Vive le difference! Sexual dimorphism and adaptive patterns in lizards of the genus *Anolis*

Marguerite A. Butler

Department of Zoology, University of Hawaii at Manoa, 2538 McCarthy Mall, Edmonson 152, Honolulu, HI 96822, USA

**Synopsis**

The repeated, convergent evolution of body shape and microhabitat use in Greater Antillean lizards of the genus *Anolis* (anoles) provides compelling evidence of the importance of microhabitat specialization in shaping morphology. Interestingly, sexual dimorphism is also extensive, with males and females differing in body size as well as in shape. It is important to note that the components of shape analyzed in these studies is related to locomotion and are size-adjusted, including: relative limb and body lengths and mass of the body. Numbers of lamellae were also used and these do not vary with size. Furthermore, dimorphism in both size and shape differs by habitat type. Thus, does functionally-relevant sexual dimorphism imply that one sex is the “ecological” sex, with the other being maladapted to it’s environment? Alternatively, sexual dimorphism may interact with adaptive diversification. Different classes of individuals within a species may act as separate ecological units if they play ecologically different roles. Here, I reanalyze a data set of morphological data for 15 species of Puerto Rican and Jamaican *Anolis*, which represent two largely independent adaptive radiations of lizards. I test for concordance between size and shape dimorphism and microhabitat (ecomorph) type, and for “parallel” patterns of sexual dimorphism among species. I integrate these results and, in the light of previous research, evaluate the relative influence that larger-scale ecological patterns have on sexual dimorphism, as well as the influence of sexual dimorphism on community structuring. I conclude that the presence of ecologically-relevant dimorphism may in fact increase the adaptive diversity present within a community.

**Introduction**

Is there any relationship between sexual variation, interspecific variation, and the environment? Early workers (Selander 1966; Schoener 1967; Emlen and Oring 1977) recognized the importance of ecology for the evolution of sexual dimorphism, especially as it relates to one of three ultimate causes of sexual dimorphism: differences in reproductive biology, reducing competition between the sexes, or independent specializations of the sexes to a bimodal distribution of resources (Slatkin 1984; Gaulin and Sailer 1985; Shine 1989). However, this interest in the role of extrinsic factors in the evolution of sexual dimorphism has been largely eclipsed by the rise of sexual selection. The head sizes of carnivores may be matched to the size distribution of prey, or larger lizards may use larger perches such that there is a linear relationship between the width of the perch and the size of the animal. In this case, sexual selection can undoubtedly be a selective force when it occurs (Andersson 1994), the loss of the greater hierarchical perspective is unfortunate because there is no theoretical or empirical justification to assume that the processes which produce variation among species and between sexes are decoupled.

Variation between the sexes has rarely been considered in studies of adaptive radiation or adaptive diversification in general (Liem 1974; Losos 1992; Schluter and McPhail 1993). Most studies have focused on one sex only (usually males), or have pooled individuals regardless of sex. However, there are at least three possible relationships between sexual differences and interspecific variation. The same processes that generate diversity between species may also produce diversity between sexes. Such a relationship between morphology and the utilization of resources may be quantitative and predictive, driven by one primary functional relationship. For example, the head sizes of carnivores may be matched to the size distribution of prey, or larger lizards may use larger perches such that there is a linear relationship between the width of the perch and the size of the animal. In this case, there is predicted to be a direct relationship between sexual differences in resource utilization and sexual...
dimorphism (Dayan and Simberloff 1994). Alternatively, niche partitioning may occur along multiple dimensions, with sexes acting as independent ecological units and adopting different patterns of resource utilization (Heatwole 1989). In this case, the sexes and species will be differentiated morphologically, such that they cluster by ecological type, but they will fit together as a complex jigsaw puzzle in multiple dimensions. Thus, it may be difficult to find a simple connection between sexual dimorphism and ecological variation (see Fig. 1 for a simplified visual representation of these alternatives). Because of the multidimensional aspect of the problem, the second alternative is more difficult to detect, even though the underlying cause is a result of the same ecological theory. The most obvious pattern in this situation is that the sexes and species in this community will cluster by ecological type and show greater “niche packing.” Finally, interspecific specialization may reflect adaptation to different resources and intersexual specialization may reflect differences in reproductive biology. The degree of sexual dimorphism possible, however, may differ under different distributions of resources. In this case, particular habitats are predicted to promote sexual differences.

Ecological context of anoles

Lizards of the genus Anolis are a particularly appropriate group to investigate the interaction of sexual and interspecific patterns. Anolis is an extremely diverse genus with over 300 species (Losos 1994). Approximately half of the species are distributed in the Caribbean, with the remainder in South and Central America. Anoles share several general characteristics: they are small, arboreal, diurnal, insectivorous lizards. Species vary, however, in size and shape of the body, degree of arboreality, prey size, locomotion and foraging, and in social behavior.

Anolis is a classic example of adaptive radiation, having experienced essentially independent radiations on each of the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico), in each case producing a suite of species morphologically and behaviorally specialized in ways that use different parts of the environment. For example, species that occupy open habitats have long legs that provide a great capacity for running and jumping. In contrast, those species that specialize on twigs have short legs that enhance maneuverability in their narrow, irregular habitat. Moreover, the same set of habitat specialists—termed ecomorphs and named for the part of the habitat they use (e.g., crown–giant, grass–bush, trunk–crown, trunk–ground, and twig)—has evolved repeatedly across the four islands (Williams 1983; Losos et al. 1998).

The different microhabitats that ecomorphs occupy seem to favor different lifestyles. For example, grass–bush anoles occupy small bushes or tall grass, which is generally a thick matrix of thin perches near the ground. They tend to have long hind limbs and short forelimbs, are good jumpers, and use jumping quite frequently to move about their habitat as well as to capture prey (Moermond 1979; Losos 1990a).

![Fig. 1 A graphic illustration of the parallel (or correlated) niches hypothesis (A) versus independent niches (B). An arrow connecting the means for males and those for females in multivariate space will produce a set of parallel vectors in (A) and vectors set at different angles in (B). Note that since these are vectors, the slope as well as the direction of the difference is important. For example, if the positions of males and females reversed in one species, their sexual dimorphism vector will be opposite in orientation to the other species, even if slopes are the same. To simplify presentation, only symbols representing the mean male and female values for three species are presented. However, the analyses presented in the text involve testing for differences among ecomorphs, each represented by multiple species. The axes are the morphological variables used in the analysis, possibly after dimension-reduction by principal components or canonical variates analysis (i.e., a form of multiple-group PCA).](https://academic.oup.com/icb/article-abstract/47/2/272/718720)
In contrast, twig anoles have short limbs, live in the canopy on the thin extremities of branches, and almost exclusively walk rather than run or jump. Twig anoles tend to be constantly moving about their habitat and are the most actively foraging of all anoles. Trunk-ground anoles, on the other hand, live on the broad, open surfaces of the lower portions of tree trunks and on the ground, and accordingly have long limbs. Trunk-ground anoles are good runners and jumpers, spend long periods essentially motionless in a perching posture scanning their environs, and tend to run when they do move. Trunk-ground anoles use the sit-and-wait strategy of foraging more than do any other Anolis.

Social behavior has been well-studied in a few specie of Anolis. Their sterotypical mating system is one of resource-defense polygyny. In most species that have been studied, large males defend high-quality territories that encompass smaller territories of several females (Rand 1967a; Jenssen 1970; Stamps 1975; Trivers 1976; Schoener and Schoener 1980; Stamps 1983; Jenssen 1995; Stamps et al. 1997). Unlike many bird species, both males and females may be territorial, although females generally have small exclusive territories and larger home ranges that they share with neighbors.

One species that lacks any degree of territoriality is the twig anole Anolis valencienni, it also differs from most other anoles in several other respects. The presence of a large colorful throat structure (dewlap) used for social signaling is a male-specific trait in most other anoles. Both male and female A. valencienni, however, possess large dewlaps which they use frequently (Hicks and Trivers 1983). Additionally, whereas females of most anoles are usually no longer receptive to males after mating (Crews 1973), A. valencienni females have been observed to copulate multiple times in one day (Hicks and Trivers 1983) and even share a communal egg-laying site.

In addition, anoles vary considerably in the extent of sexual dimorphism in body size (Schoener 1969; Stamps 1983; Butler et al. 2000), ranging from species in which the sexes are the same size to others in which adult males are more than three times the mass of adult females; the sexes also differ in ecomorphologically-relevant proportions of various parts of the body (Schoener 1967; Butler and Losos 2002). Similarly, sexual differentiation in microhabitat (Collette 1961; Rand 1967a, 1967b; Rand and Rand 1967; Schoener 1967; Jenssen 1970; Andrews 1971; Schoener and Schoener 1971a, 1971b; Lister 1976, 1981; Scott et al. 1976; Talbot, 1979; Pounds 1988; Lister and Aguayo 1992; Powell and Russell 1992; Rodriguez Schettino and Martinez Reyes 1996; Butler and Losos 2002), diet (Schoener 1967, 1968; Schoener and Gorman 1968; Lister 1976; Talbot 1979; Floyd and Jenssen 1983; Preest 1994; Parmelee and Guyer 1995; Perry 1996) and behavior is substantial among West Indian anoles.

West Indian anoles thus contain extensive ecomorphological differentiation, both among species that have radiated into specialized microhabitats on each island and between sexes within these species. In what follows, I analyze patterns of dimorphism in size and shape, and combine these new analyses with previous results in order to address the following questions: Does sexual dimorphism in size and shape suggest adaptation to microhabitat type? If adaptation is occurring, but males and females differ, can sexual variation contribute to community-wide diversity? Conversely, does the community within which the species lives provide an important context for the evolution of sex differences?

**Methods**

**Data collection**

I measured five morphological characters from adults of both sexes of members of each ecomorph class on Puerto Rico and Jamaica (sample sizes = 3–29; mean = 16.4): mass, snout-to-vent length (SVL), forelimb and hind limb length (FOREL and HINDL), and numbers of sub-digital lamella on the fourth toe of the hind foot (LAMN; lamellae are laterally expanded scales on the subdigital toepads used for clinging to inclined or vertical surfaces). Localities are described by Butler and Losos (2002). These two islands represent two independent adaptive radiations (Losos et al. 1998). I used the natural logarithm of all variables; mass was first cube-root transformed to place it on a linear scale with length measurements. I used the geometric-mean method to separate size and shape (Butler and Losos 2002), with SIZE defined as the arithmetic mean of log-adjusted SVL, MASS, FOREL, and HINDL (LAMN is not included as it does not scale intraspecifically, and only weakly interspecifically, with size). Components of shape were calculated for each individual by taking the difference of each log-variable with SIZE.

Mean values of the morphological measurements for each species and sex were presented previously (Butler et al. 2007). Previous comparative studies established that both interspecific and intersexual variation in these characters is adaptive with respect to differences in habitat use (Locos 1990 b,c; Butler and Losos 2002).
Multivariate analyses of shape dimorphism

I used analysis of variance (ANOVA) and multivariate analysis of variance (MANOVA) to test for effects of sex, ecomorph type, their interaction, and species nested within ecomorph type on shape variation (Proc Reg and Proc GLM in the SAS statistical language). Multiple comparisons were controlled at an experiment-wise error rate of 5% using the Tukey–Cramer method. The relative importance of each factor or interaction was estimated using components of partial variance explained by each term in the model (Olejnik and Algina 2000; Langerhans and DeWitt 2004) (partial $\eta^2$; because they are partial variances, their sum can exceed 100%). These analyses, including a phylogenetic version, was presented by Butler et al. (2007).

I used canonical variate analysis to reduce the dimensionality of the multiple-group data. The dependent variables were the measurements of shape described earlier. The independent variables were the species-sex classes (loadings are reported Table 1).

Correlated or independent niches

I tested the hypothesis of correlated differences between the morphology of males and females using MANOVA. If males and females have separate niches, a plot of individual measurements in a coordinate system with canonical variate scores as axes should reveal that the male and female

---

### Table 1 Results of morphological canonical variate analysis

<table>
<thead>
<tr>
<th>Variable</th>
<th>Can1</th>
<th>Can2</th>
<th>Can3</th>
<th>Can4</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Significance tests of canonical variate axes</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CAN1</td>
<td>16.99</td>
<td>0.717</td>
<td>0.00234</td>
<td>56.68</td>
</tr>
<tr>
<td>CAN2</td>
<td>4.012</td>
<td>0.887</td>
<td>0.0421</td>
<td>30.93</td>
</tr>
<tr>
<td>CAN3</td>
<td>2.206</td>
<td>0.979</td>
<td>0.211</td>
<td>20.13</td>
</tr>
<tr>
<td>CAN4</td>
<td>0.478</td>
<td>1.000</td>
<td>0.677</td>
<td>8.51</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>(B) Canonical structure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variable</td>
</tr>
<tr>
<td>Total</td>
</tr>
<tr>
<td>SSVL</td>
</tr>
<tr>
<td>SMASS</td>
</tr>
<tr>
<td>SFOREL</td>
</tr>
<tr>
<td>SHINDL</td>
</tr>
<tr>
<td>SLAMN</td>
</tr>
</tbody>
</table>

| Between species-sex classes |       |       |       |       |
| SSVL         | 0.888 | −0.427 | −0.136 | −0.103 |
| SMASS        | 0.593 | −0.380 | 0.0875 | 0.704 |
| SFOREL       | −0.608 | 0.392 | 0.670 | −0.203 |
| SHINDL       | −0.852 | 0.386 | −0.342 | −0.0820 |
| SLAMN        | 0.816 | 0.573 | −0.0607 | −0.0446 |

| Pooled within species-sex classes |       |       |       |       |
| SSVL         | 0.616 | −0.608 | −0.261 | −0.427 |
| SMASS        | 0.137 | −0.181 | 0.0562 | 0.972 |
| SFOREL       | −0.252 | 0.334 | 0.758 | −0.501 |
| SHINDL       | −0.539 | 0.503 | −0.601 | −0.309 |
| SLAMN        | 0.556 | 0.803 | −0.115 | −0.181 |

All species are of the genus Anolis. The morphological variables are size-adjusted (see below). Associated eigenvalues and significance levels of canonical variate axes (A) followed by canonical structure (B: total, between group, and pooled within group loadings of shape morphology variables on each canonical axis). Groups in this analysis were the species-sex classes.

NumDF = numerator degrees of freedom; DenDF = denominator degrees of freedom; Can1–4 = Canonical variate axes 1 through 4; SSVL = snout-to-vent length (mm); SMASS = mass (g); SFOREL = forelimb length (mm); SHINDL = hindlimb length (mm); SLAMN = lamella number; SIZE = natural log of the geometric mean size; SSVL = size-adjusted SVL = log(SVL) − SIZE; “S” preceding variable name indicates size-adjusted variables, calculated in the same fashion as SSVL.
observations form clusters. These clusters should be grouped by sex and ecomorph type (here, species is a replicate of ecomorph type).

If we draw a vector connecting the means of males and females for each species, we can think of our MANOVA as testing whether these male–female (M–F) vectors differ across ecomorph types (Fig. 1). In all cases, if males and females differ, the length of the M–F difference vector is greater than zero. Thus, when there are multiple species, differences in sexual dimorphism among species may arise because either they have differ in the lengths of their male–female difference vector (i.e., the differ in the magnitude of sexual dimorphism; Fig. 1A), or they differ in the directions or angles of their M–F difference vector (Fig. 1B). A MANOVA will find a significant difference between sexes from either or both sources.

In order to separate the alternatives of sexual dimorphism in magnitude or direction, we can employ a simple trick by normalizing (i.e., artificially equalizing) the magnitudes of the sex difference vectors. Once we remove magnitude differences, any differences that remain are from differences in direction. Thus, if species vary by ecological type, our test of correlated or independent niches comes down to testing whether the vectors of the different ecological types differ in length or direction (i.e., the slopes of the lines), which can be accomplished by two MANOVAs, one on the original data on shape testing for magnitude + direction, and the second on the normalized data on shape testing for direction only.

Thus, the difference vector between males and females in canonical variate space defines the magnitude and direction of multivariate dimorphism. I tested whether ecomorphs differed in shape dimorphism, both in magnitude and direction of sexual dimorphism difference vectors. I used the canonical variate scores as the dependent variables, and ecomorph, sex, and the term species nested within ecomorph, and the interaction between ecomorph and sex as independent variables. A significant ecomorph by sex interaction term indicates that the M–F vector differs among ecomorphs (any difference in either magnitude or direction). To clarify whether the difference can be attributed to direction in addition to magnitude, I also conducted the MANOVA after normalizing the observations for males and females so that the mean M–F vector would have the same length in each species. In this case, a significant ecomorph by sex interaction supports the hypothesis of independent niches (Fig. 1B), whereas an insignificant interaction supports the hypothesis of parallel niches (Fig. 1A).

Dimorphism in shape between ecomorphs and across islands

I computed the distance between males and females in shape (i.e., the magnitude of shape dimorphism; also equivalent to the mean Mahalanobis distance between males and female within a species). This is a means of reducing the multivariate variation between males and females within a species to a single number. I then compared mean dimorphism in shape across ecomorphs and islands and their interaction. Incorporation of phylogenetic information into this analysis is not possible because phylogenetic relationships and insular effects are for the most part confounded.

Niche-filling analyses

The above analyses of shape dimorphism examine patterns of differences between the sexes. An important conceptual distinction is that although sexual differences and ecological variation are involved, by casting the problem in terms of sexual dimorphism, what is compared is the extent to which within species variation is affected by ecology (i.e., whether some habitat types promote or constrain dimorphism, or whether the form or direction of dimorphism is different between habitat types). In contrast, niche-filling analyses measure the contribution of each sex to morphological diversity at the community level, considering each sex as a potentially independent ecological unit. Thus, conceptually, these analyses quantify the additional contribution of sexual variation, above that of (single-sex) interspecific variation, and consider each sex relative to other groups within the community, which may be of different sex, or of either sex of a different species and ecomorph type.

Niche theory predicts that organisms will evolve morphologies to match their ecological roles. Thus, by convention, the “morphospace” is the combination of possible morphologies in our set of organisms, and can be represented by plotting the organisms’ position along one or several morphological axes (Hutchinson 1957; MacArthur 1958). Morphological diversity can then be assessed by comparing the filling and overlap among groups in morphospace.

I used individual canonical variate scores to test hypotheses of morphospace filling. I binned individual observations into cubes of morphospace defined by intervals of one canonical variate unit along canonical variate axes one to three. I measured the volume of morphospace occupied by male Anolis by counting the number of cubes occupied by one or
more individuals. I then measured the increase in volume attributable to adding females by counting the number of additional cubes filled when females were included. Significance was assessed by randomizing the sex of individuals within species using 20,000 permutations of the data. Code implementing this test in the R statistical language is available at the author’s website (http://www2.hawaii.edu/~mbutler/software.html). To account for any phylogenetic confounding, analyses were re-run after eliminating the two species whose closest relatives share the same ecomorph type (A. pulchellus and A. stratulus). This test measures the amount by which morphospace is expanded when females are added to a male-only analysis and vice versa. These analyses were presented by Butler et al. (2007), but are partially reproduced here for comparison with the above MANOVA analyses. Separate analyses of niche-filling based on morphological data using an alternate ordination method (Principal Components Analysis, PCA), as well as niche-filling based on ecological data were also previously presented (Butler et al. 2007).

To visualize the position of the sexes and species in morphological space, I plotted 20% contours of the 3D kernel density using the ks package written in the R statistical language (Duong 2005). The densities were computed using kernel discriminant analysis in three dimensions (using canonical variate scores Can1–Can3) on ecomorph-sex groups.

The data entering into all analyses (both MANOVA-based and nonparametric niche-filling) were based on individual measurements, rather than on species’ means. All ANOVA and MANOVA analyses were performed in the SAS statistical language.

**Results**

Both sexual dimorphism in size and shape have strong associations with type of structural microhabitat, but not with phylogeny (Fig. 2; Butler et al. 2000; Butler and Losos 2002; Butler and King 2004). Species of anoles using different microhabitats vary greatly in shape in agreement with previous studies (Fig. 3). Within species, the sexes differ in the same morphological traits that distinguish the ecomorphs, and for which the ecological significance of morphological variation is well-understood (Losos 1990b,c; Butler and Losos 2002): females have relatively longer bodies and more lamellae in the toepad than do males, whereas males have longer limbs (Fig. 3). In addition, the extent and form of dimorphism varies among the different ecomorph
types (Fig. 3). Ecomorphs that are highly dimorphic in size, however, may not be highly in dimorphic in shape (trunk–ground and trunk–crown anoles are highly dimorphic in size but intermediate in shape; the crown–giant anole is highly dimorphic in shape but low in size), at least for the Puerto Rican and Jamaican species (compare Fig. 1B, with Fig. 1C; see also Butler and Losos 2002). Thus, dimorphism in shape reveals a different ecological pattern than does dimorphism in size.

Do males and females have independent niches?

MANOVA reveals that dimorphism in shape contributes substantially to morphological diversity within anoles (Table 2, distance + angle method), with sex accounting for 40% of the partial variance in total shape diversity and the interaction between ecomorph and sex accounting for 69% of multivariate partial variance. Furthermore, the MANOVA results support the hypothesis of independent niches. Sexual dimorphism in shape is significantly different whether we adjust for the magnitude of the difference in shape or not (Table 2; all results have P-values < 0.0054). This indicates that the sexual dimorphism in shape differs in both the magnitude of the dimorphism as well as in the angle (indicating that dimorphism in shape takes on different forms) between different species and ecomorphs. These effects are not reduced when phylogeny is taken into account (Butler et al. 2007).

Analyses of packing in morphospace reveal that sexual dimorphism is responsible for a large proportion of the total ecomorphic niche space occupied. As expected (based on previous studies), the ecomorphs occupy largely nonoverlapping portions of multivariate morphological space. However, I demonstrate here that sexes within ecomorphs also occupy unique regions of morphological space. However, I demonstrate here that sexes within ecomorphs also occupy unique regions of morphological space (Fig. 3, Table 3; Butler et al. 2007). Only 14% of occupied cells in morphological space contain both male and female individuals. By contrast, females uniquely occupy 45% of morphospace and males uniquely occupy

<table>
<thead>
<tr>
<th>Effect</th>
<th>Wilks’ λ</th>
<th>F-value</th>
<th>P-value</th>
<th>p</th>
<th>Qden</th>
<th>r</th>
<th>η²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance + Angle</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sex</td>
<td>0.599</td>
<td>78.78</td>
<td>&lt;0.0001</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td>40%</td>
</tr>
<tr>
<td>Ecomorph</td>
<td>0.00906</td>
<td>328.84</td>
<td>&lt;0.0001</td>
<td>5</td>
<td>4</td>
<td>4</td>
<td>69%</td>
</tr>
<tr>
<td>Ecomorph × Sex</td>
<td>0.838</td>
<td>5.35</td>
<td>&lt;0.0001</td>
<td>5</td>
<td>4</td>
<td>4</td>
<td>4%</td>
</tr>
<tr>
<td>Species(Ecomorph)</td>
<td>0.135</td>
<td>31.04</td>
<td>&lt;0.0001</td>
<td>5</td>
<td>10</td>
<td>5</td>
<td>33%</td>
</tr>
<tr>
<td>Angle only</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sex</td>
<td>0.748</td>
<td>39.63</td>
<td>&lt;0.0001</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td>25%</td>
</tr>
<tr>
<td>Ecomorph</td>
<td>0.00576</td>
<td>395.90</td>
<td>&lt;0.0001</td>
<td>5</td>
<td>4</td>
<td>4</td>
<td>72%</td>
</tr>
<tr>
<td>Ecomorph × Sex</td>
<td>0.136</td>
<td>30.87</td>
<td>&lt;0.0001</td>
<td>5</td>
<td>4</td>
<td>4</td>
<td>39%</td>
</tr>
<tr>
<td>Species(Ecomorph)</td>
<td>0.931</td>
<td>2.14</td>
<td>0.0054</td>
<td>5</td>
<td>10</td>
<td>5</td>
<td>1%</td>
</tr>
</tbody>
</table>

“Distance + Angle” indicates the ordinary MANOVA results, whereas the “Angle” refers to analyses of shape data after normalizing all species to the same intersexual difference in distance. All shape variables are entered into the model as dependent variables. Independent variables included in the model are listed under ‘Effect’. F-value, value from F distribution; p, number of dependent variables; Q, number of independent degrees of freedom; r, minimum of p or Q; η², multivariate partial variance = 1 − λ/278 M. A. Butler

**Fig. 3** Characterization of shape dimorphism among the ecomorphs (Butler et al. 2007). Relative means for ecomorphs and sexes (white, females; grey, males) for shape morphology variables (y-axes). Ecomorph-sex means are adjusted for all other effects in the ANOVA models (LSMEANS option in Proc GLM in the SAS statistical language; see Methods section), and plotted relative to the grand mean (centered at 0). Stars indicate significant sexual differences within ecomorphs. Sexual dimorphism in body length (SVL) occurs in ecomorphs with the shortest and longest bodies, dimorphism in forelimbs in ecomorphs with the longest forelimbs, and dimorphism in hind limbs in ecomorphs with the longest hindlimbs. All ecomorphs are dimorphic in lamella number, except twig anoles, which have the greatest lamella numbers relative to body size.

**Table 2** MANOVA results for dimorphism in shape and test of parallel versus independent niches
36% of morphospace. Thus, sexual dimorphism significantly increases the density of morphospace occupied by the anole radiations \( P = 0.0048 \): a 59% increase if the morphospace volume of both sexes is compared to that of only females, and an 88% increase compared to the male-only volume. This result remains significant when closely-related species of the same ecomorph are not included \( P = 0.0018 \) or if the analysis is repeated using principal components analysis \( P = 0.017 \; \text{Butler et al. 2007)} \).

As with the MANOVA, the extent of intersexual divergence is a function of ecomorph type (Table 3; Fig. 4): in some ecomorphs, sexes appear to have more exclusive clusters, whereas in others, the sexes form a mixed cluster. Trunk–crown anoles, and especially trunk–ground anoles, have more exclusive clusters. For example, male trunk–ground anoles form exclusive clusters and insert themselves in between clusters formed by female trunk–ground anoles and crown–giant anoles (Fig. 4B and C). These ecomorph-sex groups are neighboring adjacent ecomorph types, and thus behave as separate ecological units. The sexes of the crown–giant, grass–bush, and twig anoles, on the other hand, are more thoroughly interdigitated. Note that multiple species contribute to an ecomorph, with each ecomorph independently evolving on each island (with the exception of grass–bush anoles, which are absent from Jamaica). Thus, this analysis further demonstrates extreme morphological convergence to niches associated with habitat type.

### Discussion

#### The meaning of sexual dimorphism and adaptation

A simple question has motivated my research on sexual dimorphism in anoles. If morphology reflects adaptation to the environment, but sexes differ in morphology, what does this mean? Are females "less adapted" than males? Do sexual differences in habitat drive sexual dimorphism? Or do males and females have "independent adaptations" to the environment? If the latter is true, can there be a "female niche" and a "male niche" ("econes" in the terminology of Heatwole 1989) such that sexual dimorphism interacts with adaptive diversification such that sexual differences increase "species packing"?

#### Correlated or independent niches?

The finding here that niches of males and females cannot be described simply as "parallel" (Fig. 1A) corroborates the finding by Butler and Losos (2002) that each sex is adapted to their respective microhabitats. If the differences in shape between the sexes were simply parallel across all species, then it would be possible to find a simple functional relationship between shape and preferred habitat. For example, a small increase in hind limb length may result in a 1-cm increase in the diameter of perch used. Thus, we find that males and females can be better described as having "independent niches" (Fig. 1B). We know from previous work that neither sex is maladapted, but, rather, interspecific analyses

### Table 3 Morphospace niche-packing analysis

<table>
<thead>
<tr>
<th>Ecomorph</th>
<th>Both sexes</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( N_{ind} )</td>
<td>To tcubes</td>
<td>Uniquecubes</td>
</tr>
<tr>
<td>Trunk-ground</td>
<td>166</td>
<td>95</td>
<td>78</td>
</tr>
<tr>
<td>Trunk-crown</td>
<td>150</td>
<td>76</td>
<td>72</td>
</tr>
<tr>
<td>Crown-giant</td>
<td>31</td>
<td>29</td>
<td>21</td>
</tr>
<tr>
<td>Grass-bush</td>
<td>88</td>
<td>65</td>
<td>57</td>
</tr>
<tr>
<td>Twig</td>
<td>58</td>
<td>43</td>
<td>43</td>
</tr>
<tr>
<td>All</td>
<td>493</td>
<td>94</td>
<td>220</td>
</tr>
<tr>
<td>Total cubes</td>
<td>289</td>
<td>154</td>
<td>182</td>
</tr>
</tbody>
</table>
Fig. 4 Three-dimensional visualization of morphological space (Butler et al. 2007). The plot is based on individual data with ecomorphs (colors) and sexes (light = females, dark = males) indicated. Several species belong to each ecomorph type, thus part of the irregular shape is a result of interspecific variation. Views (A) through (C) show different views of the same three-dimensional object.
show that each sex has strong multivariate correlations between shape and microhabitat (Butler and Losos 2002). These correlations are simply slightly different for each sex.

Are these differences between ecology and morphology biologically significant? Does it imply that there is some sex-specific functional demand? Or is it something else? In the absence of functional data, it appears that the fact that sexes differ may not require special explanation related to sexual behavior. Rather, the driving pattern may be how the species and sexes fit within the community.

Niche-filling analyses

Macroevolutionary tests of niche filling often describe the idea of “niche space” as a multidimensional hypervolume, with species occupying different regions of morphospace. Thus, increasing “diversity” includes those analyses that add to the morphospace on the periphery of the cluster, as well as filling the gaps between ecological species such that the niche space is more fully occupied.

Sexual dimorphism may increase the degree of “niche packing” if the sexes of different species are interdigitated across the resource spectrum. This hypothesis is not possible to test with standard linear model or ANOVA-style analyses. If the hypothesis is true, the clusters may pack together in irregular ways. Moreover, what we really wish to know is whether the sexes are filling unique space that is left vacant by the other sex, and the classical regression-based techniques cannot detect an increase in the packing and filling of niche space. Butler et al. (2007) devised a nonparametric niche filling analysis.

If sexes are able to act as independent “species,” then sexual variation may increase “niche packing,” and ultimately, diversity at the community-wide level. Indeed, analyses of morphospace packing reveal that sexual dimorphism is responsible for a larger proportion of the total ecomorph niche space occupied (Fig. 3; Butler et al. 2007). On an ecological scale, intersexual niche packing implies that sexual variation may allow greater biomass of Anolis per area of forest. Species are often observed to expand their niche breadth in the absence of competitors (i.e., ecological release, reviewed in Dayan and Simberloff, 1994). If this variation can be converted into sexual dimorphism via disruptive selection, then it is possible to have an interplay between interspecific and intersexual variation. Thus, islands with younger faunas are predicted to have greater sexual dimorphism, which is gradually transferred to interspecific diversity as faunal buildup progresses (Butler et al. 2007).

Sexual selection

Is it natural selection or sexual selection driving the increase in morphological diversity? Differences between the sexes in use of resources have been documented in many species of Anolis. In previous studies, I have found that intersexual differences in habitat use are great and correlated with morphological dimorphism (Butler et al. 2000, 2007; Butler and Losos 2002). In contrast to environmental factors, sexual selection probably plays a lesser role in driving the evolution of sexual dimorphism in Anolis. Although sexual selection for large size in males as a means of obtaining large territories, and the females they contain, is commonly invoked as an explanation for lizard sexual dimorphism (reviewed by Stamps 1983), it is difficult to attribute the patterns observed here to that cause. For example, in those ecomorphs with significant dimorphism in shape, males have lesser relative mass than do females, shorter relative body length, and fewer lamellae. If anything, this pattern is opposite to what one might expect if the evolution of dimorphism is related to superior fighting ability in males.

Interestingly, the one pattern that is tightly associated with the pattern of dimorphism in size is whether sexes form more exclusive or mixed clusters in morphospace. The trunk–ground and trunk–crown ecomorphs with strongly sex-specific clusters are those with the largest difference between male and female body size (Fig. 2B; Butler et al. 2000), and may be the most territorial. However, from the perspective of niche partitioning, it does not matter which sex occupies which portion of the resource space; all that matters is that they are nonoverlapping. It should be equally likely that one sex or the other occupy a particular niche. Indeed, the sexes occupy roughly equal fractions of unique morphospace in each ecomorph, whether sexes form unique clusters or not (Fig. 4, Table 3). Thus, the niche space attributable to each ecomorph is similarly, and greatly, expanded whether sexual selection is operating or not. For the evolution of community-wide ecological diversity, sexual selection does not matter.

It is possible, then, that sexual selection in this morphological diversification simply biases the occupation of a particular niche by one sex or the other. The range of morphologies that can be supported within the environment, and the extent
to which sexual selection is feasible, however, should be determined by ecological opportunity.

Conclusion
Which is more important, interactions within species (e.g., sexual selection), or interactions between species (here, between sexes and species)? In the case of Anolis, the influence of the environment is pervasive. Ecological opportunity seems to set the bounds for the ranges of morphologies that can evolve, and there seems to be equal opportunity for variation to be expressed between species of different habitat types or sex-specifically. While ecology does influence within-species patterns (i.e., ecological patterns of dimorphism; MANOVA and ANOVA results presented above), by far the largest effect is in the packing and filling of morphospace (Fig. 4, Table 3). Adding females to a male-only analysis increases the volume of morphospace occupied by 88%. Some of the differences between sexes observed here are as great as if sexes formed their own ecomorph (see especially trunk–ground males and females in Fig. 4). This is truly an impressive feat of evolutionary convergence, as females are not clustering with conspecific males, or even females of related species, but rather distantly related females of the same ecological type. Since there is no theoretical or empirical reason to expect that processes which produce variation among species and between sexes are decoupled, perhaps we should not be surprised. Perhaps the question should not be “why are the sexes different,” but rather “why should the sexes be the same?”

Acknowledgments
I gratefully acknowledge Jonathan Losos for intellectual guidance, collaboration, and many stimulating discussions over the years. Jim Cheverud provided the idea for the vector-based analysis of correlated versus independent niches using MANOVA. Without the tireless field assistance of Ling-ru Chu, C. K. Wang, and Jeff Higa, this work would not have been possible. A belated thank you to my dissertation committee at Washington University, who provided stimulating guidance: Stanley Sawyer, Owen Sexton, Jane Phillips-Conroy, Bob Sussman, Alan Templeton, JC, and JBL. I thank Tarn Duong, Stanley Sawyer, and Aaron King for advice on analyses and Bob Cox, Hal Heatwole, and an anonymous reviewer for critical comments which greatly improved the manuscript. This work was supported by a grant from the National Science Foundation, the Society for the Study of Amphibians and Reptiles. I received support in the field from the Discovery Bay Marine Laboratory, Jamaica and the El Verde Field Station, Puerto Rico. Thank you also to the symposium organizers for the invitation to participate in this symposium.

References
Fairbairn DJ. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of...


