0	35.0	35.9	1.0	1.0	2,35,66
Liolaemus multiformus	81.0	5.8	18.0	2.0	1.0	57
Phrynosoma platyrhinos	76.0	7.7	22.0	1.0	1.0	61
Polychrus acutirostris	125.0	17.0	8.5	1.0	1.0	87
Sceloporus cyanogenys	106.0	13.0	35.9	2.0	1.0	36
Sceloporus clarki	97.0	12.0	12.0	1.0	3.0	40,79
Sceloporus graciosus	57.0	3.3	48.0	1.0	1.0	31,77,78,80
Sceloporus jarrovi	75.0	6.8	6.0	2.0	1.0	85
Sceloporus magister	100.0	8.4	36.0	1.0	3.0	39,72,79
Sceloporus malachitus	75.0	5.9	24.0	2.0	1.0	45
S. olivaceus biseriatus	76.0	7.7	24.0	1.0	2.0	20
Sceloporus olivaceus	100.0	15.0	12.0	1.0	1.5	6,31
Sceloporus orcutti	92.0	9.2	36.0	1.0	1.0	20,46,47
Sceloporus scalaris	56.0	10.5	9.0	1.0	1.0	55
S. undulatus hyacinthinus	44.0	5.5	12.0	1.0	5.0	20,55
Sceloporus undulatus	69.0	6.3	24.0	1.0	3.0	84
Tropidorus hispidus	82.1	5.5	9.9	1.0	3.0	64
Uma inornata	81.0	2.5	24.0	1.0	3.0	48
Uma notata	76.0	2.0	24.0	1.0	3.0	49
Urosaurus graciosus	53.0	5.3	9.9	1.0	1.5	72,88
Urosaurus ornatus	48.4	4.7	10.5	1.0	3.0	15
Urosaurus ornatus	48.1	9.0	11.0	1.0	1.5	15
Urosaurus ornatus	49.3	9.0	9.5	1.0	1.5	15
Urosaurus ornatus	50.6	7.1	8.5	1.0	3.0	15
Uta stansburiana	46.0	3.9	9.0	1.0	3.0	83
Agamidae						
Agama agama	85.0	6.0	12.0	1.0	3.0	13
Agama agama	97.0	5.5	12.0	1.0	3.0	33
Amphibolorus inermis	90.0	3.4	12.0	1.0	3.0	62
Moloch horridus	95.0	7.2	12.0	1.0	1.5	62
Anguidae						
Gerrhonotus coeruleus	100.0	6.2	35.9	2.0	1.0	16
Gerrhonotus multicavinatus	105.0	6.5	18.0	1.0	2.0	27
Ophisaurus attenautus	210.0	10.8	48.0	1.0	1.0	20
Lacertidae						
Aporosaura anchieatae	44.0	1.3	5.0	1.0	3.0	28
Takydromus tachydromoides	53.0	3.6	12.0	1.0	6.0	24,37

(*Continued*)

APPENDIX (*Continued*)

Taxon	Length	Clutch	Age	Mode	Frequency	Source
Teiidae						
Cnemidophorus exsanguis	75.0	2.7	9.9	1.0	1.0	51
Cnemidophorus gularis	74.6	4.5	10.0	1.0	2.0	4
Cnemidophorus hyperythrus	60.0	2.3	12.0	1.0	3.0	7
Cnemidophorus inornatus	57.0	2.2	9.9	1.0	3.0	51
Cnemidophorus neomexicanus	65.0	1.6	9.9	1.0	3.0	51
Cnemidophorus sexlineatus	61.0	2.3	12.0	1.0	3.0	18,19
Cnemidophorus tesselatus	83.0	3.2	24.0	1.0	3.0	70
Cnemidophorus tigris	72.0	2.0	12.0	1.0	3.0	51
Cnemidophorus tigris	82.0	2.7	22.0	1.0	1.0	9
Scincidae						
Egernia whitii	80.0	3.0	48.0	2.0	1.0	34,91
Emoia artrocostata	80.0	2.0	9.0	1.0	3.0	1
Eumaces fasciatus	72.0	9.5	24.0	1.0	1.0	17
Eumaces skiltonianus	64.0	4.4	30.0	1.0	1.0	67,81
Leiolopisma cherriei	53.8	2.0	12.0	1.0	3.0	30
Lygosoma laterale	47.0	3.8	12.0	1.0	3.0	23
Scincella laterale	48.0	3.0	12.0	1.0	3.0	3,23
Snakes						
Elapidae						
Acanthophis antarcticus	580.0	7.9	42.0	1.0	0.5	73
Cacophis squamolos	48.4	6.2	32.0	1.0	1.0	73
Cacophis harriettae	35.7	5.1	32.0	1.0	1.0	73
Cacophis krefftie	26.4	3.2	20.0	1.0	1.0	73
Micrurus fulvius (Texas)	49.0	10.0	12.0	1.0	1.0	65
Micrurus fulvius (Flor.)	727.0	6.5	26.0	1.0	1.0	38
Colubridae						
Diadophis punctatus	300.0	4.2	31.0	1.0	1.0	20
Lampropeltis triangulum	600.0	6.7	36.0	1.0	1.0	22
Viperidae						
Crotalus horridus	122.8	12.6	72.0	2.0	0.4	26
Storeria dekayia	230.0	14.9	24.0	2.0	1.0	41

SOURCES.—Alcala and Howard 1967; 2, Alvarez del Toro, 1960; 3, Anderson 1965; 4, Ballinger and Schrank 1972; 6, Blair 1960; 7, Bostic 1966; 9, Burkholder and Walker 1973; 13, Daniel 1960; 14, Droge et al. 1982; 15, Dunham 1982; 16, Fitch 1935; 17, Fitch 1954; 18, Fitch 1958; 19, Fitch 1967; 20, Fitch 1970; 21, Fitch 1972; 22, Fitch and Fleet 1970; 23, Fitch and Greene 1965; 24, Fukada 1965; 25, Gennaro 1974; 26, Gibbons 1972; 27, Goldberg 1972; 28, Goldberg and Robinson 1979; 29, Gordon 1956; 30, Greene 1969; 31, Guillete et al. 1980; 32, Hamlett 1952; 33, Harris 1964; 34, Hickman 1960; 35, Hirth 1963; 36, Hunsaker 1959; 37, Ishihara 1964; 38, Jackson and Franz 1981; 39, Johnson et al. 1948; 40, Kauffeld 1943; 41, Kofman 1979; 45, Marion and Sexton 1971; 46, Mayhew 1963*b*; 47, Mayhew 1963*a*; 48, Mayhew 1965; 49, Mayhew 1966*b*; 50, Mayhew 1966*a*; 51, Mayhew 1971; 55, Newlin 1976; 57, Pearson 1954; 59, Pianka 1971; 60, Pianka and Parker 1972; 61, Pianka and Parker 1975; 62, Pianka and Pianka 1970; 64, Prieto et al. 1976; 65, Quinn 1979; 66, Rand 1968; 67, Rodgers and Memmler 1943; 68, Ruibal et al. 1972; 70, Schall 1978; 71, Sexton et al. 1963; 72, Shaw 1952; 73, Shine 1980; 77, Stebbins 1944; 78, Stebbins 1948; 79, Stebbins 1954; 80, Stebbins and Robinson 1946; 81, Tanner 1957; 83, Tinkle 1959; 84, Tinkle 1967; 85, Tinkle 1972; 86, Tinkle and Hadley 1973; 87, Tinkle et al. 1970; 88, Vitt and Lacher 1981; 91, Worrell 1964.

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