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MULTIVARIATE SEXUAL DIMORPHISM, SEXUAL SELECTION, AND ADAPTATION IN GREATER ANTILLEAN *ANOLIS* LIZARDS

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Abstract. Sexual variation in body form is a common phenomenon in the natural world. Although most research has focused on dimorphism in size, examination of differences in shape can provide insight into ecological factors that may differ in importance to the sexes. In this study, we investigated the patterns of body shape dimorphism in 15 species of Greater Antillean *Anolis* lizards and investigated whether these patterns can be explained by allometry, phylogenetic effect, or sexual differences in habitat use.

We found extensive shape and ecological variation between males and females. Previous studies have been conducted on males only; we found that females have also evolved morphologies to match their habitats. However, we concluded that adaptive patterns differ for the sexes and that interspecific ecological variation is related more strongly to shape than to size for each sex.

Previous studies on males have revealed repeated convergent evolution of morphology to habitat types (termed ''ecomorphs''). Here, we found that ecomorphs also differ in the magnitude and direction of shape dimorphism. These results cannot be accounted for by allometric scaling or by phylogenetic similarity (regardless of assumptions regarding evolutionary process); they support previous studies that have found important life-history differences for species of different habitat types. We found some evidence for independent adaptation of the sexes, but with more complex ecological patterning occurring between sexes than can be explained by sexual selection alone. Consequently, some combination of functional differences and sexual selection is required.

Key words: adaptation; allometry; Anolis *lizards; ecomorphs; Greater Antilles; habitat use; morphometrics; multivariate analysis; phylogeny; phylo-GLS; sexual dimorphism; sexual selection.*

INTRODUCTION

Sexual dimorphism is a common and sometimes prominent feature of the animal world. Males and females differ in a variety of aspects; however, the vast majority of comparative studies of sexual dimorphism have focused only on size dimorphism (for recent reviews, see Andersson [1994] and Fairbairn [1997]), with relatively few examining variation in shape (Selander 1966, Dayan et al. 1990, Dayan and Simberloff 1994, Emerson 1994, Jablonski and Ruliang 1995, Willig and Hollander 1995, Braña 1996). However, there is no reason to believe that shape dimorphism is any less important than size dimorphism.

Selection favoring intersexual differences in body shape might result from differences between the sexes in ecology (niche partitioning between the sexes), behavior (territorial or mate choice behavior), or reproduction (physiological or anatomical differences related to different reproductive costs or roles [Darwin 1859, 1871]). Many examples are known of these phenomena. Sex differences in ecology (food and/or habitat) associated with shape dimorphism are known from many reptiles (e.g., Schoener 1967, 1968, Schoener and Gorman 1968, Lister 1970, Schoener et al. 1982, Hebrard and Madsen 1984, Powell and Russell 1984, Shine 1991, Vitt et al. 1996), birds (e.g., Selander 1966, Hakkarainen et al. 1996, Temeles et al. 2000), and mammals (Dayan and Simberloff 1994). Behavior can lead to dimorphism by the operation of sexual selection, which may result in exaggeration of body proportions in one sex, usually males (e.g., Andersson 1982, Cooper and Vitt 1989, Basolo 1990, Zuk et al. 1992, Emerson 1994, Quinn and Foote 1994, Braña 1996).

Although not as extensively studied as the other two explanations, the influence of differences in reproductive roles in producing dimorphism may be substantial. For example, sexual dimorphism in the human pelvis might reflect differences in reproductive costs because selection favors a narrow pelvis to facilitate upright locomotion in both sexes, but in females this pressure is balanced by selection for a broader pelvis to minimize mortality during childbirth (Arsuaga and Carretero 1994, LaVelle 1995). In other animals, the relative size or shape of the female's abdomen may be tightly associated with fecundity selection (Preziosi et al. 1996) or may impose a physical constraint on repro-

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ductive output (Griffith 1994, Forsman and Shine 1995, Michaud and Echternacht 1995, Qualls and Shine 1995, Braña 1996, Olsson and Shine 1997). Thus, reproductive requirements may result in different body shapes between males and females.

Shape dimorphism may also arise without being a direct target of selection. For example, shape dimorphism may arise as an allometric response to selection for size dimorphism (reviewed in Gould 1975). Alternatively, transient sexual dimorphism may evolve as a consequence of differences between the sexes in patterns of phenotypic variance (Leutenegger and Cheverud 1982, 1985, Cheverud et al. 1985). Even when the sexes experience similar selective pressures, they may temporarily exhibit different shape morphologies if males possess greater phenotypic variance for particular morphological traits such as limb length or mass. This difference will persist in the population until selective equilibrium is reached.

The causes for sexual dimorphism in shape are the same forces as those that could produce sexual dimorphism in size (Andersson 1994). Nonetheless, taxa that are dimorphic in both respects may have evolved size and shape dimorphism as a result of different selective pressures. Additionally, studies that account for both size and shape dimorphism may be aided by the multivariate nature of shape dimorphism, which allows more detailed analyses along more dimensions of differentiation than are possible with size alone.

Sexual dimorphism in Caribbean anoles

In this study, we take a comparative approach to investigate whether sexual dimorphism in shape exists for the *Anolis* lizards of Puerto Rico and Jamaica. Caribbean anoles have diversified to occupy a wide range of arboreal microhabitat types ranging from forest floor and tree trunk to canopy to tall grass, and have morphological and locomotor specializations that correspond to the physical characteristics of their microhabitats (Moermond 1979*a*, *b*, Pounds 1988, Losos 1990*a*, *b*, *c*). Williams (1972) described six types of habitat specialists, termed ''ecomorphs'' and named for the microhabitat that the lizard species most frequently occupy: trunk–ground, trunk–crown, trunk, crown–giant (giant refers to the size of the lizard), grass–bush, and twig. These ecomorphs have evolved independently on each Greater Antillean island, with the exceptions that Jamaica is missing the grass–bush ecomorph and both Jamaica and Puerto Rico lack the trunk ecomorph (Williams 1983, Losos et al. 1998).

Morphological shape variation is extensive in this group; however, previous work has focused on males only and has not considered the role of sexual dimorphism. Indeed, these lizards exhibit substantial interspecific variation in sexual size dimorphism (Andrews 1976, Stamps 1983, Stamps and Krishnan 1997), which is related to variation in habitat use (Schoener 1968, 1974, Butler et al. 2000) and not to phylogenetic relationship (Butler et al. 2000). By contrast, dimorphism in shape has received little attention.

Sexual dimorphism in shape in anoles may result from a number of reasons related to functional biology and habitat use. The males of many species are territorial (e.g., Trivers 1976, Schoener and Schoener 1982*a*, *b*, Stamps 1983, Jenssen 1995, Tokarz 1995) and spend a substantially greater portion of their time involved in conspicuous social displays and encounters than do females (e.g., Rand 1967, Jenssen 1970, Andrews 1974, Stamps 1977*a*, *b*, 1978, Schoener and Schoener 1978*a*, Talbot 1979, and previous references). As a result, males may be in need of greater predator escape abilites, such as faster sprinting ability conferred by longer limbs (Moermond 1979*a*, Losos and Sinervo 1989, Losos 1990*c*), used by most species to escape predators (Irschick and Losos 1998). Females, on the other hand, have to cope with the functional challenges posed by egg bearing. Anoles lay only one egg at time, but females may have several staggered stages of egg production simultaneously (e.g., two oviducal eggs, an enlarged follicle, and smaller follicles). As a result, egg production can account for a substantial proportion of a female's body cavity volume (M. A. Butler, *personal observation*), especially for the smallest females, given that the relative size of the egg decreases with increasing species size (Andrews and Rand 1974). For anoles, in general, shorter limbs increase stability on narrow surfaces (Losos and Sinervo 1989, Sinervo and Losos 1991). Selection particularly may favor short limbs in arboreal females to compensate for the biomechanical constraints imposed by egg bearing (altered center of gravity, reduced speed and agility) coupled with the increased difficulty of maintaining locomotor stability on the narrow surfaces of the arboreal environment.

We examine patterns of sexual dimorphism in shape in relation to selective factors and ask whether shape dimorphism is related to allometric scaling with size, habitat use, or phylogenetic effect. With regard to habitat use, we ask whether shape dimorphism occurs because the sexes maintain the same relationship between morphology and habitat, but diverge in habitat use, or because the relationship between morphology and habitat differs between the sexes.

Materials and Methods

Field studies

Field studies were conducted during the summers of 1994 and 1995 in Jamaica and Puerto Rico (study sites of Losos 1990*a*, *b*, *c*). *Anolis* species were studied at the following sites in Jamaica: Discovery Bay Marine Laboratory, St. Ann Parish (*A. garmani*, *A. grahami*, *A. lineatopus*, *A. sagrei*, *A. valencienni*); University of the West Indies, Mona, St. Andrew Parish (*A. garmani*, *A. grahami*, *A. lineatopus*, *A. opalinus*); Gold Nugget Hotel lots, Negril, Westomoreland Parish (*A. garmani*,

A. grahami, *A. lineatopus*, *A. opalinus*, *A. valencienni*). In Puerto Rico, species were studied at the following sites: Cambalache Forest (*A. cuvieri*), El Verde Biological Field Station, Caribbean National Forest (*A. cristatellus*, *A. evermanni*, *A. gundlachi*, *A. krugi*, *A. pulchellus*, *A. stratulus*); El Yunque forest (*A. cuvieri*, *A. occultus*); El Verda, Highway 186 (*A. cristatellus*, *A. krugi*, *A. pulchellus*, *A. stratulus*); and Parguera, Highway 304 (*A. cristatellus*, *A. poncensis*). To minimize the effect of interpopulation differences within species, we measured all individuals of a species from a single population whenever sufficient numbers were available. Otherwise, representative samples of both sexes were measured from each locality. Only large adults were used in this study. These animals were generally reproductively active (as revealed by palpation in females and by exhibition of territorial behavior by males) and well above size at sexual maturity from published studies.

Habitat data were collected following the methodology of previous studies (Rand 1964, 1967, Schoener and Schoener 1971*a*, *b*, Losos 1990*b*) by M. Butler and three field assistants. Briefly, the observer walked slowly through the habitat and, for each lizard sighted, recorded the species and sex and measured the lizard's perch height (PHT) and perch diameter (PD). Measurements were made using a tape measure or were estimated by comparison to poles of known length. Only observations in which the animal was not already fleeing when spotted were included. Each observer collected roughly equal proportions of observations for each species and sex. Observer bias was not detected (using ANOVA) in any of the data.

Mean values for PHT and PD are given in Table 1. We measured these variables for 14 species (all species except *A. occultus*, which is difficult to find during the day) and used the species-sex (per species, by sex) means of log-transformed values in all analyses (logPHT and logPD). Additional data on *A. cuvieri* were obtained from Leal and Rodríguez-Robles (1997) and from fieldwork at the Cambalache site conducted in 1992 by J. Losos using the methology just described. At least 40 individuals per species and sex class were measured (fewer for *A. cuvieri*, *A. poncensis*, and *A. valencienni*), for a total of 1098 individuals (Table 1).

For morphological measurements, animals were captured in the field, measured by a single researcher (M. Butler), and returned to the point of capture. Data were collected from both sexes of 15 *Anolis* species (Table 1). In total, 509 individuals were measured, with at least 11 individuals per sex and species, except for three species that were difficult to capture (*A. cuvieri*, *A. occultus*, and *A. poncensis*; see Table 1). These three species were not included in intraspecific analyses of variation due to insufficient sample size. Morphological variables included body mass and three linear measures: snout-to-vent length (SVL) and fore- and hindlimb length (FOREL and HINDL). Linear measurements were in millimeters and mass was in grams. Because mass increases linearly with the cube of body length (Andrews 1979, 1982, Powell and Russell 1992, Stamps et al. 1994), the cube root of mass was used in all analyses (CMASS). All variables were natural-log-transformed prior to analysis (logCMASS, logSVL, logFOREL, logHINDL). The variables we used were chosen, following previous studies of ecomorphological evolution in *Anolis* lizards (Moermond 1979*a*, *b*, Pounds 1988, Losos 1990*a*, *b*, *c*), for their utility in revealing patterns of adaptation to habitat use and their relation to functional biology. We recognize that there may be additional variables that may be useful to describe differences in shape variation among species and sexes (e.g., differences in head vs. body dimensions [Cooper and Vitt 1989] or tail dimensions).

Separating size and shape

To examine the influence of shape dimorphism and to compare its importance to that of size dimorphism for explaining morphological and ecological variation, we first size-adjusted the data. The relative strengths and weaknesses of various methods for the study of size and shape have been well explored (for a recent review, see Klingenberg 1996). We used Mosimann's (1970) geometric-mean method on log-transformed data for size adjustment because of the heterogeneity among groups and because the geometric interpretation of shape seemed the most natural with respect to our hypotheses of functional biology and allometric scaling.

Mosimann's (1970) method removes the effects of size for each observation on an individual-by-individual basis using a directly measured index of individual size (here the geometric mean, which equals the fourth root of the product of the variables: SVL, CMASS, FOREL, and HINDL). Thus, the log-version of geometric-mean size index (logSIZE) becomes the arithmetic average (mean) of the log-transformed variables. Each individual was adjusted for size by taking the difference of each log-variable with logSIZE (i.e., the log-ratio). For example, the size-adjusted value for forelimb length was:

$$\log(\text{FOREL/SIZE}) = \log(\text{FOREL}) - \log(\text{SIZE}).$$

We note that the use of ratios can sometimes have undesirable properties if shape variables as we have defined them have residual size effects or if the variables are highly skewed or otherwise non-normal. We tested these criteria explicitly and confirmed that they were not problematical for our data. Shape variables defined in this way are linearly dependent; thus, when the goal of analysis is to represent all shape variation at once, it is only necessary to use three of the four variables (the variation in the fourth is, by definition, built into the other three). In such multivariate analyses, we arbitrarily omitted size-adjusted logCMASS.

TABLE 1. Habitat use (perch height and diameter), morphology, and size-adjusted morphology data for female (F) and male (M) Caribbean *Anolis* lizard species used in this study, grouped by ecomorph category and island.

Ecomorph, island, and species	*N*		Perch height (m)		Perch diameter (cm)		Morphology					
							N		SVL (mm)		Mass (g)	
	F	M	F	M	F	M	F	M	F	M	F	M
Trunk–ground												
Puerto Rico												
cristatellus	55	62	0.89 (0.63)	1.20 (0.72)	16.9 (20.2)	10.8 (13.5)	19	20	46.2	66.1	2.8	9.1
gundlachi	73	88	1.13 (0.76)	1.50 (0.78)	8.3 (9.6)	14.9 (15.8)	19	18	42.6	62.9	2.2	6.7
Jamaica												
lineatopus	71	59	0.56 (0.44)	0.87 (0.60)	5.8 (5.9)	6.2 (5.9)	24	21	42.6	57.8	2.0	4.9
sagrei	58	48	0.29 (0.27)	0.42 (0.34)	8.0 (11.3)	5.8 (7.6)	25	21	38.7	47.2	1.4	2.7
Trunk–crown												
Puerto Rico												
evermanni	48	54	1.99 (2.39)	2.82 (4.28)	14.9 (19.4)	22.8 (45.5)	19	17	47.5	57.4	2.6	4.6
stratulus	45	46	6.85 (9.22)	10.49 (10.29)	14.4 (25.5)	14.2 (14.4)	26	11	38.8	43.1	1.6	1.9
Jamaica												
grahami	73	77	1.47 (1.10)	2.04 (1.77)	7.0 (7.2)	10.2 (9.5)	21	18	43.3	60.0	2.4	6.7
opalinus	36	37	1.62 (1.30)	1.84 (0.99)	9.0 (11.2)	9.5 (7.8)	21	18	37.6	46.8	1.1	2.2
Crown–giant												
Puerto Rico												
cuvieri	8	20	2.77 (0.66)	2.84 (1.69)	9.8 (0.6)	10.8 (4.6)	3	6	118.0	133.7	38.4	48.7
Jamaica												
garmani	39	44	2.60 (1.98)	3.55 (1.95)	17.6 (14.1)	13.0 (8.8)	12	10	78.2	115.3	11.7	40.3
Grass–bush												
Puerto Rico												
krugi	27	46	0.67 (0.56)	0.91 (0.63)	3.9 (9.6)	6.2 (10.1)	19	18	37.1	42.8	1.3	1.8
poncensis	27	30	0.30 (0.17)	0.31 (0.14)	3.4 (5.6)	2.3 (1.5)	6	6	36.0	43.2	1.3	1.8
pulchellus	51	64	0.30 (0.20)	0.51 (0.32)	1.8 (4.0)	4.5 (11.1)	20	19	35.1	41.6	1.0	1.5
Twig												
Puerto Rico												
occultus	0	0					10	4	38.1	37.3	0.6	0.7
Jamaica												
valencienni	35	22	2.18 (1.67)	2.62 (1.66)	2.3 (6.0)	7.0 (21.5)	29	15	54.8	58.4	2.8	3.8

Notes: N, numbers of individuals. Means (with 1 SD for habitat data in parentheses) are given by sex and species. Morphological variables are: SVL, snout-to-vent length; MASS, mass; HINDL, hind-limb length; FOREL, forelimb length. SIZE is the geometric mean of the three linear measures plus the cube root of mass (logSIZE is given). Size-adjusted morphology (shape) variables are the log-ratio of each variable with SIZE. Sexual dimorphism in shape variables was tested for significance using mean male and female values (asterisks [*] next to male value indicates $P < 0.05$ after sequential Bonferroni correction, paired *t* test). *Anolis cuvieri, A. occultus*, and *A. poncensis* were not tested (because of small intraspecific sample size).

Previous studies of the relationship between morphology and habitat use in *Anolis* lizards (males only) have employed SVL as an estimate of overall body size and have used regression residuals as size-corrected variables (e.g., Losos and Sinervo 1989, Losos 1990*b*, *c*, Irschick et al. 1997). However, the present study has shown that males and females differ in relative SVL, with females generally having longer relative SVL. Thus, using SVL as an indicator of size can be problematical in studies of shape dimorphism.

The relationship between size and shape

We investigated the relationship between size and shape using multivariate linear models. The full model specified log(shape variables) as the dependent variables, with SEX, ECOMORPH, and SPECIES nested

TABLE 1. Extended.

Morphology				Size-adjusted morphology									
HINDL(mm)		FOREL(mm)		logSIZE		logSVL/SIZE		logMASS/SIZE		logHINDL/SIZE		logFOREL/SIZE	
F	M	F	M	F	M	F	M	F	M	F	M	F	M
36.9	55.6	22.2	32.5	2.72	3.10*	1.10	1.08	−2.38	−2.37	0.89	0.91	0.38	0.38
37.9	56.1	21.7	32.0	2.68	3.06*	1.07	1.08	−2.42	−2.44	0.95	0.96	0.40	0.40
33.8	46.6	19.6	27.6	2.62	2.93*	1.13	1.12	−2.39	−2.41	0.90	0.91	0.36	0.38
28.6	35.7	16.6	21.0	2.48	2.70*	1.17	1.16	−2.37	−2.38	0.87	0.88	0.33	0.35
37.7	45.6	23.7	29.0	2.74	2.93*	1.12	1.11	−2.43	−2.44	0.89	0.89	0.42	0.44
28.6	32.1	18.8	21.1	2.52	2.62*	1.13	1.14	−2.37	−2.40*	0.83	0.84	0.41	0.42
31.7	45.1	19.8	27.7	2.62	2.95*	1.14	1.14	−2.34	−2.35	0.84	0.84	0.36	0.37
26.7	34.3	17.1	22.2	2.44	2.68*	1.18	1.16	−2.42	−2.43	0.84	0.85	0.39	0.42
88.7	102.4	53.7	61.3	3.61	3.73	1.16	1.16	−2.40	−2.44	0.87	0.90	0.37	0.38
54.1	79.6	32.9	50.4	3.16	3.56*	1.20	1.18	−2.35	−2.34	0.83	0.81	0.33	0.35
30.5	35.8	16.0	19.1	2.47	2.60*	1.14	1.14	−2.40	−2.44	0.95	0.97	0.30	0.33*
25.9	31.4	14.7	17.8	2.41	2.57	1.19	1.19	−2.35	−2.38	0.86	0.88	0.30	0.31
25.7	30.9	14.4	16.7	2.36	2.52*	1.20	1.20	−2.38	−2.40	0.88	0.91	0.30	0.29
16.5	16.6	10.9	10.8	2.16	2.16	1.47	1.45	−2.34	−2.31	0.64	0.65	0.22	0.21
29.4	32.3	19.3	21.1	2.67	2.74*	1.33	1.31	−2.33	−2.33	0.71	0.72	0.29	0.29

within ECOMORPH as independent variables, logSIZE as the covariate, and all interactions. Because of the one significant interaction (SPECIES nested within ECOMORPH crossed with SEX) in the overall model including all species, MANCOVAs were also conducted for each ecomorph separately.

Our MANCOVA tested for a significant multivariate difference between sexes in shape after controlling for size. If the SEX effect was significant, we examined both the magnitude and direction of the eigenvector describing sex differences. The magnitude indicates the degree to which sexes differ along similar shape trajectories (e.g., both males and females vary in hindlimb length relative to body size, but males have relatively much longer hindlimbs than females), whereas the eigenvector direction indicates differences in the weightings on the different shape variables (e.g., males have variation in hindlimb length relative to body size, but females do not and instead exhibit variation in mass relative to body size [Bernstein 1988]).

We tested for allometric scaling both between species (the model just described) and within species (separate models for each species). A significant logSIZE effect would indicate that shape increases or decreases with size (positive or negative allometry, respectively, also referred to as hyper- or hypo-allometry).

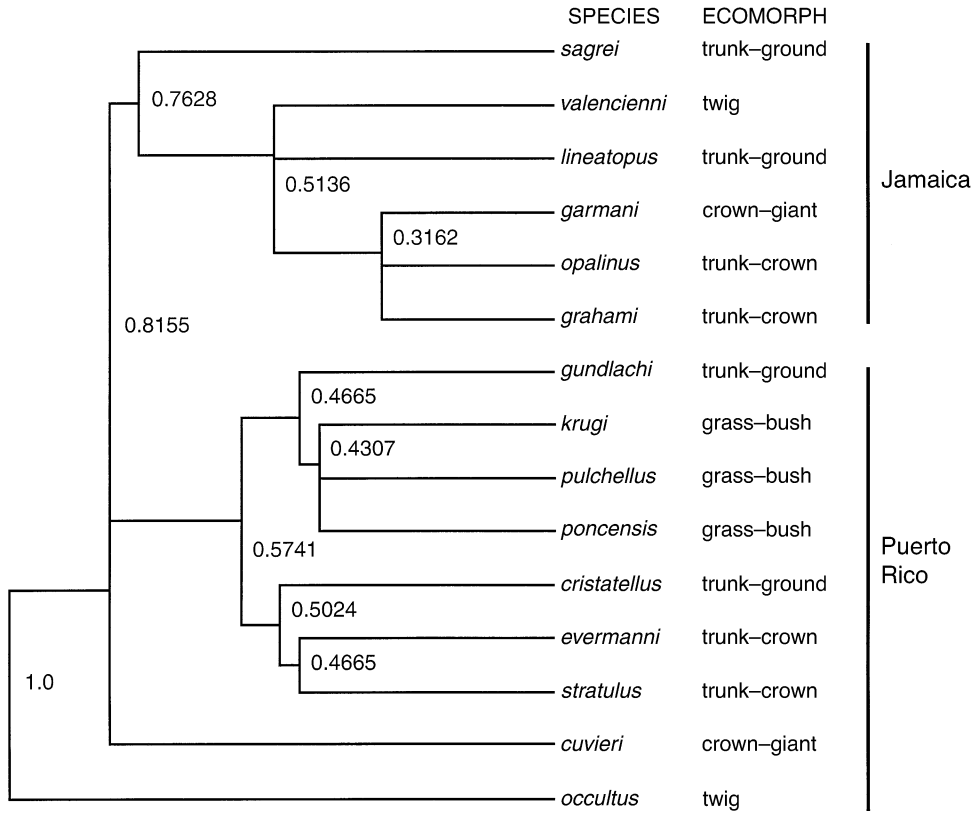

FIG. 1. A phylogenetic hypothesis for the *Anolis* lizard species included in this study, based on Jackman et al. (1999). The tree is drawn to reflect relative branch lengths assuming a molecular clock (numbers refer to the distance from the tips to each node). The tree is scaled so that the distance from the tips to the most basal node is 1.0.

Ecology and morphology

We investigated the relationship between morphology, ecology, and sex differences using correlation analyses on sex-specific mean data. We used canonical correlation analysis to investigate the multivariate correlation relationships among ecological and morphological variables. We conducted these analyses separately for males and females and compared results.

To examine how much variation in ecology could maximally be related to size vs. shape, we used MANOVA and examined the range of variation potentially accounted for by each type of variable (logSIZE and all size-adjusted variables). The amount of variation attributable to a variable (e.g., logSIZE) in MANOVA is given by the Hotelling-Lawley trace for that variable (the multivariate analogue of the mean-square term in ANOVA; Bernstein 1988). The contribution by overall shape was the sum of the Hotelling-Lawley trace values for all shape variables. The maximum variation attributable to SIZE is obtained from a Type I model (the sums of squares computed sequentially as terms are added to the model; SAS Institute 1989), with SIZE entered first, followed by shape variables. The minimum value is obtained by using a Type III model (sums of squares for SIZE computed after all shape variables are included in model, also called ''partial sums of squares''; SAS Institute 1989). Analogous models were computed to obtain maximum and minimum variation from overall shape.

We also tested whether sex differences in ecology correlate with sex differences in morphology. Sex difference variables were computed as the difference between mean male and mean female values for log-transformed morphological or ecological variables, e.g.,

$$\text{dimorphism in logFOREL/SIZE} = (\text{logFOREL/SIZE})_{\text{males}} - (\text{logFOREL/SIZE})_{\text{females}}.$$

Comparative analyses

A phylogeny for Caribbean *Anolis* lizards was used to conduct comparative analyses (Fig. 1). Most Puerto Rican and Jamaican species were included in a recent phylogenetic analysis based on mtDNA (Jackman et al. 1999). Branch lengths, based on the amount of genetic differentiation assuming a molecular clock, were kindly provided by T. Jackman (personal communication). Additional *Anolis* species (*A. evermanni*, *A. gundlachi*, *A. poncensis*, *A. pulchellus*, and *A. opalinus*) were added to the phylogeny following previous studies (Gorman et al. 1983, Guyer and Savage 1986, 1992, Burnell

TABLE 2. Bivariate correlations between ecological and morphological (shape and size) log-variables for Caribbean *Anolis* lizards.

Variable	Habitat variables		Morphological variables				
	logPHT†	logPD‡	logSVL/SIZE	logCMASS/SIZE	logHINDL/SIZE	logFOREL/SIZE	logSIZE
logPHT	1.0	0.521	0.0729	−0.0275	−0.4025	0.4458	0.6336*
logPD	0.6814*	1.0	−0.5085	−0.2582	0.1275	0.6953*	0.6114*
logSVL/SIZE	−0.0024	−0.5810*	1.0	0.6178*	−0.8234*	−0.6929*	−0.0396
logCMASS/SIZE	0.0109	−0.2743	0.5339*	1.0	−0.6847*	−0.6134*	−0.0617
logHINDL/SIZE	−0.3913	0.0844	−0.7570*	−0.7316*	1.0	0.2681	−0.0713
logFOREL/SIZE	0.5100	0.8418*	−0.6936*	−0.5330*	0.2341	1.0	0.1882
logSIZE	0.4638	0.6642*	−0.1998	0.0196	−0.0193	0.2586	1.0

Notes: Abbreviations for shape variables are given in Table 1; log refers to natural log transformation. Correlations among females are above the diagonal; correlations among males are below. All significant correlations (*$P < 0.05$) remained significant in all phylogenetic analyses (see *Results: Phylogenetic analyses* for further explanation).

† PHT, perch height.

‡ PD, perch diameter.

and Hedges 1990, Hedges and Burnell 1990, Hass et al. 1993) that have established their phylogenetic affinities to those taxa included in Jackman et al. (1999).

Organismal traits are determined both by historical legacy and as a result of adaptation to environmental factors. Thus, one goal of phylogenetic comparative methods is to statistically account for the similarity due to phylogeny so that hypotheses of adaptive evolution can be tested. The phylogenetic generalized least squares method (hereafter, phylo-GLS; Grafen 1989, Hansen and Martins 1996, Martins and Hansen 1997) statistically accounts for the expected covariance between species resulting from phylogenetic relationship for regression-based or ANOVA analyses, while simultaneously incorporating an explicit model of evolution (which can be varied). The phylogenetic covariance matrix (**G**) is assumed to be known, and is computed using a phylogenetic tree with branch lengths and the expected pattern of phylogenetic covariance being specified by each evolutionary model that one wishes to test.

We used two models of character evolution, the Brownian Motion (BM) and Ornstein-Uhlenbeck (OU) models. The combination of BM and OU models has been found to cover a broad range of evolutionary mechanisms in simulations ranging from simulations of very strong stabilizing selection to neutral drift (Hansen and Martins 1996) and thus may provide a reasonable assessment of the robustness of phylogenetic tests. For details of our implemetation of Phylo-GLS, see Butler et al. (2000). We tested eight different evolutionary models for our data set: NP (nonphylogenetic), BM, and six OU models (with $\alpha = 0.0004$, 0.004, 0.04, 0.4, 4.0, and 40). The phylo-GLS approach, because it is based on generalized least squares regression theory, exploits already existing maximum likelihood theory for selecting the best-fit model (Hansen 1997). We simply add a term for the covariance due to phylogeny (**G**; for detailed explanation, see Butler et al. 2000):

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

Note that the likelihood is a general formula; when there is no phylogenetic correlation (nonphylogenetic analysis), the **G** matrix becomes the identity matrix so that the phylogenetic covariance term disappears, as it should. Correlation statistics are not a type of least squares method. However, we can use the fact that the *t* test for the bivariate correlation coefficient is mathematically identical to the *t* test for the slope of the least squares regression line (Sokal and Rolf 1981:583) to find the best-fitting model while accounting for phylogeny.

RESULTS

Size and shape dimorphism: univariate analyses

Nearly all species are dimorphic in logSIZE (Table 1), the exception being *Anolis occultus*. In contrast, univariate differences in shape variables (between sexes within species) are mostly nonsignificant after sequential Bonferroni correction (Table 1).

Sex differences in the relationship between ecology and morphology

Bivariate correlations among ecological and morphological variables, sexes analyzed separately.—In general, pairwise correlations of ecology and morphology are quite similar between males and females. The correlation between ecological variables (logPHT and logPD) is moderate in magnitude, but significant only in males (although nearly so in females; correlation $P < 0.056$). Correlations between perch diameter and morphological variables are similar among males and females (Table 2). LogPD is associated positively with logFOREL/SIZE and logSIZE and negatively with logSVL/SIZE (significant for males; $P < 0.063$ for females). Perch height is significantly correlated only with size and only among females. The highest cor-

relation for perch height among males is with logFOREL/SIZE (although not significant at $P < 0.062$).

The sexes have similar patterns of bivariate correlation among morphological variables (Table 2). Size is not significantly correlated with any of the shape variables. Among shape variables, relative body length (logSVL/SIZE) is negatively correlated with relative limb lengths (logHINDL/SIZE and logFOREL/SIZE). Similarly, relative mass (logCMASS/SIZE) is also negatively associated with relative limb lengths.

Multivariate (canonical) correlations, sexes analyzed separately.—We examined two components of the multivariate correlation between ecology and morphology: the magnitude of the correlation and the variables involved in the correlation. Canonical correlations are equally strong for males and females, and the first canonical correlation (hereafter, CC preceded by F or M for sex) is higher than any of the bivariate correlations between ecological and morphological variables (FCC1 = 0.935, MCC1 = 0.969). The second canonical correlation is also high (FCC2 = 0.640, MCC2 = 0.674). The canonical correlations, considered together, are statistically significant (females, Wilks' lambda = 0.074, $F_{8,16} = 5.348$, $P < 0.0022$; males, Wilks' lambda = 0.033, $F_{8,16} = 8.971$, $P < 0.0001$). The second canonical correlation by itself is not significant (females, Wilks' lambda = 0.591, $F_{3,9} = 2.080$, $P < 0.1732$; males, Wilks' lambda = 0.546, $F_{3,9} = 2.491$, $P < 0.1263$). However, we report it because its magnitude is substantial, which suggests that the lack of significance might be related to small sample size rather than to spurious association.

Although the magnitudes of the correlations are similar, the variables that contribute to the correlation differ between males and females. In females, the first canonical correlation between ecology and morphology (FCC1) describes a positive correlation between the ecological variables (perch height and perch diameter) and the two morphological variables: relative forelimb length and overall size (Fig. 2). (Because the variables are log-transformed, the original variables would be expressed as a product for positive correlations and as ratios for negative correlations.) In contrast, the first canonical correlation in males (MCC1) relates perch diameter with relative forelimb length and, to a lesser extent, to overall size and negatively to relative body length. The second canonical correlation also differs between the sexes (Fig. 3). Among females, the second canonical correlation axis relates a negative correlation between perch height and perch diameter to a positive correlation between relative body length and relative hindlimb length. In males, MCC2 relates perch height to relative body length and relative hindlimb length.

The sex difference in the ecology–morphology relationship is corroborated by multiple correlation analysis among the original ecological and morphological variables. The difference between the sexes appears in the differential importance of the two ecological variables. Multiple correlations for females are significant and similar for both perch height and perch diameter (logPHT with morphology: $R^2 = 0.741$, $F_{4,9} = 6.443$, $P < 0.010$; logPD with morphology: $R^2 = 0.784$, $F_{4,9} = 8.167$, $P < 0.005$). Male multiple correlations differ by ecological variable: logPD is highly correlated with morphology ($R^2 = 0.937$, $F_{4,9} = 33.348$; $P < 0.0001$), whereas logPHT demonstrates a weaker association ($R^2 = 0.645$, $F_{4,9} = 4.100$, $P < 0.040$).

We also determined that shape generally accounts for greater variation in ecology than does size (as revealed by a comparison of F ratios for size vs. shape variables in Type I and Type III MANOVA models; Fig. 4). In males, however, shape dominates to a greater extent.

Dimorphism in ecology vs. dimorphism in morphology.—We examined whether, among species, the magnitude of dimorphism in ecology is correlated with the magnitude of dimorphism in morphology. However, only one ecological sex difference variable is related to dimorphism in morphology. The bivariate correlation between sex difference in perch diameter ($\text{logPD}_{\text{males}} - \text{logPD}_{\text{females}}$) and dimorphism in log-size-adjusted SVL is significant (Table 3, Fig. 5).

Morphological variation and its relationship to ecomorph type, species, sex, and allometric scaling

Sources of variation in overall model.—The overall MANCOVA model for shape variation was conducted on individual data. Only one interaction is significant (SPECIES by SEX nested within ECOMORPH: Wilks' lambda = 0.876, $F_{42,\,1365} = 1.478$, $P < 0.026$), although this interaction is weak relative to the strength of the other effects. All main effects are highly significant ($P < 0.0001$). Difference among ECOMORPHs explain most of the variance in the multivariate model (Wilks' lambda = 0.0493, $F_{42,\,1365} = 80.222$), followed by differences among SPECIES nested within ECOMORPH (Wilks' lambda = 0.3267, $F_{30,\,1351} = 20.893$), differences between the SEXes (Wilks' lambda = 0.8846, $F_{3,\,460} = 20.002$), and differences due to logSIZE (Wilks' lambda = 0.9207; $F_{3,\,460} = 13.214$). Individual models for each ecomorph produced similar results among the remaining sources of variation (SPECIES, SEX, logSIZE; results are not shown). There are no significant (SPECIES × SEX) interactions except among the trunk–ground ecomorphs. A residual size effect remains in trunk–crown, trunk–ground, and crown–giant anoles (also marginally nonsignificant in grass–bush anoles; results are not shown).

Patterns of shape variation: ecomorphs analyzed separately.—A major axis of shape variation in the Puerto Rican and Jamaican anoles as a whole (all species and sexes considered together) is a negative correlation between relative SVL and limb lengths (partial correlations are associated with the error sums of squares matrix after accounting for the effects of SEX, SPECIES, and logSIZE; Table 4). Grass–bush, trunk–

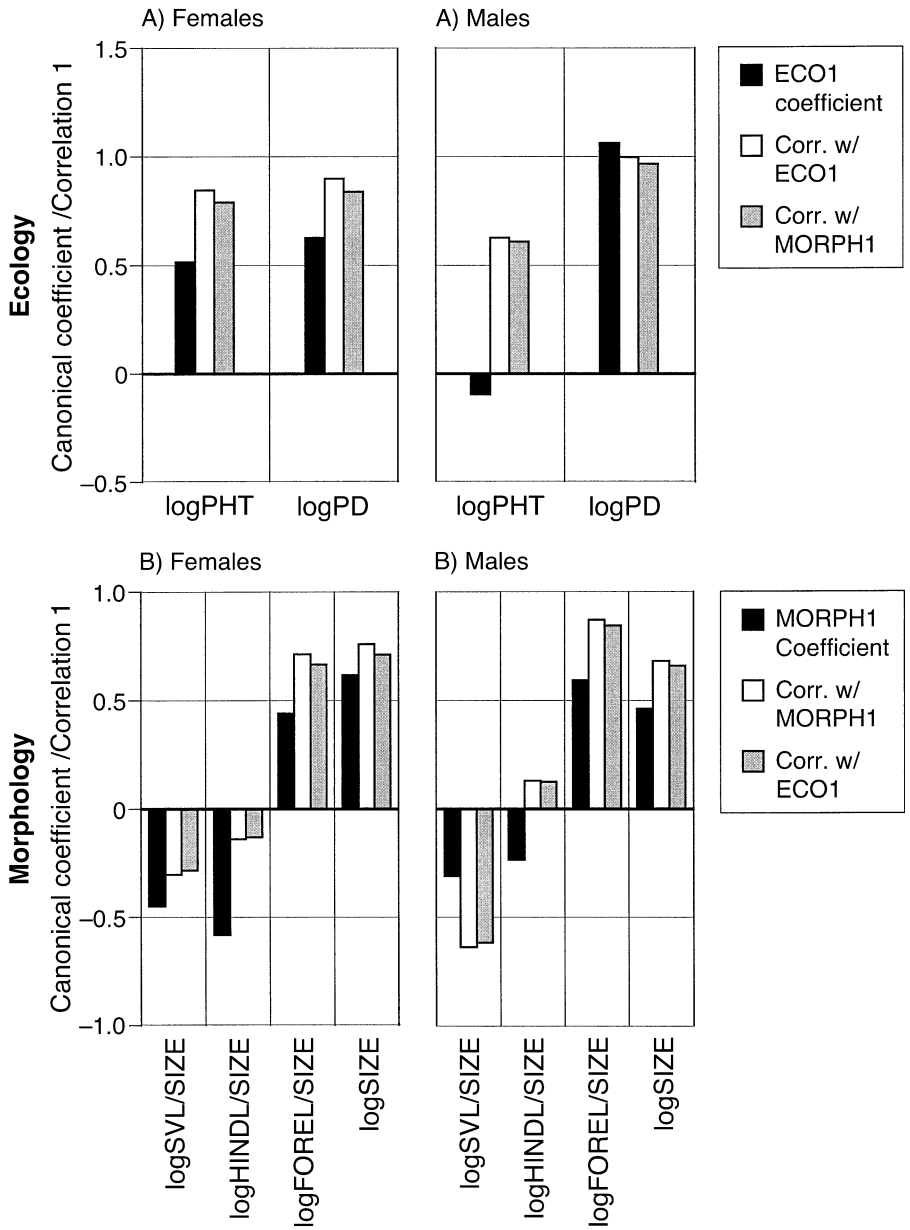

FIG. 2. The relationship between ecological variables (perch height, log PHT; perch diameter, log PD) and the first ecological canonical variable (ECO1), and between morphological variables (geometric mean size index, logSIZE; size-adjusted snout-to-vent length, logSVL/SIZE; and size-adjusted hind-limb and forelimb length, logHINDL/SIZE and logFOREL/SIZE) and the first morphological canonical variable (MORPH1). Male and female *Anolis* lizards were analyzed separately. (A) Relationships for ECO1: black bars indicate the ecological variable coefficients for ECO1; open bars indicate the correlation of ecological variables with ECO1; and gray bars indicate the correlation of ecological variables with MORPH1. Note that the overall association between an ecological variable and ECO1 is a function of both the coefficient and the correlation. If the correlation is very small, there is no explanatory power. (B) Relationships for MORPH1. All variables are species-sex (per species, by sex) mean values.

crown, and trunk–ground anoles share identical patterns: logFOREL/SIZE and logHINDL/SIZE are negatively correlated with logSVL/SIZE, but not with each other. Crown–giant anoles have large but nonsignificant correlation values that may have been affected by small sample size. The pattern exhibited by crown–giant anoles differs from the previous ecomorphs mainly in possessing a large negative correlation value between logFOREL/SIZE and logHINDL/SIZE.

We examined sex differences in shape by eigenanalysis. Multivariate differences have both a magnitude component (eigenvalue) and a directional component (eigenvector; i.e., indicating the variables by which they differ). Comparing the eigenvalues of sex shape

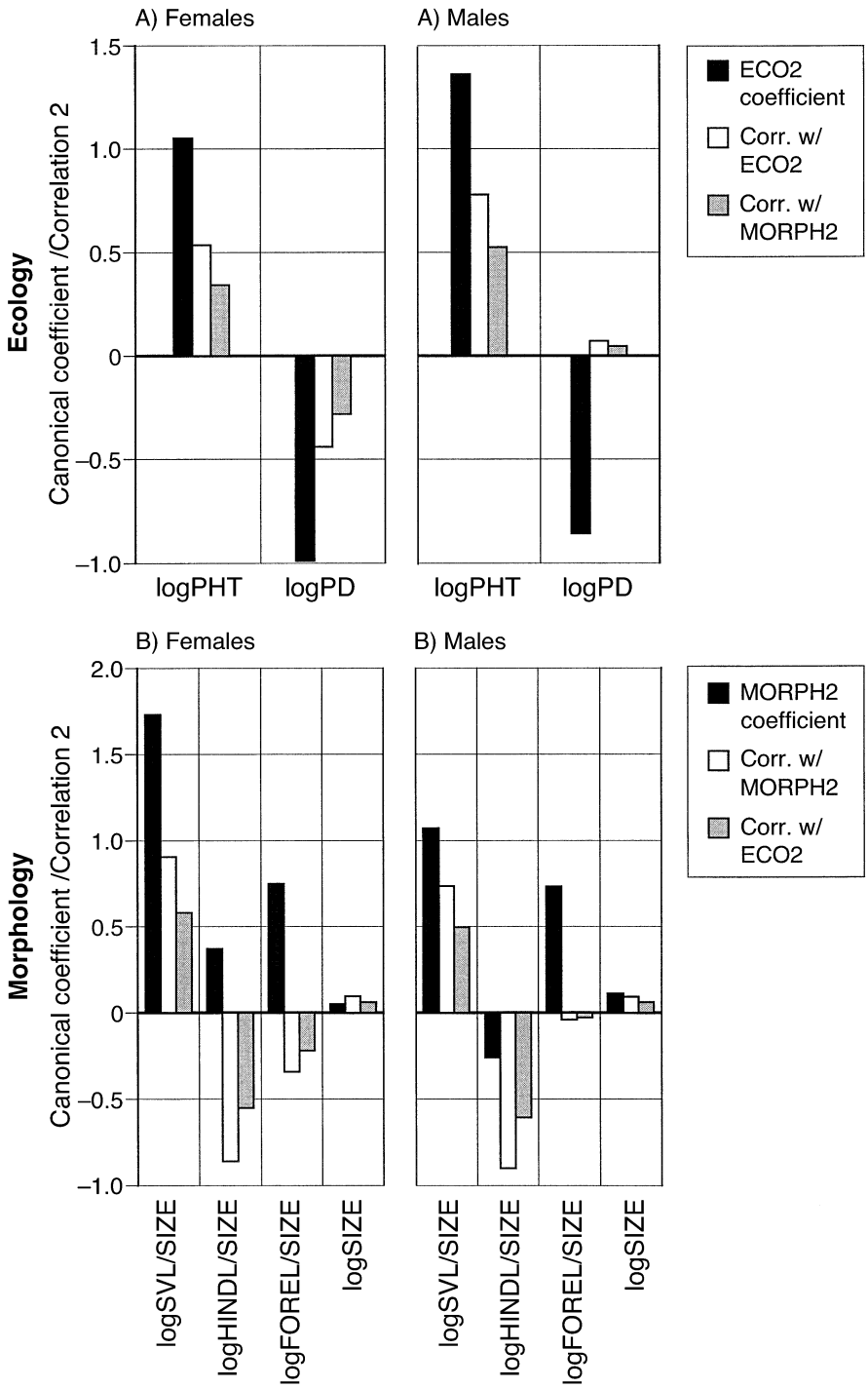

FIG. 3. The relationship between ecological and morphological variables (as in Fig. 2) and their second canonical variables (ECO2 and MORPH2) for males and females. See the explanation in Fig. 2.

differences, we find that crown–giant anoles have the greatest shape dimorphism, grass–bush and trunk–crown anoles have intermediate levels, and trunk–ground and twig anoles have the lowest magnitude of shape dimorphism (Fig. 6). Four of these ecomorphs have shape dimorphism that is significantly different from zero: grass–bush (eigenvalue = 0.256, $F_{3,81} = 6.9$, $P < 0.0003$), trunk–crown (eigenvalue = 0.244, $F_{3,142} = 11.5$, $P < 0.0001$), trunk–ground (eigenvalue = 0.147, $F_{3,155} = 7.0$, $P < 0.0002$), and crown–giant (eigenvalue = 0.447, $F_{3,25} = 3.7$, $P < 0.0242$). The weak significance of crown–giant anoles may result from a

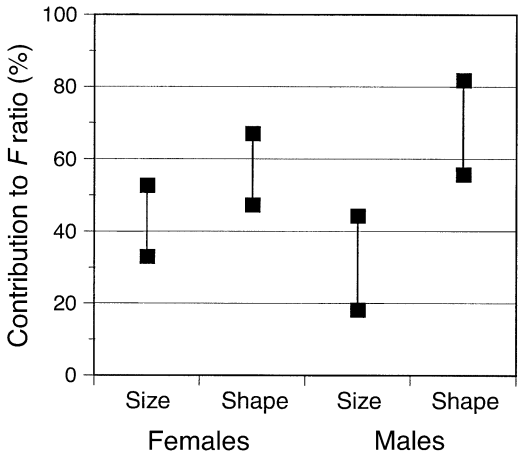

FIG. 4. Percentage of ecological variation explained by size vs. shape in male and female *Anolis* lizards. The MANOVA *F* approximation to the Hotelling-Lawley trace is depicted. The lower end of each range is the independent percentage contribution of shape or size variables to ecological variation (the minimum amount of explanatory power), whereas the top of the range indicates the maximum percentage contribution of size or shape variables, but includes variation that may be shared among the two variable types. See *Methods: Ecology and morphology* for further explanation.

small sample size, as the eigenvalue is quite large. Shape dimorphism in twig anoles is not significant, despite being similar in magnitude to that of trunk–ground anoles (eigenvalue = 0.126, $F_{3,52} = 2.2$, $P < 0.1009$).

Three ecomorphs share similar eigenvectors of sexual dimorphism in shape: trunk–crown, grass–bush, and crown–giant anoles (Fig. 7). Males have greater values than females in all three variables, with the largest difference in logHINDL/SIZE. In particular, trunk–crown and grass–bush anoles have very similar eigenvectors (Fig. 7; shape variables listed as logSVL/SIZE, logHINDL/SIZE, logFOREL/SIZE). The sexes of trunk–ground anoles, however, differ most strongly by logFOREL/SIZE, which is twice as strong as the difference in logHINDL/SIZE, with the least difference in logSVL/SIZE. The negative sign of the logSVL/SIZE weight indicates that females have greater size-adjusted SVL. The eigenvector for twig anoles is weighted strongly and negatively by logSVL/SIZE, which is more than three times greater than the positive difference in logHINDL/SIZE. In twig anoles, sex difference in logFOREL/SIZE is weak.

Intraspecific allometric scaling.—Within species, shape changes allometrically in at least three species (*A. evermanni*, *A. grahami*, and *A. sagrei* are significant at alpha = 5%, whereas *A. gundlachi* and *A. krugi* are marginally nonsignificant at alpha = 10%; Table 5). Isometric variation in shape occurs in seven species (*A. cristatellus*, *A. garmani*, *A. lineatopus*, *A. opalinus*, *A. stratulus*, *A. pulchellus*, and *A. valencienni*). Sexes are

TABLE 3. Correlations between sex differences in ecological variables and dimorphism in shape and size variables for *Anolis* lizards.

Sex differences in habitat	Sex differences in dimorphism			
	ΔlogSVL/SIZE	Δlog-HINDL/SIZE	Δlog-FOREL/SIZE	ΔSIZE
ΔlogPHT	0.1077	−0.0288	0.0394	0.1410
ΔlogPD	0.5788*	0.1551	−0.2564	−0.3524

Notes: Table entries are correlation coefficients. Sex differences are denoted by Δ and are defined as male value minus female value. See Tables 1 and 2 for abbreviations of ecological and morphological variables.
* $P < 0.05$.

significantly different in shape after accounting for any potential allometric scaling in seven species (*A. cristatellus*, *A. lineatopus*, *A. sagrei*, *A. evermanni*, *A. grahami*, *A. opalinus*, and *A. krugi*), marginally so in two species (*A. gundlachi* and *A. stratulus*), and not significant in three species (*A. garmani*, *A. pulchellus*, and *A. valencienni*).

Phylogenetic analyses

All ecological and morphological variables were tested for sensitivity to phylogenetic assumptions, either simultaneously in multiple regression or pairwise via bivariate correlations.

Multiple regressions with ecological variables as de-

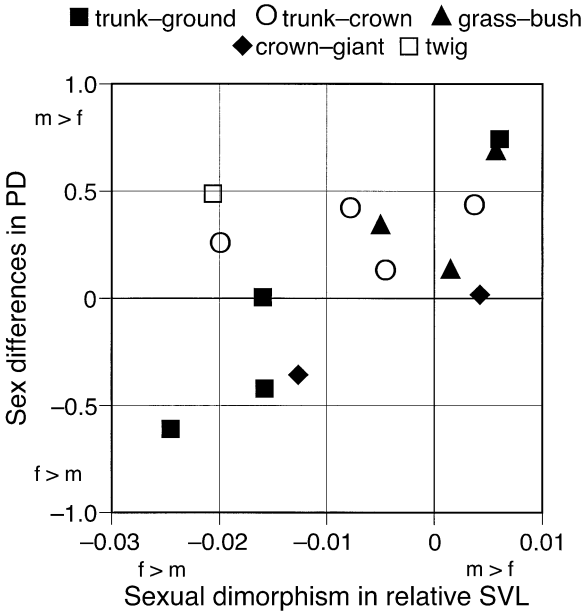

FIG. 5. Sexual dimorphism in size-adjusted SVL (logSVL/SIZE) vs. sex differences in perch diameter (logPD). Both variables are log(male) minus log(female), calculated from species mean values. Thus, species with males larger than females are at the top right (m > f), and those with females larger than males (f > m) are at the bottom left of the plot. Each point represents one species; symbols indicate ecomorph type.

TABLE 4. MANCOVA partial correlations among *Anolis* shape variables associated with the error sums of squares matrix.

Ecomorph	Partial correlation coefficients: logSVL/SIZE logHINDL/SIZE	logSVL/SIZE logFOREL/SIZE	logHINDL/SIZE logFOREL/SIZE	df
Crown–giant	−0.198	−0.482[b]	−0.362	27
Grass–bush	−0.413[a]	−0.367[a]	0.015	83
Trunk–crown	−0.319[a]	−0.380[a]	−0.056	144
Trunk–ground	−0.399[a]	−0.327[a]	0.046	160
Twig	−0.290[c]	−0.181	−0.078	54

Notes: The model explained shape variation as a function of sex, species, and size for ecomorphs analyzed separately. These partial correlations represent residual correlation among shape variables after accounting for the other shape variables and variation due to SEX, SPECIES, and logSIZE. Superscript letters indicate significance level: a, $P < 0.001$, significant at 0.05 level after sequential Bonferroni correction; b, $P = 0.009$, not significant after Bonferroni correction; and c, $P = 0.032$.

pendent variables and all morphological variables as independent variables indicate no detectable influence of phylogeny. All regressions remain highly significant no matter which evolutionary model is used (results for female-only regression of logPD on morphology are given in Table 6; all other analyses are similar). In general, the nonphylogenetic and OU (Ornstein-Uhlenbeck) models with alpha parameters in the range of 40–400 share the maximum likelihood among models (Fig. 8). The only exception is the male logPD-morphology model in which the OU alpha 4 model has similar, but slightly higher, likelihood (Fig. 8). Even models with the lowest likelihood have similar model R^2 values and significance levels (Table 6), indicating that results are not sensitive to phylogenetic assumptions.

A plot of the maximum likelihood values for OU models shows that the likelihood increases steeply as the alpha parameter of the model increases, but the likelihood surface becomes very flat once high values of alpha are attained. Thus, it is probably more informative to know where the flat region occurs rather than the precise maximum. High values of alpha correspond to very little correction for phylogeny and, in fact, the nonphylogenetic model shares the maximum likelihood value with alpha values of 40 or higher (Fig. 8).

Analyses for bivariate correlations among all ecological and morphological variables produced qualitatively identical results (thus, results are not shown). All bivariate correlations that were significant in nonphylogenetic correlations remained so in all phyloge-

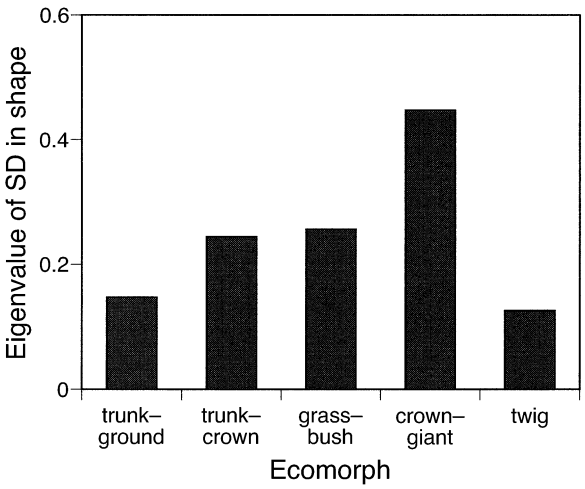

FIG. 6. Magnitude of shape dimorphism by ecomorph category. Shape dimorphism SD eigenvalues were obtained from MANCOVA, with shape variables as the dependent terms, SEX and SPECIES as independent terms, and logSIZE as the covariate. The eigenvectors of the multivariate SEX effect are plotted. The ecomorphs were analyzed in separate MANCOVAs.

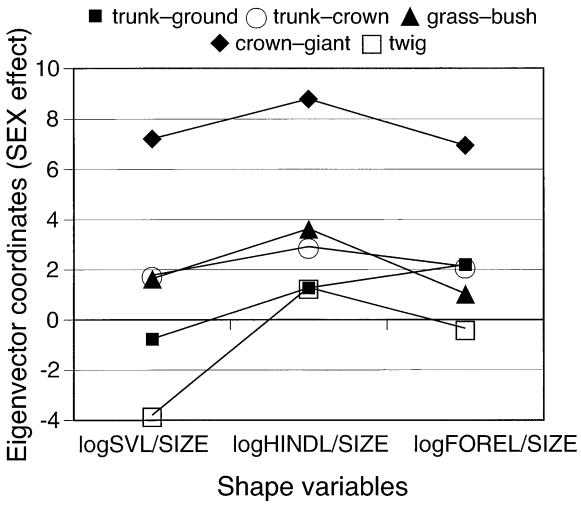

FIG. 7. Directions of shape differences by ecomorph category. The eigenvector coefficients of shape differences are plotted. Eigenvectors correspond to eigenvalues plotted in Figs. 4 or 6. A positive value for a shape variable indicates that males are greater in that shape variable, after accounting for variation due to logSIZE and SPECIES, and reflects correlation among shape variables. Similarly, a negative value indicates that females are greater in that variable. The magnitude is proportional to the degree of difference in the given shape variable.

TABLE 5. Results of MANCOVA testing each *Anolis* species for intraspecific sexual dimorphism in shape and allometric scaling of shape with size, with shape morphology as the dependent variables and SEX as the independent variable and with logSIZE as a covariate.

Anolis species	Denominator df	logSIZE			SEX hypothesis type	SEX Type I			SEX Type III		
		Wilks' lambda	*F*	*P*		Wilks' lambda	*F*	*P*	Wilks' lambda	*F*	*P*
cristatellus	34	0.877	1.60	0.209	I	0.771	3.37	0.030	0.845	2.08	0.121
evermanni	30	0.738	3.55	0.026	III	0.914	0.94	0.432	0.732	3.66	0.023
garmani	17	0.711	2.31	0.113	I	0.802	1.40	0.276	0.792	1.49	0.253
grahami	34	0.748	3.83	0.018	III	0.962	0.45	0.719	0.765	3.47	0.027
gundlachi	31	0.803	2.54	0.075	I	0.905	1.08	0.372	0.771	3.06	0.043
krugi	32	0.824	2.27	0.099	I	0.719	4.16	0.013	0.631	6.25	0.002
lineatopus	40	0.917	1.20	0.321	I	0.799	3.35	0.028	0.846	2.43	0.080
opalinus	34	0.886	1.46	0.244	I	0.768	3.42	0.028	0.844	2.09	0.120
pulchellus	34	0.919	1.00	0.406	I	0.870	1.69	0.187	0.817	2.54	0.073
sagrei	41	0.747	4.64	0.007	III	0.776	3.94	0.015	0.640	7.70	0.000†
stratulus	32	0.847	1.93	0.145	I	0.807	2.54	0.074	0.738	3.79	0.020
valencienni	39	0.938	0.87	0.467	I	0.909	1.31	0.286	0.873	1.89	0.147

Notes: A significant logSIZE effect indicates that shape scales allometrically with size (nonsignificance indicates isometry). The test for sex difference in shape depends on whether logSIZE differs between the sexes. If logSIZE is not significant, then we examine the Type I *P* value for SEX (difference between the sexes without accounting for size). If logSIZE is significant, we examine the Type III *P* value (difference between the sexes after accounting for size). Only one species (*A. sagrei*) remains significantly dimorphic in shape (SEX effect) when we examine the tests individually after Bonferroni correction. However, considering all species together, the binomial probability of obtaining seven SEX effects at the $\alpha = 0.05$ level (out of 12 species) is highly significant ($P = 4.6 \times 10^{-7}$).

† Significant at $\alpha = 0.05$ level after Bonferroni correction.

netic analyses. The nonphylogenetic model was either the same as the maximum likelihood model or produced very similar correlations and identical levels of statistical significance as the maximum likelihood model.

TABLE 6. An example of the effect of phylogeny on interspecific regressions and correlation analyses relating ecology and morphology in Caribbean *Anolis* lizards.

Evolutionary model†	α	logL	R^2	$F_{4,9}$	*P*
NP		−8.48‡	0.78	8.17	0.005
BM		−10.02	0.64	6.96	0.008
OU	0.0004	−14.15	0.63	6.96	0.008
OU	0.004	−12.99	0.63	6.96	0.008
OU	0.04	−11.81	0.63	6.97	0.008
OU	0.4	−10.39	0.63	7.09	0.007
OU	4	−8.53	0.77	7.96	0.005
OU	40	−8.48‡	0.78	8.17	0.005
OU	400	−8.48‡	0.78	8.17	0.005

Notes: We tested a wide range of evolutionary models in multiple regression of ecological variables (logPD or logPHT) on all morphological variables and for bivariate correlations in Table 4. Only the table for multiple regression of logPD on morphology for females is given because all analyses produced qualitatively identical results. The nonphylogenetic (NP) model was either selected as the maximum likelihood model or with virtually identical likelihoods. In addition, wherever a significant effect is detected in nonphylogenetic analyses, all phylogenetic models also produce significant results irrespective of the evolutionary model. The α parameter of the OU model; the log-likelihood value (logL), the model R^2, *F* ratio (with numerator and denominator degrees of freedom), and *P* values are given.

† NP, nonphylogenetic model; BM, Brownian motion model; OU, Ornstein-Uhlenbeck model.

‡ Maximum-likelihood model.

DISCUSSION

We find extensive shape dimorphism that is not related to phylogenetic similarity or to allometric scaling relationships. This dimorphism is notable in two respects. First, we have demonstrated that a relationship exists between shape dimorphism and habitat use by demonstrating that interspecific variation in perch height and perch diameter correlate with shape dimorphism, and by showing that species that are specialized to use different habitats (ecomorphs) differ in the patterns and extent of dimorphism. These findings suggest that whatever mechanism regulates shape dimorphism (e.g., sexual selection or intersexual adaptive divergence to different microhabitats) must operate differently among habitats.

Second, we document that ecomorphs vary greatly in the extent of dimorphism in both size and shape, but no ecomorph is highly dimorphic in both aspects. Although shape and size dimorphism are not necessarily concordant in invertebrates (Hamel and Himmelman 1992, Prenter et al. 1995), this is a novel finding for vertebrates, for which comparative patterns of dimorphism in shape have thus far been found to be concordant with those of size (Wiig 1986*a*, *b*, Lynch and O'Sullivan 1993, Willig and Hollander 1995). This suggests that different mechanisms may regulate size and shape dimorphism.

We first briefly discuss patterns of allometric scaling (both generally and with respect to sexual dimorphism) and then discuss our findings with respect to potential ecological and sexual selection mechanisms.

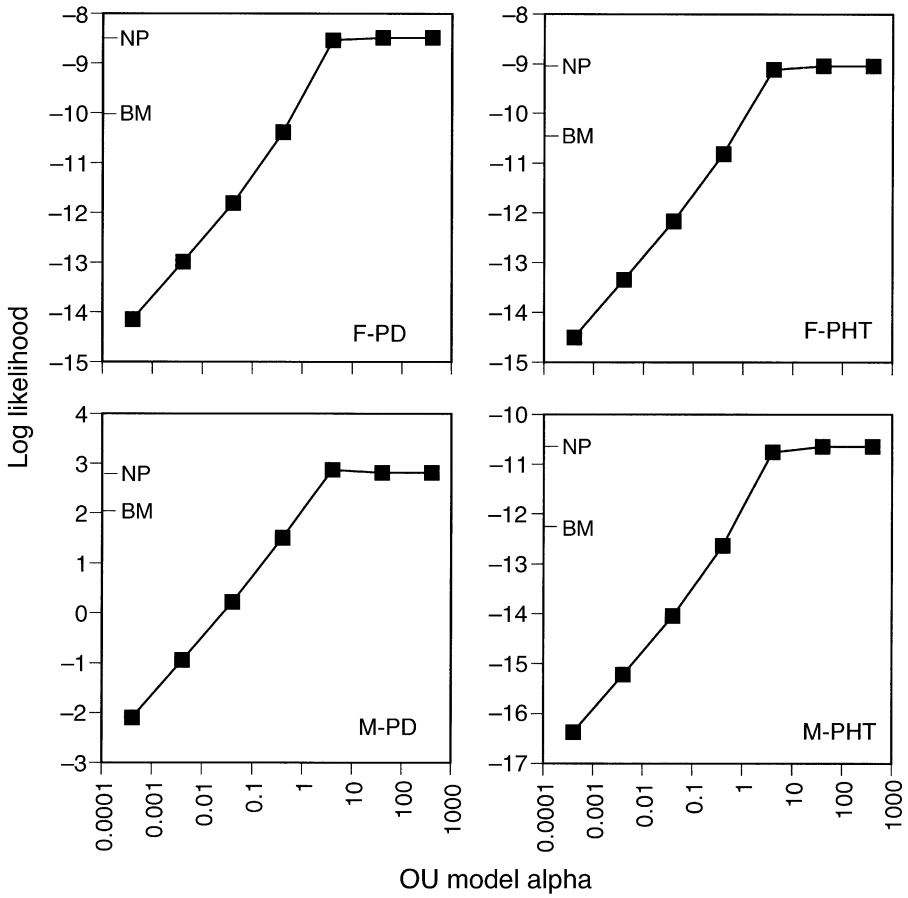

FIG. 8. Effect of phylogenetic model on statistical tests. Multiple regressions were performed on ecological variables with all size and shape morphological variables as dependent variables. Likelihood values are plotted for regression analyses performed under an OU (Ornstein-Uhlenbeck) model of evolution with varying alpha parameters on a log scale (range 0.004–400). Likelihood values for BM (Brownian motion) and NP (nonphylogenetic) models are also indicated along the *y*-axis. Female regression of logPD on morphological variables (F-PD); female regression of logPHT on morphological variables (F-PHT); and similar analyses for males (M-PD and M-PHT) are presented. See *Results: Phylogenetic analyses* for further explanation.

Allometric scaling

Shape change is commonly observed to follow patterns of allometric scaling (reviewed in Reiss 1989). In our study, we investigated potential patterns of scaling both within species (static allometry; i.e., patterns of shape variation with size that occur among adults or same-aged individuals within a species) and between species (evolutionary allometry; i.e., the scaling of shape with size when comparing different species). We had no data to address ontogenetic allometry.

Applied to sexual dimorphism within species, allometric scaling could account for sex differences if shape were to scale geometrically with size, and male and female growth trajectories were to differ. Previous studies on *Anolis* have established that growth trajectories within species tend to be conservative; intrinsic growth rate and age at sexual maturity vary little, and the only parameter that differs between the sexes is asymptotic size (note: these studies focused on size only and did not examine shape change; Andrews 1976, Schoener and Schoener 1978*b*, Stamps 1995). Thus, a simple null model for adult shape dimorphism is that shape scales geometrically with size and males grow to larger size, resulting in the observed shape differences. Admittedly, this is a naive expectation (for more complex treatments and models, see Cheverud 1982, Lande 1985, Klingenberg and Zimmerman 1992, Klingenberg 1996) because sex-specific morphologies may diverge suddenly at a particular growth stage (e.g., Cvetkovic et al. 1997). However, it is an expectation that is easily tested without further information on developmental trajectories.

At the within-species level, we find very little evidence for allometric scaling as an explanation for either shape variation or shape dimorphism. Shape generally varies isometrically with size, as we cannot detect significant allometric trends in nine of 12 *Anolis* species (the logSIZE effect is not significant; Table 5). Addi-

tionally, we find non-allometric sexual shape dimorphism in seven species (Table 5). This is consistent with a previous study (Powell and Russell 1992) that found relatively minor sex differences among bivariate scaling relationships in three species of *Anolis*.

Among species, body size does explain some variation in shape. Thus, to the extent that allometric scaling occurs, it is interspecific (evolutionary) rather than intraspecific (static). Nonetheless, residual size effects explain a small portion of shape variation in these anole radiations. The greatest portion of shape variation is explained by ecomorph class, confirming the extraordinary ecologically based morphological diversification in Caribbean anoles previously reported (see references in the *Introduction*).

Relationship between morphology and habitat

Anolis lizards have experienced primarily independent evolutionary radiations on each of the islands of the Greater Antilles (Jackman et al. 1999). Remarkably, essentially the same set of habitat specialists (ecomorphs) have evolved independently on each island as species have adapted morphologically and behaviorally to utilize different parts of the habitat (Williams 1983, Losos et al. 1998). Shape variation is particularly important to microhabitat specialization in this group. Here we have shown that shape variation explains a greater proportion of variation in ecological variables (perch height and perch diameter) than does body size variation (Fig. 4). Previous morphological analyses (e.g., Losos 1992, Losos et al. 1998) have focused only on males. We have documented in this study that differences in habitat use among anole species are related not only to morphology and locomotor behavior, but also to the extent of sexual dimorphism in body proportions (Figs. 6 and 7).

We investigated two hypotheses about why a relationship between habitat use and extent of sexual dimorphism in shape might occur:

1. *Sexes adapt differently to the environment*.—Males and females may interact in different ways with the environment, thus leading to a quantitative sex difference in the relationship between morphology and habitat use. This implies that sexes may or may not differ in habitat use, but regardless, the relationship between morphology and ecology will differ between the sexes.

2. *Intersexual niche partitioning occurs, with sexes similarly adapted*.—The relationship between morphology and habitat use does not differ between the sexes, but the sexes differ in microhabitat use more in some habitats than in others. The amount of ecological difference between the sexes may differ qualitatively among habitats, leading to greater morphological difference in habitats where sexes are more ecologically distinct.

Most of the evidence suggests that the sexes do adapt differently to the environment, with very little support for the hypothesis that sexes are similarly adapted. The sexes have different relationships of intercorrelation between habitat use and morphology. This difference is not a result of only one sex being adapted to the environment, with the other sex being ''misfit;'' the degree to which female morphologies correlate to their respective environments is just as strong as that in males (FCC1 = 0.935, MCC1 = 0.969; FCC2 = 0.640, MCC2 = 0.674), despite the existence of significant sex differences in body size, shape, and habitat use.

The general lack of correlation between sexual dimorphism and sex differences in ecology also argues against the hypothesis that sexes are similarly adapted. We found only one relationship: species that exhibit greater sexual differences in perch diameter also have greater sexual dimorphism in relative body length. Fig. 5 reveals three trends. First, at the extremes, the sex that uses broader perches tends to have a relatively longer body. This suggests a functionally adaptive relationship, although further research is needed to clarify why shorter bodies are favored on narrower surfaces. Second, when the sexes do not differ in perch diameter, females have longer relative body length. One potential explanation is that females need longer bodies to provide room for eggs. Third, there is no pattern with respect to ecomorph, suggesting that this relationship is a general one such as a reproductive requirement, rather than one determined by habitat type.

These findings extend previous studies, which, based only on data from adult males, indicated the pervasiveness of convergent adaptive evolution in the Caribbean anole radiation. Our results, which show a predictive relationship between ecology and morphology irrespective of phylogenetic distance, indicate not only that convergence has been just as common among female anoles as it has been among males, but also that shape dimorphism itself evolves convergently.

A role for sexual selection

An alternative explanation for shape differences is that sexual selection varies among habitats, selecting for great shape divergence between the sexes in some habitats, but not in others. This is certainly plausible, given that the ecomorphs vary in their degree of territoriality. Studies to date suggest that trunk–ground and trunk–crown anoles are the most territorial, whereas twig anoles are not territorial (although more studies are needed, particularly of the other ecomorphs; see Butler et al. [2000] and references therein). Nonetheless, morphological correlates of sexual selection, other than overall body size, have been surprisingly little studied in anoles (see review in Tokarz 1995), but we can make two predictions. First, in species in which sexual selection is greatest, traits should be favored that enhance the abilities of males to acquire choice territories and attract females. One such trait is relative hindlimb length. Males perform prominent displays in open situations (e.g., Jenssen [1977] and references in

the *Introduction*) and are thus vulnerable to predators (e.g., Leal 1999). As a result, in species in which sexual selection is most intense, males may need to evolve traits that allow them to escape predators; long limbs enhance sprint speed (Irschick and Losos 1998, 1999). Thus, we would predict a correlation between the degree of sexual selection and dimorphism in relative limb length. If magnitude of sexual selection varies among habitats, then a habitat–dimorphism relationship would be predicted.

With regard to shape dimorphism, crown–giant, grass–bush, and trunk–crown ecomorphs differ to the highest degree in relative limb length, especially relative hindlimb length (Fig. 7). Trunk–ground anoles are also dimorphic: males primarily have longer forelimbs, followed by longer hindlimbs and shorter SVL. Twig anoles differ primarily in relative SVL (females longer) and not in relative limb lengths. Although the magnitude of shape dimorphism agrees with predictions for the trunk–crown (high) and twig (low) ecomorphs, it clearly does not for the trunk–ground ecomorph (predicted to be high, but actually low). The twig ecomorph is the most unusual in many respects; it moves slowly and deliberately throughout its habitat of thin twigs and branches, is most actively foraging, is not territorial, and has the most derived morphology (Schoener and Schoener 1980, Hicks and Trivers 1983, Irschick and Losos 1996). Thus, it is not surprising that its pattern of shape dimorphism is also unusual. However, it is not clear why the trunk–ground ecomorph should have a different axis of shape dimorphism from the first group (crown–giant, grass–bush, and trunk–crown ecomorphs). Detailed functional studies are needed to determine whether these dimorphisms translate into different performance abilities and whether, in turn, such differences in performance are related to sexual selection.

Butler et al. (2000) indicated that sexual size dimorphism varies among habitats. Here we have shown that shape dimorphism not only varies among habitats, but also reveals a different pattern of variation than does size dimorphism. We find some evidence for independent adaptation of the sexes, but with more complex ecological patterning occurring between sexes than can be explained by sexual selection alone. Some combination of functional differences and sexual selection is required. Nevertheless, the suggestion that the ecomorphs vary in sexual selection, which was suggested for the *Anolis* radiation by the finding that size dimorphism varies by habitat type (Butler et al. 2000), is partly corroborated by complex patterns of shape variation. If confirmed by direct ecological or genetic studies, ecologically based variation in sexual selection could have profound implications for understanding the ecology and evolution of the *Anolis*, and possibly other, radiations.

Previous studies have established that morphology of male *Anolis* lizards has evolved to enhance functional capabilities in their respective habitats (Losos 1990*b*, *c*, Losos and Irschick 1996, Irschick and Losos 1998, 1999). Given that performance capabilities thus may be the mechanistic link between morphology and ecology, and that the relationship between morphology and ecology differs between the sexes, one would predict that the relationship between morphology and performance capability should differ between the sexes. Constraints imposed by reproductive biology also predict that the relationship between morphology and performance ability may differ between the sexes. For example, females, at least when gravid, must bear the additional mass and thus may have reduced capabilities. Moreover, female lizards often have increased body volume, even when not gravid, which might also affect performance abilities. Both phenomena are known for other squamates (e.g., van Damme et al. 1989, Schwarzkopf and Shine 1992, Qualls and Shine 1997), but surprisingly little research has been conducted on the capabilities of female anoles (see Macrini and Irschick 1998). To better understand the extent to which females are well adapted to their habitats and why the extent of dimorphism in shape varies among habitats, future studies along these lines will be necessary.

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