Evolution of dorsal pattern variation in Greater Antillean *Anolis* lizards

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Dorsal patterning in animals can serve as an antipredator defence and may be involved in sexual selection, and is thus likely to be the target of multiple selective forces. Intraspecific variation in dorsal patterning is not rare, but the reasons behind it are poorly understood. *Anolis* lizards offer an ideal system to test for a role of ecological factors in driving variation in dorsal pattern. Anoles show a high degree of variation in dorsal pattern not only among species, but also between and within sexes. We use a comparative framework to explore whether ecological variables such as habitat use and perch height can explain the evolution of sexual dimorphism in dorsal pattern and the presence of female pattern polymorphism (FPP) in 36 Greater Antillean *Anolis* species. We provide evidence that anoles that perch closer to the ground are more likely to exhibit sexual dimorphism in dorsal pattern, and we suggest that habitat-use differences between sexes in ground-affiliated ecomorphs may drive the evolution of dorsal pattern dimorphism. In contrast, the ecological variables we investigated cannot explain the presence of FPP. Our results demonstrate that niche-associated diversification can generate phenotypic diversity within as well as among species, but the factors responsible for intrasexual polymorphism in some anole species remain cryptic. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **00**, 000–000.

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INTRODUCTION

The coloration and patterning of animals have profound effects on organismal fitness and adaptation, playing important roles in thermoregulation, crypsis, escape, aposematism, and sexual selection (Endler, 1984; Forsman, 1995; Hoffman & Blouin, 2008; Punzalan, Rodd & Rowe, 2008; Chen *et al.*, 2013). For example, many birds, snakes, lizards, and other animals are adorned with spots or stripes that may help them elude detection by predators or aid escape once detected (Brodie, 1989, 1992; Stevens & Cuthill, 2006; Dreiss *et al.*, 2012; Van den Brink *et al.*, 2011). Many other animals exhibit background pattern matching, in which colour patterns that match common background elements disrupt the outline of the

body or obscure features that predators commonly use to detect prey (Stevens & Cuthill, 2006). Regardless of the function of a given dorsal pattern, its adaptive value depends critically on the visual environment in which the animal occurs (Hoekstra, Drumm & Nachman, 2004), and the effectiveness of the pattern has been shown to vary according to the background appearance of the organism's habitat (Merilaita, Lyytinen & Mappes, 2001; Leal & Fleishman, 2004; Vignieri, Larson & Hoekstra, 2010).

Dorsal pattern can often be variable within species, and identifying the ultimate causes of this variation remains an outstanding challenge for many systems. Selection on dorsal pattern can vary between the sexes of a species, generating sexual dimorphism in pattern. Sexual selection has been widely proposed as an explanation for dimorphism in dorsal pattern in a number of animals, including

guppies (Endler, 1984), a swordtail fish (Morris, Nicoletto & Hesselman, 2003), birds (Burns, 1998), butterflies (Kemp, 2007), and many other species (Andersson, 1994). Ecological differences between the sexes may also explain sexual dimorphism in colour pattern (Slatkin, 1984). Although this is a less well-explored possibility, several examples are known. For instance, in Eclectus parrots (*Eclectus roratus*), selection for camouflage while foraging has resulted in cryptic males while females, which stay up to 11 months in the nest, are more conspicuous (Heinsohn, Legge & Endler, 2005). Similarly, in fairy-wrens (*Malurus* spp.), natural selection may impose greater pressures on females than males, generating differences in plumage coloration (Johnson, Price & Pruett-Jones, 2013).

In addition to sexual dimorphism in patterning, many species express polymorphisms in which one or both sexes exhibit a polymorphic dorsal colour pattern (Andres, Sanchez-Guillen & Rivera, 2002; Hoffman & Blouin, 2008; Vignieri *et al.*, 2010). The existence of pattern polymorphism may be habitat-dependent, and certain colour patterns may be better adapted to certain backgrounds (Schoener & Schoener, 1976). In the sexually dimorphic adder *Vipera berus* and the pigmy grasshopper *Tetrix subulata*, survival of colour morphs is different for males and females, and such differences can be explained by sex-specific microhabitat use, which ultimately determines susceptibility to visual predators (Forsman, 1995; Forsman & Appelqvist, 1999). Differential survival of morphs may help explain the maintenance of polymorphisms in both sexes, but in many species only females are polymorphic, and the reasons for this are less clear. One possibility is that higher heterogeneity in habitat use and increased predation risk in females may have led to the evolution of dorsal pattern polymorphism in females, but not in males. Females may also be more nutritious than males, and thus subject to stronger selection for crypsis (Stamps & Gons, 1983). Alternatively, selection for crypsis may be weaker in males than females because of the need for the former to conspicuously advertise and defend resources from conspecifics (Schoener & Schoener, 1976; Stamps & Gon, 1983).

Lizards in the genus *Anolis* are particularly well suited for studying the evolution of dorsal pattern variation. Anole species vary greatly in their dorsal patterning; some species lack pattern, whereas other possess stripes (e.g. *A. krugi*), spots (e.g. *A. sabanus*) or chevrons (e.g. *A. sagrei*, Fig. 1). Dorsal pattern not only varies among anole species, but in many species, it also varies between the sexes (sexual dimorphism) and within sexes (e.g. female pattern polymorphism, FPP). The latter has been documented in a number of anole species, and several studies have suggested a link between habitat and female polymorphism in dorsal pattern (Cox & Calsbeek, 2011; Paemelaere, Guyer & Dobson, 2011a). Both sexual dimorphism and FPP have evolved multiple times in anoles (Butler, Schoener & Losos, 2000; Butler & Losos, 2002; Butler, Sawyer & Losos, 2007; Paemelaere *et al.*, 2011a), making it an ideal system to test which conditions can influence the evolution of variation in dorsal pattern within species.

Anoles have radiated largely independently on each of the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica and Puerto Rico), and on each they have diversified to produce ecologically and

Figure 1. Examples of dorsal pattern in *Anolis* lizards. A, *A. sagrei*, B, *A. krugi*, C, *A. sabanus* (photograph by B. Falk). D, *A. pulchellus*. Photographs A, B and D by D. L. Mahler.

morphologically similar sets of habitat specialists, called ecomorphs (Williams, 1972; Williams, 1983; Losos, 2009). Six distinct ecomorph classes are traditionally recognized, and each possesses a unique suite of phenotypic traits, such as body size, toepad lamella number, relative limb and tail length, and body mass (Losos *et al.*, 1998; Langerhans, Knouft & Losos, 2006; Mahler *et al.*, 2013). In addition to this among-ecomorph variation, some of the ecomorphs exhibit sexual dimorphism in these ecologically relevant traits (Butler *et al.*, 2000, 2007; Butler & Losos, 2002). These differences likely trace to both behavioral and ecological differences among the sexes, especially in the more territorial ecomorphs. By having several independent origins of different ecomorphs we can statistically test whether ecology plays a role in the evolution of dorsal pattern in anoles.

In this study, we investigated whether dorsal pattern dimorphism and polymorphism in *Anolis* lizards are associated with habitat type. First, we asked whether ecomorph class and average perch height could explain the presence and magnitude of sexual dimorphism in dorsal pattern. Then, we asked whether sexual dimorphism in dorsal pattern was correlated with sexual size dimorphism, which would suggest that these two types of dimorphism evolve in concert. Finally, we quantified the extent of female pattern polymorphism among species, and tested whether FPP was more likely to be present in some ecomorphs than in others. All these questions were addressed in a phylogenetic framework using 36 *Anolis* species from the Greater Antilles.

METHODS
DATA COLLECTION

We examined fluid-preserved specimens of 36 *Anolis* species chosen to represent nearly all independent lineages of the six Greater Antillean ecomorph classes (grass-bush, trunk-ground, trunk, trunk-crown, crown-giant and twig) (Williams, 1972). Species were chosen based on specimen availability in the Museum of Comparative Zoology at Harvard University (MCZ). For each species, we aimed to examine 15 adult specimens of each sex, although we examined fewer individuals for some species that were poorly represented in the MCZ (males, mean = 9.4, SD = 4.1; females, mean = 10.0, SD = 4.2, Total specimens: 696). We took dorsal photographs of each specimen submerged in alcohol, because dorsal patterning in many preserved anoles is more easily discerned when the specimen is submerged than when it is in hand.

PATTERN ANALYSES
We quantified dorsal pattern variation by measuring or scoring 11 variables from the dorsal images (Table 1). We measured continuous variables using the software program ImageJ v.1.44 (Rasband, 1997–2011), and we scored discrete variables by eye. When possible, dorsal patterns were divided into entities (e.g. spots, chevrons or stripes), which were easily discernible. Continuous variables (entity shape and relative size) were natural log-transformed after we added the smallest non-zero value in the data set to every entry for these variables (following Warton & Hui, 2011) to replace zero values. The number of entities, strength of the pattern, number of sides and body location were specified as ordinal factors with different levels. The presence of a straight line, borders, symmetry, multiple colours and colour darker than background were specified as symmetric binary variables. After recording the 11 variables for each specimen, we performed a Principal Coordinate Analysis (PCO; Gower, 1966). First we constructed a dissimilarity matrix of all variables (ordinal, continuous and binary) with the *daisy* function in the *cluster* R

Table 1. Variables measured to characterize dorsal pattern

Variable	Possible values
Is the pattern a straight line?	0 = no; 1 = yes
Does it have borders?	0 = no; 1 = yes
Number of discrete entities in the pattern	0 = 0 discrete entities; 1 = 1–10 discrete entities; 2 = >10 discrete entities
Shape of the entity	0 = no entity; positive values = length/width (log-transformed)
Number of sides of entity	0 = no entity; 1 = line; 2 = triangle; 3 = rectangle/diamond; 4 = circle
Is the pattern symmetrical?	0 = no or no entity; 1 = yes
How strong is the pattern?	0 = no pattern; 1 = light; 2 = visible; 3 = strong
Where is the pattern found?	0 = no pattern; 1 = one part of body only (either sides or centre); 2 = all over the body
Is there more than one colour?	0 = no; 1 = yes
Size of the entity (e.g. spot size)	0–1 (proportion of dorsal area covered by each entity, log-transformed)
Is the pattern darker than background?	0 = lighter or no pattern; 1 = darker

package, using the 'Gower' method of variable standardization (Maechler *et al.*, 2015). Then, we used this matrix and the function *cmdscale* to obtain a set of coordinates for two dimensions such that the spatial distances between the points are proportional to the dissimilarities in the dissimilarity matrix. This yielded a data set containing two coordinates describing dorsal pattern for each individual.

CALCULATION OF SEXUAL DIMORPHISM IN DORSAL PATTERN

To calculate the degree of sexual dimorphism for each species, we first calculated the centroid for females and males in the PCO space for each species. Then we calculated the Euclidean distance between the centroids, which served as our measure of the degree of pattern dimorphism within each species. As an alternative approach for measuring sexual dimorphism, we performed a MANOVA between sexes for each species, using the two factors obtained in the PCO analysis as response variables. We then used Wilks' lambda as an index of degree of dimorphism between sexes. Low values of Wilks' lambda suggest that there is high differentiation between sexes. Thus, we transformed this value into a more intuitive dimorphism score using the formula: 1 − Wilks' lambda. The greater this value, the greater the difference between sexes of a given species. We report results for both measures of pattern dimorphism (Euclidean and Wilks' lambda).

CALCULATION OF FEMALE OR MALE BIASED POLYMORPHISM

To measure the amount of variation in dorsal pattern within each sex (i.e. the amount of female or male polymorphism), we calculated the average distance between each individual and the centroid for its sex, within each species. Following this, we calculated the difference in variability between females and males in each species by subtracting the male polymorphism value from the female polymorphism value. In addition, we examined for a difference in polymorphism by performing an analysis of variance (ANOVA) between average distance to centroid and sex; high F-values represent species where the sexes differ significantly in polymorphism.

ADDITIONAL SPECIES-SPECIFIC TRAITS

All species investigated are members of one of the six traditional *Anolis* ecomorph classes (grass-bush, trunk-ground, trunk, twig, trunk-crown and crowngiant), and we assigned species to ecomorph class following Butler & Losos (2002) and Butler *et al.* (2007,

2000). We obtained perch height estimates for 29 different species from several sources (Losos, 1990, 1992; Rodriguez-Schettino *et al.*, 2010; J. B. Losos, unpubl. data). Finally, we gathered continuous measures of sexual size dimorphism from Butler *et al.* (2000). All pattern scores, dimorphism metrics, and perch height values used in this study are included in the Supporting Information (Table S1).

STATISTICAL ANALYSES

To test whether dorsal pattern dimorphism varies as a function of ecomorph class, we performed a phylogenetic ANOVA using the function *phylANOVA* in the *phytools* package in R (Revell, 2012). This test compares the F statistic from the empirical ANOVA to a null distribution of F statistics obtained from analyses of phylogenetically simulated data (we conducted 10 000 simulations). To test the association between perch height and dorsal pattern dimorphism, we natural log-transformed perch height to achieve normality and then performed a phylogenetic correlation using the *PGLS* function in the *caper* R package (Orme *et al.*, 2012). Because we were conducting a correlation, we used a fixed λ value, which was calculated using the *phyl.pca* function in phytools. Additionally, we tested whether dorsal pattern dimorphism was related to sexual size dimorphism using a data set collected by Butler *et al.* (2000) and a phylogenetic correlation using the *PGLS* function in the *caper* R package and the same procedure described above (Orme *et al.*, 2012). For all of these analyses, we used the ultrametric maximum clade credibility phylogeny of Gamble *et al.* (2014), pruned to include only the species for which we measured dorsal pattern (results of analyses using an alternative topology [Mahler *et al.*, 2010] were qualitatively similar and can be found in the Supporting Information).

To test whether differences in male and female polymorphism were associated with ecomorph class, we first performed a phylogenetic ANOVA using ecomorph class as the predictor variable and polymorphism (within males and within females) as the response variable. We also used a phylogenetic ANOVA to test whether the difference between sexes in polymorphism was related to ecomorph class. Additionally, we tested whether male and female polymorphism were correlated by conducting a phylogenetic correlation as described above.

RESULTS

PATTERN QUANTIFICATION

Most of the dorsal patterns of the species analyzed could be qualitatively ascribed to one of the following

categories: stripes, chevrons, spots, diamonds, and intermediate between stripes and diamonds. The most common of these was an intermediate pattern between diamonds and a central stripe, followed by a pattern of a clear dorsal stripe. The presence of a dorsal pattern was uncommon for both males and females from crown-giant, twig and trunk ecomorph species, while trunk-ground and grass-bush species usually had a stripe, spots or chevrons.

DORSAL PATTERN DIMORPHISM AND ECOMORPHOLOGY

Among the 36 species, 20 (56%) presented significant dorsal pattern dimorphism according to the MAN-OVA. Our results also show a significant association between ecomorph class and pattern dimorphism when we used the Wilks' lambda dimorphism measure ($F = 3.66$, $P = 0.046$), although this relationship was non-significant when we used the Euclidean distance between male and female centroids as a measure of pattern dimorphism ($F = 3.11$, $P = 0.099$, Fig. 2). Trunk-ground and grass-bush ecomorphs exhibited greater pattern dimorphism than the other ecomorphs (Supporting Information, Fig. S1).

Anole species that perch closer to the ground are more dimorphic in dorsal pattern than more arboreal species. We found a significant negative correlation between perch height and dorsal pattern dimorphism regardless of the measure of dimorphism used (Euclidean method: $\lambda = 0.170$, $\beta = -0.114$, $P = 0.0099$, Wilks' lambda: $\lambda = 0.509$, $\beta = -0.170$, $P = 0.016$, Fig. 3A). The high level of dimorphism in the trunk-ground anoles results from the presence of a dorsal pattern in females and lack of pattern in males of most species. In contrast, in grass-bush species, both males and females exhibit a dorsal pattern (in four out of six species), but the pattern often differs between the sexes (e.g. diamonds in males and stripes in females in *A. bahorucoensis*, or lateral chevrons in males and central stripes in females in *A. pulchellus*). Dorsal pattern dimorphism and sexual size dimorphism are positively correlated (Euclidean method: $\lambda = 0.22$, $\beta = 0.54$, $P = 0.027$, Wilks' lambda: $\lambda = 0.381$, $\beta = 0.77$, $P = 0.047$, Fig. 3B).

SEX-DEPENDENT POLYMORPHISM

In 16 of the 36 species, females were significantly more polymorphic than males, in one species (*A. porcatus*), males were significantly more polymorphic, and in 19 species there was no significant difference in the degree of polymorphism between males and females. Differences in polymorphism between males and females were not related to ecomorph class or

Figure 2. Association between sexual dimorphism in dorsal pattern and ecomorph in 36 species of *Anolis*. A, Phylogenetic tree with coloured branches representing values of dimorphism in dorsal pattern (Euclidean distance). Circles at tips represent ecomorph and the colour legend is the same as in (B). B, Values of dorsal pattern dimorphism according to ecomorph class.
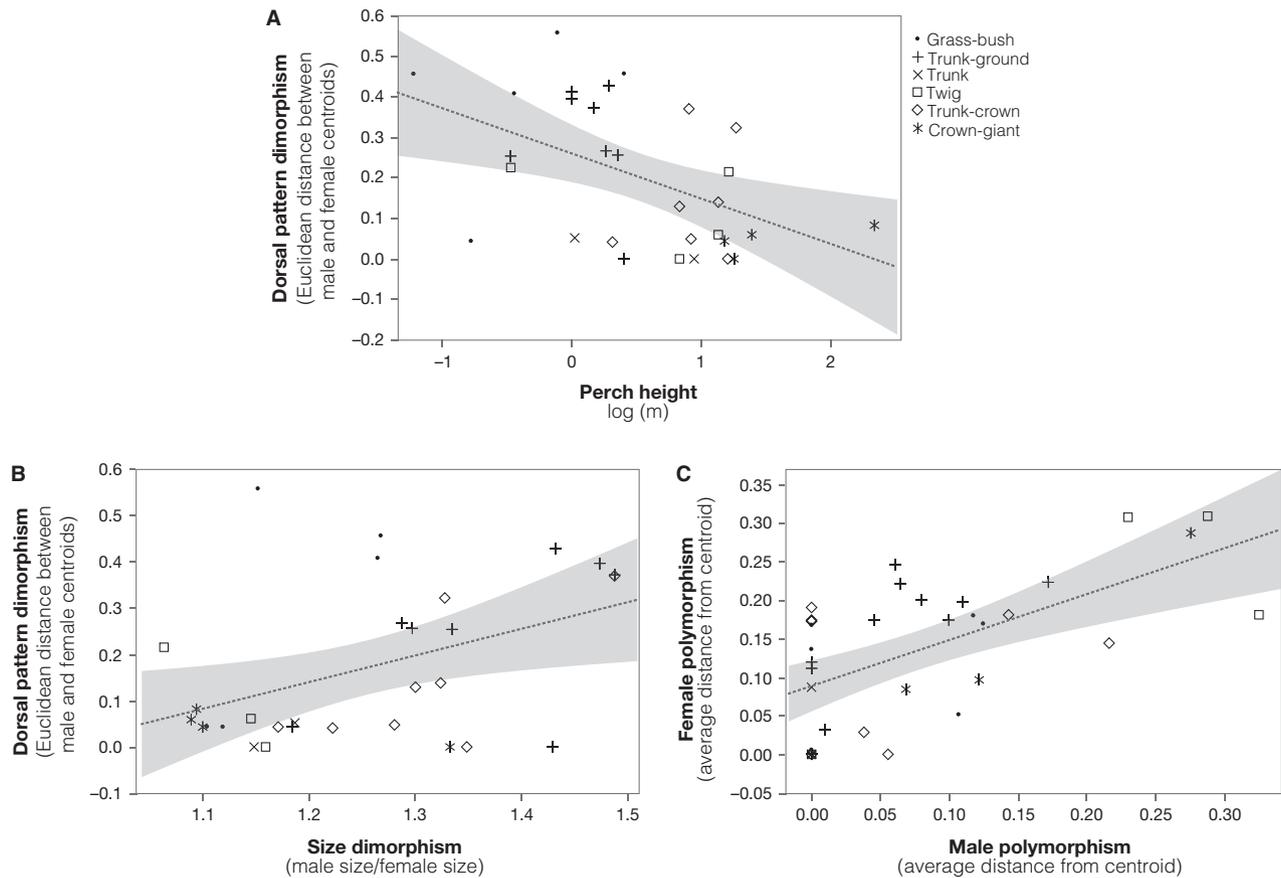
Figure 3. A, Species that perch higher are less dimorphic in their dorsal pattern than species that perch close to the ground. B, Sexual dimorphism in size is positively correlated to dorsal pattern dimorphism. C, Species with higher levels of male polymorphism also present high levels of female polymorphism.

perch height (F = 1.55, P = 0.408, β = −0.03, P = 0.15, Supporting Information, Fig. S2). Within sexes, the amount of polymorphism was not related to either ecomorph class (females F = 0.99, P = 0.64, males F = 2.971, P = 0.107) or perch height (females F = 0.22, P = 0.73, males F = 1.21, P = 0.42). However, a positive correlation existed between female and male polymorphism across species (λ = 0.004, β = 0.594, P = 0.0001, Fig. 3C).

DISCUSSION

Variation in dorsal pattern occurs in many species, both between and within sexes. Previous work has shown that ecological conditions, like habitat type and risk of predation, can generate divergence in dorsal pattern not only across, but also within, species. For instance, in the scincid lizard *Lampropholis delicata*, white stripes decrease susceptibility to predators in gravid females, but increase the risk of predation in males (Forsman & Shine, 1995). The frequency of females with white stripes varies

geographically, and is thought be related to geographic variation in female microhabitat use. Likewise, in Australian agamid lizards, individuals with dorsal stripes tend to use grass substrates, whereas arboreal individuals tend to be patternless (Chen *et al.*, 2013). Within anoles, Thorpe & Stenson (2003) found an association of certain patterns (e.g. spots or amount of black) with xeric habitats in *Anolis roquet*; other Lesser Antillean anole species show parallel evolutionary trends of pattern variation in response to climate variation (Thorpe *et al.*, 2015). More generally, a number of anole studies suggest an adaptive value for such pattern variation (e.g. Schoener & Schoener, 1976; Steffen, 2010; Paemelaere, Guyer & Dobson, 2011b).

For years, the idea that sexual selection (e.g. mate choice) drives phenotypic divergence between sexes has been accepted, but ecology may also play an important role in the evolution of sexual dimorphism (Slatkin, 1984). Our results show that the evolution of dorsal pattern dimorphism in Greater Antillean *Anolis* is linked to ecology. We demonstrate in a comparative framework that habitat use and the degree of sex

differences in dorsal pattern are strongly correlated. Species that have lower average perch height and hence live closer to the ground possess a higher degree of pattern dimorphism. Most of these species belong to the grass-bush and trunk-ground ecomorphs.

Although ecology and dorsal pattern dimorphism are strongly linked, it remains possible that dorsal pattern is a sexually selected trait, and sexual selection is stronger in some microhabitats than in others (Butler & Losos, 2002; Stuart-Fox & Ord, 2004). According to this hypothesis, we would expect to see lower amounts of dimorphism in more cluttered, low-visibility habitats because animals have a harder time seeing each other in such habitats, and this would prevent males from holding exclusive territories and hinder females from choosing among possible mates (Butler *et al.*, 2000). On one hand we did find that arboreal ecomorphs exhibited modest levels of pattern dimorphism, as might be predicted for anoles living in a complex arboreal matrix. However, the grass-bush anoles exhibited very high levels of pattern dimorphism, and the members of this ecomorph occur in extremely cluttered habitats. The sexual selection hypothesis seems unlikely for additional reasons. First, sexual selection through male territoriality or female mate choice would most likely select for prominent dorsal patterns in males, but it is females that more frequently exhibit dorsal patterning. In addition, sexual selection would likely select for conspicuous ornamentation, but the dorsal patterns of both male and female Greater Antillean anoles are cryptic. Nonetheless, we note the possibility that natural and sexual selection on males are aligned, such that females prefer cryptic, unpatterned males that blend in well with their backgrounds. Such a possibility would be difficult to rule out, but we note that females are attracted to very gaudy displays in another phenotypic trait – the extensible dewlap (Butler & Losos, 2002; Butler *et al.*, 2007).

Our results show a positive correlation between sexual size dimorphism and sexual pattern dimorphism (Fig. 3B); moreover, the same ecomorphs that are sexually dimorphic for pattern (trunk-ground and grass-bush) are also highly sexually dimorphic for other morphological traits such as toepad lamella number and relative hindlimb and forelimb length (Butler *et al.*, 2007). The correlation between different types of dimorphism suggests that these traits might be under similar pressures, which are likely to be ecological, because sexual selection would be unlikely to favour a shorter body length and fewer lamellae (Butler *et al.*, 2007). Differences in habitat between sexes may explain many aspects of sexual dimorphism in *Anolis*. For instance, males of *A. polylepis* have higher perches, eat smaller food items and are more sedentary compared to females (Perry, 1996), and similar differences between sexes in perch height and diameter have been found in many other *Anolis* species (Butler & Losos, 2002). In fact, trunk-ground ecomorphs present the largest differences in perch diameter between sexes, and sex differences in habitat use are correlated with dimorphism in size (Butler & Losos, 2002). Our results indicate that sexual dimorphism in dorsal patterning may be added to the list of traits that vary among anole ecomorphs, and its variation is possibly related to differences in microhabitat between sexes.

Female pattern polymorphism (FPP) has evolved independently several times across the phylogeny of anoles. The ancestral condition is likely to be absence of FPP, and it has been gained more frequently than lost, suggesting that it may be under selective pressures that favour its emergence and maintenance (Paemelaere *et al.*, 2011a). Stamps & Gon (1983) suggested that predation on females is stronger because they are less agile and more nutritious, and FPP may arise as a type of protection against avian predators (Stamps & Gon, 1983). Specifically, they suggested that heterogeneity in habitat use among females may explain why that sex is more polymorphic (Stamps & Gon, 1983). Previous work has shown that females differing in dorsal pattern occur at different perch heights (Steffen, 2010; Cox & Calsbeek, 2011; Paemelaere *et al.*, 2011b; Calsbeek & Cox, 2012), but at least in *A. sagrei* and *A. humilis*, morphs experience similar mortality rates (Cox & Calsbeek, 2011; Paemelaere *et al.*, 2011b; Calsbeek & Cox, 2012). In our study, we found that in 16 of 36 species studied, females were significantly more polymorphic than males. However, we found no support for a role of ecomorph class explaining such sex differences. FPP was found in roughly similar frequencies across most ecomorph classes. Although ecomorph class could not explain why some species are polymorphic, male and female polymorphism were correlated. This finding suggests that selective pressures favoring polymorphism may be coarsely similar for both males and females.

Williams (1972) initially characterized the ecomorphs in terms of their limb lengths and toepad proportions, adaptations for which part of the habitat they occupied and how they move. More recently, however, we have learned that the ecomorphs differ in many traits other than those related to locomotion and substrate use, including differences in territoriality, dimorphism in size and body proportions, and foraging behaviour, among others (Butler *et al.*, 2000, 2007; Butler & Losos, 2002). These broad-ranging correlations suggest that the different ecomorphs represent different ways of life, driven by some combination of differences of food availability, predator pressure, competition, and habitat structure.

To these differences we now add two others: dorsal patterning and extent of dimorphism in this trait. How these relate to the other ecomorph traits is not clear, but the finding that different aspects of dimorphism are correlated suggests a common cause for the myriad differences among the sexes. We encourage future research to investigate why greater sexual differences in dorsal pattern have evolved in species living near the ground. Experiments on differences in predation rates between males and females across different ecomorphs may help elucidate an adaptive basis for the occurrence of dimorphism and female polymorphism. Regarding the latter, acquiring data on within-sex variation in habitat use may be the key to understand why some species are polymorphic and others are not, even within an ecomorph class.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Figure S1. Differences in dorsal pattern between sexes (blue: males, red: females) and within each ecomorph.
Figure S2. Differences in dorsal pattern polymorphism for males (black) and females (gray) across different ecomorphs.
Table S1. Values calculated for each species.