# A COMPARATIVE TEST OF ADAPTIVE HYPOTHESES FOR SEXUAL SIZE DIMORPHISM IN LIZARDS

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*Abstract.*—It is commonly argued that sexual size dimorphism (SSD) in lizards has evolved in response to two primary, nonexclusive processes: (1) sexual selection for large male size, which confers an advantage in intrasexual mate competition (intrasexual selection hypothesis), and (2) natural selection for large female size, which confers a fecundity advantage (fecundity advantage hypothesis). However, outside of several well-studied lizard genera, the empirical support for these hypotheses has not been examined with appropriate phylogenetic control. We conducted a comparative phylogenetic analysis to test these hypotheses using literature data from 497 lizard populations representing 302 species and 18 families. As predicted by the intrasexual selection hypothesis, male aggression and territoriality are correlated with SSD, but evolutionary shifts in these categorical variables each explain less than 2% of the inferred evolutionary change in SSD. We found stronger correlations between SSD and continuous estimates of intrasexual selection such as male to female home range ratio and female home range size. These results are consistent with the criticism that categorical variables may obscure much of the actual variation in intrasexual selection intensity needed to explain patterns in SSD. In accordance with the fecundity advantage hypothesis, SSD is correlated with clutch size, reproductive frequency, and reproductive mode (but not fecundity slope, reduced major axis estimator of fecundity slope, length of reproductive season, or latitude). However, evolutionary shifts in clutch size explain less than 8% of the associated change in SSD, which also varies significantly in the absence of evolutionary shifts in reproductive frequency and mode. A multiple regression model retained territoriality and clutch size as significant predictors of SSD, but only 16% of the variation in SSD is explained using these variables. Intrasexual selection for large male size and fecundity selection for large female size have undoubtedly helped to shape patterns of SSD across lizards, but the comparative data at present provide only weak support for these hypotheses as general explanations for SSD in this group. Future work would benefit from the consideration of alternatives to these traditional evolutionary hypotheses, and the elucidation of proximate mechanisms influencing growth and SSD within populations.

*Key words.*—Body size, comparative method, fecundity, phylogeny, sexual selection.

Sexual size dimorphism (SSD) is a fundamental and widespread biological phenomenon in which individuals of one sex are characteristically larger than those of the opposite sex for a given population or species. SSD is of considerable interest because it can arise from, and contribute to, differences in the behavior, demography, life history, physiology, ecology, and evolution of males and females within a population. Studies of the selective mechanisms leading to SSD have figured prominently in the evolutionary literature since the pioneering efforts of Darwin (1871). However, recent advances in statistical methodology (reviewed in Harvey and Pagel 1991), coupled with the increasing availability of phylogenetic hypotheses for many groups, have renewed interest in comparative analyses of SSD across diverse taxa (birds: Oakes 1992; Webster 1992; Fairbairn and Shine 1993; Figuerola 1999; Colwell 2000; Székely et al. 2000; Dunn et al. 2001; fishes: Pyron 1996; mites: Colwell 2000; nematodes: Poulin 1997; Morand and Hugot 1998; primates: Mitani et al. 1996; snakes: Shine 1994a; spiders: Head 1995; Prenter et al. 1997; ungulates: Loison et al. 1999; Pérez-Barbería et al. 2002; water striders: Fairbairn 1990; Andersen 1997; multiple taxa: Abouheif and Fairbairn 1997; Fairbairn 1997). Lizards have historically served as important models for the study of SSD, due in large part to the considerable variation in both direction and magnitude of SSD observed in this group. However, all previous comparative analyses involving lizards either predate contemporary methods of controlling

for statistical nonindependence due to shared evolutionary history (Fitch 1976, 1978, 1981; Schoener et al. 1982; Stamps 1983; Carothers 1984), or focus only on particular genera (*Podarcis* and *Lacerta*: Braña 1996; *Anolis*: Stamps et al. 1997; Stamps 1999; Butler et al. 2000; *Draco*: Shine et al. 1998; *Phrynosoma*: Zamudio 1998). As such, a synthetic analysis of SSD in lizards using phylogenetically based statistical methods is needed.

The present study focuses on adaptive hypotheses for the evolution of SSD, which we define as hypotheses viewing SSD as the result of selection favoring different body sizes in males and females. Many authors have suggested that sexual differences in physiology (e.g., Abell 1998), behavior (e.g., Cooper and Vitt 1989), reproductive investment (e.g., Sugg et al. 1995), and ecology (e.g., Shine 1989) can result in sexually divergent growth trajectories in lizards, thus indirectly producing SSD. Although these fundamental sexual differences are presumably adaptive in their own right, we view such hypotheses as essentially nonadaptive with regard to SSD, insofar as they do not explicitly invoke selection on body size. Thus defined, two of the primary adaptive hypotheses for SSD in lizards involve (1) sexual selection for large male size, which confers an advantage in intrasexual mate competition (intrasexual selection hypothesis), and (2) natural selection for large female size, which confers a fecundity advantage (fecundity advantage hypothesis). Other adaptive hypotheses for SSD have been postulated, but we

limit our analysis to these two because they are likely to apply with generality across diverse lizard taxa and because sufficient data are available in the literature to support a broad comparative study. In this analysis, we use a taxonomically diverse dataset obtained from an extensive literature review to test several predictions of the intrasexual selection and fecundity advantage hypotheses with phylogenetically based statistical methods.

### Intrasexual Selection Hypothesis

Sexual selection arises from variance in mating success and can act via intrasexual (e.g., male aggression) or intersexual (e.g., female choice) processes (Darwin 1871). Female preference for large males has rarely been documented in lizards (reviewed in Tokarz 1995; Olsson and Madsen 1995; but see Cooper and Vitt 1993; Censky 1997). Thus, intrasexual selective pressures are believed to be of primary importance in establishing male size. If intrasexual selection for large male body size is mediated via agonistic encounters among males, then large size must confer an advantage in these encounters, and dominance in these encounters must translate into increased reproductive success. Many studies have demonstrated that dominance among male lizards is strongly influenced by size and that dominant or territorial males gain increased access to females (reviewed in Stamps 1983; see also Ruby 1984; Tokarz 1985; Vitt and Cooper 1985; Lewis and Saliva 1987; Anderson and Vitt 1990; Hews 1990; Olsson 1992; Haenel et al. 2003a). Accordingly, male size is often correlated with measures of reproductive success, such as number of females within a territory, number of copulations achieved, or number of offspring sired (reviewed in Stamps 1983; see also Anderson and Vitt 1990; M'Closkey et al. 1990; Abell 1997; Wikelski and Trillmich 1997; Haenel et al. 2003b). Several descriptive studies have also concluded that intrasexual selection for large male size has shaped SSD within lizard populations (Trivers 1976; Vitt and Cooper 1985; Anderson and Vitt 1990; Wikelski and Trillmich 1997), although other investigators have found little evidence that SSD is the result of this process (Cordes et al. 1995).

Recent comparative studies have found support for the intrasexual selection hypothesis based on relationships between SSD and categorical measures of intrasexual selection such as mating system (Oakes 1992; Székely et al. 2000; Dunn et al. 2001; Pérez-Barbería et al. 2002) and male combat or contest behavior (Shine 1994a; Pyron 1996). Correlations have also been found between SSD and quantitative measures of intrasexual selection such as sex ratio (Mitani et al. 1996; Poulin 1997) and breeding group size (Loison et al. 1999). In lizards, patterns in SSD have been linked to male aggression (Carothers 1984), territoriality (Stamps 1983), male to female home range ratio or female home range size (Stamps 1983), and female density (Stamps et al. 1997, Stamps 1999). In the present study, we test the intrasexual selection hypothesis using both categorical (male aggression, territoriality) and continuous (home range ratio, female home range size) measures of intrasexual selection intensity.

### Fecundity Advantage Hypothesis

Darwin (1871) proposed that natural selection should favor large female body size when female size is positively correlated with fecundity within a population, as appears to be the case for most lizards in which clutch size is variable (Fitch 1970). Alternatively, selection for large female size is expected to be relatively weak in the absence of a strong relationship between female size and clutch size, or in species in which clutch size is fixed (Fitch 1978; Vitt 1986; Shine 1988). The fecundity advantage hypothesis focuses on selection to maximize clutch size in a given reproductive episode, but several investigators have extended it to predict a correlation between SSD and reproductive frequency. This argument states that species that reproduce frequently should generally experience selection for early reproduction and increased clutch number, whereas species that reproduce infrequently should primarily experience fecundity selection for large female size, to maximize clutch size in each reproductive episode (Tinkle et al. 1970; Fitch 1978, 1981; Vitt 1986). The assumptions of this argument would be violated if reproductive frequency were to increase with female body size within a population, but there is little empirical support or theoretical justification for such a relationship in lizards (Shine 1988). The fecundity advantage hypothesis therefore predicts a relationship between female-larger SSD and variables associated with low reproductive frequency, such as viviparity, a short reproductive season, and high latitude (Fitch 1970, 1978, 1981; Tinkle et al. 1970).

Support for the fecundity advantage hypothesis has come from numerous recent comparative analyses documenting correlations between SSD and clutch or litter size (Fairbairn and Shine 1993; Head 1995; Braña 1996; but see Shine 1994a; Zamudio 1998). In squamate reptiles, SSD has also been found to correlate with several measures reproductive frequency (Fitch 1978, 1981; but see Shine 1994a). In this study, we test the fecundity advantage hypothesis using correlates of fecundity selection measured in a single reproductive episode (clutch size, fecundity slope, reduced major axis estimator of fecundity slope) and several measures of reproductive frequency (reproductive frequency, reproductive mode, length of reproductive season, and latitude).

## MATERIALS AND METHODS

### Sexual Size Dimorphism

We used mean snout-vent length (SVL) of adult lizards to calculate an index of SSD as:

$$SSD = \frac{\text{size of larger sex}}{\text{size of smaller sex}} - 1,$$

arbitrarily expressed as positive if females are larger and negative if males are larger (Lovich and Gibbons 1992). However, there has recently been much debate regarding the proper method for expressing and analyzing SSD in comparative studies (reviewed in Smith 1999). Discussion has focused on (1) the use of alternative ratios as measures of SSD, (2) the use of residuals of male size on female size as measures of SSD, and (3) the direct analysis of male and female body

size as opposed to some measure of SSD. We briefly address each of these issues below.

(1) In a comparison of popular ratio indices of SSD across 25 real datasets, Smith (1999) concluded that there was no convincing statistical argument for the use of any ratio other than the Lovich and Gibbons (1992) index or a logarithmic transformation of (male size / female size). We chose the former method because it generates values that are intuitive, directional, properly scaled, and symmetrical around zero (for a discussion of these attributes, see Lovich and Gibbons 1992; Smith 1999). We subsequently performed a logarithmic transformation of all of our variables (see below); thus the values used in our analyses do not exhibit distributional problems that might otherwise make the latter index preferable.

(2) When relationships between SSD and body size are examined, it has been suggested that ratio measures of SSD can lead to spurious correlations, since both variables contain body size and thus are not mathematically independent (Ranta et al. 1994; Abouheif and Fairbairn 1997; Fairbairn 1997). Residuals from the regression of male size on female size (or vice versa) have been proposed as alternative measures of SSD, and many recent comparative analyses have followed this procedure (Head 1995; Braña 1996; Mitani et al. 1996; Poulin 1997; Stamps et al. 1997; Dunn et al. 2001). However, Smith (1999) has argued that it makes no difference whether SSD or male or female size is used as the dependent variable in analyses such as ours. We empirically tested the equivalence of these methods by conducting all analyses using both the Lovich and Gibbons (1992) index of SSD and the residuals of male SVL on female SVL (or vice versa).

(3) The intrasexual selection and fecundity advantage hypotheses identify male and female body size, rather than their ratio, as the targets of selection. Given this, it may seem more appropriate to separately examine evolutionary patterns in male and female body size as opposed to SSD. However, although the hypotheses in question assume that body size in one sex or the other is the target of selection, the pattern of interest (i.e., SSD) evolves due to the direct response of the sex under selection and the genetically correlated response of the opposite sex (Lande 1980; Cheverud et al. 1985; reviewed in Badyaev 2002). An index of SSD is the most straightforward way to account for this correlated genetic response. However, analyses of the direct targets of selection could potentially be used to determine whether intrasexual selection and fecundity selection are actually favoring large male and female size, irrespective of their effects on SSD. Accordingly, we examined the relationships between each of our measures of selection and both male and female SVL.

### Measures of Intrasexual Selection

We categorized male aggression as present or absent based on literature reports of agonistic male-male behavior in any context, since large size generally confers an advantage in both aggressive encounters involving physical contact (e.g., wrestling, biting) and threat displays lacking physical contact (e.g., push-ups, head-bobs). If one study reported information regarding male aggression for a species, we extended this classification to all populations of the species, but not to congeneric species.

We used the broad familial generalizations of Martins (1994; derived from Stamps 1977) and the available data for male aggression to generate three categories of territoriality: (1) defense of all or most of the home range or displaying male aggression, (2) defense of specific sites within the home range, and (3) no defense of any particular area or lacking male aggression. We extended this classification to all members of a given family, except in instances in which it contradicted reports of the presence or absence of territoriality or male aggression for a particular species.

Male aggression and territoriality are useful variables in that they are widely reported for lizards, but they reduce the presumably continuous variation in sexual selection intensity to a discrete variable with a limited number of classes. Thus, it has been argued that analyses involving such variables have little power to detect functional relationships with SSD (Fairbairn 1997). Unfortunately, suitable quantitative measures of intrasexual selection intensity are rarely reported for lizards. However, Stamps (1983) suggested that the ratio of male to female home range size provides an estimate of the degree of polygyny, and thus the intensity of intrasexual selection, in breeding territorial lizards. Similarly, she used a simple model incorporating the hypothetical energetic costs and reproductive benefits of male territoriality to argue that the intensity of intrasexual selection should increase as female home range size decreases. As predicted by the intrasexual selection hypothesis, Stamps (1983) found that SSD is related to both home range ratio ($r = 0.57$, $P < 0.01$) and $\log_{10}$ mass-adjusted female home range size ($r = -0.78$, $P < 0.001$) across 24 populations of territorial lizards. We repeated her analysis of home range ratio and female home range size using our index of SSD and phylogenetically based statistical methods to test the intrasexual selection hypothesis with continuous measures of selection intensity.

### Measures of Fecundity Selection

We obtained measures of mean clutch size from counts of oviposited eggs or young in a litter, enlarged vitellogenic follicles, oviductal eggs or developing embryos, and corpora lutea. When more than one measure of clutch size was reported, we used the combined mean of all available data. To quantify the relationship between female SVL and clutch size within a population, we calculated fecundity slope as the slope of the linear regression of clutch size on female SVL (Goodman 1982). We calculated the reduced major axis estimator of fecundity slope as the ratio of the standard deviation in clutch size to the standard deviation in female SVL to allow for error in both variables (Harvey and Pagel 1991; Shine 1994a; Braña 1996). We did not include species characterized by invariant clutch size (i.e., *Anolis*, most gekkonids) in any analyses involving measures of clutch size, fecundity slope, or the reduced major axis estimator of fecundity slope (see Clobert et al. 1998).

We classified reproductive frequency as single or multiple based on the number of clutches or litters produced in a typical reproductive season. We classified species as multiple if any members of the population were observed to produce multiple clutches or were found to simultaneously contain vitellogenic follicles, oviductal eggs, or corpora lutea. We

classified all viviparous species as single due to the time required for gestation in most lizards (Fitch 1970, 1978; Tinkle et al. 1970). We dichotomized reproductive mode as either oviparous or viviparous, with ''ovoviviparous'' species classified as effectively viviparous due to the length of time invested in retaining each clutch. We calculated length of reproductive season for oviparous species as the number of months between the earliest record of vitellogenesis in a population and the latest date on which oviposition occurred. We excluded viviparous lizards from this analysis, since length of reproductive season measured in this fashion would not be related to the potential for multiple clutches because of the time investment required for gestation. We recorded latitude for each population based on published coordinates or estimates derived from descriptions of site locations and treated northern and southern hemisphere latitudes as equivalent in our analyses. We obtained all measures of clutch size, fecundity slope, reduced major axis estimator of fecundity slope, reproductive frequency, length of reproductive season, and latitude from the same population from which the SSD data were recorded.

### Conventional Statistical Analyses

Previous studies have demonstrated that many of our variables are often correlated with body size in reptiles (Tinkle et al. 1970; Fitch 1978, 1981; Berry and Shine 1980; Shine 1994a,b; Clobert et al. 1998; Perry and Garland 2002). To correct for allometry, we calculated residuals from the least-squares regression of each logarithmically ($log_{10}$)-transformed variable on $log_{10}$ average SVL. We hereafter refer to these $log_{10}$-transformed, size-corrected variables as residual SSD, residual clutch size, and so forth. To obtain results directly comparable to those of Stamps (1983), we did not perform any transformations of home range ratio or SSD in the analyses using her data. However, because home range size scales with body size (Perry and Garland 2002), we calculated size-corrected residuals for female home range size in the above fashion, which we found preferable to her ''mass-adjusted'' measure. For consistency, we conducted all other regression analyses using size-corrected residuals, even in the absence of significant allometry.

Relationships between pairs of variables were initially examined using conventional least-squares regression (Smith 1999). We also performed a backward elimination stepwise multiple regression with residual SSD as the dependent variable and residual territoriality, residual clutch size, residual reproductive frequency, residual reproductive mode, and residual latitude as independent variables. The remaining measures of selection intensity were omitted because their inclusion in the model would have substantially reduced the sample size. The significance level for the retention of a variable in the model was set to $P = 0.05$. Alternative multiple regression methods (i.e., forward, stepwise) yielded results identical to backward elimination. We hereafter refer to our conventional analyses as ''tips'' analyses because they utilize datapoints (i.e., species or populations) drawn from the tips of a phylogeny.

### Phylogenetically Based Statistical Analyses

Conventional statistical analyses assume that datapoints are independent, an assumption that is violated when species, which share parts of their evolutionary history, are used as datapoints (Felsenstein 1985; Harvey and Pagel 1991). We used the independent contrast approach of Felsenstein (1985) to remove the confounding effects of phylogeny and infer correlated evolution between traits. We calculated independent contrasts using the PDTREE module of the Phenotypic Diversity Analysis Program (PDAP, Ver. 5.0, Garland et al. 2001). To correct for allometric scaling effects, residuals were obtained from the regression through the origin of the contrasts for each $log_{10}$-transformed variable against the contrasts for $log_{10}$ average SVL (Garland et al. 1992). These $log_{10}$-transformed, size-corrected, phylogenetically independent variables are hereafter referred to as residual contrast of SSD, residual contrast of clutch size, and so forth. We initially examined relationships between residual contrasts using conventional least-squares regression forced through the origin (Garland et al. 1992). As in the tips analyses, we conducted all regression analyses using residual contrasts, except in the case of home range ratio and SSD in the datasets taken from Stamps (1983).

Our categorical variables generated a large number of contrasts equal to zero (i.e., no discernable evolutionary change between taxa). Datapoints with contrast scores of zero for the independent variable are important because they confer degrees of freedom in hypothesis testing and because they provide information on variance about the regression line (Garland et. al 1992). However, some investigators have examined the relationship between SSD and categorical variables by restricting comparisons to nodes that differ with regard to the independent variable (e.g., Shine 1994a). Accordingly, we used two different approaches for each analysis involving a categorical independent variable. With either approach, contrast scores were first calculated using a complete phylogeny with all available datapoints. In the first approach, we performed our regression analysis using residual contrasts from all available datapoints, as in our analyses involving continuous variables. The results of these regressions therefore reflect the ability of these variables to explain evolutionary patterns in SSD among all lizards included in our analyses. In the second approach, we omitted all datapoints with contrasts of zero for the independent variable, calculated size-corrected residuals using only the remaining subset of datapoints, and used only these residual contrasts in subsequent analyses. We hereafter refer to these analyses as ''trimmed'' regressions. It is important to note that these trimmed regressions are limited to nodes of the phylogeny that differ with regard to the categorical variable, thus ignoring instances in which SSD varies in the absence of change in the independent variable. Significant results can therefore be interpreted only as support for the predicted relationship in which changes in the independent variable are accompanied by changes in SSD, not as evidence for the ability of these variables to explain broader patterns of SSD among all lizards.

We also performed a backward elimination stepwise multiple regression through the origin using the residual contrasts

of the variables previously examined in the tips analysis. The significance level for retention of a variable in the model was again set to $P = 0.05$. As in the tips analyses, alternative multiple regression methods yielded identical results. We hereafter refer to our phylogenetic analyses as ''contrasts'' analyses because they use independent contrast scores calculated between all nodes in a phylogeny.

### Phylogenetic Hypothesis

Felsenstein's (1985) independent contrasts method requires information regarding both the topology and the branch lengths of the phylogeny being employed. We used numerous published sources to construct a composite phylogenetic hypothesis describing relationships among the species considered in this study (Fig. 1). Because of differences in species composition among datasets, the phylogeny for each separate analysis represents a unique, ''pruned'' version of this composite phylogeny. We performed our analyses on a paraphyletic Squamata exclusive of snakes because (1) the placement of Serpentes within Squamata is uncertain (Estes et al. 1988); (2) snakes and lizards differ markedly in ecology, behavior, and morphology; and (3) an analogous study has already been conducted for snakes (i.e., Shine 1994a). For consistency regarding the second criterion, we also excluded fossorial lizards exhibiting significant reduction or loss of limbs (as recommended by Losos 1994), although we recognize the possibility that our results might differ if these lineages were included (e.g., Bininda-Emonds and Gittleman 2000). We assumed that named families, subfamilies, genera, and species are monophyletic unless published analyses suggested otherwise. Multiple populations within species were treated as species-level polytomies. In most instances in which phylogenetic relationships were questionable, we conservatively adopted a polytomous phylogeny, since an incompletely resolved phylogeny is likely to violate the assumptions of the independent contrasts method to a lesser degree than an incorrectly resolved phylogeny (Purvis and Garland 1993; Garland and Díaz-Uriarte 1999). Simulation studies suggest that polytomies have little effect on Type 1 error rates (Garland and Díaz-Uriarte 1999), thus we did not attempt to correct for them in our analyses.

Branch lengths provide a measure of the expected variance of character change and are thus necessary to properly standardize independent contrasts and assure that they will receive equal weighting in statistical analyses. Because insufficient data were available to accurately establish divergence times, we employed constant branch lengths for all traits. For each trait, we empirically validated this approach by examining the diagnostic plot of the absolute value of each standardized independent contrast against its standard deviation (Garland et al. 1992). Constant branch lengths provide adequate standardization for SSD in all datasets, and diagnostic correlation coefficients are generally weak ($r \leq 0.2$) for all other traits except fecundity slope ($r = 0.27$, $P < 0.05$), reduced major axis estimator of fecundity slope ($r = 0.65$, $P < 0.01$), and female home range size ($r = 0.60$, $P < 0.01$). However, the results of subsequent analyses conducted with alternative branch-length transformations are similar to those obtained using constant branch lengths for these traits. We

therefore report only the results obtained using constant branch lengths.

### RESULTS

Our literature review yielded useful data for a total of 652 populations representing 426 species and 22 families of lizards (see Electronic Appendix, currently available from the *Evolution* Editorial Office at evolution@asu.edu). Many of these species could not be included in our study due to uncertain phylogenetic placement. The final dataset used in our analysis included 497 populations representing 302 species and 18 families.
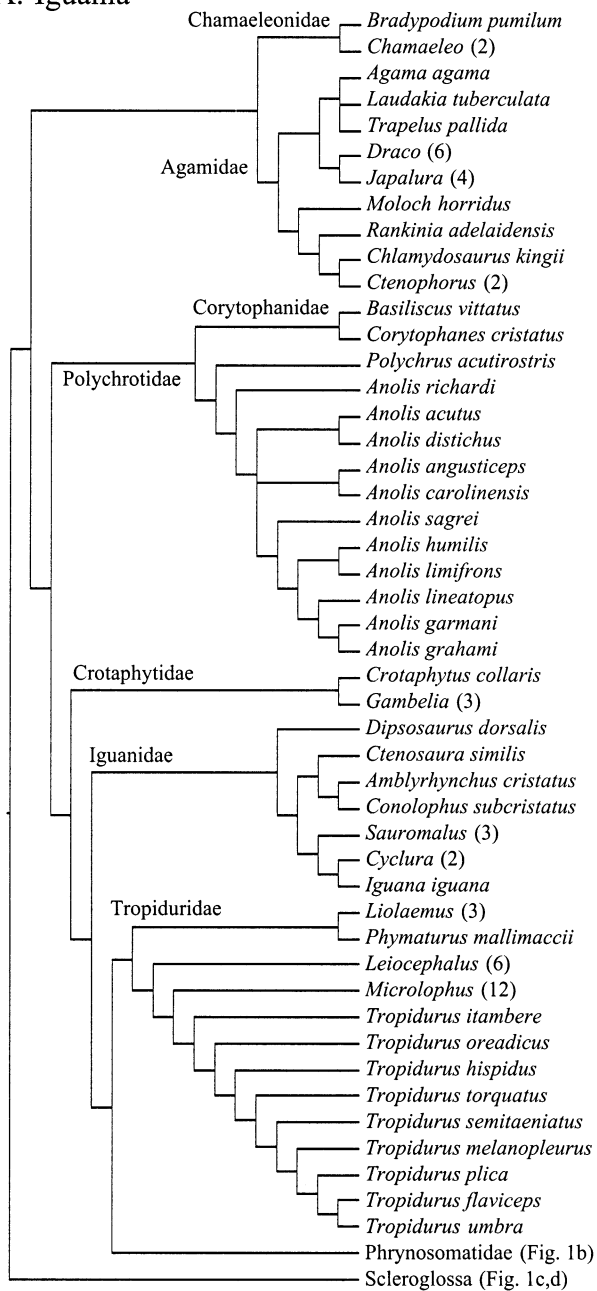
### Allometry

The scaling relationships for each trait regressed against male SVL, female SVL, and average SVL are summarized in Table 1. Due to the high interspecific correlation between male and female size and the considerable variation in body size across species, we obtained similar results regardless of whether we used male SVL, female SVL, or average SVL as a measure of body size (Table 1). Thus, the hypothesized targets of selection, male and female size, do little more than describe allometric trends when regressed against our measures of selection. This demonstrates the importance of examining variance in the size of one sex relative to size in the opposite sex (i.e., with an index of SSD or with the residuals of male size on female size).

In most of our datasets, the magnitude of male-larger SSD increases with body size, a phenomenon known as Rensch's rule (Abouheif and Fairbairn 1997; Fairbairn 1997; Colwell 2000). Other studies have demonstrated similar allometric patterns in SSD among squamate reptiles (Fitch 1978, 1981; Shine 1994b). We found a positive correlation between female home range size and body size in our tips analysis ($r = 0.615$, $P < 0.001$), but not our contrasts analysis ($r = 0.048$, $P = 0.824$), although such a relationship has been demonstrated in one phylogenetic analysis involving a substantially larger sample size (Perry and Garland 2002). In both our tips and our contrasts analyses, we found that clutch size increases with body size in lizards (Tinkle et al. 1970; Clobert et al. 1998). Both our tips and our contrasts analyses revealed that reproductive frequency scales negatively with body size, as previously documented by Clobert et al. (1998). We also found a positive correlation between latitude and body size in both our tips and our contrasts analyses. Although our tips analysis suggests a negative relationship between length of reproductive season and average SVL, we found no evidence for allometry once phylogeny was taken into account. Body size is not correlated with male aggression, territoriality, fecundity slope, or reproductive mode in either our tips or our contrasts analyses.

### Intrasexual Selection Hypothesis

The results from both our tips and our contrasts analyses for residual SSD and residual male or female SVL regressed against our measures of intrasexual selection are presented in Table 2. Residual SSD and residual male or female SVL generated nearly identical results for every analysis in which

A. Iguania

Chamaeleonidae — *Bradypodium pumilum*
*Chamaeleo* (2)
*Agama agama*
*Laudakia tuberculata*
*Trapelus pallida*
*Draco* (6)
Agamidae — *Japalura* (4)
*Moloch horridus*
*Rankinia adelaidensis*
*Chlamydosaurus kingii*
*Ctenophorus* (2)
Corytophanidae — *Basiliscus vittatus*
*Corytophanes cristatus*
Polychrotidae — *Polychrus acutirostris*
*Anolis richardi*
*Anolis acutus*
*Anolis distichus*
*Anolis angusticeps*
*Anolis carolinensis*
*Anolis sagrei*
*Anolis humilis*
*Anolis limifrons*
*Anolis lineatopus*
*Anolis garmani*
*Anolis grahami*
Crotaphytidae — *Crotaphytus collaris*
*Gambelia* (3)
Iguanidae — *Dipsosaurus dorsalis*
*Ctenosaura similis*
*Amblyrhynchus cristatus*
*Conolophus subcristatus*
*Sauromalus* (3)
*Cyclura* (2)
*Iguana iguana*
Tropiduridae — *Liolaemus* (3)
*Phymaturus mallimaccii*
*Leiocephalus* (6)
*Microlophus* (12)
*Tropidurus itambere*
*Tropidurus oreadicus*
*Tropidurus hispidus*
*Tropidurus torquatus*
*Tropidurus semitaeniatus*
*Tropidurus melanopleurus*
*Tropidurus plica*
*Tropidurus flaviceps*
*Tropidurus umbra*
Phrynosomatidae (Fig. 1b)
Scleroglossa (Fig. 1c,d)

B. Phrynosomatidae

*Uma scoparia*
*Uma inornata*
*Uma notata*
*Callisaurus draconoides*
*Cophosaurus texanus*
*Holbrookia* (2)
*Phrynosoma orbiculare*
*Phrynosoma hernandesi*
*Phrynosoma coronatum*
*Phrynosoma cornutum*
*Phrynosoma modestum*
*Phrynosoma platyrhinos*
*Uta* (5)
*Urosaurus bicarinatus*
*Urosaurus graciosus*
*Urosaurus ornatus*
*Sceloporus chrysosticus*
*Sceloporus cozumelae*
*Sceloporus teapensis*
*Sceloporus variabilis*
*Sceloporus siniferous*
*Sceloporus utiformis*
*Sceloporus merriami*
*Sceloporus nelsoni*
*Sceloporus pyrocephalus*
*Sceloporus graciosus*
*Sceloporus vandenburgianus*
*Sceloporus bicanthalis*
*Sceloporus aeneus*
*Sceloporus scalaris*
*Sceloporus megalepidurus*
*Sceloporus pictus*
*Sceloporus grammicus*
*Sceloporus mucronatus*
*Sceloporus cyanogenys*
*Sceloporus poinsetti*
*Sceloporus jarrovi*
*Sceloporus insignis*
*Sceloporus bulleri*
*Sceloporus torquatus*
*Sceloporus virgatus*
*S. undulatus consobrinus*
*S. undulatus garmani*
*Sceloporus occidentalis*
*S. undulatus elongatus*
*S. undulatus erythrocheilus*
*S. undulatus tristichus*
*Sceloporus woodi*
*S. undulatus hyacinthinus*
*S. undulatus undulatus*
*Sceloporus olivaceous*
*Sceloporus clarki*
*Sceloporus magister*
*Sceloporus orcutti*
*Sceloporus spinosus*
*Sceloporus lundelli*
*Sceloporus adleri*
*Sceloporus formosus*
*Sceloporus malachiticus*
*Sceloporus smaragdinus*
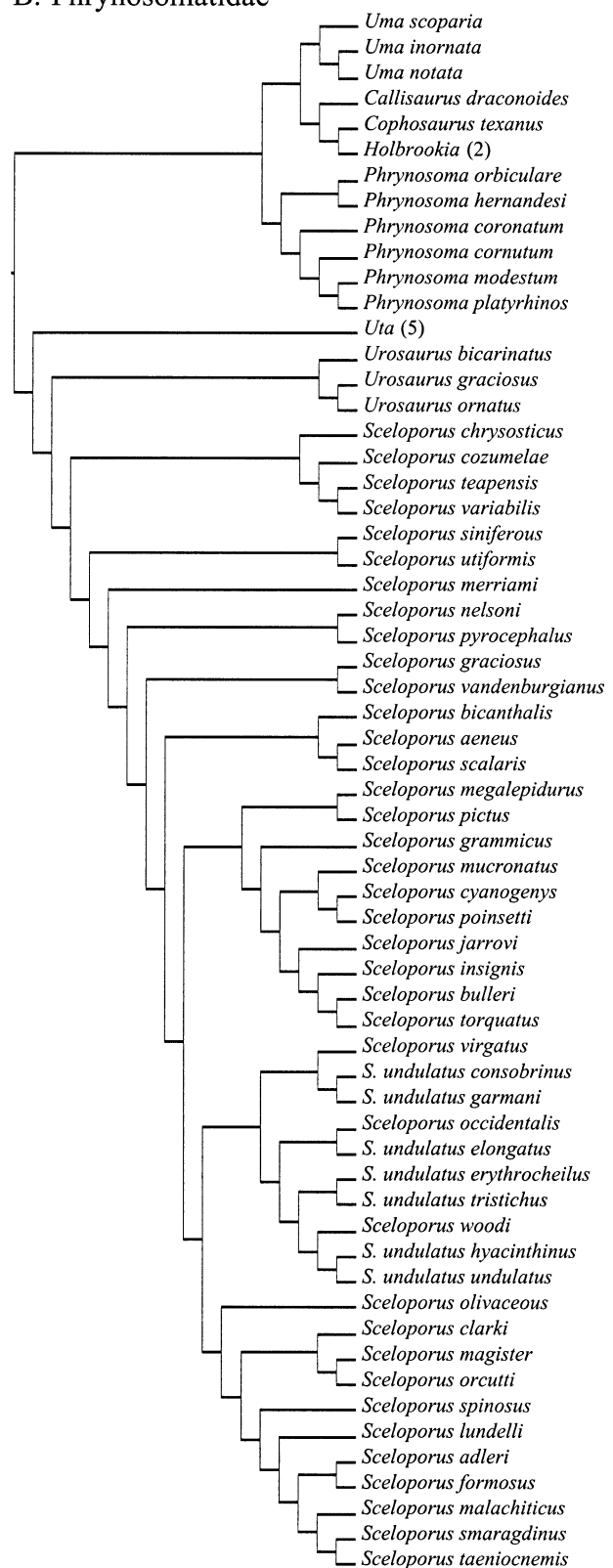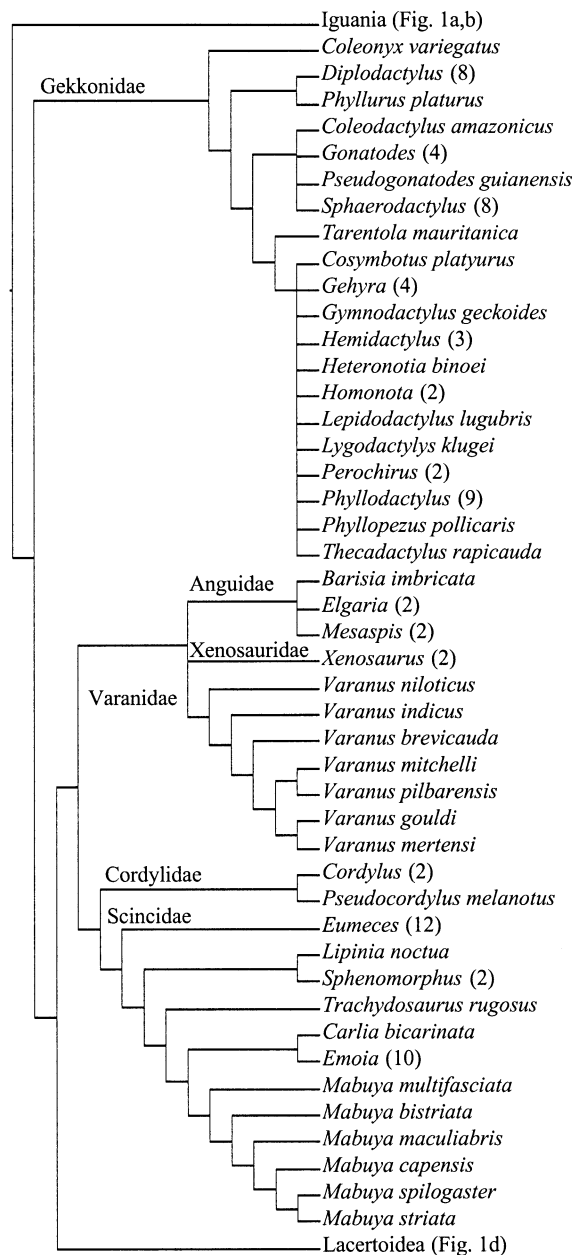*Sceloporus taeniocnemis*

FIG. 1. Composite of published phylogenetic hypotheses used to calculate independent contrasts. Branch lengths are arbitrary for illustrative purposes. Numbers in parentheses following genera indicate the number of species included in a genus with either two species or a completely polytomous topology. (A) Iguania, after Estes et al. (1988), Etheridge and de Queiroz (1988), Rassman (1997), Stamps et al. (1997), Jackman et al. (1999), Harvey and Gutberlet (2000), Macey et al. (2000), and Wiens and Hollingsworth (2000). (B) Phrynosomatidae, after Reeder and Wiens (1996), Wiens and Reeder (1997), and Reeder and Montanucci (2001). (C) Scleroglossa, after Kluge (1967,1987), Estes et al. (1988), Fuller et al. (1998), Honda et al. (2000), and Mausfeld et al. (2000). (D) Lacertoidea, after Presch (1974, 1980), Harris et al. (1998), Forstner et al. (1998), Harris and Arnold (1999), and Fu (2000).
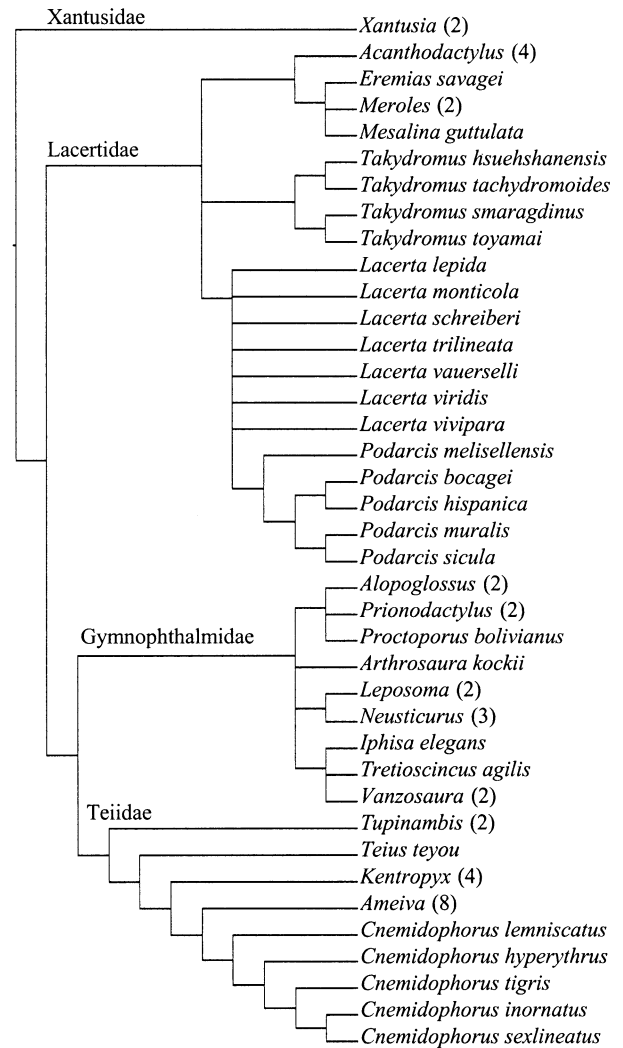
## C. Scleroglossa

Gekkonidae

- Iguania (Fig. 1a,b)
- *Coleonyx variegatus*
- *Diplodactylus* (8)
- *Phyllurus platurus*
- *Coleodactylus amazonicus*
- *Gonatodes* (4)
- *Pseudogonatodes guianensis*
- *Sphaerodactylus* (8)
- *Tarentola mauritanica*
- *Cosymbotus platyurus*
- *Gehyra* (4)
- *Gymnodactylus geckoides*
- *Hemidactylus* (3)
- *Heteronotia binoei*
- *Homonota* (2)
- *Lepidodactylus lugubris*
- *Lygodactylys klugei*
- *Perochirus* (2)
- *Phyllodactylus* (9)
- *Phyllopezus pollicaris*
- *Thecadactylus rapicauda*

Anguidae
- *Barisia imbricata*
- *Elgaria* (2)
- *Mesaspis* (2)

Xenosauridae
- *Xenosaurus* (2)

Varanidae
- *Varanus niloticus*
- *Varanus indicus*
- *Varanus brevicauda*
- *Varanus mitchelli*
- *Varanus pilbarensis*
- *Varanus gouldi*
- *Varanus mertensi*

Cordylidae
- *Cordylus* (2)
- *Pseudocordylus melanotus*

Scincidae
- *Eumeces* (12)
- *Lipinia noctua*
- *Sphenomorphus* (2)
- *Trachydosaurus rugosus*
- *Carlia bicarinata*
- *Emoia* (10)
- *Mabuya multifasciata*
- *Mabuya bistriata*
- *Mabuya maculiabris*
- *Mabuya capensis*
- *Mabuya spilogaster*
- *Mabuya striata*
- Lacertoidea (Fig. 1d)

## D. Lacertoidea

Xantusidae
- *Xantusia* (2)

Lacertidae
- *Acanthodactylus* (4)
- *Eremias savagei*
- *Meroles* (2)
- *Mesalina guttulata*
- *Takydromus hsuehshanensis*
- *Takydromus tachydromoides*
- *Takydromus smaragdinus*
- *Takydromus toyamai*
- *Lacerta lepida*
- *Lacerta monticola*
- *Lacerta schreiberi*
- *Lacerta trilineata*
- *Lacerta vauerselli*
- *Lacerta viridis*
- *Lacerta vivipara*
- *Podarcis melisellensis*
- *Podarcis bocagei*
- *Podarcis hispanica*
- *Podarcis muralis*
- *Podarcis sicula*

Gymnophthalmidae
- *Alopoglossus* (2)
- *Prionodactylus* (2)
- *Proctoporus bolivianus*
- *Arthrosaura kockii*
- *Leposoma* (2)
- *Neusticurus* (3)
- *Iphisa elegans*
- *Tretioscincus agilis*
- *Vanzosaura* (2)

Teiidae
- *Tupinambis* (2)
- *Teius teyou*
- *Kentropyx* (4)
- *Ameiva* (8)
- *Cnemidophorus lemniscatus*
- *Cnemidophorus hyperythrus*
- *Cnemidophorus tigris*
- *Cnemidophorus inornatus*
- *Cnemidophorus sexlineatus*

Fig. 1. Continued.

they were regressed against a measure of selection (Table 2; for similar results, see Stamps et al. 1997; Smith 1999; Butler et al. 2000). Thus, we only discuss the results obtained using residual SSD. Visual presentations of our contrasts analyses for residual SSD and comparisons of our full and trimmed regressions for measures of intrasexual selection are provided in Figure 2.

In our tips analyses, we found a significant negative correlation between residual SSD and both residual male aggression and residual territoriality (Table 2). Our contrasts analyses show that residual contrast of SSD is correlated with both residual contrast of male aggression (Fig. 2A) and residual contrast of territoriality (Fig. 2B), but neither of these variables can explain more than 2% of the inferred evolutionary change in SSD. Our trimmed regressions show that the predicted changes in SSD generally accompany evolutionary shifts in male aggression (Fig. 2A), and territoriality (Fig. 2B). However, even when considering only those instances in which male aggression and territoriality differ between sister taxa, the residual contrasts of these variables still explain less than 25% of the variance in residual contrast of SSD.

TABLE 1. Correlations between log$_{10}$-transformed measures of intrasexual and fecundity selection and several log$_{10}$-transformed measures of body size. Note that male snout-vent length (SVL) and female SVL are highly correlated in all datasets; thus the relationships are similar between each measure of selection and either male SVL, female SVL, or average SVL. We used the residuals from these regressions as size-corrected measures of selection and sexual size dimorphism (SSD) in subsequent analyses (see Table 2). Home range ratio and female home range size are not included here because male SVL and female SVL data were unavailable, and because size-corrected residuals were not used in subsequent analyses of SSD and home range ratio in these datasets (see Materials and Methods). RMAE, reduced major axis estimator of fecundity slope.

| Measure of selection | Analysis | df | Male SVL vs. female SVL | | Measure vs. male SVL | | Measure vs. female SVL | | Measure vs. average SVL | | SSD vs. average SVL | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | r | P | r | P | r | P | r | P | r | P |
| Male aggression | tips | 211 | 0.985 | <0.001 | 0.053 | 0.443 | 0.000 | 0.971 | 0.030 | 0.669 | −0.381 | <0.001 |
| | contrasts | 211 | 0.946 | <0.001 | 0.048 | 0.487 | 0.000 | 0.963 | 0.026 | 0.697 | −0.207 | 0.002 |
| Territoriality | tips | 496 | 0.985 | <0.001 | −0.020 | 0.660 | −0.070 | 0.117 | −0.044 | 0.337 | −0.390 | <0.001 |
| | contrasts | 496 | 0.965 | <0.001 | 0.028 | 0.539 | 0.000 | 0.929 | 0.017 | 0.686 | −0.208 | <0.001 |
| Clutch size | tips | 153 | 0.974 | <0.001 | 0.310 | <0.001 | 0.395 | <0.001 | 0.353 | <0.001 | −0.181 | 0.024 |
| | contrasts | 153 | 0.972 | <0.001 | 0.420 | <0.001 | 0.479 | <0.001 | 0.456 | <0.001 | −0.261 | 0.001 |
| Fecundity slope | tips | 50 | 0.964 | <0.001 | 0.039 | 0.789 | 0.059 | 0.676 | 0.010 | 0.937 | −0.028 | 0.847 |
| | contrasts | 50 | 0.969 | <0.001 | 0.050 | 0.723 | 0.087 | 0.538 | 0.070 | 0.622 | −0.125 | 0.376 |
| Fecundity slope (RMAE) | tips | 17 | 0.964 | <0.001 | −0.371 | 0.118 | −0.317 | 0.186 | 0.349 | 0.143 | −0.277 | 0.252 |
| | contrasts | 17 | 0.978 | <0.001 | −0.366 | 0.123 | −0.396 | 0.093 | 0.382 | 0.106 | −0.410 | 0.081 |
| Reproductive frequency | tips | 207 | 0.986 | <0.001 | 0.451 | <0.001 | 0.498 | <0.001 | 0.475 | <0.001 | −0.480 | <0.001 |
| | contrasts | 207 | 0.965 | <0.001 | 0.180 | 0.009 | 0.238 | 0.005 | 0.209 | 0.024 | −0.214 | 0.002 |
| Reproductive mode | tips | 458 | 0.986 | <0.001 | −0.010 | 0.815 | 0.022 | 0.643 | 0.000 | 0.929 | −0.416 | <0.001 |
| | contrasts | 458 | 0.967 | <0.001 | −0.049 | 0.295 | −0.017 | 0.728 | 0.033 | 0.475 | −0.244 | <0.001 |
| Length of reproductive season | tips | 76 | 0.973 | <0.001 | −0.248 | 0.039 | −0.271 | 0.016 | −0.261 | 0.021 | −0.278 | 0.014 |
| | contrasts | 76 | 0.971 | <0.001 | −0.090 | 0.433 | −0.092 | 0.424 | −0.092 | 0.426 | −0.239 | 0.035 |
| Latitude | tips | 274 | 0.990 | <0.001 | 0.488 | <0.001 | 0.448 | <0.001 | 0.471 | <0.001 | −0.480 | <0.001 |
| | contrasts | 274 | 0.974 | <0.001 | 0.157 | 0.009 | 0.141 | 0.019 | 0.151 | 0.012 | −0.287 | <0.001 |

Similar to Stamps (1983), we found strong correlations between SSD and both home range ratio and residual female home range size (Table 2). Both of these relationships remain significant and essentially unchanged when phylogeny is taken into account. Contrast of SSD is strongly correlated with contrast of home range ratio (Fig. 2C) and residual contrast of female home range size (Fig. 2D).

### Fecundity Advantage Hypothesis

The results from both our tips and our contrasts analyses for residual SSD and residual male or female SVL regressed against our measures of fecundity selection are summarized in Table 2. Visual presentations of our contrasts analyses and comparisons of our full and trimmed regressions for residual contrast of SSD and our measures of fecundity selection are provided in Figure 3.

As predicted by the fecundity advantage hypothesis, we found a strong positive correlation between residual SSD and residual clutch size in our tips analysis (Table 2). Residual contrast of SSD is also positively correlated with residual contrast of clutch size (Fig. 3A), but evolutionary changes in clutch size explain less than 8% of the associated variance in residual contrast of SSD. We found a significant positive relationship between residual SSD and residual fecundity slope, but the results of our contrasts analysis for these traits provided no support for the fecundity advantage hypothesis (Table 2; Fig. 3B). We did not observe a significant relationship between SSD and reduced major axis estimator of fecundity slope in either our tips or our contrasts analysis (Table 2).

We found significant relationships between residual SSD and both residual reproductive frequency and residual reproductive mode in our tips analyses (Table 2). Our contrasts analyses show that residual contrast of SSD is negatively correlated with residual contrast of reproductive frequency (Fig. 3C), and positively correlated with residual contrast of reproductive mode (Fig. 3D), but neither of these variables can explain more than 2% of the variance in residual contrast of SSD. Our trimmed regressions suggest that the predicted changes in SSD generally accompany evolutionary shifts in reproductive frequency (Fig. 3C) and reproductive mode (Fig. 3D). However, even when considering only those instances in which reproductive frequency and mode differ between sister taxa, the residual contrasts of these variables each explain less than 12% of the inferred evolutionary change in SSD. We did not observe significant correlations between SSD and length of reproductive season in either our tips or our contrasts analysis (Table 2; Fig. 3E). We found a significant positive correlation between residual SSD and residual latitude, but the results of our contrasts analysis suggest that this relationship is due to shared evolutionary history (Table 2; Fig. 3F).

### Multiple Regression

In our tips analysis, backward elimination stepwise multiple regression with residual SSD as the dependent variable resulted in a significant model ($r = 0.577$, $F_{1,81} = 13.51$, $P < 0.001$) that retained residual clutch size (partial $r = 0.444$, $P < 0.001$), residual territoriality (partial $r = 0.297$, $P =$

TABLE 2. Correlations between our measures of intrasexual and fecundity selection and two alternative measures of sexual size dimorphism (SSD): (1) residuals from the regression of our index of SSD on average snout-vent length (SVL), and (2) residuals from the regression of male SVL on female SVL (intrasexual selection analyses) or female SVL on male SVL (fecundity selection analyses). Note that these two measures of SSD yield nearly identical results. We did not use the latter measure of SSD in the home range ratio or female home range size analyses because male SVL and female SVL data were unavailable. We also did not use size-corrected residuals for home range ratio or SSD in these analyses (see Materials and Methods). For all other analyses, we used the residuals from the regression of each measure of selection on average SVL (see Table 1). RMAE, reduced major axis estimator of fecundity slope.

| Measure of intrasexual selection | Analysis | df | Residual SSD vs. measure | | Residual male SVL vs. measure | |
|---|---|---|---|---|---|---|
| | | | r | P | r | P |
| Male aggression | tips | 211 | −0.295 | <0.001 | −0.293 | <0.001 |
| | contrasts | 211 | −0.136 | 0.048 | −0.133 | 0.052 |
| Territoriality | tips | 496 | −0.288 | <0.001 | −0.287 | <0.001 |
| | contrasts | 496 | −0.133 | 0.003 | −0.118 | 0.001 |
| Home range ratio | tips | 22 | −0.510 | 0.011 | NA | NA |
| | contrasts | 22 | −0.547 | 0.006 | NA | NA |
| Female home range size | tips | 22 | 0.709 | <0.001 | NA | NA |
| | contrasts | 22 | 0.723 | <0.001 | NA | NA |

| Measure of fecundity selection | Analysis | df | Residual SSD vs. measure | | Residual female SVL vs. measure | |
|---|---|---|---|---|---|---|
| | | | r | P | r | P |
| Clutch size | tips | 153 | 0.403 | <0.001 | 0.400 | <0.001 |
| | contrasts | 153 | 0.273 | <0.001 | 0.277 | <0.001 |
| Fecundity slope | tips | 50 | 0.364 | 0.008 | 0.361 | 0.009 |
| | contrasts | 50 | 0.148 | 0.296 | 0.147 | 0.299 |
| Fecundity slope (RMAE) | tips | 17 | 0.211 | 0.386 | 0.210 | 0.390 |
| | contrasts | 17 | 0.161 | 0.509 | 0.159 | 0.517 |
| Reproductive frequency | tips | 207 | −0.320 | <0.001 | −0.320 | <0.001 |
| | contrasts | 207 | −0.223 | 0.001 | −0.223 | 0.001 |
| Reproductive mode | tips | 458 | 0.192 | <0.001 | 0.192 | <0.001 |
| | contrasts | 458 | 0.126 | 0.007 | 0.126 | 0.007 |
| Length of reproductive season | tips | 76 | −0.104 | 0.366 | −0.103 | 0.370 |
| | contrasts | 76 | −0.010 | 0.932 | −0.010 | 0.944 |
| Latitude | tips | 274 | 0.318 | <0.001 | 0.317 | <0.001 |
| | contrasts | 274 | 0.070 | 0.245 | 0.070 | 0.248 |

0.002), and residual reproductive mode (partial $r = 0.289$, $P = 0.002$). In our contrasts analysis, backward elimination stepwise multiple regression with residual contrast of SSD as the dependent variable resulted in a significant model ($r = 0.396$, $F_{1,82} = 7.61$, $P < 0.001$) that retained residual contrast of clutch size (partial $r = 0.277$, $P = 0.008$) and residual contrast of territoriality (partial $r = 0.277$, $P = 0.008$). Thus, once phylogeny was taken into account, the variables employed in this analysis could explain only about 16% of the variance in SSD as the result of intrasexual selection for large male size and fecundity selection for large female size.

## DISCUSSION

### Intrasexual Selection Hypothesis

Male-larger SSD is generally more pronounced in lizards exhibiting male aggression and territoriality than in species lacking these behaviors, as previously suggested by several interspecific studies (Stamps 1983; Carothers 1984). Our phylogenetic analyses show that evolutionary changes in male aggression and territoriality are generally correlated with shifts in SSD, as predicted by the intrasexual selection hypothesis. However, SSD also varies considerably between sister taxa in the absence of discernable evolutionary change in these variables, which each only explain 2% of the inferred

evolutionary change in SSD. Further, even when considering only those sister taxa that differ with regard to male aggression and territoriality, these variables each explain less than 25% of the associated evolutionary change in SSD. Thus, although our results are qualitatively consistent with the predictions of the intrasexual selection hypothesis, we conclude that these variables do not explain much of the variance in SSD across lizard taxa as the result of intrasexual selection for large male body size.

The lack of a strong relationship between SSD and these correlates of intrasexual selection could be due to their simple categorical coding, which may obscure much of the actual variation in male aggression and territorial behavior needed to explain patterns in SSD. The diversity of aggressive behaviors and territorial defense strategies exhibited by lizards (e.g., Stamps 1977, 1983; Martins 1994), coupled with the uncertain extent to which this variation is likely to reflect differences in the intensity of sexual selection, makes this a legitimate concern. To accurately estimate the intensity of intrasexual selection, information concerning both the intensity of intrasexual mate competition and the relative magnitude of the reproductive reward attained from successful competition is ideally required. The ratio of breeding males to total adult males offers a measure of the former parameter, whereas the ratio of breeding males to breeding females approximates the latter (Jehl and Murray 1986). Unfortunately,
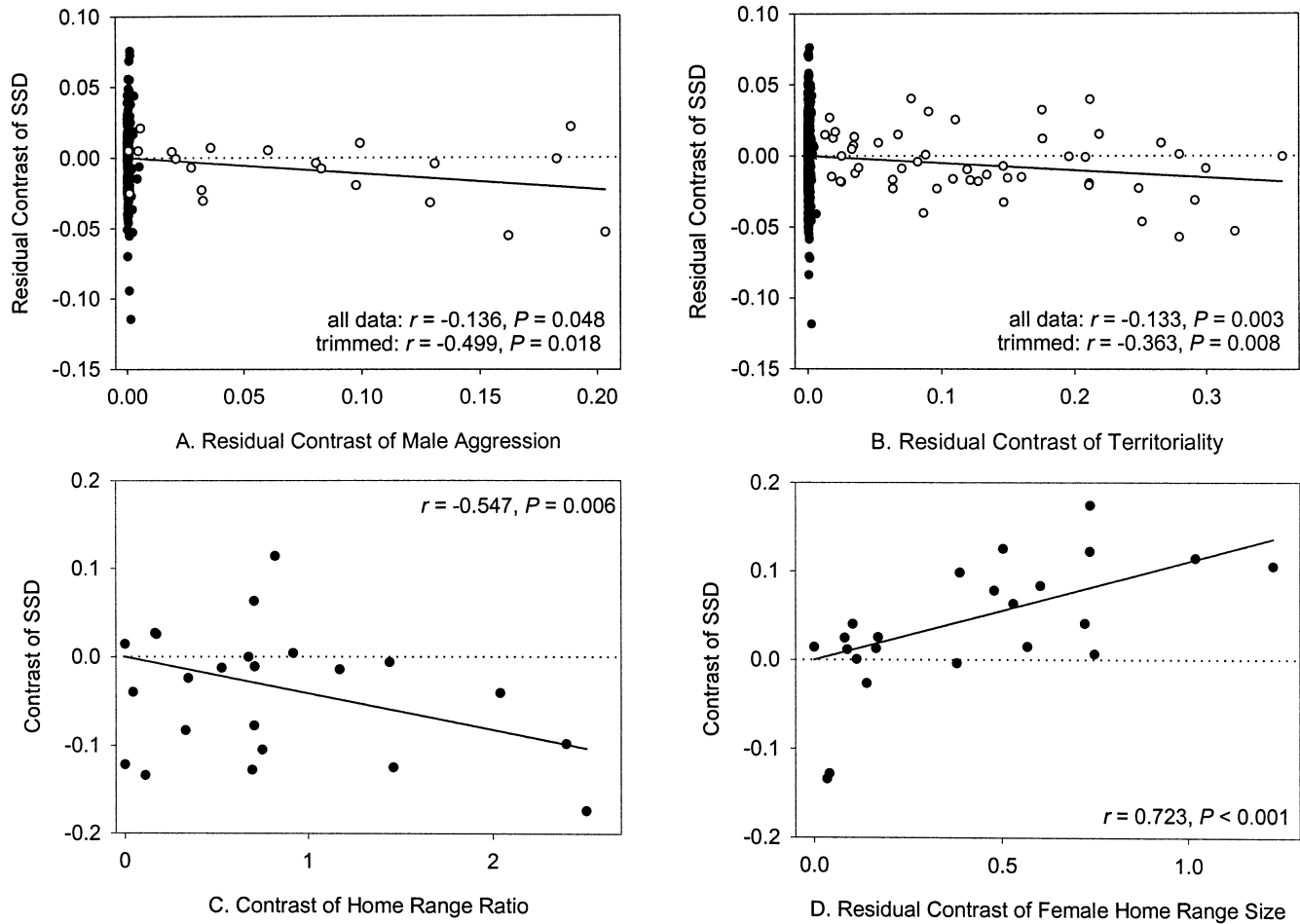
FIG. 2. Results of the least-squares regression through the origin of residual contrast of sexual size dimorphism (SSD) on residual contrasts of (A) male aggression and (B) territoriality, and of contrast of SSD on (C) contrast of home range ratio and (D) residual contrast of female home range size. Contrasts are "positivized" (see Garland et al. 1992) for illustrative purposes. Open circles denote datapoints used in our "trimmed" regressions (see Materials and Methods).

the accurate identification of breeding male lizards is difficult in the absence of paternity analyses (Haenel et al. 2003b), thus suitable data are seldom reported for natural populations. Adult sex ratio has been used to estimate intrasexual selection intensity in other taxa (e.g., Poulin 1997), and Stamps (1983) documented a correlation between adult sex ratio and SSD across 29 populations of territorial lizards. However, it would be inappropriate to consider these results as supportive of the intrasexual selection hypothesis due to the uncertain extent to which the adult sex ratio reflects the ratio of breeding males to breeding females in a given lizard population. In any case, Stamps employed SSD itself as a measure of intrasexual selection and interpreted this relationship as consistent with Trivers' (1972) prediction that intense male mate competition should lead to higher male mortality relative to females. Any such relationship between SSD and adult sex ratio could therefore be predicted from separate hypotheses arguing opposite causation.

Stamps (1983, 1999; Stamps et al. 1997) has suggested that information regarding male and female distributional patterns and population densities can be used to estimate intrasexual selection intensity in territorial species. As pre-

dicted by the intrasexual selection hypothesis, we found relatively strong evidence for a functional relationship between SSD and both home range ratio and female home range size in territorial species. Similarly, Stamps et al. (1997; Stamps 1999) documented the predicted correlation between SSD and female density in phylogenetic analyses of the genus *Anolis*. Although similar relationships between SSD and home range ratio or female density can be predicted from the alternative hypothesis that SSD functions to reduce intersexual trophic resource competition, the assumptions and additional predictions of this hypothesis were not supported in previous analyses (Stamps 1983, 1999; Stamps et al. 1997). The strong relationships between SSD and these continuous estimates of intrasexual selection intensity are consistent with the criticism that simple categorical variables such as male aggression and territoriality may lack the ability to uncover patterns of correlated evolution between SSD and intrasexual selection. However, with the exception of the lacertid *Podarcis muralis*, all species considered in the analyses of Stamps et al. (1997; Stamps 1983; 1999) belong to a single large clade of territorial lizards. The ability of the intrasexual selection
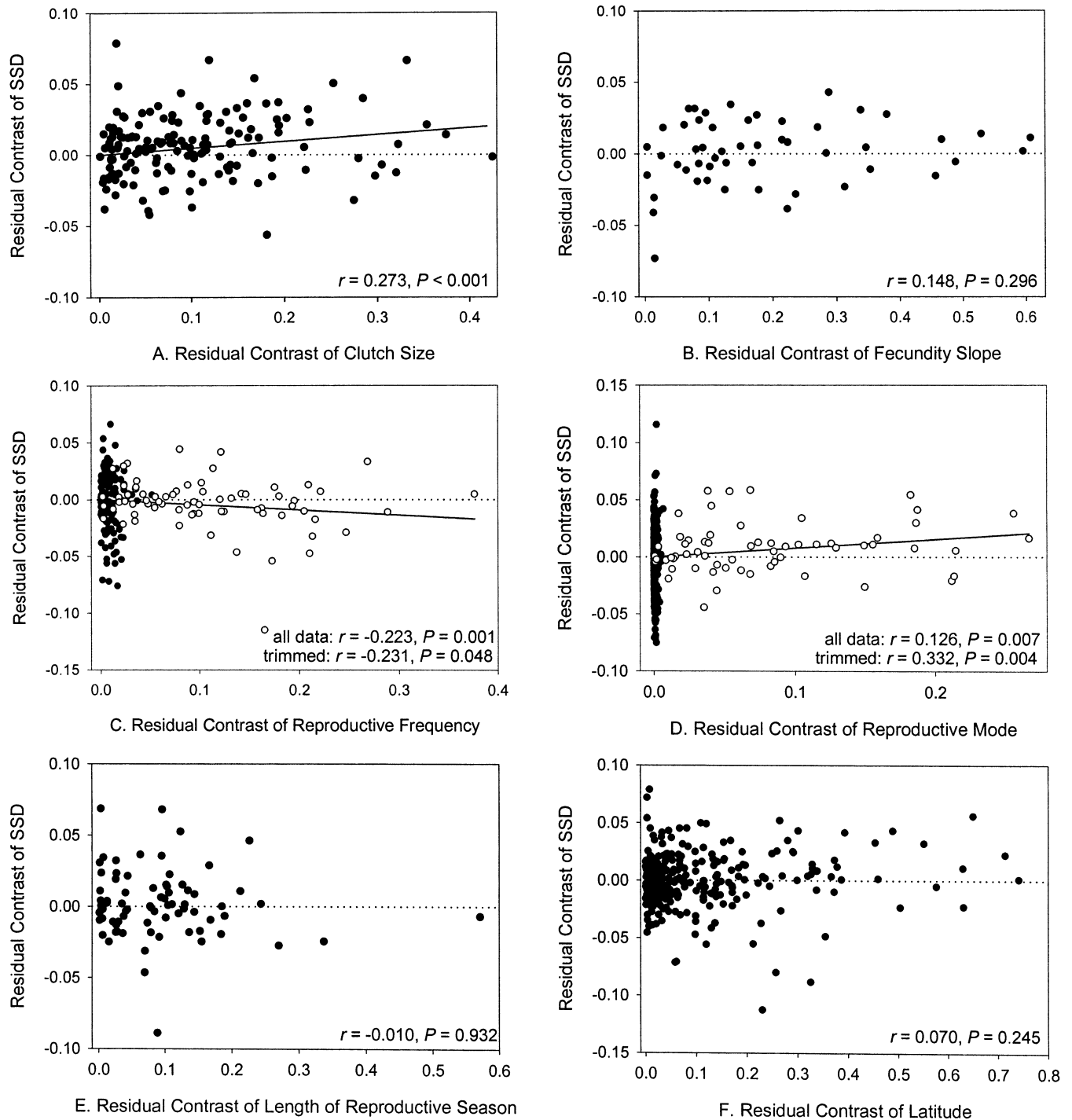
FIG. 3. Results of the least-squares regression through the origin of residual contrast of sexual size dimorphism (SSD) on residual contrasts of (A) clutch size, (B) fecundity slope, (C) reproductive frequency, (D) reproductive mode, (E) length of reproductive season, and (F) latitude. Contrasts are "positivized" (see Garland et al. 1992) for illustrative purposes. Open circles denote datapoints used in our "trimmed" regressions (see Materials and Methods).

hypothesis to explain patterns of SSD within other clades and across nonterritorial species therefore remains uncertain.

It is also important to note that measures such as home range ratio and female home range size only provide accurate estimates of intrasexual selection when there is a high probability that a territory holder will sire the clutches of the

females within his territory. Although this "probability of paternity" is believed to be high in many territorial species (see Stamps 1983), genetic analyses reveal considerable uncertainty in the use of home range overlap as a predictor of paternity in other territorial species (Abell 1997; Haenel et al. 2003b). In a New Jersey population of *Sceloporus un-*

*dulatus*, a relatively small average female home range size (147 m²) and an exceptionally large home range ratio (23:1) suggest strong intrasexual selection for male size (Haenel et al. 2003b). In a comparative analysis, these estimates of intrasexual selection intensity would correlate poorly with the significant female-larger SSD observed in this population (Haenel and John-Alder 2002). This unexpected relationship could be explained in light of the fact that home range overlap accurately predicted paternity in only 42% of the clutches examined (Haenel et al. 2003b). We present these data only as a cautionary example to stress the importance of validating the assumption that home range overlap is strongly related to reproductive success when using such estimates of intrasexual selection intensity.

Snakes comprise a highly derived lizard clade, thus a comparison of our results with those of Shine (1994a) is appropriate. In both lizards and snakes, patterns of SSD are such that males are generally larger, relative to females, in taxa characterized by the presence of male aggression and combat. Shine concluded that male combat favors the evolution of large male body size in snakes, and our trimmed regressions suggest a similar relationship between male aggression (or territoriality) and SSD in lizards. However, we question the general explanatory power of these variables in light of the substantial differences in SSD observed between sister taxa in the absence of discernable evolutionary changes in male aggression or territoriality. Shine's phylogenetic analysis is analogous to our trimmed regressions because it is limited to contrasts of SSD calculated between clades that differ with respect to male combat, thus ignoring the variance in SSD that occurs within these clades in the absence of evolutionary change in male combat. Although Shine incorporated data from 374 species in his analysis, support for the intrasexual selection hypothesis in snakes is based on a comparison of only 11 clades. We do not believe it is satisfactory to consider only instances of evolutionary change in testing hypotheses, and the inclusion of all contrast scores in our analyses leaves 98% of the variance in SSD unexplained by either male aggression or territoriality.

*Fecundity Advantage Hypothesis*

Sexual size dimorphism is positively correlated with clutch size across lizard species, and our phylogenetic analysis suggests that evolutionary changes in clutch size are generally accompanied by the predicted shifts in SSD. Although these results are consistent with the predictions of the fecundity advantage hypothesis, evolutionary changes in clutch size explain less than 8% of the variance in residual contrast of SSD. Previous studies have also documented a positive relationship between clutch size and SSD in squamates (Fitch 1978, 1981), but the results of several phylogenetic analyses are equivocal. As did Braña (1996), we found a significant positive correlation between residual contrast of clutch size and residual contrast of SSD in lizards, whereas Shine (1994a) and Zamudio (1998) found no relationship between clutch size and SSD in phylogenetic analyses involving Australian snakes and horned lizards of the genus *Phrynosoma*, respectively. Mean clutch size is a useful variable because it is widely reported in the literature, but the validity of this

measure as an estimate of the intensity of fecundity selection depends upon the assumption that, all else being equal, species with relatively larger clutch sizes have experienced stronger fecundity selection. Interpretation of causation from correlations between size-corrected measures of clutch size and SSD may be complicated because, for any given average body size, species with relatively larger females would be expected to produce relatively larger clutches, regardless of the source of SSD.

Fecundity slope presumably offers a more informative estimate of the intensity of fecundity selection because it describes the dynamic relationship between female SVL and clutch size within a population, thus providing a measure of the extent to which selection for large body size is likely to increase fecundity. Although SSD increases with fecundity slope across lizard species, our phylogenetic analysis suggests that much of this relationship is due to artifacts of shared evolutionary history. This conclusion is similar to that reached by Shine (1994a) for the reduced major axis estimator of fecundity slope in snakes, although Braña (1996) reported a strong positive relationship between fecundity slope and SSD after controlling for phylogenetic relationships among lacertids. The reduced major axis estimator of fecundity slope did not correlate significantly with SSD in either our tips or our contrasts analyses, although our sample size was relatively small (N = 19 populations). Shine (1994a) discussed several conditions under which fecundity slope is likely to yield a biased estimate of the intensity of fecundity selection and suggested that data linking growth rate, adult size, and lifetime reproductive success would be necessary for an ideal test of the fecundity advantage hypothesis.

The fecundity advantage hypothesis can also be indirectly tested by examining the relationship between SSD and reproductive frequency, assuming that species that reproduce infrequently are under greater selective pressure to increase clutch size per reproductive episode relative to species that reproduce frequently. Lizard species characterized by single annual reproductive frequency and a viviparous reproductive mode exhibit SSD in which females are relatively larger than in species that produce multiple annual clutches and reproduce oviparously, as previously reported by Fitch (1978, 1981). Our phylogenetic analyses suggest that evolutionary shifts in both reproductive frequency and reproductive mode are associated with the predicted changes in SSD. However, residual contrast of SSD also varies substantially in the absence of discernable evolutionary change in either independent variable, such that evolutionary shifts in reproductive frequency or mode each explain less than 5% of the inferred evolutionary change in SSD. Further, even when considering only those sister taxa that differ with regard to reproductive frequency and reproductive mode, these variables each explain less than 25% of the associated evolutionary change in SSD. Shine (1994a) found a similar relationship between reproductive mode and SSD in snakes, although his analysis was again limited to a comparison of only 10 clades that differ with respect to reproductive mode. Shine found no relationship between SSD and a continuous measure of reproductive frequency (proportion of reproductive females in a sample).

As predicted by the fecundity advantage hypothesis, we observed a positive correlation between latitude and SSD

across lizard species. Similar relationships have previously been reported across populations of *Uta stansburiana* (Parker and Pianka 1975), within the lizard genera *Sceloporus* (Fitch 1978) and *Leiocephalus* (Schoener et al. 1982), and across lizards and snakes in general (Fitch 1981). However, several studies have also found correlations in the opposite direction (Fitch 1976; Shine 1994a). In either case, these relationships appear to be driven by phylogeny, because neither our study nor that of Shine (1994a) found evidence that changes in latitude are accompanied by evolutionary shifts in SSD. To our knowledge, no previous comparative study has directly examined the relationship between SSD and length of reproductive season in squamate reptiles, but neither our tips nor our contrasts analysis suggested a relationship between these variables.

As with our male aggression and territoriality variables, it could be argued that categorical variables such as reproductive frequency and reproductive mode obscure much of the actual variation in fecundity selection intensity necessary for a strong correlation with SSD. However, we also examined the relationship between SSD and reproductive frequency using alternative, continuous variables such as length of reproductive season and latitude, neither of which suggested any functional relationship between reproductive frequency and SSD once phylogeny was taken into account. We also tested additional predictions of the fecundity advantage hypothesis using quantitative measures such as clutch size and fecundity slope. We therefore conclude that our analyses provide only weak support for the role of fecundity selection in shaping patterns of SSD across lizards.

Life-history theory predicts that lifetime reproductive success should be maximized by allocating energy to reproduction, rather than growth, when energy is limited. Shine (1988) therefore argued that the fecundity advantage hypothesis may be of limited utility because it implicitly assumes that the population in question is not energy-limited. Consistent with this critique, Shine found little support for the predicted trend toward relatively smaller females in lizard species characterized by invariant clutch size. However, the extent to which lizard populations are energy-limited, and thus violate this assumption, is not generally known (but see Dunham 1978; Ballinger and Congdon 1980).

### *Explaining Sexual Size Dimorphism in Lizards*

Intrasexual selection for large male size and fecundity selection for large female size have undoubtedly influenced patterns of SSD in lizards, as evidenced by the qualitative agreement between several of our results and the predictions of these hypotheses. However, our multiple regression analysis employed correlates of both intrasexual and fecundity selection, and although both territoriality and clutch size are significantly correlated with SSD, only 16% of the inferred evolutionary change in SSD can be explained by evolutionary shifts in either of these variables. Based on the weak explanatory power of our variables in both the bivariate and multiple regression analyses, we conclude that the comparative data at present do not strongly support these hypotheses as general explanations for SSD in lizards. This conclusion contradicts several previous comparative analyses involving

squamate reptiles, questions the generality of results obtained from descriptive studies of individual populations, and challenges the utility of the prevailing adaptive hypotheses for SSD in this group. In the following sections, we suggest several explanations for the discrepancies between our conclusions and those of previous comparative studies and conclude with a brief consideration of several alternative factors potentially influencing SSD in lizards.

Our results can be interpreted as evidence for or against the intrasexual selection and fecundity advantage hypotheses only to the extent that our variables provide reliable estimates of the intensity of selection on male or female body size. We have already discussed the limitations of our data and the potential biases inherent in our variables, many of which provide only coarse estimates of selection intensity and were chosen primarily because they were widely reported in the literature. However, many of these variables were also chosen because they were used in previous studies of SSD in squamate reptiles. Thus, much of the existing support for these hypotheses was derived from similar data.

Our study differs from several earlier investigations of SSD in lizards because we control for both allometry and phylogeny in our analyses. Although the biological basis for allometry in SSD is poorly understood and the validity of statistically controlling for this relationship has been questioned (Webster 1992; Fairbairn 1997; Smith 1999), it is generally accepted that phylogenetic relationships must be accounted for in interspecific analyses (Harvey and Pagel 1991). Additionally, aside from the nonphylogenetic analyses of Stamps (1983) and Fitch (1981), previous comparative studies have examined the intrasexual selection and fecundity advantage hypotheses only within particular squamate clades. It is conceivable that these hypotheses are of variable explanatory power across lineages, particularly given the diversity in morphology, behavior, ecology, and life history observed across lizards and snakes. For example, Clobert et al. (1998) found significant differences between major clades in their phylogenetic analysis of lizard life-history evolution. However, the relationships between SSD and our quantititative measures of fecundity selection did not differ in any consistent fashion when assessed using separate tips analyses for each family or major clade (i.e., Iguania and Scleroglossa; data not shown). Similarly, Perry and Garland (2002) found no evidence for significant family or major clade effects in their phylogenetic analysis of factors influencing lizard home range size. Our dataset did not support separate analyses for many of our variables (particularly our categorical measures) at the family level, but future studies may find it informative to conduct similar studies and compare results between major and minor clades.

Finally, and perhaps most importantly, our conclusions differ from those of previous studies (i.e., Shine 1994a) because we do not believe that it is appropriate to consider only those clades that differ with respect to categorical variables when attempting to explain the extensive variation in SSD that occurs both within and between these clades. Collapsing a phylogeny down to nodes that differ with respect to male combat or reproductive mode (see Shine 1994a) or conducting paired comparisons of sister taxa that differ with respect to mating system (see Oakes 1992; Székely et al. 2000) are

procedures analogous to our trimmed regressions. As such, they can informatively test the prediction that evolutionary changes in a categorical variable are associated with changes in the magnitude of SSD. However, the results of such analyses cannot be taken as evidence for the general explanatory power of the hypotheses in question because the variance in SSD that occurs within each category is not examined. Furthermore, the demonstration of a statistically significant effect of some variable on SSD should not be interpreted as strong support for the hypothesis being tested in the absence of some quantitative consideration of the unexplained variance in SSD. Similar to other studies, our results show statistically significant relationships between SSD and several of our measures of intrasexual and fecundity selection. However, because 84% of the variance in SSD was unexplained in our multiple regression analysis, we conclude that our results provide only weak support for these hypotheses as general explanations for SSD in this group.

*Additional Adaptive Hypotheses for Sexual Size Dimorphism*

Blanckenhorn (2000, p. 385) began a recent review on the evolution of body size by observing that ''it is widely agreed that fecundity selection and sexual selection are the major evolutionary forces that select for larger body size in most organisms,'' but concluded that alternative factors selecting against large body size are poorly understood and rarely investigated. In accordance with this view, adaptive hypotheses involving sexual selection for large male size and fecundity selection for large female size have historically been given preferential status as the primary explanations for SSD. The results of numerous descriptive studies suggest that intrasexual selection and fecundity selection favor large body size in lizards, but relatively few investigators have examined the potential deleterious fitness consequences of large size (Hecht 1952; Sinervo et al. 1992), or the resultant effects of counterbalancing natural selection on SSD (Wikelski and Trillmich 1997). Adaptive hypotheses for SSD that focus only on selection favoring large body size in either sex may ignore the important constraints introduced by stabilizing selection against large body size.

In this study, we considered sexual selection only in the context of intrasexual selection for large male size, thus neglecting the possibility that SSD is related to intersexual selection or intrasexual selection favoring small male size. In species with low population densities, females may be widely dispersed and male-male agonistic encounters are presumably less common. Under these conditions, intrasexual selection acting on males should favor the evolution of early reproduction, high mobility, and time and energy budgets allowing for substantial mate searching (Trivers 1972; Ghiselin 1974), thus selecting for small males. This ''small male advantage'' hypothesis is essentially an extension of the intrasexual selection hypothesis to conditions (i.e., low population density) under which male mate competition favors efficient search behavior over aggressive exclusion. Consistent with this hypothesis, Zamudio (1998) found that changes in SSD could be explained by decreases in average male size and male size at maturity in a phylogenetic analysis of 24 populations of *Phrynosoma* lizards. Sexual selection could

also influence SSD via female preference for large males, a phenomenon that has been documented in several lizard species (Cooper and Vitt 1993; Censky 1997). However, the available data suggest that although these processes may be important determinants of SSD within particular groups, they do not occur with enough frequency to warrant consideration as general explanatory hypotheses for SSD across lizards.

Rand (1967) and Schoener (1967) were among the first to suggest that SSD in lizards could result from selection for intersexual trophic niche divergence, under the assumption that differences in body size between the sexes are directly related to differences in prey size. Many investigators have documented correlations between SSD and intersexual trophic resource partitioning, but numerous others have reported SSD in the absence of trophic resource partitioning, differences in prey size in the absence of SSD, or differences in prey size in the opposite direction of SSD (reviewed in Stamps et al. 1997). Even in cases in which SSD and dietary differences appear correlated, it is often difficult to determine the causal relationship between the two, since divergence in prey size would not be an unusual consequence of SSD resulting from other factors (Vitt 1983; Powell and Russell 1984; Vitt and Cooper 1985). The trophic resource partitioning hypothesis also assumes that SSD reduces dietary overlap between the sexes and thus decreases intersexual food competition. Estimates of the intensity of food competition between males and females are generally lacking, but Stamps et al. (1997) showed that this assumption is not met in *Anolis aeneus*, in which intersexual competition coefficients are actually lower when males and females are the same size than when one sex is larger than the other. Although selection for intrasexual trophic resource partitioning may produce or reinforce SSD in some taxa, most direct tests have found little evidence in support of this hypothesis (Perry 1996; Stamps et al. 1997), and none have convincingly demonstrated that trophic divergence is driving SSD rather than vice versa.

*Nonadaptive Hypotheses for Sexual Size Dimorphism*

Since the pioneering work of Darwin (1871), investigators have focused primarily on adaptive hypotheses for SSD, often to the exclusion of alternative, nonadaptive explanations. For example, Butler et al. (2000, p. 259) begin their investigation of SSD in *Anolis* lizards by stating that ''sexual size dimorphism is the evolutionary result of selection operating differently on the body sizes of males and females,'' whereas Braña (1996, p. 518) considers SSD to be ''the result of a variety of selective forces acting on both male and female size.'' The rationale for this exclusively adaptive paradigm is provided by Fairbairn (1997, p. 680), who argues that, ''given the importance of body size in the ecology, life history, and reproductive fitness of most organisms. . . the patterns of variation in SSD among species should reflect differences in the patterns of adaptive divergence of males and females.'' However, recent studies have begun to consider the alternative that SSD may be an incidental consequence of sexual dimorphism in growth, which may in turn result from fundamental sexual differences in physiology, behavior, ecology, and reproductive investment. Although such sexual differences may be adaptive, we view these alternative hy-

potheses as nonadaptive with regard to SSD, in that they do not explicitly invoke differential selection on male and female body size. To illustrate the potential importance of such nonadaptive hypotheses, we present several of the many possible mechanisms whereby fundamental sexual differences could influence growth and SSD.

In several lizards in which males are larger than females, it has been suggested that SSD could result from the preferential allocation of energy to the production of offspring, rather than growth, in sexually mature females (e.g., Cordes et al. 1995; Sugg et al. 1995). However, the relative importance of female reproductive investment and selection on body size in shaping SSD within some populations may be difficult to determine in the absence of careful manipulative studies (Wikelski and Trillmich 1997). SSD could also arise because of fundamental sexual differences in the production of hormones associated with growth regulation (e.g., Abell 1998; see Badyaev 2002). In species in which females are the larger sex, SSD could develop as a result of investment in energetically expensive reproductive behaviors (i.e., territorial defense, mate searching) on the part of males (Cooper and Vitt 1989). Thus, SSD could result from sexual selection on behavioral traits or patterns of energy use rather than on male body size or morphology per se. For these reasons, investigators may find it more informative to focus on the ontogenetic and mechanistic basis of sexual differences in growth rather than on evolutionary correlates such as intrasexual or fecundity selection. To accomplish this, we believe that future studies will need to combine detailed demographic data regarding male and female growth with careful experimental manipulations of the physiological, behavioral, and ecological mechanisms potentially responsible for sexual dimorphisms in growth and body size. The importance of elucidating proximate causation and adopting an ontogenetic perspective in studies of SSD has recently been emphasized by numerous investigators (Shine 1990; Stamps 1993; Andrews and Stamps 1994; Watkins 1996; Duval and Beaupre 1998; Badyaev 2002), but at present this field is still dominated by studies, such as ours, that focus on evolutionary explanations.

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