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THE RELATIONSHIP BETWEEN SEXUAL SIZE DIMORPHISM AND HABITAT USE IN GREATER ANTILLEAN *ANOLIS* LIZARDS

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Abstract.—Sexual size dimorphism (SSD) is the evolutionary result of selection operating differently on the body sizes of males and females. *Anolis* lizard species of the Greater Antilles have been classified into ecomorph classes, largely on the basis of their structural habitat (perch height and diameter). We show that the major ecomorph classes differ in degree of SSD. At least two SSD classes are supported: high SSD (trunk-crown, trunk-ground) and low SSD (trunk, crown-giant, grass-bush, twig). Differences cannot be attributed to an allometric increase of SSD with body size or to a phylogenetic effect. A third explanation, that selective pressures on male and/or female body size vary among habitat types, is examined by evaluating expectations from the major relevant kinds of selective pressures. Although no one kind of selective pressure produces expectations consistent with all of the information, competition with respect to structural habitat and sexual selection pressures are more likely possibilities than competition with respect to prey size or optimal feeding pressures. The existence of habitat-specific sexual dimorphism suggests that adaptation of *Anolis* species to their environment is more complex than previously appreciated.

Key words.—Allometry, *Anolis* lizards, ANOVA, body size, comparative methods, phylogenetic effect, sexual selection.

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Although sexual size dimorphism (SSD) is ubiquitous throughout the animal kingdom, the relationship between SSD and environmental factors remains largely to be established. Darwin (1859, 1871) identified three types of selective pressures as potentially influencing the degree of sexual dimorphism: those resulting from intersexual competition for mates (sexual selection), from differences in the two sexes' reproductive roles, and from independent adaptations that the males and females may have in relation to ''differences in their habits of life.'' The importance of environmental factors is obvious when investigating the latter two selective pressures; however, even when SSD evolves as a result of sexual selection, the degree to which males and/or females are able to diverge may be determined by the environmental context of the species (Selander 1972). Food quality and dispersion are environmental variables that are thought sometimes to determine whether territorial mating systems are energetically feasible and, in particular, what degree of polygyny is possible. For example, mating systems are thought to evolve in response to food quality in primates (Leutenegger and Cheverud 1982; Cheverud et al. 1985; Gaulin and Sailer 1985; Ford 1994) and in response to food dispersion in ungulates (Jarman 1974; Geist 1977; Geist and Bayer 1988), gallinaceous birds (Geist 1977), and, possibly, seabirds (Fairbairn and Shine 1993).

In addition to food properties, an enormously important environmental factor potentially related to SSD is habitat type. Species living in different habitats may experience a broad array of different conditions, including differences in food availability, visibility, and density of competitors and predators, any of which could be related to SSD (Selander 1966). Nonetheless, few comparative studies have investigated whether a relationship exists between SSD and habitat use. Several studies of primate species have found weak or nonexistent effects of habitat on SSD, although the ability to detect any relationship may have been impaired by using only two categories to describe the full range of habitat variation (terrestrial/arboreal: Cheverud et al. 1985; Leutenegger and Cheverud 1982; primary/secondary forest: Ford 1994). By contrast, studies of ungulates (e.g., Jarman 1974) using more complex habitat categorizations have found an SSD-habitat relationship, but most were done without statistically rigorous methodology (for an exception, see Geist and Bayer 1988) and were conducted before the development of methods to account for phylogeny. Thus, the evolutionary relationship between habitat type and SSD remains uncertain.

Lizards of the genus *Anolis* are a particularly appropriate group to investigate the effect of habitat use on SSD for two reasons. First, *Anolis* species differ greatly in habitat use (Schoener and Schoener 1971a,b; Williams 1972, 1983). *Anolis* lizards are semiarboreal, insectivorous lizards. However, they have diversified into a wide range of lifestyles, the breadth of which is not typical among other lizard genera (Williams 1983; Losos 1994). For example, species that belong to the trunk-ground ecomorph type live close to the ground in relatively open habitat, tend to use a sit-and-wait foraging style, and are thought to be the most territorial. In contrast, twig anoles tend to live in the crowns of trees in dense matrices of thin twigs and tend to use an active-foraging mode of searching for prey (Schoener 1968, 1979; Schoener and Schoener 1980). Further, microhabitat differences have profound and evolutionarily repeated effects on morphology, and foraging and social behavior (Moermond 1979a,b; Pounds 1988; Losos 1990a,b,c, 1992; Losos et al. 1998). Williams (1972) described six ecomorph types, based on the structural habitat that the lizard species most frequently occupy: trunk-ground, trunk-crown, trunk, crown-giant, grass-bush, and twig. These ecomorphs have evolved independently on each of the Greater Antillean islands: Cuba, Hispaniola, Puerto Rico, and Jamaica (with the exception that

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TABLE 1. Taxa used in the study. Species for which phylogenetic information is available are indicated in bold. Only adults were measured, and female and male snout-to-vent length (SVL) is the mean of the largest third of these respective samples.

Ecomorph	Island	*Anolis* species	Sexual dimorphism log-ratio	Female SVL (mm)	Female number	Male SVL (mm)	Male number
Trunk-ground	Cuba	***sagrei***	0.28893	40.0	140	53.4	426
		homolechis	0.25268	40.7	111	52.4	371
		allogus	0.28119	42.5	108	56.3	262
	Hispaniola	***cybotes***	0.26024	50.8	157	65.9	258
		shrevei	0.16888	46.2	48	54.7	28
		whitemani	0.20933	48.1	18	59.3	19
	Jamaica	***lineatopus***	0.38873	44.2	132	65.2	421
	Puerto Rico	***cristatellus***	0.39796	44.6	245	66.4	440
		gundlachi	0.36021	45.2	28	64.8	50
		cooki	0.35788	41.6	6	59.5	22
Trunk-crown	Cuba	*allisoni*	0.28104	60.4	90	80.0	172
		porcatus	0.26307	54.5	125	70.9	237
	Hispaniola	***aliniger***	0.24837	45.4	4	58.2	10
		chlorocyanus	0.28399	54.2	102	72.0	208
		coelestinus	0.24703	54.6	155	69.9	347
	Jamaica	***grahami***	0.39786	44.0	53	65.5	186
		opalinus	0.20067	40.5	129	49.5	252
	Puerto Rico	*evermanni*	0.29954	52.4	73	70.7	80
		stratulus	0.15737	39.9	51	46.7	135
Grass-bush	Cuba	***alutaceus***	0.08216	32.7	111	35.5	103
		ophiolepis	0.15963	31.2	48	36.6	79
	Hispaniola	*hendersoni*	0.17525	40.2	86	47.9	165
		olssoni	0.09844	40.6	114	44.8	141
		semilineatus	0.11179	37.2	48	41.6	16
	Puerto Rico	*pulchellus*	0.23710	37.0	98	46.9	143
		poncensis	0.14108	39.6	28	45.6	55
		krugi	0.23478	39.3	56	49.7	83
Crown-giant	Cuba	***equestris***	0.08454	155.3	104	169	132
	Hispaniola	***ricordi***	0.08947	138.9	40	151.9	88
	Jamaica	***garmani***	0.28768	82.5	71	110.0	85
	Puerto Rico	***cuvieri***	0.09501	119.4	17	131.3	25
Twig	Cuba	***angusticeps***	0.13547	38.6	60	44.2	41
	Hispaniola	***insolitus***	0.06137	39.5	19	42.0	20
	Jamaica	***valencienni***	0.14766	68.5	32	79.4	43
	Puerto Rico	***occultus***	−0.00512	39.2	18	39.0	7
Trunk	Cuba	***loysiana***	0.13108	35.7	15	40.7	20
	Hispaniola	***brevirostrus***	0.17106	40.2	33	47.7	25
		distichus	0.13801	44.6	303	51.2	217

Jamaica is missing the grass-bush ecomorph and both Jamaica and Puerto Rico lack the trunk ecomorph; Jackman et al. 1997; Losos et al. 1998). Second, anoles vary considerably in extent of sexual dimorphism (Andrews 1976; Stamps 1983; Stamps et al. 1997). Sexual differences in body size have wide ranging correlates in anoles, including differences in prey size (Schoener 1967, 1968; Schoener and Gorman 1968) and microhabitat use (Schoener 1967; Schoener and Schoener 1971a,b; Scott et al. 1976).

In this study, we test the hypothesis that habitat differences influence the evolution of SSD. We test the additional alternative hypotheses that differences in SSD are an allometric consequence of differences in body size among ecomorphs or are simply a reflection of phylogenetic relationships.

MATERIALS AND METHODS

Stamps and coworkers (Stamps 1993, 1995; Stamps et al. 1994; Stamps and Krishnan 1997) have advocated the use of growth models in the study of sexual size dimorphism in species that continue to grow after sexual maturity. Although this approach captures the biological comparisons more accurately than simply comparing measures of standard adult body size, the data required to compare growth models are not as widely available. Therefore, to obtain a reasonable sample size of species, we measured snout-to-vent length (SVL, a standard measure of body size in lizards) of adults of both sexes of 40 species of *Anolis* lizards from the islands of Cuba, Hispaniola, Puerto Rico, and Jamaica (some of these data were published in Schoener 1969a, 1970a). Most species and sex classes had sample sizes of many more than 15 individuals for a total of 8488 individuals measured (Table 1). Of the 40 taxa, two species were excluded from the analysis because one had fewer than four specimens per sex class (*A. singularis*) and one species was represented twice (we included *A. sagrei* from Cuba because it has only recently colonized Jamaica; Williams 1969). We used the means of the largest third of all individuals for each species-sex class as indices of body size (Table 1). These indices are reasonable given that *Anolis* lizards follow asymptotic growth curves (Stamps and Andrews 1992).

As our measure of sexual dimorphism, we chose the ratio of male size to female size because it is intuitively simple and easily interpretable. Sexual size dimorphism ratios were natural-log (log) transformed prior to analysis (logSSD = log

TABLE 2. Ecomorph means for male size, female size, and dimorphism log-ratio for all species for which data were available. Size values were snout-to-vent lengths measured in millimeters and are reported as means with standard errors.

Ecomorph	Number of species	Female size (mm)	Male size (mm)	Dimorphism Log-ratio
Trunk-ground	10	44.4 ± 1.1	59.8 ± 1.7	0.297 ± 0.025
Trunk-crown	9	49.5 ± 2.4	64.8 ± 3.7	0.264 ± 0.022
Grass-bush	8	37.2 ± 1.2	43.6 ± 1.8	0.155 ± 0.021
Trunk	3	40.2 ± 2.6	46.5 ± 3.1	0.147 ± 0.012
Crown-giant	4	124.0 ± 15.7	140.6 ± 12.8	0.139 ± 0.050
Twig	4	46.4 ± 7.4	51.2 ± 9.5	0.085 ± 0.036

[male SVL/female SVL]) so that the distribution of SSD better approximated normality. However, this transformation made no qualitative difference in the analyses. Although more complicated models incorporating genetic covariances between the sexes could be devised, treating SSD as a single trait is sufficient for these analyses.

Effect of Habitat on Sexual Size Dimorphism

Each species belongs to a single ecomorph class (sensu Williams 1972; Table 1). LogSSD, female SVL, and male SVL appeared to differ among ecomorph classes (Table 2). We tested the null hypothesis that sexual dimorphism does not vary between ecomorph types using both the one-way ANOVA and Kruskal-Wallis tests. (Kruskal-Wallis tests were used in addition to ANOVA to compare with results from phylogenetic simulation, described below, for which it is not possible to use ANOVA). Significance was assessed at the 0.05 level. Which ecomorph classes differed from each other in sexual size dimorphism was determined using standard multiple comparisons procedures at the experiment-wise error rate of 0.05. For the ANOVA, we used the sequential Bonferroni method (Rice 1989). Because the Kruskal-Wallis test does not produce a table of *P*-values with a separate *P*-value for each treatment difference, it was not possible to apply the sequential Bonferroni method to this test. Instead, we used Bonferroni's (or Dunn's) distribution-free multiple comparisons test (Hollander and Wolfe 1973). This test compares each of the pairwise absolute differences in rank sums between ecomorphs against the largest pairwise difference in the randomized data. An observed difference is considered significant if it was greater than the largest difference in 95% of the 1000 randomization trials. This test is considered to be conservative with respect to Type I error (Hollander and Wolfe 1973); thus, we also compared the observed pairwise differences to the second and third largest randomized differences (Table 3). In no case was a pairwise difference considered significant by comparison to the second (or third) largest difference in the randomization if it was not also significant in comparison to the first (or second) difference.

Allometry

A potential explanation for the relationship between habitat and SSD is that SSD increases with increasing body size (hyperallometry) and body size is correlated with habitat

TABLE 3. Effect of habitat type on sexual size dimorphism. ANOVA analyses were conducted on logSSD with habitat type (trunk-ground, trunk-crown, grass-bush, trunk, crown-giant, or twig) as the treatment effect. The standard ANOVA model was used: logSSD = intercept + habitat type, with habitat type effect coded as a categorical variable. Phylogeny was accounted for by the GLS transformation (see text) using either BM or OU. Model, evolutionary model (NP, nonphylogenetic, BM, or OU); α, level of α-parameter in OU model; LogL, log-likelihood value for model; MSE, mean squared error of the ANOVA model; R^2, percent of variation in logSSD explained by the above model (i.e., interspecific variation in habitat); parameter estimates, estimated effects for each ecomorph type plus or minus one standard error; and *F*-ratios and *P*-values, hypothesis test for the pooled habitat effect (i.e., that at least one habitat type is different from the others). As is usual for ANOVAs, effects are estimable for only $n - 1$ of n categories; the final category has an effect of zero. Note that the parameter estimates were identical for the BM and four of the OU models (α = 0.0004, 0.004, 0.04, 0.4).

					Parameter estimates					Hypothesis test	
Model	α	LogL	MSE	R^2	Crown-giant	Grass-bush	Trunk-crown	Trunk-ground	Trunk	$F_{5,17}$	*P*-value
NP		28.9	0.00613	62%	−0.046 ±0.036	−0.041 ±0.036	0.077 ±0.036	0.149 ±0.036	−0.038 ±0.040	5.63	0.0031
BM		31.592[1]	0.0239	68%	−0.044 ±0.032	−0.023 ±0.029	0.059 ±0.030	0.138 ±0.028	−0.036 ±0.039	7.03	0.0010
OU	0.0004	27.2	7.701	67%	same as BM model					7.03	0.0010
	0.004	28.4	0.772	67%	same as BM model					7.03	0.0010
	0.04	29.5	0.079	67%	same as BM model					7.00	0.0010
	0.4	30.5	0.0105	68%	same as BM model					6.80	0.0012
OU	0.7578	30.562[2]	0.00714	69%	−0.046 ±0.033	−0.027 ±0.031	0.064 ±0.032	0.141 ±0.030	−0.035 ±0.039	6.64	0.0013
	4	29.4	0.00592	62%	−0.045 ±0.032	−0.026 ±0.030	0.063 ±0.031	0.140 ±0.030	−0.035 ±0.039	5.81	0.0026
	40	28.9	0.00613	62%	−0.047 ±0.036	−0.040 ±0.036	0.076 ±0.036	0.149 ±0.036	−0.038 ±0.040	5.63	0.0029

[1] Overall maximum-likelihood model.
[2] Maximum-likelihood model among OU models.

type. To investigate whether sexual size dimorphism increased with increasing overall size and could possibly account for the effect of habitat on SSD, we tested for differences in male size after controlling for female size (Fairbairn 1997). All body sizes were natural-log transformed prior to analysis, so that we tested for a multiplicative (or proportional) difference in SSD among ecomorph types. We conducted an ANCOVA on male size with ecomorph type as a treatment effect and female size as a covariate. The influence of phylogeny was accounted for by phylogenetic ANCOVA.

Phylogenetic Effect

Of the 38 species measured, 23 were included in a recent phylogenetic analysis (Jackman et al. 1997, 1999). Two species (*A. cybotes* and *A. ricordi*) were not included in the phylogeny, but had very closely related sibling species (*A. marcanoi* and *A. barahonae*, respectively) included in the phylogeny. Substituting *A. cybotes* for *A. marcanoi* and *A. ricordi* for *A. barahonae* is not likely to introduce error because each of these sister pairs is closely related (*A. cybotes* and *A. marcanoi* differ in immunological distance by only five albumin immunological distance units, and *A. ricordi* and *A. barahonae* react nearly identically to closely related species in immunological comparisons [Hass et al. 1993]). In all, 23 species (four species per ecomorph, except for trunk anoles represented by three species) were used in phylogenetic analyses (Fig. 1). Whenever possible, we conducted all analyses in three ways to compare the relative effects of sample size reduction and phylogeny: (1) nonphylogenetic analyses with the full 38 species dataset; (2) nonphylogenetic analyses with the 23 species for which there is a molecular phylogeny available; and (3) phylogenetic analyses with the 23 species.

To determine whether closely related species were more similar in logSSD than expected by chance (i.e., whether a phylogenetic effect existed), we calculated the phylogenetic autocorrelation statistic, ρ (Cheverud et al. 1985) for 23 species for which we had phylogenetic information. Branch lengths from the phylogeny (Fig. 1) were used to construct the phylogenetic similarity matrix (note that the basal polytomy is apparently real and represents a rapid radiation early in the history of anoles; Jackman et al. 1999). We note that results of this analysis should be received cautiously because Martins (1996) suggested that power to detect significant autocorrelation may be a function of sample size, and our sample size is below the recommended 40 taxa.

Phylogenetic Analyses

Statistical analyses can be confounded because of the nonindependence of species. Consequently, we also conducted habitat and allometry analyses incorporating phylogenetic information. We followed the generalized least-squares (GLS) approach of Martins and Hansen (Martins 1994; Hansen and Martins 1996; Martins and Hansen 1997) using both the Brownian motion (BM) and Ornstein-Uhlenbeck (OU) models for evolutionary change, as well as performing phylogenetic simulation tests. The GLS approach is described first. Brownian motion describes a stochastic process in which evolutionary changes at each generation are independent and

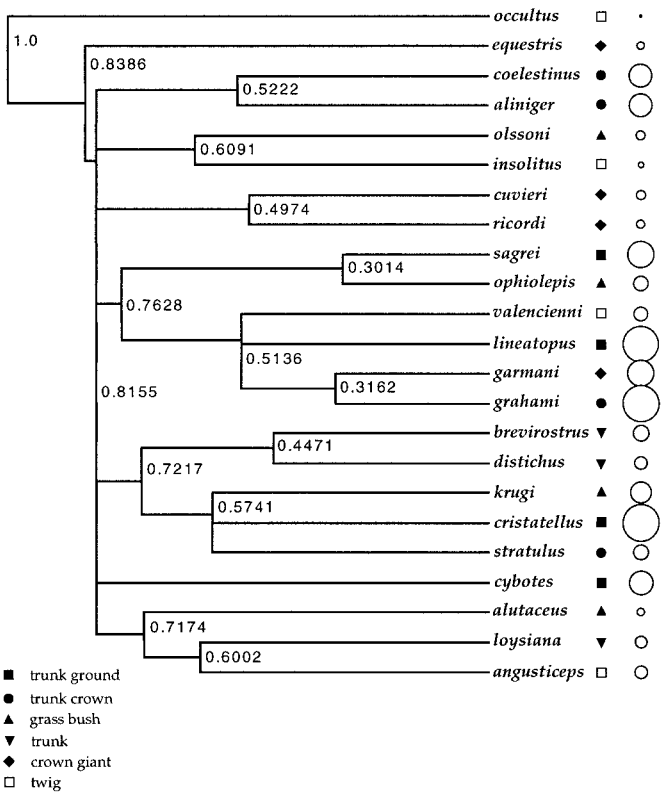

FIG. 1. Phylogenetic relationships for 23 of the taxa included in this study, based on Jackman et al. (1999; a complete phylogeny for Greater Antillean anoles is not available). The tree is drawn to reflect relative branch lengths assuming a molecular clock (numbers refer to the distance from the tips to each node). The tree is scaled so that the distance from the tips to the root is 1.0. LogSSD is proportional to the diameter of the circles. Ecomorph (habitat) types are coded as follows: ■, trunk-ground; ●, trunk-crown; ▲, grass-bush; ▽, trunk; ◆, crown-giant; and □, twig.

normally distributed (for further explanation, see Felsenstein 1973, 1985, 1988). BM is often used to approximate neutral drift or selection with a randomly changing selection gradient. OU is similar to BM, but with the added parameter of a restraining force, which tends to ''reign in'' evolutionary changes (drawn from a normal distribution as in BM). Thus, the pattern resulting from OU is one in which phenotypes, on average, tend to remain clustered near some ''optimal'' value, but with large changes occurring at low frequency that move the phenotypes farther from the optima. Several workers have used this process to describe a form of stabilizing selection because it resembles the expected behavior (phenotypes remaining near an optima with occasional peak shifts; Felsenstein 1988; Martins 1994; Hansen and Martins 1996). The extent to which phenotypes remain near their ancestral value or are free to change is determined by the strength of the restraining force. The salient difference between the models for comparative studies is that, with BM, similarity among species is expected to drop off linearly with time so that distantly related species will still resemble each other (although possibly only slightly); whereas with the OU model, expected similarity drops off much faster (exponentially), so that only closely related species resemble each

other and more distantly related species bear no phylogenetic similarity (Martins 1994; Hansen and Martins 1996; Martins and Hansen 1997).

The method of Martins and Hansen (Martins 1994, 1995; Hansen and Martins 1996; Martins and Hansen 1997) can accommodate detailed evolutionary models, such as estimating adaptive optima (Hansen 1997), here we only concern ourselves with correcting for the phylogenetic interdependence of the data while simultaneously incorporating an explicit model of evolution. This is done using a relatively simple transformation derived from the statistical theory of GLS (Grafen 1989; for a general reference, see Rao 1965). All that is needed is a phylogeny with branch length information and to select a model of evolution. The phylogenetic GLS transformation is explained below. SAS/IML code to conduct all steps of this methodology is provided in Appendix 1, and a worked example is given at the website http://biosgi.wustl.edu/lososlab/butler01/appendix.html.

If there were no phylogenetic interdependence among species (e.g., a star phylogeny), a regression of a dependent variable (y) on independent variables ($x_{.1}$, $x_{.2}$, . . . $x_{.m}$) could be described by a least-squares regression (Rao 1965, ch. 4). For species i:

$$y_i = x_{i1}\beta_1 + \cdots + x_{im}\beta_m + \epsilon, \quad (1)$$

where β_1, β_2, . . . β_m are the regression parameters, and ε represents random error. (In the usual case, an intercept is included by setting $x_{i1} = 1$, so that β_1 becomes the intercept term.) The expectation (mean) and variance of y is:

$$E[y_i] = x_{i1}\beta_1 + \cdots + x_{im}\beta_m \qquad \text{var}[y_i] = \sigma^2, \quad (2)$$

or, in matrix notation:

$$E[\mathbf{Y}] = \mathbf{X\beta} \qquad \text{var}[\mathbf{Y}] = \sigma^2\mathbf{I}, \quad (3)$$

where **Y** is now a vector, **X** is a matrix of independent variables (including any categorical variables), and **I** is the identity matrix.

However, if there are known correlations among the observations (as with data from a group of phylogenetically related organisms), then the variance of **Y** changes as follows (Rao 1965):

$$E[\mathbf{Y}] = \mathbf{X\beta} \qquad \text{var}[\mathbf{Y}] = \sigma^2\mathbf{G}, \quad (4)$$

where **G** is the matrix of covariances that we expect as a result of phylogeny (**G** is assumed to be known, and is described below). We can convert equations with correlations among observations (4) to equations with zero correlations (2; Rao 1965) by the phylogenetic GLS transformation:

$$\mathbf{Z} = \mathbf{G}^{-1/2}\mathbf{Y} \qquad \mathbf{U} = \mathbf{G}^{-1/2}\mathbf{X}, \quad (5)$$

where $\mathbf{G}^{-1/2}$ is the root (e.g., Cholesky decomposition) of the inverse of **G.** This results in:

$$E[\mathbf{Z}] = \mathbf{G}^{-1/2}\mathbf{X\beta} = \mathbf{U\beta} \qquad \text{var}[\mathbf{Z}] = \sigma^2\mathbf{I}. \quad (6)$$

This transformation is analogous to the univariate procedure of adjusting the data to unit variance by dividing each observation by the standard deviation. After transformation under the appropriate evolutionary model, the data are suitable for many standard statisitical procedures (e.g., ANOVA, ANCOVA, correlation analysis, linear regression).

The form of the **G** matrix (the covariance due to phylogenetic relationship) is a function of the phylogeny (both topology and branch lengths, which we assume are known) and the evolutionary process. Because we usually do not have any information regarding the form of the actual evolutionary process, a reasonable approach is to try a variety of different models. This has two benefits: we can determine which model fits the data best, and whether the conclusions are sensitive to the models selected. Hansen and Martins (1996) investigated a variety of different microevolutionary scenarios (combinations of drift, directional and stabilizing selection, changing evironment, and speciational evolution) and found that all produced covariance structures that were well approximated by either the BM or OU models.

Under BM, the elements of the **G** matrix are simply the amount of time (t_{bm}) from the root of the phylogeny to the most recent common ancestor of the pair of taxa. The diagonal entries (species variances) are the amounts of time from the root of the tree to each species (the depth of the tree if a molecular clock is assumed). The covariance between two species i and j in the OU model is (Hansen and Martins 1996; Hansen 1997):

$$\text{cov}[Y_i, Y_j] = v\exp[-\alpha t_{ou}][1 - \exp(-2\alpha t_{ra})], \quad (7)$$

where α is the magnitude of the restraining force, t_{ou} is the time that the the two species have been evolving independently (i.e., the branch length from one sister taxon to its ancestor plus the branch length from the other sister to their ancestor, or, if we can assume a molecular clock, t_{OU} = 2*[total time depth of tree $- t_{BM}$]), v is the variance term for evolutionary change in a small time interval (for OU, $v = \sigma^2/2\alpha$), and t_{ra} is the time separating their most recent common ancestor from some root of the tree. Following Hansen (1997), we assume here that this root point is far back in time, and that all ancestors have the same variance, v, so that the above equation reduces to:

$$\text{cov}[Y_i, Y_j] = v\exp[-\alpha t_{ou}] = v\mathbf{G}_{ij}. \quad (8)$$

Setting the elements of **G** equal to $\text{Exp}[-\alpha t_{ou}]$ with diagonal elements as ones, the expression (8) for the variance-covariance matrix becomes the same as (4). Alpha can be estimated using the RATES.C program (Martins 1994); Martins (1994) recommends trying several different values for alpha to bound the range of possiblities. After applying the phylogenetic GLS transformation (5), we get data that are suitable for ordinary (nonphylogenetic) statistics (i.e., expression 3). In addition, the fit of the models can be monitored by tracking the log-likelihood (LogL) value of the regression or ANOVA and finding the model with the largest LogL (Hansen 1997):

$$\log L = [\log|\mathbf{G}^{-1/2}|] - \left[\frac{n}{2}\log(2\pi\text{MSE})\right] - \left[\frac{(n-p)}{2}\right], \quad (9)$$

where n is the number of species, MSE is the mean squared error term from the ANOVA or regression model, and p is the number of parameters included in the model (see Appendix 1 for derivation). Thus, the only remaining task is to find the square-root of the inverse of the **G** matrix, which can be carried out using a matrix-language package (e.g.,

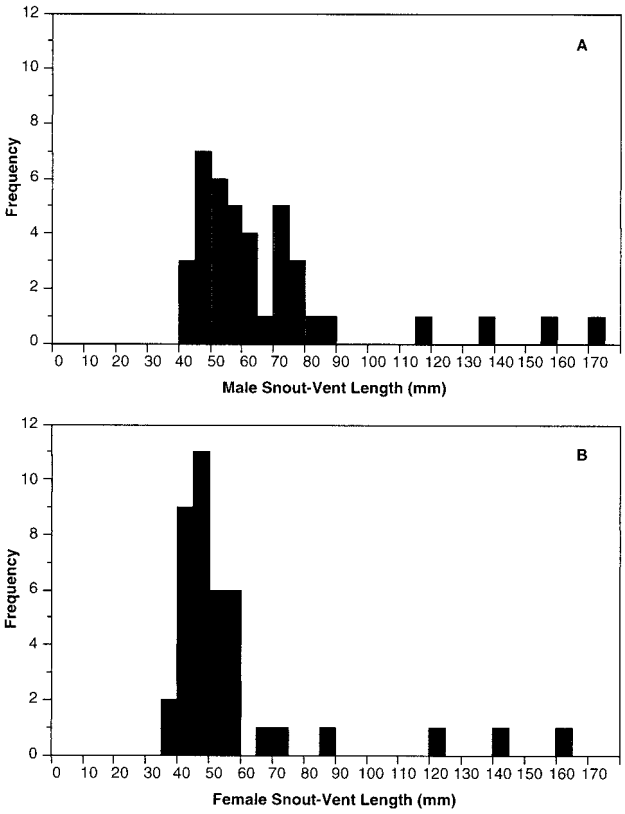

FIG. 2. Frequency histogram of male size (A) and female size (B) in 38 species of Greater Antillean *Anolis.* Species' sizes are grouped by intervals of 5 mm; labels indicate the upper end of the range.

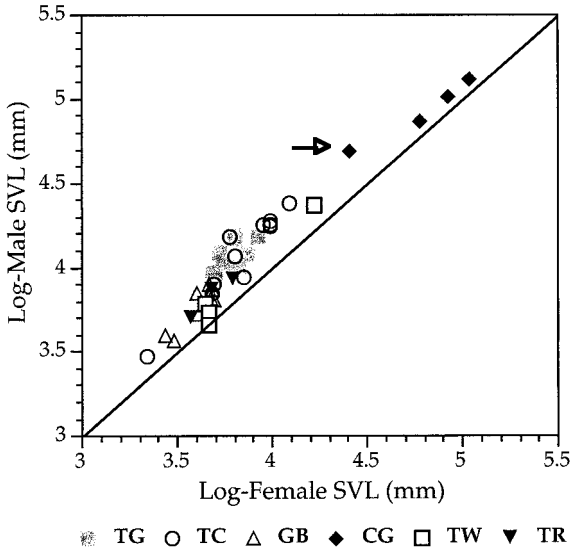

FIG. 3. Natural-log-transformed male size versus log(female size). Common slope of male size regressed on female size is not significantly different from one (diagonal line indicates unit allometry; common slope = 0.95 ± 0.10 SE, BM common slope = 0.95 ± 0.08 SE, OU common slopes = 0.95–0.96 ± 0.10 SE, Table 4). *Anolis garmani,* a likely outlier, is labeled with an arrow. Ecomorph (habitat) types are as indicated.

SAS or Mathematica). The transformed data can be used directly in statistical packages for regression of continuous variables. However, available packages for ANOVA or ANCOVA (involving the association of a continuous variable from one or more categorical variables) cannot automatically accept transformed categorical variables. In this case, the ANOVA or ANCOVA must be entered as a regression and the hypothesis tests specified manually.

We note that Garland et al. (1992) advocate a different approach, namely various transformations of the branch lengths until the data conform to BM expectations after applying independent contrasts. Although statistically valid, these transformations yield data that may not conform to any model of evolutionary change (Martins and Hansen 1997).

For the habitat effect and allometry hypotheses, LogSSD, male and female body size, and ecomorph category (effect coded for ANOVA; for an excellent treatment, see Bernstein 1987, p. 123) were transformed using the above procedure. These transformed data were used to compute ANOVAs or ANCOVAs using Proc REG from SAS Institute (1989). Branch lengths from the phylogeny in Figure 1 were used in the analyses. For an example and SAS/IML code required to do the effect coding of categorical variables, phylogenetic GLS transformation, and hypothesis test using ANCOVA or ANOVA, see Appendix 2 and website http://biosgi.wustl.edu/lososlab/butler01/appendix.html for updates.

For comparison among phylogenetic methods, we also conducted analyses using phylogenetic simulation with a BM model of evolution. Null distributions were generated by starting at the root of the phylogeny and simulating evolution of variables (LogSSD, log male size, or log female size) up the tree. Simulations were conducted using Martins's (1995) SIMULATE.C program in the COMPARE package, using both a gradual BM model incorporating branch lengths and a speciational model (i.e., BM model using equal branch lengths). One thousand simulations were conducted for each model in the LogSSD analysis. For the phylogenetic ANCOVA, only 250 simulations were conducted because they were labor intensive. Expectation tests were conducted in the manner of standard Kruskal-Wallis tests, with the exception that the observed scores were compared to the simulated null distributions to obtain *P*-values.

RESULTS

Males are larger than females in all Greater Antillean *Anolis* lizards measured, with only one small exception (*A. occultus* females are larger than males by 0.2 mm, LogSSD = −0.005, Table 1). Male size and female size have similar ranges of variation (male SVL 35.5–169 mm, female SVL 31.2–155.3 mm; Fig. 2, Table 1). The intermediate-sized species are the most highly size dimorphic (Fig. 3, Table 2), which results in a greater concentration of female sizes in the lower extreme of the distribution (SVL < 55 mm) and few female sizes in the intermediate range (55 mm < SVL < 85 mm) as compared to the distribution of male sizes (Fig. 2). Phylogenetic autocorrelation indicates that closely related species are no more similar in LogSSD than would be expected by chance ($\rho = -0.40$, $Z = -0.57$, $P > 0.75$; Fig. 1; note, however, that the power to detect a significant effect may have been reduced by small sample size).

TABLE 4. Test for allometric relationship in sexual size dimorphism (SSD) using ANCOVA. SSD may increase with overall species size (and thus eliminate the habitat effect on SSD). Thus, the ANCOVA tested for the effect of habitat on male size after controlling for female size. Terminology follows that used in Table 3. None of the models produced significant interaction effects (model: male size = intercept + female size + habitat type + female size × habitat type). Therefore, we can adequately describe the plot of log (male size) versus log (female size) (FSIZE; Fig. 3) as a set of parallel lines (one for each ecomorph), and all statistics are for the model: male size = intercept + female size + habitat type. The FSIZE parameter (± 1 SE) can be interpreted as the common slope for all data points. None of the model slopes are significantly different from 1.0, indicating no effect of allometry on SSD. *F*-ratios (with numerator and denominator degrees of freedom) and *P*-values are given for the pooled habitat effect; the FSIZE effect was highly significant (for each model: $F_{1,16} > 86.6$, $P < 0.0001$).

						Habitat effect	
Model	α	LogL	MSE	R^2	FSIZE	$F_{5,16}$	*P*-value
NP		28.956	0.0064	98%	0.95 ± 0.10	5.25	0.0048
BM		31.616[1]	0.0064	99%	0.95 ± 0.082	6.42	0.0019
OU	0.0004	27.226	8.027	98%	0.95 ± 0.082	6.42	0.0019
	0.004	28.376	0.8050	98%	0.95 ± 0.082	6.42	0.0019
	0.04	29.510	0.0828	98%	0.95 ± 0.082	6.40	0.0019
	0.4	30.461	0.0109	99%	0.96 ± 0.086	6.22	0.0022
OU	0.723	30.545[2]	0.0076	99%	0.96 ± 0.084	6.10	0.0024
	4	29.339	0.0062	98%	0.95 ± 0.100	5.40	0.0043
	40	28.956	0.0064	98%	0.95 ± 0.10	5.26	0.0048

[1] Overall maximum-likelihood model
[2] Maximum-likelihood model among OU models.

Does Variation Exist in Sexual Size Dimorphism among Ecomorphs?

Ecomorphs are significantly different in sexual size dimorphism in both nonphylogenetic and phylogenetic analyses. Using the nonphylogenetic ANOVA with the 38 Greater Antillean species, the ecomorphs were significantly different in SSD ($P < 0.001$). Considering only the 23 for which we have phylogenetic information, the test is still significant ($P < 0.003$, Table 3). Phylogenetic ANOVA results were also significant whether using BM ($P < 0.0010$, Table 3) or OU models (*P*-values ranged from 0.0010 to 0.0029). Moreover, nonphylogenetic and phylogenetic estimates for the ecomorph effects on SSD were very similar (Table 3). Note that the goal of this analysis, and that of ANOVAs generally, is to find a significant difference among treatments (ecomorph types), rather than to obtain precise estimates for the effect of each ecomorph category on SSD. Thus, the parameter estimates for the ecomorph effects are given mainly for the purpose of comparing analyses using different evolutionary models.

Log-likelihood (LogL) values for the models tested ranged from 27.2 to 31.6 (Table 3). The maximum likelihood (ML) model was the BM model (LogL = 31.562), which was followed by the OU with α-parameter = 0.758 (LogL = 30.562). However, our conclusions above remain robust to variation in evolutionary model, even if the ML model is not the correct one. Kruskal-Wallis tests produced results similar to that of ANOVA whether conducted nonphylogenetically (38 species: $P < 0.001$; 23 species: $P < 0.006$) or using phylogenetic simulation with a gradual or speciational model of evolution (23 species: $P = 0.004$ and 0.008, respectively).

Female size is highly correlated with male size (nonphylogenetic correlation, $r = 0.961$, Fig. 3; correlation after independent contrasts, $r = 0.967$). ANCOVA indicates that male size adjusted for female size is significantly different among ecomorph types whether assessed nonphylogenetically ($P < 0.0048$, using 23 species; Table 4) or phylogenetically using BM ($P < 0.0019$) or OU models ($P < 0.0019$–0.0048, Table 4). The interaction term between female size and ecomorph type was not significant (nonphylogenetic: $P < 0.475$; BM: $P < 0.99$; OU: $P < 0.506$), indicating that the slope of male size regressed on female size was not significantly different among ecomorphs. Accounting for phylogeny made no difference to the estimate of the common slope; common slopes are nearly identical among models and not significantly different from 1.0 (common slopes (± 1 SE ranged from 0.95 ± 0.10 to 0.96 ± 0.085, Table 4) . Thus, there is no evidence that SSD changes with overall size. The ML model was again the BM model (LogL = 31.616) followed by the OU model with α = 0.723 (LogL = 30.545). When statistical significance of these ANCOVA results is assessed by phylogenetic simulation, only three of 250 simulations provided results more significant than the analyses on the real data ($P \leq 0.012$). Thus, the difference between male and female size between ecomorph types cannot be explained by size differences among ecomorphs (Fig. 3).

We note in passing that a recent analysis of SSD (Stamps et al. 1997) recommends using residuals of size plots rather than absolute values to represent SSD. When this procedure is applied, ecomorph classes rank in exactly the same order (using residuals of male size regressed against female size as the measure of SSD) as when adjusted means from the above ANCOVA (nonphylogenetic) are used.

Which Ecomorphs Differ in Sexual Size Dimorphism?

Ecomorph classes overlap in SSD, but the means differ with the following order (Table 2): trunk ground (TG) > trunk crown (TC) > grass bush (GB) > trunk (TR) > crown giant (CG) > twig (TW). Multiple comparisons tests support the general pattern of high SSD for TG and TC anoles and low SSD for GB, CG, TR, and TW anoles. ANOVA for the full dataset with sequential Bonferroni post hoc comparisons indicates that the following pairs of ecomorph classes differ in SSD at the experiment-wise error rate of α = 0.05: TG versus TR, GB, CG, and TW and TC versus TW (Table 5, Fig. 4a); in addition, the comparison of TC versus CG is

TABLE 5. Pairwise differences in sexual size dimorphism by ecomorph. The Kruskal-Wallis differences between ecomorph categories in average SSD rank (with correction for unequal sample size) are given. Above diagonal, 23 species for which we have phylogenetic information; below diagonal, complete 38-species dataset. Significance of multiple comparisons at the experimentwise error rate of $\alpha = 0.05$ were determined by the Bonferroni distribution-free multiple comparisons procedure for the Kruskal-Wallis test (see text for further explanation). Significance was assessed in three ways: using randomization with replacement (nonphylogenetic approach) or using gradual or speciational evolution simulations for the reduced dataset. All three methods yielded the same conclusions. Superscripts a, b, and c indicate which ecomorphs are significantly different at the first, second, and third sequential comparisons, respectively. ANOVA with the sequential Bonferroni procedure produced similar results, with the exception that two comparisons become marginally nonsignificant (TC vs. CG in 38-species analysis; TC vs. TW in 23-species nonphylogenetic or phylogenetic ANOVA analyses).

vs.	Crown-giant	Trunk-crown	Trunk-ground	Grass-bush	Trunk	Twig
Crown-giant		11.67	16.97[b]	1.41	2.84	3.89
Trunk-crown	24.31[c]		5.30	10.25	7.96	15.56[c]
Trunk-ground	29.75[a]	6.51		15.56[c]	12.87	20.86[a]
Grass-bush	2.86	26.47[b]	33.41[a]		1.53	5.30
Trunk	1.09	20.67	25.47[c]	1.35		6.44
Twig	7.07	32.63[a]	38.20[a]	11.02	7.64	

marginally nonsignificant (this comparison becomes significant if $\alpha = 0.10$ is used). The reduced (23 species) dataset, which was analyzed nonphylogenetically, produced fewer significant comparisons (TG vs. TR, GB, CG, and TW; TC vs. TW is marginally nonsignificant $P = 0.061$, Table 5, Fig. 4b). This trend of high dimorphsim for TG and TC and low dimorphism for GB, and CG is also consistent with the estimated effects from the ANOVA models (with 23 species; TW was not estimable; see Table 3). There was no difference between the nonphylogenetic results for these 23 species and the phylogenetic ANOVA, whether the BM or OU models were used. The Kruskal-Wallis rank sums analyses (nonphylogenetic or phylogenetic simulation) produced parallel results to the ANOVAs with two minor differences. The comparison of TC versus CG becomes significant at $\alpha = 0.05$ in the 38-species, nonphylogenetic analysis and TC versus TW is significant in both the 23-species, nonphylogenetic and phylogenetic simulation analyses (Table 5, Fig. 4a).

DISCUSSION

Sexual size dimorphism differs among microhabitat types in Greater Antillean *Anolis* lizards. At least two classes of SSD exist, high dimorphism (trunk-ground and trunk-crown) and low dimorphism (trunk, crown-giant, grass-bush, and twig). Although habitat has been suggested to influence the evolution of SSD, this hypothesis has rarely been demonstrated. We present three possible explanations for the differences in SSD among habitat types: (1) habitat type and SSD are both strongly associated with phylogeny such that the relationship between them is a phylogenetic artifact; (2) the ecomorphs tend to differ in body size so that the difference in SSD may be a result of allometry; or (3) selective pressures on male and/or female body size differ among habitat types. As we now show, the first two explanations are inadequate, whereas the third (in rather complex form) is sufficient.

Allometry

Body size has been implicated as a good predictor of SSD (e.g., Leutenegger and Cheverud 1982; Cheverud et al. 1985; Björklund 1990; Fairbairn and Preziosi 1994; several authors [Gaulin and Sailer 1984; Reiss 1989; Fairbairn 1997], however, argue that allometry is a description of, rather than an explanation for, SSD). An indirect relationship between SSD and habitat use in *Anolis* could result if SSD changed allometrically with body size and if species using different structural habitats differed in body size. This expectation assumes that the relationship between SSD and body size does not vary among ecomorph classes. However, our analyses disprove this assumption: the relationship between SSD and body size varies among ecomorph classes and, when the effect of body size is removed, variation among ecomorphs in size-adjusted SSD still exists. Thus, variation among ecomorphs in body size alone cannot explain the overall relationship between SSD and structural habitat use.

Phylogenetic Effects

Several investigators have found large (Cheverud et al. 1985; Ely and Kurland 1989; Höglund 1989) or small, but significant (Björklund 1990), effects of phylogeny on SSD, whereas others have found little (Pyron 1996) or no effect (Zeh 1987; Fairbairn and Shine 1993; Willig and Hollander 1995). Comparative studies should incorporate methods that take phylogenetic relationships into account because species are historically related units and, thus, species' trait values may not be independent datapoints for statistical analysis (Felsenstein 1985; Huey and Bennett 1987; Grafen 1989). Failure to account for phylogeny can potentially result in either over- or underestimation of significance levels in statistical tests (Martins and Garland 1991; Butler and Losos 1997). Using the phylogenetic GLS method, we found that the BM model had the highest log-likelihood, and a close second was the OU $\alpha = 0.72$ model (or $\alpha = 0.77$, depending on the variables included). Thus, the influence of phylogeny can be detected in the evolution of SSD. However, phylogeny had no impact on our conclusions regarding the evolutionary association of SSD with habitat type or allometry. Thus, several lines of evidence indicate that SSD in Greater Antillean anoles is not an evolutionarily conservative trait. First, evolutionary changes in SSD cannot be localized to a few branches of the phylogenetic tree (Fig. 1). Second, SSD does not display any significant phylogenetic autocorrelation. Third,

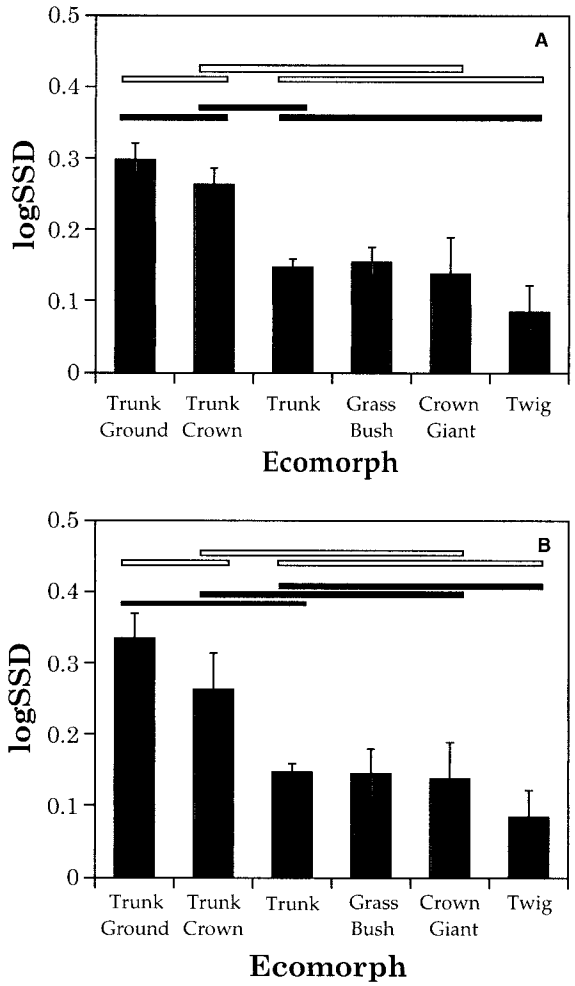

FIG. 4. (A) LogSSD by ecomorph (habitat) type for the complete (38 species) dataset. Plotted values are means with standard error bars. Ecomorphs that are not significantly different are indicated by lines above ecomorph categories. Both sequential Bonferroni (with ANOVA; open bars in figure) and randomization (with Kruskal-Wallis rank sums; closed bars) methods of assessing multiple comparisons were used. (B) LogSSD by ecomorph for the reduced dataset (23 species). Open bars indicate sequential Bonferroni as for part (A). Multiple comparisons using the Kruskal-Wallis rank sum randomizations gave identical results, whether conducted nonphylogenetically or by phylogenetic simulation using either a gradual or speciational model of evolution (closed bars).

conclusions from all phylogenetic analyses were identical to those for nonphylogenetic analyses.

Selective Pressures

Selective pressures that might influence SSD as it relates to structural habitat can be grouped into three classes: (1) Sexual selection may favor relatively large size in males when that trait results in greater mating success. Male anoles in many species maintain territories that provide access to the females residing within the territories. In highly territorial species, larger males have larger territories that encompass the territories of more females and thereby obtain more matings (Rand 1967a; Trivers 1976 [This reference also documents a relation between male body size and number of copulations]; Stamps 1977a; Schoener and Schoener 1982a; Hicks and Trivers 1983; Stamps 1983; Ruby 1984; Andrews 1985). Because the larger male usually prevails in agonistic encounters (Rand 1967a; Trivers 1976; Stamps 1977b, 1983; Andrews 1982, 1985; Tokarz 1985), selection may favor large size in males to gain the best territories and, indeed, the degree of polygyny is correlated with SSD in territorial lizards (Stamps 1983). Note that in nonterritorial systems, small male size may actually be favored (e.g., Zamudio 1998). (2) Intraspecific competition may select for large SSD if different sizes are most effective with different resource types (reviewed in Schoener 1977; Shine 1989, 1991). Relevant resource axes include prey size and one or more features of the microhabitat. For *Anolis*, the most frequently used habitat axes are perch height and perch diameter (together called ''structural habitat''). Slatkin's (1984) theoretical treatment shows competition is as likely (or as unlikely) to produce intersexual as interspecific differences; genetic correlations do not affect the likelihood of a species evolving sexual dimorphism. (3) Optimal feeding models predict unimodal or bimodal plots of optimal body size, depending on assumptions that inter alia incorporate foraging style (Schoener 1969b): sit-and-wait predators have bimodal plots, whereas active searchers have unimodal plots. Thus, SSD should be more prevalent among the former. These models are of a solitary species or morph, that is, competition is not explicitly included. Slatkin's (1984) theoretical treatment shows that, in part because of genetic correlations, this type of dimorphism can be difficult to evolve. This is in contrast to competition, which is as likely (or unlikely) to produce intersexual as interspecific differences; genetic correlations are not an issue.

Theory for the three classes of selection pressures makes various predictions about SSD. We now evaluate those predictions in which the degree of SSD is explicitly related to variation in some major property of the structural habitat.

The structural habitats occupied by the ecomorphs differ in their degree of visibility. Trunk-ground anoles occur in the most open habitats and have the highest SSD, whereas twig, grass-bush, and crown-giant anoles occupy the most closed habitats and have low SSD. In contrast to the general pattern, trunk anoles, which use relatively open habitats, have low SSD. Additionally, trunk-crown anoles, whose habitat is partly open but partly relatively dense branches and leaves, have high SSD. Thus, there is a tendency, albeit imperfect, for anoles in low-visibility microhabitats to have low SSD and vice versa. The tendency is consistent with both sexual selection and optimal feeding selective pressures. High visibility facilitates successful control of sexual access to females via territoriality in two ways. First, if territory holders can easily see intruders, they will be able quickly to expel them. Second, if intruders can easily see territory holders, then territorial displays become an effective deterrent. Thus sexual selection is likely to have greater effects the more open the microhabitat. Similarly, sit-and-wait predation on arthropods is more likely to be effective in open microhabitats, where prey can be spotted at relatively great distances. Indeed, anoles in the most open habitats, the trunk-ground species, can be classic sit-and-wait predators, for example,

A. sagrei and *A. lineatopus*, whereas anoles in cluttered twig habitats can be classic active searchers, for example, *A. angusticeps* and *A. valencienni* (Schoener and Schoener 1980; Hicks and Trivers 1983). Correspondingly, sit-and-wait predation favors a large SSD, whereas active searching favors the reverse. Visibility per se gives no obvious relation to competition selective pressures.

To evaluate competition, two basic characteristics of niche theory are relevant: SSD should be smaller (1) the smaller the range of available resources; and (2) the greater the number of species. The first expectation is an obvious one that follows directly from a positive relation of niche breadth to the width of the resource spectrum (e.g., Taper and Case 1992). Because each species' total niche can be decomposed into the two ''subniches'' corresponding to each sex, on average, the subniches should be closer the smaller the total niche width. The second (Selander 1966) argues that the greater the number of species, the smaller the average species' total niche width, and, as before, the closer the subniches should be. Interdigitation of sexes between species can occur and would disrupt the trend if great enough, but then total niche width would show little relation to number of species.

From the ecomorph designations alone, we can qualitatively surmise the range of the structural habitat axes available to each. Of those axes, perch diameter is the one most obviously related to body size and thus SSD; a within-species tendency for larger anoles to use thicker perches is well documented (Rand 1967b; Schoener 1967, 1968, 1970b; Schoener and Gorman 1968; Andrews 1971; Schoener and Schoener 1971a,b). Particularly the trunk-ground and, to a lesser extent, the trunk-crown ecomorphs occupy a wide range of perch diameters (at least on an arithmetic scale—see references just cited), and both have large SSD. Trunk, twig, and grass-bush anoles occupy a smaller range of diameters (note that the name for each denotes a particular subset of perch sizes), and those ecomorphs have small SSD. The crown-giant ecomorph may be an exception. Although few data are available on its structural habitat, it may be similar in perch-diameter range to the trunk-crown ecomorph. Reliable information exists for *A. garmani* (Rand 1967b, table 1), which does indeed support great similarity in structural habitat to large individuals of the trunk-crown *A. grahami*, to which it is closely related (Fig. 1). However, we do not know the extent to which this is typical for crown giants because no other precise information exists. Moreover, *A. garmani* is in fact atypical in SSD for the crown-giant ecomorph; it has an unusually high SSD, even higher than all but one trunk-crown species. Thus, *A. garmani* may be the ''exception that proves the rule.''

Evaluation of the second aspect of niche theory is more difficult. Ideally, we would like to know the number of potentially competing species averaged over the appropriate sites for the average species in each ecomorph. Such information is not available, so we are left with qualitatively surmising spatial co-occurrence directly from the ecomorph designations. Thus, we use as a measure of (maximum) ''crowdedness'' the number of ecomorphs each ecomorph overlaps with; these numbers range from 0 to 4. (Note that there are only a few known examples of more than one species from a given ecomorph occurring sympatrically in the Greater Antilles; Schoener 1970a, figs. 1–3.) Table 6 shows that the number of overlapping ecomorphs is not related to SSD. The trunk-crown ecomorph, which overlaps with the greatest number of other ecomorphs, has high SSD; moreover, the two ecomorphs with the least overlap, twig and grass-bush, have low SSD. The only obviously consistent ecomorph is trunk. Interestingly, on the satellite island of Bimini, only four ecomorphs occur, the trunk species has the smallest SSD and the largest average interspecific spatial overlap (Schoener 1968; table 11.)

TABLE 6. Overlap (X) or nonoverlap (—) between ecomorph classes (TC, trunk-crown; TG, trunk-ground; GB, grass-bush; TW, twig; CG, crown-giant; TR, trunk).

	TC	TG	GB	TW	CG	TR	Number of overlaps
TC	*						4
TG	X	*					2
GB	—	—	*				0
TW	X	—	—	*			1
CG	X	—	—	—	*		2
TR	X	X	—	—	X	*	3

In summary, each class of selective pressures has some substantial support, but no single class can account for all the evidence. The visibility expectations lend support to both sexual selection and optimal feeding, although a few ecomorphs seem inconsistent. Selective pressures related to competition are supported with regard to the available range of a habitat axis, perch diameter, to be partitioned by the sexes, but are not supported by interspecific crowdedness as surmised from the number of overlapping ecomorphs. Note further that the range of available perch diameters could also be considered a constraint for the other classes of selective pressures. For example, sexual selection favoring increased male size may not be realizable if available perches are all small. Further, although number of co-occurring species appears mostly irrelevant here, note that on a per-island basis, a rather strong correlation exists between SSD and number of species (Schoener 1977). Apposite to our study, it is interesting that the trunk-ground and trunk-crown are those West Indian species most frequently found in a solitary state, that is, on islands with no other *Anolis* (Schoener 1969a, 1975; Williams 1969). Thus, lack of sympatric competitors, perhaps followed by evolutionary stasis, may have resulted in a broad structural habitat and a higher SSD in these two ecomorphs. Moreover, even on islands where more than one species occurs, the trunk-ground representative in particular may often be in near solitary condition by virtue of its using habitats unused by other anoles (as on Bimini; Schoener and Schoener 1980); thus, some selective pressure may be ongoing.

Uncertainty over its selective basis should not obscure the primary finding of this paper. Despite the extensive literature on causal mechanisms involved in the evolution of SSD, relatively few studies have considered the ecological context in which this evolution occurs, and the role of habitat has not been adequately investigated. Our analysis clearly indicates that evolutionary change in degree of SSD has occurred repeatedly within greater Antillean Anolis lizards, and that this change is closely linked with shifts in habitat use.

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Appendix 1

In this appendix, we derive the likelihood equation (9) for general ANOVA assuming a model of evolution (nonphylogenetic, BM, or OU). Recall from the Materials and Methods that we used the transformation (5), $\mathbf{Z} = \mathbf{G}^{-1/2}\mathbf{Y}$, to transform our phylogenetically correlated data (Y,**X**) to uncorrelated data (**Z,U**), which we could use in standard statistical tests. Thus, we can obtain the likelihood expression for our transformed data by starting with the standard likelihood equation and simply making a change of variables.

The standard likelihood equation for ANOVA models with uncorrelated data is (Rao 1965):

$$L(\mathbf{Z}) = \frac{1}{(2\pi\sigma^2)^{n/2}}\exp\left[\frac{-(\mathbf{Z} - \hat{\mathbf{Z}})'(\mathbf{Z} - \hat{\mathbf{Z}})}{2\sigma^2}\right], \quad \text{(A1)}$$

where **Z** is the vector of dependent observations (e.g., SSD in this study), n is the number of observations, and σ^2 is the variance. The Jacobian of transformation for $\mathbf{Z} = \mathbf{G}^{-1/2}\mathbf{Y}$ is then:

$$d\mathbf{Z} = |\mathbf{G}^{-1/2}|d\mathbf{Y}. \quad \text{(A2)}$$

In terms of our observed data, substituting evolutionary variance v for σ^2, the likelihood equation becomes:

$$L(\mathbf{Y}) = \frac{1}{(2\pi v)^{n/2}}\exp\left[\frac{-(\mathbf{Y} - \hat{\mathbf{Y}})'\mathbf{G}^{-1}(\mathbf{Y} - \hat{\mathbf{Y}})}{2v}\right]|\mathbf{G}^{-1/2}|. \quad \text{(A3)}$$

We now take the natural logarithm and substitute the maximum-likelihood estimates (MLEs) for the parameters in the model. We can greatly simplify the likelihood equation by noting three items: (1) $(\mathbf{Y} - \hat{\mathbf{Y}})'\mathbf{G}^{-1}(\mathbf{Y} - \hat{\mathbf{Y}})$ is simply the RSS (residual sum of squares) from the ANOVA using the transformed data; (2) the MLE for the variance term is simply the model MSE (Rao 1965); and (3) that MSE = RSS/(n − p), where p = number of parameters in the model (note also that n − p is equivalent to the error degrees of freedom). We finally obtain equation (A4):

$$\log L(\mathbf{Y}) = [\log|\mathbf{G}^{-1/2}|] - \left[\frac{n}{2}\log(2\pi\text{MSE})\right] - \left[\frac{n - p}{2}\right]. \quad \text{(A4)}$$

Equation (A4) can be used to calculate log-likelihood equations for any ANOVA or regression-based hypothesis tests using various evolutionary models. The first term in the likelihood equation is the contribution from the evolutionary model and the remaining terms are the contribution from the ANOVA or regression model. Thus, different evolutionary models can be accomodated by substituting the appropriate **G** matrix as described in the text. In the nonphylogenetic model, the **G** matrix is the identity matrix, so that the first term, $\log|\mathbf{G}^{-1/2}|$, equals zero.

Appendix 2

Here we describe how to effect code categorical variables and provide sample code to carry out the calculations and conduct a phylogenetic ANCOVA using SAS/IML.

Effect coding (what commercially available ANOVA programs do for us ''behind the scenes''; Bernstein 1987; SAS Institute 1989) involves splitting up a categorical variable with k categories into k − 1 presence/absence variables (each pseudovariable represents membership to one category, with the last category represented as not belonging to any of the first k − 1 categories). For example, the categorical variable, food type, with three categories is recoded as two pseudovariables X_3 and X_4:

Food type	X_3	X_4
fruit	1	0
snails	0	1
ants	−1	−1

It is the pseudovariables (here, X_3 and X_4) that are included in the regression model as independent variables (along with any other independent variables, such as a continuous covariate). Testing for a treatment effect is testing whether at least one of the regression parameters for the pseudovariables is significantly different from the others. (Note that the effect coding above refers to the specification of the regression model, not the specification of the hypothesis tests, which also use the same terminology, for example, effect, dummy, or orthogonal coding.) For further explanation and other methods of coding, see Bernstein (1987, p. 123).

The phylogenetic GLS transformation involves premultiplying the vector of dependent variables (**Y**) and the matrix of independent variables (**X**) with the square root of the inverse of the expected phylogenetic covariance matrix (**G**) to produce transformed variables (**Z, U,** respectively) with the phylogenetic covariance removed (see Materials and Methods for an explanation).

The SAS/IML code to perform these transformations and conduct a phylogenetic ANCOVA is provided below (the nonphylogenetic ANCOVA would simply involve performing the ANCOVA on the original data, and an ANOVA is specified in the same way, but without a continuous covariate and check for interactions). In the following example, we have one dependent variable, head length (Y), a continuous covariate, body size (X_2, the second column of the design matrix **X**), and a categorical independent variable, food type (X_3,X_4). An intercept term (X_1) is also included because the data were not adjusted to zero mean prior to analysis. The main hypothesis tests for an evolutionary association between head length and food type after controlling for body size. If there is a significant treatment effect, often we are interested in knowing which of the treatments is significantly different from the others. The code to produce all pairwise comparisons among food types (fruit vs. snail, fruit vs. ant, snail vs. ant) is also provided (but the significance levels must be adjusted for the number of multiple tests). The sample code performs the calculations using the OU model, but this can easily be changed to the BM model by substituting ''gg = tbm;'' for ''gg = exp(-1*a*tou);''. Please note that is only a ficticious example for illustrative purposes. It is not possible to test for interactions among three categories and a continuous variable with only five datapoints.

BeginSAScode:

```
proc iml;
y = {1, 6, 2, 3, 5};                                   /* a 1 × 5 vector, e.g., head length */
x = {1 3 1 0, 1 7 0 1, 1 3 -1 -1, 1 4 0 1, 1 8 1 0};   /* a 4 × 5 matrix */
                                                       /* each row represents one species */
                                                       /* columns represent variables X1–X4 */
tbm = {5 3 0 0 0, 3 5 0 0 0, 0 0 5 2 2, 0 0 2 5 4, 0 0 2 4 5};
tou = {0 4 10 10 10, 4 0 10 10 10, 10 10 0 6 6, 10 10 6 0 2, 10 10 6 2 0};

print 'Ornstein-Uhlenbeck Transformation';
a = 0.1;
gg = exp(-1*a*tou);                                    /* compute OU G-matrix. For BM, use gg = tbm */
ggi = inv(gg);                                         /* compute inverse of G-matrix */
rootggi = half(ggi);                                   /* compute square-root ggi by Cholesky decomposition */
detrggi = det(rootggi);
logdet = log(detrggi);

                                                       /* use this to compute log-likelihood */
print detrggi logdet;                                  /* or detrggi to compute likilihood */
u = rootggi*x;
z = rootggi*y;                                         /* transform X variables */
print gg u z;                                          /* transform Y variables */

filename out 'ou.dat';                                 /* print transformation to file ou.dat */
file out;                                              /* each line has y x1 x2 x3 x4 */
do i = 1 to nrow(u); put (z[i]) 9.6 + 2 @;
do j = 1 to ncol(u); put (u[i,j]) 9.6 + 2 @;
end; put;
end;
closefile out;
quit; /* Exit IML */

data ou; infile 'ou.dat';
input y intercept x c1 c2;
int1 = x*c1;
int2= x*c2;
run;
/*** Compute ANCOVA for OU model ***/
proc reg data = ou;
model y = intercept x c1 c2 intl int2 / noint;
interxns: test int1, int2 / print;                     /* tests for interaction effect */
proc reg data = ou;
model y = intercept x c1 c2 / noint;
effect: test c1, c2 / print;                           /* tests for treatment effect */
onetwo: test c1 = c2 / print;                          /* pairwise test of treatment 1 vs 2 */
onethr: test c1 = -c1-c2 / print;                      /* 1 vs 3 */
twothr: test c2 = -c1-c2 / print;                      /* 2 vs 3 */
run;
endsas;
```