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1996

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Smith, Geoffrey R.; Rowe, John W.; and Ballinger, Royce E., "Intraspecific Life History Variation in *Sceloporus undulatus*: A Factor Analysis" (1996). *Transactions of the Nebraska Academy of Sciences and Affiliated Societies*. 87.
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**INTRASPECIFIC LIFE HISTORY VARIATION IN
SCELOPORUS UNDULATUS: A FACTOR ANALYSIS**

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ABSTRACT

We examined life history variation in the lizard, *Sceloporus undulatus*, across its range. Data from published studies on 14 populations of *S. undulatus* were analyzed using factor analysis. Four factors were generated from the data. Factor 1 reflected the influence of body size on lizard life histories and explained 31% of the variance in *S. undulatus* life histories. Factor 2 represented the negative relationship of relative clutch mass and number of clutches per year and explained 17% of the variance. The third factor had strong positive loadings of egg mass, age at maturity, and adult survivorship, with a weaker negative loading of the number of eggs per year and explained just over 24% of the variance. The fourth and final factor consisted of strong loading on a single variable, survivorship to maturity, and explained nearly 12% of the variance. Factor 1 was negatively related to Factor 2, but positively related to Factors 3 and 4. Factor 2 was negatively correlated with Factor 4. Factor 2 scores were correlated with the latitude of the study populations; however, no other factor scores were related to latitude, longitude, or altitude of the study populations. Our results suggest that there is an underlying structure to the life histories of *S. undulatus* that may constrain or limit both local adaptations and proximate environmental effects.

† † †

Life history theory has often predicted and sometimes assumed that certain life history traits are linked to other life history traits (see Sibly, 1991; Stearns, 1976, 1989). Linkage and correlations among individual traits can ultimately determine the direction of and possibly the extent to which life history strategies can evolve (see Ricklefs, 1991; Smith, 1991). For example, if two traits are correlated, selection on one trait will influence the other trait and through a network of

interrelated traits the entire life history strategy will be influenced. Therefore, a key to understanding the evolution of life history strategies is the identification of covariation in life history traits.

In this study we consider the covariation of life history traits in the eastern fence lizard, *Sceloporus undulatus*, one of the most-studied lizards in North America. Its life history across its geographical range has been particularly well studied, and more importantly has been the subject of experiments aimed at identifying sources of life history variation among populations (e.g., Ferguson and Talent, 1993; Niewiarowski, 1995, Niewiarowski and Roosenburg, 1993). Several reviews have considered correlations among life history traits (primarily reproductive traits) among populations (Adolph and Porter, 1993; Dunham et al., 1988; Gillis and Ballinger, 1992; Niewiarowski, 1994; Tinkle and Ballinger, 1972). Most of these studies have attempted to determine the source of differences in life history traits among populations. Here we focus on similarities and correlations in traits rather than differences in traits. We attempt to determine if certain life history traits in *S. undulatus* are consistently correlated with other life history traits (i.e., if there are suites of traits). Since life history variation among populations may be in part the result of adaptation to local environmental conditions (see Ballinger, 1983) or proximate environmental differences (see Adolph and Porter, 1993), we also consider whether these suites of traits are correlated with environmental parameters.

We ask the following questions: (1) Are there suites of life history traits apparent in *S. undulatus*?, and (2) Are there relationships between suites of life history

Table 1. Biotic characters for 14 populations of *Sceloporus undulatus* from across its range in North America. Data were gathered from the literature.

	Clutch Size	Clutches per Year	Eggs per Year	Egg Mass	Relative Clutch Mass	SVL	Age at Maturity	Size at Maturity	Adult Survivorship	Survivorship to Maturity	Relative Egg Mass	Adult BM
South Carolina ¹	7.4	3	22	0.33	0.23	63	12	55	0.49	0.11	0.031	10.6
Ohio ¹	11.8	2	24	0.35	0.25	75	20	66	0.44	0.03	0.021	16.6
Mississippi ¹	9.4	2	19	0.36	0.24	67	10	58	0.32	0.18	0.026	15.5
Alabama ³	8.3	3	25	0.28	0.23	72	12	60	0.12	0.18	0.028	10.0
Kansas ⁴	7.0	2	14	0.26	0.28	57	12	47	0.27	0.14	0.040	6.5
Texas ¹	9.5	3	29	0.22	0.27	57	12	47	0.11	0.06	0.028	7.8
Nebraska ⁵	5.5	2	11	0.23	0.33	55	9.5	45	0.33	0.12	0.060	3.8
México ⁶	10.0	3	30	0.23	0.20	63	10	58	0.41	0.09	0.020	12.2
E. Colorado ⁷	10.8	2	22	0.32	0.34	72	20.5	62	0.35	0.10	0.031	10.3
New Mexico ⁸	7.2	3	22	0.29	0.22	63	18	53	0.32	0.02	0.030	9.7
desert New Mexico ⁸	9.9	4	40	0.24	0.21	68	12	54	0.20	0.03	0.021	11.4
W. Colorado ¹	7.9	2	16	0.42	0.23	70	20.5	58	0.37	0.11	0.029	14.5
Arizona ⁹	8.3	3	25	0.29	0.22	65	11.5	59	0.24	0.07	0.026	11.2
Utah ¹⁰	6.3	3	19	0.36	0.21	69	22.8	58	0.48	0.05	0.033	10.9

¹Tinkle and Ballinger (1972), ²Parker (1994), ³McKinney (1982), ⁴Ferguson et al. (1980), ⁵Ballinger et al. (1981), ⁶Gadsen and Aguirre (1993),⁷Gillis and Ballinger (1992), ⁸Vinegar (1975), ⁹Tinkle and Dunham (1986), ¹⁰Tinkle (1972)

Table 2. Factor analysis for biotic characters listed in Table 1 for 14 populations of *Sceloporus undulatus*. See text for explanation of characters. Boldface indicates relatively strong loading on factor.

	Factor 1	Factor 2	Factor 3	Factor 4
Eigenvalue	4.76	3.06	1.30	1.01
Percent variation explained	31.2	17.0	24.1	12.0
Factor weights				
Clutch size	0.921	0.143	-0.205	0.157
Clutches per year	0.012	-0.690	-0.412	0.440
Eggs per year	0.535	-0.460	-0.546	0.452
Egg mass	0.294	-0.037	0.878	-0.207
Relative clutch mass	-0.186	0.963	-0.124	-0.052
Snout-vent length	0.748	-0.090	0.460	0.058
Age at maturity	0.211	0.159	0.757	0.458
Size at maturity	0.794	-0.110	0.458	-0.006
Adult survivorship	0.010	0.012	0.630	0.045
Survivorship to maturity	-0.067	0.178	-0.084	-0.846
Relative egg mass	-0.802	0.494	0.036	-0.160
Adult female body mass	0.783	-0.298	0.441	-0.102

traits and abiotic environmental characters?. To determine if suites of life history traits exist in *S. undulatus*, we used factor analysis (see James and McCulloch, 1990; Reyment and Jöreskog, 1993) which generates multiple factors that are linear combinations of variables that explain a portion of the total variation in the data in question. In a sense, factor analysis reduces several potentially correlated variables into a smaller number of variables (i.e., factors). Gillis and Ballinger (1992) used principal component analysis to analyze life history variation in *S. undulatus*; however, factor analysis appears to be more appropriate to understand the intercorrelations between traits. The goals of each analysis are different: principal component analysis explains the greatest amount of variation in the variables in question using the smallest number of components, whereas factor analysis is used to recognize correlations among variables (see James and McCulloch, 1990; Reyment and Jöreskog, 1993). Therefore we use factor analysis to examine correlations in the life histories of *S. undulatus* from across its range with the goal of determining whether common suites of life history traits exist in this species.

METHODS

Data were gathered from published accounts of the life history traits of 14 populations of *S. undulatus* (Table 1). Variables included: (1) clutch size, (2) number of clutches produced in a year, (3) number of eggs per year, (4) mean egg mass (g), (5) relative clutch mass (mean total clutch mass/mean female body mass), (8) size (snout-vent length, SVL) at maturity of females (mm), (9) adult female annual survivorship, (10)

survivorship to maturity (hatching to maturity), (11) relative egg mass (mean egg mass/mean female body mass), and (12) mean body mass (BM) of adult females (g). Where possible data on longitude, latitude, and altitude (m) were taken from the original studies, otherwise, they were based on data taken from geographic atlases.

We conducted factor analyses using SYSTAT for the Macintosh (Systat Inc., 1989). Results of the varimax rotation technique are reported, which were qualitatively the same as results obtained using equamax and quartimax rotation techniques. Factors were considered to be relevant and useful when the eigenvalue was > 1. Factors are numbered as numbered by the SYSTAT program, and reflect the percent variation explained by the unrotated factor analysis and are based on the size of the eigenvalue. Factor weights were used to generate factor scores.

RESULTS

Biotic factors

The factor analysis resulted in the generation of four factors (Table 2). The first factor explained 31.2% of the variance. The primary biotic characters loading on factor 1 (i.e., characters having high factor weights) were (in order of absolute loading) clutch size, relative egg mass, size at maturity, adult female body mass, snout-vent length. The number of eggs per year was somewhat heavily loaded on factor 1, but much less strongly than the other biotic parameters just listed. Relative egg mass had a negative loading, whereas all the other variables had positive loadings.

The second factor explained 17.0% of the variance. The major loadings on this factor were relative clutch mass and the number of clutches per year. Relative clutch mass was positively loaded, but the number of clutches per year was negatively loaded.

Factor 3 explained 24.1% of the variation. The major positive loading variables were egg mass, age at maturity, and adult survivorship. The number of eggs per year was negatively loaded on factor 3, but as in factor 1, the strength of this loading was lower than the other major variables.

The final factor (factor 4) consisted of a single strongly and negatively loading variable, survivorship to maturity. This factor explained nearly 12% of the variance.

Relationships among factors and environmental parameters

In several cases, factor scores were significantly

Table 3. Correlations between the four factor scores for the 14 populations of *Sceloporus undulatus*.

		r^2	P	slope
Factor 1	Factor 2	0.53	0.003	-0.23
	Factor 3	0.34	0.027	0.38
	Factor 4	0.53	0.003	0.20
Factor 2	Factor 3	0.01	0.73	
	Factor 4	0.66	0.0004	-0.72
Factor 3	Factor 4	0.02	0.63	

related to each other (Table 3). Factor 1 was negatively related to factor 2, and positively related to factor 3 and factor 4 (Table 3). Factor 2 was negatively correlated with factor 4, but was not related to factor 3 (Table 3). There was no relationship between factor 3 and factor 4 (Table 3).

Factor 2 scores were significantly and positively correlated with the latitude of the study populations ($N = 14$, $r^2 = 0.46$, $P = 0.0073$; $y = -49.7 + 0.76x$). However, latitude was not significantly related to any of the other factor scores ($P > 0.10$ in all 3 cases). No factor scores were correlated to the longitude of the study populations ($P > 0.35$ in all 4 cases). Altitude of the study population also did not have any significant relationships with any of the factor scores ($P > 0.25$ in all 4 cases).

DISCUSSION

The results of our factor analysis suggest that there are indeed several suites of correlated traits in *Sceloporus undulatus*. The first factor presumably reflects the importance of body size (SVL and body mass) in lizard life histories, especially the effects on clutch size and size at maturity. Several previous studies on the life histories of lizards, and reptiles in general, have demonstrated the importance of body size in interspecific as well as intraspecific life history variation (Gillis and Ballinger, 1992; Miles and Dunham, 1992; Tinkle and Ballinger, 1972). In addition to body size, body shape may also be playing a role, especially if foraging mode differs among populations (see Vitt and Congdon, 1978).

Our second factor reflects an apparent correlation between the number of clutches per year and relative clutch mass (an index of energy invested in a clutch of eggs). The relationship between these two variables is negative (i.e., number of clutches per year had a negative loading, whereas RCM had a positive loading). Thus a large quantity of energy invested in a single clutch may reduce the production of future clutches.

The third factor had strong positive loadings on egg mass, age at maturity, and adult survivorship. The only major loading on factor 4 was survivorship to maturity. This single variable factor explained 12% of the variation in *S. undulatus* life history variation among populations. The fact that this factor is significant supports the contention that survivorship to maturity is a critical life history parameter (Ballinger, 1983; Cole, 1954; Dunham et al., 1988; Tinkle, 1969; Tinkle et al., 1970). Indeed, work that has attempted to explain differences in two populations of *S. jarrovi* at different elevations strongly suggests that survivorship to maturity may have a strong role in the evolution of growth and age at maturity (Ballinger, 1979; Ballinger et al., in press; Smith et al., 1993).

In addition to the relationships of variables within a factor, factors are also related to some, but not all other, factors. That factor 1 is positively correlated with factors 3 and 4, and negatively with factor 2 again stresses the importance of body size in the generation of life history variation in lizards. The only other significant correlation between factors was the negative relationship between factors 2 and 4, which suggests that there may be a negative relationship between survivorship to maturity and relative clutch mass.

Factor scores do not appear to be influenced by longitude and altitude, which is somewhat surprising considering the influence of altitude on some aspects of lizard life histories (e.g., Grant and Dunham, 1990; Smith and Ballinger, 1994). Latitude was significantly related to factor 2 only (relative clutch mass and number of clutches per year). Lower latitudes presumably allow longer annual activity periods (e.g., for lizards see Adolph and Porter, 1993). Longer annual activity periods would in turn allow lizards in southern populations to produce more clutches per year (assuming the time needed to produce a clutch does not vary among populations). Such a trend has been observed in other reptiles such as the painted turtle, *Chrysemys picta* (Iverson and Smith, 1993).

Our results point to an underlying structure to the life histories of *S. undulatus* throughout its range that is consistent with many basic assumptions or findings about the source of life history variation in organisms in general, such as a trade-off between quantity and quality of propagules, and the importance of survivorship to maturity as a life history trait. However, our results do not necessarily suggest that the variation between populations of *S. undulatus* can be explained solely on the basis of local adaptation or solely on the basis of proximate environmental variation (see Ballinger, 1983). Our results do suggest that local adaptation and proximate environmental variation op-

erate within a broader framework that may constrain the direction and extent of life history variation through the correlation of suites of traits (e.g., the factors). Recent research has begun to focus on experimentally testing and partitioning the sources of life history variation in *S. undulatus* (e.g., Ferguson and Talent, 1993; Niewiarowski, 1995; Niewiarowski and Roosenburg, 1993), but this is proving to be a very difficult task despite a relative plethora of data (see Niewiarowski, 1994). Future research using more manipulative methods (e.g., Landwer, 1994; Sinervo and Huey, 1990; Sinervo et al., 1992) will be necessary to examine how the interplay among traits may vary between populations, and how this in turn contributes to intraspecific life history variation. In addition, a definitive phylogeny of these populations would be very useful in assessing the potential influences of phylogeny in constraining or influencing life history evolution in *S. undulatus*.

ACKNOWLEDGMENTS

Comments by P. Niewiarowski, J. Rettig, and several anonymous reviewers improved primitive versions of this manuscript. We thank C. Garbin for suggesting the use of factor analysis on this data set. Data compilation was aided by S. Jones. Some financial support provided by an NSF Predoctoral Fellowship to GRS at the University of Nebraska, as well as some logistic support from the Kellogg Biological Station, Michigan State University to GRS during data analysis and manuscript preparation.

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