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PHYLOGENETIC COMPARATIVE ANALYSIS OF LIFE-HISTORY VARIATION AMONG POPULATIONS OF THE LIZARD *SCELOPORUS UNDULATUS*: AN EXAMPLE AND PROGNOSIS

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Abstract.—Over the past 15 years, phylogenetic comparative methods (PCMs) have become standard in the study of life-history evolution. To date, most studies have focused on variation among species or higher taxonomic levels, generally revealing the presence of significant phylogenetic effects as well as residual variation potentially attributable to adaptive evolution. Recently, population-level phylogenetic hypotheses have become available for many species, making it possible to apply PCMs directly to the level at which experiments are typically used to test adaptive hypotheses. In this study, we present the results of PCMs applied to life-history variation among populations of the widespread and well-studied lizard *Sceloporus undulatus*. Using *S. undulatus* (which may represent four closely related species) as an example, we explore the benefits of using PCMs at the population level, as well as consider the importance of several thorny methodological problems including but not limited to nonindependence of populations, lack of sufficient variation in traits, and the typically small sample sizes dictated by the difficulty of collecting detailed demographic data. We show that phylogenetic effects on life-history variation among populations of *S. undulatus* appear to be unimportant, and that several classic trade-offs expected by theory and revealed by many interspecific comparisons are absent. Our results suggest that PCMs applied to variation in life-history traits below the species level may be of limited value, but more studies like ours are needed to draw a general conclusion. Finally, we discuss several outstanding problems that face studies seeking to apply PCMs below the species level.

Key words.—Independent contrasts, life history, phrynosomatid, phylogenetic comparative method, *Sceloporus undulatus*.

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Sparked by comparative studies of mammals (Stearns 1983) and reptiles (Stearns 1984; Dunham and Miles 1985; Miles and Dunham 1992), the analysis of phenotypic variation using phylogenetic comparative methods (PCMs) has become a dominant theme in studies of the evolution of life histories. The growth of phylogenetic comparative studies has been fueled by a rapid increase in the diversity of analytical techniques along with an unprecedented availability of molecular phylogenetic hypotheses (Losos 1999). Traditional (nonphylogenetic) comparative approaches have been virtually replaced by phylogenetic comparative analyses as a means of testing evolutionary hypotheses, advancing the role of comparative methods as a powerful complement to experimental methods (Doughty 1996).

The original goal of phylogenetic comparative analysis of life-history variation was to account for phylogenetic relatedness when estimating and interpreting patterns of covariation among life-history traits (Dunham and Miles 1985; Harvey and Clutton-Brock 1985; Miles and Dunham 1992). When taxa share suites of life-history traits, traditional comparative analyses do not distinguish between the sharing of traits due to descent from a common ancestor versus the sharing of traits due to a common response to similar selective environments (Felsenstein 1985; Miles and Dunham 1992). Consequently, a phylogenetic approach has helped move forward studies of life-history variation by allowing more rigorous tests of major theoretical predictions or assumptions. In general, phylogenetic comparative analyses of life-history variation at interspecific and higher taxonomic levels have found evidence for significant phylogenetic effects (i.e., similarity of traits due to descent), but also significant residual variation (i.e., response to selective environments and plasticity) after accounting for phylogenetic effects (see e.g., Miles and Dunham 1992).

Clearly, phylogenetic comparative analyses at the interspecific level have provided and will continue to provide insight into the evolution of life histories (Stearns 2000; Roff 2002). However, whether such analyses are likely to yield significant insights about life-history evolution at lower levels remains to be seen. In principle, life-history theory stands to gain substantially from the application of complementary approaches (comparative and experimental) at the interface between populations and species. That is, experimental tests of the sources of life-history variation among populations (e.g., transplant and common garden experiments) can help reveal the putative role of contemporary selective environments, but interpretation of the adaptive significance of particular patterns of population divergence/similarity is ultimately constrained or facilitated by our understanding of the phylogenetic history of the populations (Wanntorp et al. 1990; Niewiarowski 1994; Niewiarowski 2001). At a time when PCMs are increasing in diversity and capability (see review by Martins 2000) and molecular phylogenies of populations are becoming increasingly common (Losos 1999), there has never been a greater opportunity to answer questions about the role of natural selection in the evolution of life histories by bringing together comparative and experimental analyses at the interface between species and populations.

In light of significant advances in molecular techniques and comparative analyses, our overarching goal in this paper is to raise a simple question: Is it important (or even useful) to apply PCMs to the analysis of life-history variation below the species level (i.e., variation among populations)? To address this question, we provide an example of the application of PCMs to the study of life-history variation among populations of the eastern fence lizard *Sceloporus undulatus*. Clearly, no single study will be able to answer the question we raise; however, *S. undulatus* has several characteristics suggesting our example will offer a prognosis for the utility of phylogenetic comparative analyses of life-history variation at the population level. First, life-history variation among populations has been documented (using both comparative and experimental approaches) for an uncommonly large number of populations (nearly 20 over the last 30 years of study), and this variation is rather extensive (reviewed by Niewiarowski 1994). Second, a phylogenetic hypothesis for 56 populations of *S. undulatus* has recently become available (Leaché and Reeder 2002), providing a detailed phylogeographic context in which to examine patterns of life-history variation in extant populations. So, whereas phylogenetic comparative study below the species level might be feasible for many taxa, those like *S. undulatus* are most likely to help bridge the gap in temporal and spatial scales between micro- and macroevolutionary studies of life histories.

In addition to providing a phylogenetic hypothesis, Leaché and Reeder (2002) argue that *S. undulatus* should be recognized as consisting of four monophyletic clades proposed as ''evolutionary species'' (Figure 1). Phylogenetic comparative methods do not explicitly recognize taxonomic rank as a formal component of analysis; therefore, our use of relationships hypothesized by Leaché and Reeder (2002) is independent of their specific recommendations for species delimitation. However, a central rationale of our study is that it applies PCMs below the species level, and although all of the populations in our study likely do not belong to a single species, there is considerable intraspecific analysis in our study. Following Leaché and Reeder (2002), our dataset is comprised of populations belonging to four different proposed species (clades): an eastern clade (A; six populations), western clade (B; four populations), central clade (C; two populations), and a southwestern clade (D; two populations). Therefore our current analysis of life-history variation among ''populations'' of *S. undulatus* (sensu lato) falls squarely at the interface of populations and species. For the purposes of simplicity, and because proposals for taxonomic revisions for *S. undulatus* (sensu lato) will benefit from more data (see also Miles et al. 2002), we refer to populations of *S. undulatus* (sensu lato) simply as *S. undulatus*.

Although the development and use of PCMs have traditionally been limited to analyses at the interspecific and higher taxonomic levels, for as many as 10 years the leading methodologies (e.g., independent contrasts and phylogenetic autocorrelation) have provided techniques for incorporating within-species variation (cf., Garland et al. 1992; Edwards and Kot 1995; Martins and Hansen 1997). There are a few notable exceptions to the rule that comparative analyses predominantly focus on strictly interspecific variation, including a study of sexual dichromatism among populations of Yarrow's spiny lizard, *Sceloporus jarrovii* (Wiens et al. 1999), a population-level comparative study of sexual size dimorphism among closely related species of horned lizards, *Phrynosoma* (Zamudio 1998), and a comparative analysis of morphology and group size in grey-crowned babblers, *Pomatostomus temporalis* (Edwards and Kot 1995). Our study shares with these a desire to call attention to the role that PCMs can play at taxonomic levels below those at which they have been traditionally applied. Perhaps a more novel aspect of our study is that we explicitly ask whether patterns of variation in life-history traits that have been well established by interspecific comparative analyses are apparent at lower taxonomic levels: a question that has garnered relatively little attention in the life-history literature. So, although we are

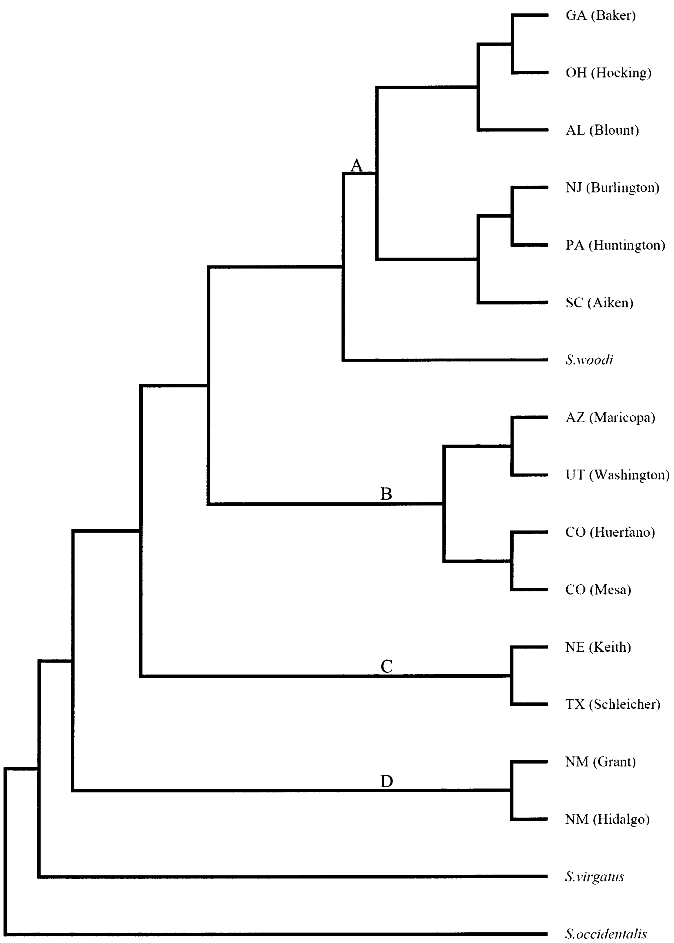

FIG. 1. Phylogeny of *Sceloporus undulatus* populations used in the comparative analysis. Our tree is based on a larger tree of 56 populations (Leaché and Reeder 2002); populations without life-history data were pruned and the tree was redrawn. A, B, C, and D mark the bases of the eastern, western, central, and southwestern clades, respectively, which were proposed to be separate species by Leaché and Reeder (2002). Populations of *S. undulatus* are identified by state and county of mtDNA sample collection.

not the first to apply PCMs to a set of taxa that is a mixture of species and populations, such studies are nevertheless rare.

Given our overarching goal, we were particularly interested in the following questions: (1) Are there patterns of covariation in life-history traits among populations of *S. undulatus* that are predicted by life-history theory and that are observed at higher taxonomic scales? (2) Do two different methods of phylogenetic comparative analysis yield different results? (3) Do the results of our analysis suggest a prognosis for applying PCMs below the species level?

MATERIALS AND METHODS

Study Species

The eastern fence lizard, *Sceloporus undulatus*, is widely distributed throughout the United States and northern Mexico. Life histories have been documented in many disjunct populations throughout its range, and some life-history phenotypes vary more than twofold among populations (reviewed by Tinkle and Ballinger 1972; Tinkle and Dunham 1986; Gillis and Ballinger 1992; Niewiarowski 1994). Comparative, experimental, and theoretical studies have suggested many hypotheses (adaptive and nonadaptive) to account for this geographic variation in life histories (Stearns and Crandall 1981; Grant and Porter 1992; Adolph and Porter 1993, 1996; Niewiarowski 1994, 2001; Angilletta 2001). Proposed adaptive hypotheses are all based on general expectations of covariation among traits based on traditional life-history theory. Until now comparative studies of *S. undulatus* have not benefited from the incorporation of a rigorous phylogenetic hypothesis.

Patterns of Covariation Expected under Life-History Theory

A review of life-history theory is beyond the scope of this paper (see Stearns 1992 and Roff 2002 for comprehensive reviews), but to understand our expectations for the covariation among life-history phenotypes, we note some fundamental aspects of the theoretical and empirical findings relevant to our analysis. Life-history theory is formulated to explain how traits such as body size, life span, and reproductive output evolve by natural selection. Most theory is based on two guiding principles: optimality and trade-offs (Stearns 2000). Although the predictions of specific models vary, the assumptions of optimality and trade-offs have given rise to a set of fairly ubiquitous and simple predictions about the covariation among life-history phenotypes: a pattern that has been referred to as the ''slow-fast'' continuum (Stearns 1983). On the slow end of this continuum are individuals exhibiting delayed maturity, large body size, small clutches, large offspring, and high survivorship; the fast end is characterized by individuals exhibiting the opposite suite of traits.

Several theories predict relationships among life-history phenotypes that are consistent with the notion of a slow-fast continuum. Certain pairwise relationships are expected from the assumption of intraindividual trade-offs (Stearns 1989) or from demographically based theories (Gadgil and Bossert 1970; Hirshfield and Tinkle 1975; Law 1979; Michod 1979). For example, in the case of intraindividual trade-offs, it is commonly expected that allocating energy to offspring in a single reproductive episode will lead to a negative relationship between the number and size of offspring (e.g., Sinervo 1999; Ernsting and Isaaks 2000; Jordan and Snell 2002), which can be detected through experimental manipulation of offspring size or number (e.g., Sinervo 1999; Oksanen et al. 2001; Williams 2001). Similarly, the allocation of energy to reproduction may result in a decrease in energy available for maintenance, activity, and growth, which could lead to reduced survival to the next reproductive episode (reviewed by Reznick 1985; Schwarzkopf 1993; Landwer 1994; Miles et al. 2000). Consequently, a negative relationship between the magnitude of reproduction (as estimated by clutch size, clutch frequency, or reproductive effort) and survivorship is expected. In the case of demographically driven relationships, a negative relationship between reproduction and survivorship is expected because an increase in the rate of extrinsic mortality favors an increase in reproductive effort (Gadgil and Bossert 1970; Hirshfield and Tinkle 1975; Law 1979; Michod 1979). Finally, some recent demographically based theory predicts a positive relationship between age at maturity and adult survivorship (Charnov 1993). For our study, we narrowed the range of possible pairwise relationships to those that have been most frequently reported in the theoretical and empirical literature (see Table 2). Although we recognize that these relationships may not always be detected by comparative analysis, the expectation that they exist is not a point of contention.

Life-History Data

We compiled life-history data for *S. undulatus* from published and unpublished sources (Table 1). Although some kinds of demographic data have been collected for more populations, we restricted our analysis to 14 populations for which a complete set of demographic data has been compiled. We also included one population of *S. woodi* and a single population each of *S. virgatus* and *S. occidentalis* (Leaché and Reeder 2002). We assumed that variation among taxa included in the analysis represented population-specific differences not attributable to simple phenotypic plasticity arising from temporal variation in environmental factors. We cannot directly test the validity of this assumption, but several experimental studies with *S. undulatus* have demonstrated that there are significant population-specific sources of variation in life-history traits that are not attributable to proximate environmental effects (Ferguson and Brockman 1980; Ferguson and Talent 1992; Niewiarowski and Roosenburg 1993).

Phylogeny

The phylogeny used in this study (Figure 1) was based on a Bayesian analysis of 3688 base pairs of mitochondrial DNA (mtDNA) from 56 populations of *S. undulatus* and nine closely related species (Leaché and Reeder 2002). Branch lengths were calculated using PAUP* Version 4.0b8 (Swofford 2001) on a pruned phylogeny containing only those populations included in the current study, and including only those sequences that were available for all individuals. Estimates of branch length were calculated using maximum parsimony, but maximum likelihood (ML) produced similar estimates.

TABLE 1. Variables for all *Sceloporus* populations used in our phylogenetic comparative analysis of life history. Data are means for each population reported in the literature. Source of data is listed in the last two columns.

Locality	Size at maturity (mm)	Average size (mm)	Age at maturity (mo)	Egg mass (g)	Clutch size	Clutches per year	Clutch mass (g)	Eggs per year	Adult survi-vorship	Life-history source	mtDNA source
S. occidentalis	70	84	22	0.50	11.2	1	5.60	11.2	0.70	Ruth 1955	San Diego County, CA
S. virgatus	47	57	10	0.23	9.5	1	2.18	9.5	0.50	Vinegar 1975a	Cochise County, AZ
S. woodi	47	54	10.5	0.25	4.1	3	1.02	12.3	0.09	Hokit et al. 2001; D.G. Hokit, unpubl. data	Highlands County, FL
S. undulatus											
Aiken County, SC	55	63	12	0.33	7.4	3	2.44	22.2	0.49	Tinkle and Ballinger 1972	Aiken County
Baker County, GA	52	62	12	0.33	7.6	3	2.51	22.8	0.07	Crenshaw 1955	Hamilton County
Blount County, AL	60	72	12	0.28	8.3	3	2.32	24.9	0.12	McKinney 1982	Madison County
Burlington County, NJ	60	73	20	0.36	8.9	2	3.20	17.8	0.44	Niewiarowski 1994; P. H. Niewiarowski, unpubl. data	Burlington County
Grant County, NM	53	63	18	0.29	7.2	3	2.09	21.6	0.32	Vinegar 1975b	Grant County
Hidalgo County, NM	54	68	12	0.24	9.9	4	2.38	39.6	0.20	Vinegar 1975b	Hidalgo County
Hocking County, OH	66	75	20	0.35	11.8	2	4.13	23.6	0.44	Tinkle and Ballinger 1972	Muskingum County
Huerfano County, CO	62	72	20.5	0.32	10.8	2	3.46	21.6	0.35	Gillis and Ballinger 1992	Costillo County
Huntingdon County, PA	62	72	22	0.42	11.0	2	4.62	22.0	0.57	J. Matter, unpubl. data	Huntingdon County
Keith County, NE	45	55	9.5	0.23	5.5	2	1.27	11.0	0.33	Jones et al. 1987	Keith County
Mesa County, CO	58	70	20.5	0.42	7.9	2	3.32	15.8	0.37	Tinkle and Ballinger 1972	Uintah County, UT*
Maricopa County, AZ	60	65	11.5	0.29	8.3	3	2.41	24.9	0.24	Tinkle and Dunham 1986	Pinal County
Schleicher County, TX	47	57	12	0.22	9.5	3	2.09	28.5	0.11	Tinkle and Ballinger 1972	Kimbal County
Washington County, UT	58	69	22.8	0.36	6.3	3	2.27	18.9	0.48	Tinkle 1972	Washington County

* The only population for which life-history and mtDNA data were collected from neighboring counties located in two different states.

TABLE 2. Correlation coefficients and significance level for five planned comparisons of life-history traits of *Sceloporus undulatus*. Expected relationship refers to the direction of the correlation expected based on previous empirical studies or on life-history theory.

		Independent contrasts			Phylogenetic autocorrelation		
	Expected relationship	Observed relationship	Squared correlation coefficient (R^2)	Significance (P)	Observed relationship	Squared correlation coefficient (R^2)	Significance (P)
Clutch size vs. adult survival	negative	none	0.015	0.635	none	0.067	0.164
Age at maturity vs. adult survival	positive	positive	0.254	0.039	none	0	0.618
Egg mass/year vs. adult survival	negative	none	0.018	0.612	none	0.133	0.083
Age at maturity vs. clutch size	negative	none	0.017	0.616	none	0	0.548
Egg mass vs. clutch size	negative	none	0.022	0.574	none	0.083	0.138

For ML calculations of branch lengths, the GTR + I + Γ model was used (selected using the program Modeltest; Posada and Crandall 1998) with the ML parameter values from Leaché and Reeder (2002). Although ML is a superior method for estimating branch lengths, our results should be largely independent of the exact method used because our phylogenetic comparative analyses used branch lengths set to unity to meet assumptions of the methods (see below). Note that another phylogeny based on allozyme variation among 12 populations has recently been published by Miles et al. (2002). Relationships among populations are broadly consistent between Miles et al. (2002) and Leaché and Reeder (2002) but the former phylogeny is less extensive. Although the potential benefits of using multiple unlinked loci (allozymes) as a source of genetic data should not be ignored, given the probable level of divergence of taxa in our study, such data are unlikely to yield as complete a resolution of relationships among populations as a phylogeny based on variation in mtDNA (Moore 1995; Wiens and Penkrot 2002). Furthermore, sample localities for phylogenetic analyses in Leaché and Reeder (2002) were coordinated to correspond with sample localities for published and unpublished life-history data. In 16 of 17 cases, the localities of populations that were the source of life-history data are not separated from those where mtDNA was sampled by more than a single county (Table 1). Therefore, the phylogeny of Leaché and Reeder (2002) provides the larger and more appropriate dataset for comparative analyses. Nevertheless, a comparative analysis of life-history variation using the phylogeny of Miles et al. (2002) is in progress (D. Miles, pers. comm.).

Comparative Analyses

Methods for comparative analyses have increased rapidly in number over the last five years, helping to rekindle an ongoing debate about which techniques are most appropriate under any given circumstance (Miles and Dunham 1992; Martins and Hansen 1997; Martins 2000; Pagel 2000; Martins et al. 2002). We elected to employ two different approaches in analyzing variation in life-history traits: independent contrasts (Felsenstein 1985) and phylogenetic autocorrelation (Cheverud et al. 1985). These two approaches are at opposite ends of a spectrum of analytical techniques (Gittleman and Luh 1992, 1994), handling phylogenetic effects differently and making different assumptions about evolutionary processes. Because these and other techniques have been extensively described elsewhere (Gittleman and Luh 1994; Wenzel and Carpenter 1994; Garland et al. 1999; Martins 2000; Martins et al. 2002) we restrict our description here to how we carried out analyses.

Independent Contrasts

We used the program COMPARE (Martins 1999) to generate independent contrasts. Prior to analyses, all life-history traits were $\log_{10}$-transformed to improve linearity and homogeneity of variances. We followed the procedures of Garland et al. (1992) in performing the independent contrasts analysis, using plots of the absolute values of standardized independent contrasts versus their standard deviations to diagnose the adequacy of branch lengths. Although there are other diagnostic procedures, none are understood as well (Garland et al. 1999). Body size is an important correlate of life-history trait variation in squamate reptiles (Dunham and Miles 1985; Miles and Dunham 1992), so we regressed contrasts of each trait on contrasts of the average snout-vent length of adults (SVL) and used the residuals (size-adjusted contrasts) in all subsequent analyses (Clobert et al. 1998).

Size-adjusted contrasts were used in two separate but conceptually related analyses. First, we constructed five planned pairwise relationships (linear regressions) to test for significant relationships predicted by life-history theory (see Table 2). Second, we subjected the size-adjusted contrasts to a principal components analysis (PCA) to explore the multivariate space in two dimensions defined by principal components PC1 and PC2. Unrotated factors from the PCA based on the correlation matrix were used to explore whether the set of life-history phenotypes in *S. undulatus* exhibit the covariation predicted by life-history theory (i.e., the slow-fast continuum; Clobert et al. 1998). We used the broken-stick method to determine how many principal components to interpret (Jackson 1993). Two PCAs were performed for both the independent contrasts and the autocorrelation results. First, we did a PCA on the full set of life-history traits excluding adult SVL (clutch frequency, egg mass, age at maturity, annual adult survival, size at maturity, and clutch size). Second, we combined all reproductive traits into a single summary variable (total mass of eggs produced annually) to produce a reduced dataset that provided a better ratio of observations to variables (17:4), which usually improves the performance of PCA (Grossman et al. 1991).

Phylogenetic Autocorrelation

We also used COMPARE (Martins 1999) to perform a phylogenetic autocorrelation analysis of the size-adjusted life-history phenotypes (Cheverud et al. 1985; Gittleman and Luh 1992, 1994). We adjusted life-history traits for size by regressing each trait on SVL. In analyzing the results of the autocorrelation analysis, we checked whether Moran's *I* for each trait varied from its expected value by more than 1.96 standard deviations along small, regular intervals of phylogenetic distance (Gittleman and Kot 1990). Whenever this condition held, we concluded that the trait under consideration had a significant phylogenetic autocorrelation. Subsequent to autocorrelation analyses, we constructed pairwise comparisons and PCA as described for independent contrasts above. In these tests, we used either the standardized value or the phylogenetically corrected value as indicated by the significance of Moran's *I* (Gittleman and Kot 1990; Martins 1999).

Examining Assumptions about Gene Flow

Phylogenetic comparative analyses such as Felsenstein's (1985) independent contrasts assume that the taxa subject to analysis have a phylogenetic history that represents hierarchical descent. When analyses are conducted among species, this assumption is usually not questioned. However, analysis among populations might not satisfy this assumption due to the confounding process of gene flow. For *S. undulatus*, a high degree of genetic substructuring revealed by the analysis of mtDNA (Leaché and Reeder 2002) suggests that gene flow is not high enough to warrant concern about the efficacy of our phylogenetic comparative analyses. Nevertheless, we wanted to bolster confidence in this assumption using all available data. Therefore, we used a quantitative analysis of the life-history traits themselves to determine whether gene flow among populations is likely. Specifically, we used a regression to test a model of isolation by distance that might be expected if gene flow was high enough to make the application of phylogenetic comparative analyses suspect (Thompson 1990). If gene flow among populations is high enough, it should be detectable by regressing the differences between means of a given life-history trait for each pair of populations against the geographic distance separating the populations. Regressions showing a significant positive relationship between the difference in trait means and the geographic distance would cause us to re-evaluate whether we are justified in applying phylogenetic methods to our dataset. Note that if gene flow is very high, isolation by distance might not be revealed by a regression analysis, however, the genetic structuring evident in the phylogeny of Leaché and Reeder (2002) makes extremely high levels of gene flow a very unlikely possibility.

We structured regressions of trait differences on geographic distance in two ways. First, we tested the regressions of all pairwise combinations among populations within the four proposed species, and second, among all pairwise combinations between populations belonging to different proposed species (based on the recommended taxonomy of Leaché and Reeder 2002). The former comparison gives an intraspecific estimate of the importance of gene flow, whereas the latter comparison gives an estimate among populations belonging to different proposed species. Since distances in these regression analyses are not independent, we did not use standard regression statistics to judge statistical significance. Instead, we used Mantel tests to determine whether regression slopes were significant, following methods outlined in Hellberg (1994) and Manly (1991). Lack of a significant positive relationship between difference in life-history traits and geographic distance either within or between proposed species would be consistent with the assumption that gene flow is not confounding our comparative analysis.

RESULTS

Testing the Potential Importance of Gene Flow and Evolutionary Independence of Populations

There were no apparent trends in regressions between difference in life-history traits and geographic distance (Figure 2); pairwise differences in life-history traits appeared to either increase or decrease with distance. Furthermore, within versus between proposed species regressions were not always identical. However, none of these trends even approached significance as judged by Mantel tests (Figure 2). Overall, the regressions are consistent with the assumption that gene flow either within or between proposed species is apparently low. Given these results and the high genetic substructuring revealed in the original phylogeny (Leaché and Reeder 2002), we believe using phylogenetically independent contrasts for this dataset is reasonable.

Relationships Between Life-History Traits: Independent Contrasts

Consistent with other studies of life-history variation in squamates (see review in Dunham et al. 1988), body size expressed as SVL is an important correlate of variation in life-history traits in *S. undulatus*. Contrasts for minimum SVL at maturity, age at maturity, egg mass, clutch size, and total egg mass per year all showed significant regressions on average adult SVL (Table 3). Only the contrasts for clutch frequency and average annual female survival were not significantly related to SVL (Table 3; survival was marginally nonsignificant); all other life-history traits examined were positively related to body size.

Planned pairwise comparisons showed that only one of the relationships between life-history traits (age at maturity vs. adult survival) was significant (Table 2). As expected by theory, age at maturity and adult survival were positively related.

Multivariate analyses (PCA) of seven life-history traits revealed structure in the variation of life-history traits not easily anticipated from the pairwise regressions. Two significant components were identified for both the full and reduced set of life-history traits, explaining a total of 64% and 73% of the variance, respectively, in size-adjusted life-history traits (Table 4; Fig. 3). For all six variables, PC1 represented an axis contrasting survival, age at maturity, and egg size with clutch frequency. When individual measures of reproductive output were combined and expressed as total mass of eggs produced per year, PC1 revealed a clearer trade-off between adult survival and reproduction. The second principal component represented an axis contrasting clutch size and size at maturity with egg mass for the full dataset, and the co-

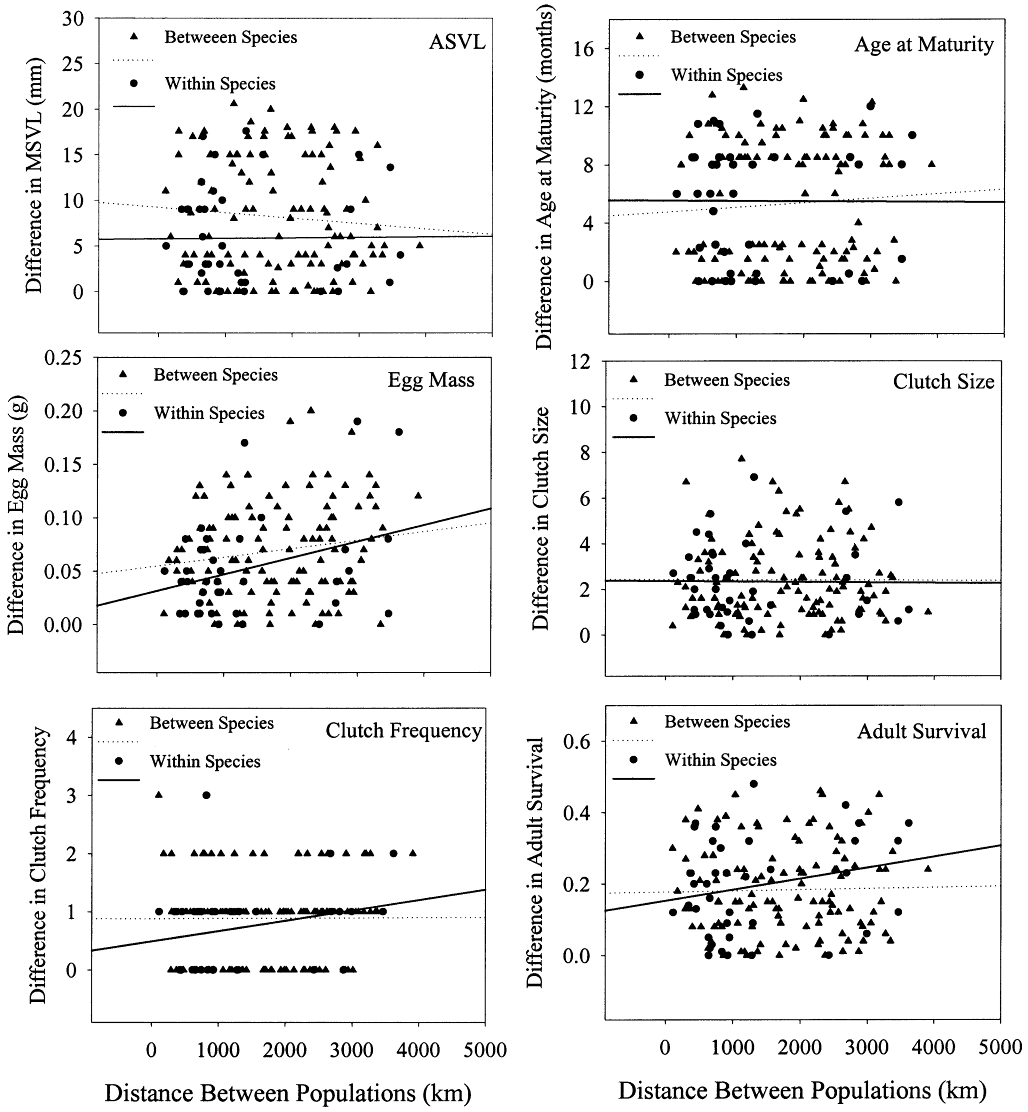

FIG. 2. Geographic distance versus pairwise differences between selected life-history traits. Within and between refer to within versus between sets of analyses described in the text.

variation between size at maturity and reproductive output was preserved in the reduced dataset with combined reproductive traits.

Relationships between Life-History Traits: Phylogenetic Autocorrelation

Of the seven life-history traits included in the analysis, only clutch frequency showed the effects of a significant phylogenetic autocorrelation, consistent with the idea that there is not a significant phylogenetic effect on life-history variation in *S. undulatus*. Using the residuals from the autocorrelation analysis for clutch frequency and the standardized values for the other traits (Martins 1993), regressions revealed none of the expected pairwise relationships. However, there was a trend for a negative relationship between egg mass per year and adult survival (Table 2).

The main axes of variation in life-history traits identified by PCA on the autocorrelation results were very similar to those identified from independent contrasts (Table 4; Fig. 3). For the full set of variables, PC1 contrasted clutch frequency and adult survival, and PC2 contrasted clutch frequency and clutch size. When reproductive traits were combined in the reduced set of variables, adult survival contrasted strongly with egg mass produced per year (PC1), but all traits loaded positively on PC2. Overall, the results of PCAs on the independent contrast and autocorrelation datasets are very comparable.

DISCUSSION

Consistent with studies of life-history variation in other vertebrates (Stearns 1983, 1984; Dunham and Miles 1985; Miles and Dunham 1992; Shine and Charnov 1992; Bauwens and Diaz-Uriarte 1997; Clobert et al. 1998), body size is an important correlate of variation in life-history traits of *S. undulatus* (Table 3). However, apart from this general result, our study stands in stark contrast to previous studies in two

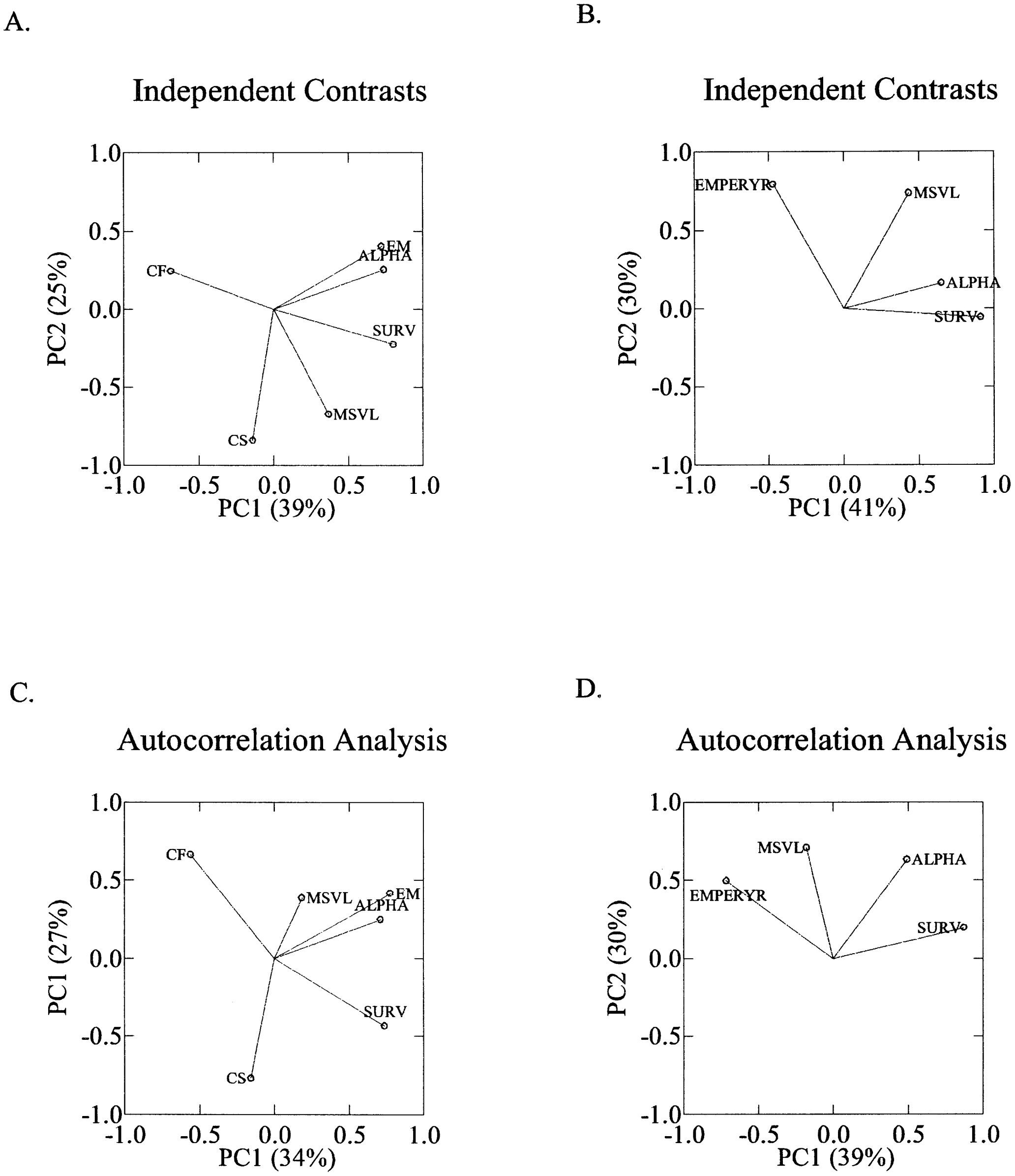

FIG. 3. Principal components analysis of life-history traits of *Sceloporus undulatus*, using the correlation matrix. Factors were not rotated. Reproductive output variables visible in the left panels are combined into gram equivalents per year (egg mass per year). CF, clutch frequency; EM, egg mass; ALPHA, age at maturity; SURV, annual adult survival; MSVL, minimum size at maturity; CS, clutch size.

important ways. First, pairwise relationships among traits that were expected to covary strongly were essentially absent, even though significant covariation was revealed by PCA. Second, phylogenetic effects on life-history variation in *S. undulatus* appear to be unimportant. We draw this conclusion mainly from the lack of significant phylogenetic autocorrelation found in the life-history data; the method of independent contrasts does not speak to this issue. Both of these results have important implications for studying life-history variation within *S. undulatus* and we think they raise important issues for phylogenetic comparative studies of life-history variation at the interface between species and populations. We explore these implications below.

Where Are the Expected Patterns of Covariation?

Our expectation that pairs of life-history traits would covary in predictable ways in *S. undulatus* is based on life-history theory as well as previous empirical studies (including phylogenetic and nonphylogenetic comparative analyses). One of the most pervasive assumptions of life-history theory is that of the cost of reproduction (Bell and Koufopanou 1985; Reznick 1985; Roff 2002; Stearns 1992). We expected to see evidence of two fundamental trade-offs given a cost of reproduction: clutch size versus adult survival and egg mass per year versus adult survival. However, the independent contrasts showed no evidence of a trade-off between survival and reproductive output (Table 2), nor did our analysis after phylogenetic autocorrelation. Similarly, clutch size and egg size, and age at maturity and fecundity (clutch size) were not negatively related (Table 2). A significant positive relationship between age at maturity and adult survival was detected for independent contrasts but not for the phylogenetic autocorrelation dataset. One reasonable interpretation of the difference between PCMs in detecting this trade-off is that the trade-off itself is not particularly strong. Consequently, we suggest there is only partial support for an important dimension of covariation implicit in the slow-fast continuum.

The lack of support for all but one of the expected relationships (age at maturity vs. survival) is surprising and our inability to detect patterns of covariation predicted by theory and by comparative studies may have several explanations. First, the degree of covariation in traits may be too small for there to be a signal; perhaps too little time has elapsed since divergence of populations for selection to have produced coadapted suites of traits. Second, but not unrelated, our sample size (number of populations) may be too small to detect the bivariate relationships we expected from theory. To consider the likelihood that either or both of these explanations apply to our results, we compare our study to similar studies performed on other squamate lineages (including those with similar and larger samples sizes).

In a study of covariation of life-history traits among 18 species of lizards in the family Lacertidae, Bauwens and Diaz-Uriarte (1997) found significant negative relationships between egg mass and clutch size, as well as egg mass and clutch frequency. Both results are consistent with expectations from life-history theory, based on assumptions about physiological trade-offs. However, neither relationship was observed in our study. We also failed to detect a consistent significant positive relationship between age at maturity and adult survival (significant for independent contrasts but not phylogenetic autocorrelation), again in contrast to the highly significant relationship detected by Bauwens and Diaz-Uriarte (1997). Consequently, using approximately the same sample size but running their analysis at the interspecific level (in a different family of lizards), Bauwens and Diaz-Uriarte (1997) found substantial evidence of predicted pairwise relationships between several life-history traits whereas we did not.

Clearly the difference between their study and ours is not simply that the range of variation in life-history traits among species of lacertids is greater than that among populations of *S. undulatus*. By several measures, variation in life-history traits is largely comparable in both studies. For example, coefficients of variation (CV) for seven traits common to both studies are similar, although there was substantially greater variation in body size in their study (Table 5). In fact, although the CV provides a simple comparison of life-history variation between groups, it may actually be inadequate because the CV includes the effect of body size and body size drives much of the variation in life-history traits in both studies (Table 3; Bauwens and Diaz-Uriarte 1997, table 2). An alternative estimate of variation can be obtained by comparing the root mean square errors (RMSE) for each trait after they have been regressed on average body size; this reveals variation in each trait that remains after body size effects are removed. The RMSE estimates the standard deviation of the residual error in the model and therefore represents variation not explained by body size. Note that with the exception of egg mass, RMSE for *S. undulatus* are similar to or greater than the RMSE for the lacertids (Table 5). Comparison of RMSE supports the view that our inability to detect expected relationships among life-history traits in *S. undulatus* is not a result of insufficient variation in life-history traits among populations. Apparently, a lack of variation is not limiting the detection of expected trade-offs among traits.

Another possibility is that processes leading to variation in life-history traits among populations masks or obscures the expected trade-offs. Several authors have pointed out that trade-offs occurring within individuals will be difficult to detect via comparative analyses (van Noordwijk and de Jong 1986; Pease and Bull 1988). The problem is that variation among individuals results from two processes: the acquisition of resources and the allocation of those resources to competing functions (e.g., maintenance, activity, growth, and reproduction). Variation in allocation produces the ''signal'' that might be detected through comparative analysis, whereas variation in acquisition causes ''noise'' that can obscure a trade-off. When variation in acquisition among individuals (i.e., the noise) is relatively large and variation in allocation (i.e., the signal) is relatively small, physiological trade-offs will not be detected easily. Thus, the power of a phylogenetic comparative analyses cannot simply be determined by a measure of the total variation in life-history traits, but also de-

TABLE 3. Squared correlations and significance tests from regressions of life-history traits on average adult snout-vent length (SVL) using independent contrasts. Residuals from these regressions were used in subsequent analyses (pairwise correlations and PCAs) as ''size-adjusted'' life-history traits (see Materials and Methods for details). ns, nonsignificant.

Trait	Squared correlation (R^2)	P
Minimum SVL at maturity	0.890	<0.0001
Age at maturity	0.447	0.0028
Egg mass	0.364	0.0079
Clutch size	0.354	0.0089
Clutch frequency	0.007	ns
Survival	0.185	0.0542
Total egg mass per year	0.316	0.0137

TABLE 4. Principal components analysis of independent contrasts and phylogenetic autocorrelation datasets. Analysis was performed on the correlation matrix, and factors are unrotated to simplify interpretation of loadings (see Fig. 3).

	Full dataset		Reduced dataset	
	PC1	PC2	PC1	PC2
Independent contrasts				
Eigenvalue	2.333	1.498	1.667	1.200
% of variance	38.884	24.964	41.685	30.009
Cumulative %	38.884	63.848	41.685	71.694
Phylogenetic autocorrelation				
Eigenvalue	2.024	1.603	1.546	1.180
% of variance	33.727	26.721	41.685	30.009
Cumulative %	33.727	60.448	41.685	71.694

TABLE 5. Means and coefficients of variation for life-history traits of *Sceloporus undulatus* included in this study and for species in the family Lacertidae included in a similar study by Bauwens and Diaz-Uriarte (1997). RMSE is root mean square error (see text for details).

Species group	Size at maturity (mm)	Average size (mm)	Age at maturity (mo)	Egg mass (g)	Clutch size	Clutches per year	Adult survivorship
S. undulatus							
Mean	56.1	66.6	16.0	0.3	8.7	2.5	0.3
CV(%)	12	12	31	24	25	31	54
RMSE	2.160	—	3.360	0.048	1.690	0.770	0.455[1]
Lacertids							
Mean	59.4	71.3	10.9	0.4	5.9	1.6	34.5[2]
CV(%)	38	40	32	47	66	38	42
RMSE	2.49	—	2.31	0.11	1.56	0.54	9.75[1]

[1] The root mean square error is divided by the mean trait value to provide comparable variables.

[2] Adult survivorship was expressed as maximum life span in months.

pends on the potential for variation in acquisition to obscure the expected trade-offs; in other words, the power to detect some of the relationships that we expected may depend on the ratio of the variation in allocation to the variation in acquisition.

How does this phenomenon apply to the apparent existence of trade-offs at the interspecific level and their absence in our study of *S. undulatus*? The trade-offs that we expected could be masked at lower taxonomic levels if either the relative variation in allocation decreases or the relative variation in acquisition increases as one focuses on more closely related taxa. Although both of these possibilities might have played a role in generating the difference between our results and those of Bauwens and Diaz-Uriarte (1997), we believe the former is a more likely explanation than the latter. We expect life-history variation arising from differences in allocation to decrease as the divergence among taxa decreases; that is, allocation should vary less among populations of a species than it does among species, particularly when these belong to nested clades. However, life-history variation arising from differences in acquisition is not likely to increase as one broadens the phylogenetic scope of a comparative analysis, because much of the variation in acquisition among taxa is removed when traits are adjusted for body size. Because body size is highly correlated with the energetic requirements of animals (Nagy 2001), adjusting life-history traits for body size should eliminate an equal portion of the variation at the interspecific and intraspecific levels. Therefore, we predict that the ability to detect trade-offs through comparative analysis decreases as the phylogenetic scope of the comparative analysis decreases.

To see whether the signal-to-noise ratio depends on the phylogenetic scale, we examined the trade-off between the size and the number of offspring. Specifically, we compared the signal-noise ratio for two sets of data: populations of *S. undulatus* and species of Phrynosomatidae, the family to which *S. undulatus* belongs. For this comparison, a reasonable measure of acquisition is the total mass invested in reproduction (i.e., clutch mass), whereas the appropriate measure of allocation is the fraction of clutch mass that is allocated to each offspring (Table 6). The signal-to-noise ratio for the trade-off is proportional to the variation in allocation divided by the variation in acquisition, after both variables have been adjusted for body size. The coefficients of variation (error mean squares divided by the means) of the size-adjusted allocation and size-adjusted acquisition are scale-independent estimates of the signal and noise, respectively, for the trade-off between the size and the number of offspring. We calculated these values for both sets of data using independent contrasts of allocation and acquisition. Contrasts for the Phrynosomatidae were obtained using the phylogenetic hypothesis of Reeder and Wiens (1996), assuming all branch lengths were equal to one.

Overall, the analysis did not support our hypothesis about

TABLE 6. Reproductive characteristics for lizards of the family Phrynosomatidae that were included in our analysis of strategies of acquisition and allocation at different phylogenetic scales (see Fig. 4). When data for two or more populations of a species were available, we used the average values for all populations of each species.

Species	SVL	Egg mass	Clutch size	Clutch mass	Egg mass/ clutch mass	Source
Cophosaurus texanus	64	.27	3.2	0.88	0.31	Sugg et al. 1995
C. texanus	59	.31	3.8	1.18	0.26	Punzo 2000
Sceloporus clarki	102	.66	19.6	12.94	0.05	Tinkle and Dunham 1986
S. graciosus	55	.32	3.8	1.22	0.26	Tinkle 1973
S. merriami	50	.20	4.3	0.86	0.23	Dunham 1981
S. occidentalis	70	.50	11.2	5.60	0.09	Goldberg 1973; Sinervo 1990
S. undulatus	56	.32	8.7	2.86	0.12	see Table 1
S. virgatus	47	.23	9.5	2.19	0.11	Vinegar 1975a
S. virgatus	62	.23	10.2	2.37	0.10	Smith et al. 1995
Urosaurus graciosus	52	.21	4.4	0.93	0.23	Vitt et al. 1978
U. ornatus	50	.14	7.1	0.99	0.14	Tinkle and Dunham 1983

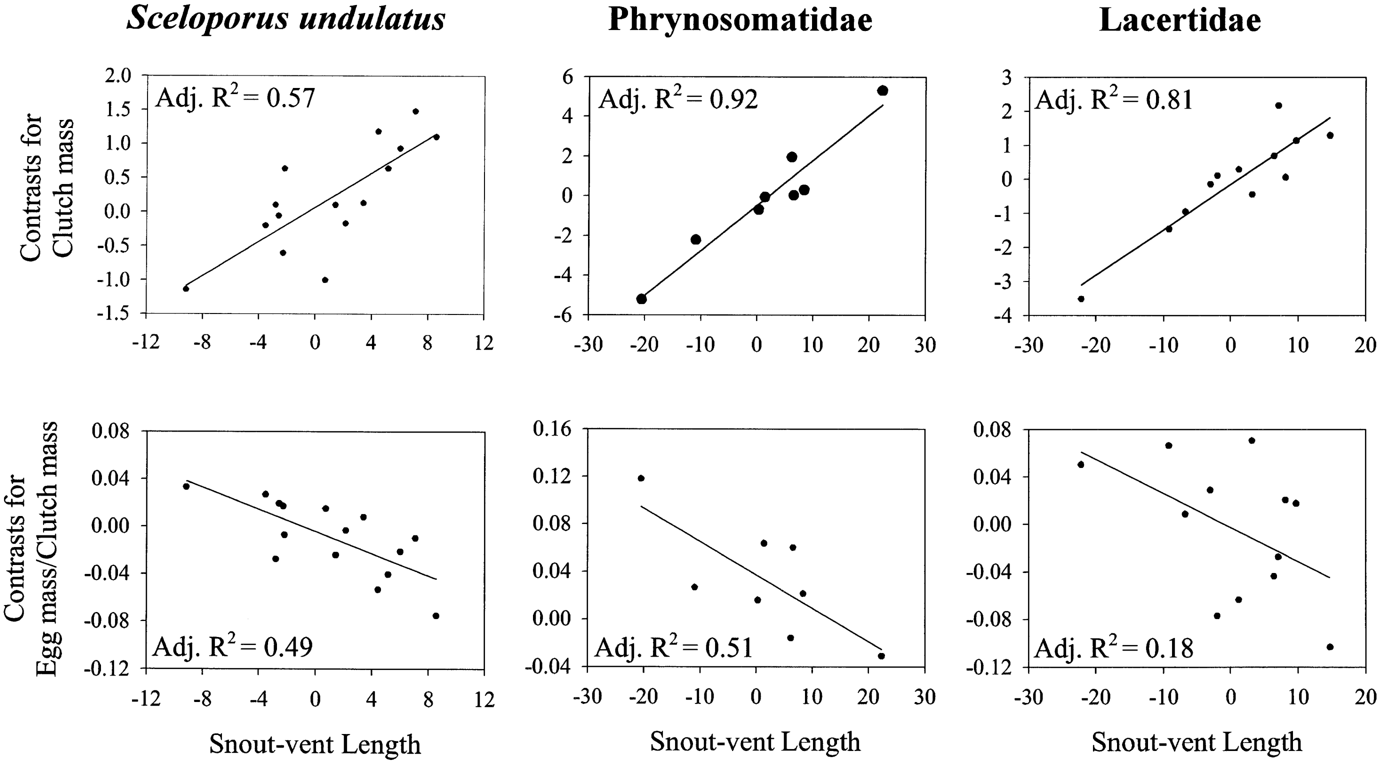

FIG. 4. Comparison of variation in resource acquisition (clutch mass) to resource allocation (egg mass/clutch mass) for three datasets: (1) populations of *S. undulatus*, (Table 1), (2) species of Lacertids in the study by Bauwens and Diaz-Uriarte (1997), and (3) species of the Phrynosomatidae (see Table 6).

the signal-noise ratio at different phylogenetic scales. Variation in acquisition and allocation was strongly related to body size in *S. undulatus* and in the Phrynosomatidae (Fig. 4). The signal-to-noise ratio for the trade-off between the size and the number of offspring differed between the two sets of taxa, but did so in a direction opposite to our prediction: the signal-to-noise ratio (CV of contrasts for allocation/CV for contrasts for acquisition) for *S. undulatus* (0.040) was 13 times greater than that for the Phrynosomatidae (0.003). Much to our chagrin, this example indicates that trade-offs should be easier to detect through comparative analysis of life-history variation among populations of *S. undulatus* than it would be through a similar analysis of life-history variation among species of the Phrynosomatidae. Nevertheless, the signal-to-noise ratio for 13 species of the Lacertidae (0.092), computed from data summarized by Bauwens and Diaz-Uriarte (1997), was more than twice that obtained for either *S. undulatus* or the Phrynosomatidae. Thus, although our initial hypothesis was not supported, the relative variation in allocation and acquisition is consistent with the difference between our ability to detect a trade-off between egg mass and clutch size in *S. undulatus*, and that of Bauwens and Diaz-Uriarte (1997) to detect this trade-off in Lacertidae. We encourage additional analyses to determine whether variation in acquisition and allocation changes across phylogenetic scales. Such analyses will be particularly worthwhile if the increasing number of population-level phylogenetic hypotheses sparks an increase in population-level comparative analyses.

Although expected pairwise relationships were generally not evident in our analysis, PCA did reveal patterns of covariation consistent with the slow-fast continuum (Clobert et al. 1998). Based on either independent contrasts or phylogenetic autocorrelation, PCA extracted two significant dimensions explaining 62–71% of the total variance in life-history traits (Fig. 3, Table 4). When all six traits were included in the analysis, egg size, age at maturity, and adult survival were strongly negatively related to clutch frequency. The largest loadings on PC1 from both the independent contrast and autocorrelation datasets describe an inverse relationship between clutch frequency and survival. Possibly, the ability to produce an extra clutch, or the sensitivity of survival to the production of an extra clutch is closely related to reproductive seasonality. Adolph and Porter (1993, 1996) modeled life-history variation in *S. undulatus* using a physiologically based simulation. Their model showed that activity season length can be an important source of variation in age and size at maturity, as well as the clutch frequency of *S. undulatus*. Patterns described by PC2 are less clear. Clutch size and clutch frequency were negatively related, even more strongly so in the autocorrelation dataset. Furthermore, clutch size was negatively related to egg size in both datasets. The latter relationship represents a classic trade-off in life-history theory.

The PCA from the reduced dataset more clearly describes the expected trade-off between reproductive output and survival. In both the standardized contrasts and the autocorrelation analyses, reproductive output and survival load most strongly onto PC1. All of the variables either did not appear to significantly covary on PC2, or they were positively related. Considering both PCAs (the reduced and the full datasets) our results reinforce similar analyses for other lizards (Clobert et al. 1998).

Why Are Phylogenetic Effects on Life-History Variation Weak or Absent in S. undulatus?

Our study suggests that phylogenetic effects on life-history variation in *S. undulatus* are very weak or absent. We draw this conclusion largely from the phylogenetic autocorrelation analysis in which only clutch frequency showed a significant phylogenetic autocorrelation. Consequently, the bivariate analyses and PCA on life-history traits after autocorrelation analysis are essentially analyses on the original data since one of the primary uses of the autocorrelation analysis is to remove the effect of phylogeny by partitioning the original trait variation into two components (phylogenetic and nonphylogenetic; Martins 1995) when a significant autocorrelation is found. However, phylogenetic autocorrelation is not necessarily a very powerful technique to detect phylogenetic effects for the sample size in our study (Martins 1996). Nevertheless, both the bivariate (Table 2) and PCA (Fig. 3) analyses from independent contrasts and phylogenetic autocorrelation show very concordant patterns of variation. We interpret this to mean that phylogenetic effects on life-history variation are weak or absent among the populations of *S. undulatus* we studied. This interpretation is further supported by a comparison of bivariate relationships on contrasts with those on the original, body-size-corrected variables (analysis not shown). Analysis of the phylogenetically uncorrected traits found no evidence of the expected relationships (Table 2).

How do our results compare with other studies? We can only make comparisons with studies done at very broad phylogenetic scales using large sample sizes because other studies of life-history variation at the population-species interface do not exist. Dunham and Miles (1985) analyzed data from 112 species of squamate reptiles (91 lizards and 21 snakes) using phylogenetic autocorrelation. They found significant phylogenetic effects on three of the life-history traits included in our study (clutch size, clutch frequency, and age at maturity), and also a significant negative relationship between clutch size and clutch frequency. In a subsequent analysis with a different but not independent dataset, Miles and Dunham (1992) estimated that 14–64% of the variation in life-history traits among 130 species of lizards in the Iguanidae (sensu lato) was attributable to phylogenetic effects at the family level. They noted that even after correcting for phylogenetic effects, a substantial amount of variation in life-history traits remained, suggesting that microevolutionary processes (e.g., natural selection) are an important source of life-history variation. Our study of *S. undulatus* is consistent with this view.

Two other sources of comparison with our study are worth noting. Shine and Charnov (1992) and Clobert et al. (1998) used independent contrasts to test for life-history ‘‘invariants’’ (sensu Charnov 1993). Using 36 species of squamate reptiles, Shine and Charnov (1992) found evidence for approximately constant relationships between adult mortality rate, adult body size, and age at maturity, as predicted by theory (Charnov et al. 1993). However, Clobert et al. (1998) used data for 90 species of lizards and found strong evidence that invariants did not exist, and that substantial variation in life-history traits remains after phylogenetic correction. They concluded that some of the difference between their findings and those of Shine and Charnov (1992) might be due to the removal of the effects of body size in the analysis of life-history variation; Shine and Charnov (1992) did not account for variation in body size. However, it is impossible to determine whether differences in findings between the two studies are a consequence of the different data or the different analytical procedures (Clobert et al. 1998).

Phylogenetic Comparative Studies at the Population-Species Interface: Prognosis

We would be unwise to conclude from our study that only comparative analyses of taxa at the species level and above are likely to yield significant insight into the evolution of life-history traits. More examples will be required to evaluate exactly how phylogenetic information may inform hypotheses about the evolution of traits within species (or mixtures of populations and species). Although the analysis of life-history variation provides an excellent context in which to raise this question, it obviously extends to other contexts such as morphology and behavior (Edwards and Kot 1995; Zamudio 1998; Wiens et al. 1999). Because of the dearth of analyses carried out at this level, we do not know what general pattern (if any) will emerge; however, the importance of applying PCMs below the species level is likely to vary with taxon and with the traits that are analyzed (Martins and Housworth 2002).

Apart from conclusions about character evolution in specific datasets, phylogenetic comparative analyses applied below the species level will help to direct attention toward several important and nagging issues in comparative biology. Two such issues are (1) estimating gene flow among populations, and (2) delimiting species. For example, using the indirect method of Thompson (1990), we argued that gene flow among populations was unlikely to be important in *S. undulatus*. However, a more rigorous approach is desirable, especially as population-level phylogenies become more common. Perhaps incorporating phylogenetic information at the population level will require the more extensive sampling that could lead to explicit genetic tests of gene flow (such as nested clade analysis; Templeton 2001). Moreover, new PCMs may be able to use such population-level networks directly, either in place of or in addition to standard bifurcating phylogenies (Martins and Housworth 2002).

Finally, if the application of phylogenetic comparative analyses at lower and lower taxonomic levels could benefit from a different form of phylogenetic information (e.g., gene trees and population-level networks rather than bifurcating phylogenies) than is used at the interspecific level, then species delimitation may become a central issue when PCMs are used at the population-species interface. Consequently, phylogenetic comparative analyses that include taxa below the species level may help foster recognition of the complex relationship between the processes of phylogeny estimation and species delimitation. There is no question that the field of systematics and evolutionary analyses in general would benefit from more attention given to objective means for delimiting species (Wiens and Penkrot 2002).

If phylogenetic effects on life-history traits in taxa other than *S. undulatus* are similarly shown to be unimportant (or too small to estimate), then PCMs applied below the species level may have little to offer experimental analyses of life-history variation. Such a conclusion would not obviate other obvious benefits to phylogenetic information being accounted for in population-level studies, such as cases in which multiple populations of a single species are revealed as multiple species (Wiens et al. 1999). In light of the rapid growth of PCMs and our ability to reconstruct robust phylogenies, population-level analyses may yet play a critical role in understanding the evolution of life-history traits, especially as methods for incorporating population-level phylogenetic information are developed (e.g., Cornillon et al. 2000; Rochet et al. 2000; Martins and Housworth 2002).

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