

Sex-specific ecomorphological variation and the evolution of sexual dimorphism in dwarf chameleons (*Bradypodion* spp.)

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Abstract

Natural selection can influence the evolution of sexual dimorphism through selection for sex-specific ecomorphological adaptations. The role of natural selection in the evolution of sexual dimorphism, however, has received much less attention than that of sexual selection. We examined the relationship between habitat structure and both male and female morphology, and sexual dimorphism in size and shape, across 21 populations of dwarf chameleon (genus *Bradypodion*). Morphological variation in dwarf chameleons was strongly associated with quantitative, multivariate aspects of habitat structure and, in most cases, relationships were congruent between the sexes. However, we also found consistent relationships between habitat and sexual dimorphism. These resulted from both differences in magnitude of ecomorphological relationships that were otherwise congruent between the sexes, as well as in sex-specific ecomorphological adaptations. Our study provides evidence that natural selection plays an important role in the evolution of sexual dimorphism.

Introduction

The evolution of sexual dimorphism is often thought to be driven primarily by sexual selection, however, natural selection may also play an important role when the relationship between ecology and morphology (ecomorphology) differs between the sexes. Natural selection can influence the evolution of sexual dimorphism via three main mechanisms. First, males and females may occupy slightly different ecological niches, for example because of exploitation of different food resources (Shine, 1989). Secondly, sexual dimorphism may be associated with ecological factors as a secondary consequence of sex-specific selective pressures (Shine, 1989; Andersson, 1994). For example, fecundity selection on females may differ between habitat types (e.g. between habitats with high and low fire frequency) and consequently, female body size and shape may be expected to show a different association with habitat compared to males (Shine,

1989). Thirdly, habitat structure may influence the opportunity and nature of sexual selection with predictable, but different consequences for male and female morphology (discussed in Butler *et al.*, 2000; Butler & Losos, 2002; Perez-Barberia *et al.*, 2002; Losos *et al.*, 2003). As a corollary, habitat structure may influence the net cost of sexually selected traits if different habitats are associated with different predation risks (Endler, 1983). Despite the numerous ways in which natural selection may influence the evolution of sexual dimorphism, it has received little attention in comparison with the role of sexual selection.

Lizards are model organisms in the study of ecomorphology and have provided convincing evidence of ecologically driven morphological adaptation and convergence (Losos, 1990a, 1992; Garland & Losos, 1994; Losos *et al.*, 1997, 1998, 2006; Vanhooydonck & Van Damme, 1999; Melville & Swain, 2000; Kohlsdorf *et al.*, 2001; Elstrott & Irschick, 2004; Schulte *et al.*, 2004; Harmon *et al.*, 2005; Irschick *et al.*, 2005; Langerhans *et al.*, 2006; Melville *et al.*, 2006). The great majority of ecomorphological studies using lizards, however, have either looked at one sex only (usually males, e.g. Losos *et al.*, 1998; Kohlsdorf *et al.*, 2001; Bickel & Losos, 2002;

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Elstrott & Irschick, 2004; Harmon *et al.*, 2005) or lumped the sexes (e.g. Vitt *et al.*, 1997; Melville & Swain, 2000). Furthermore, the relationship between habitat use and sexual dimorphism has been examined in only one group, Caribbean *Anolis* lizards (Butler *et al.*, 2000; Butler & Losos, 2002; Losos *et al.*, 2003). These studies showed a relationship between habitat and sexual dimorphism in both size (Butler *et al.*, 2000; Losos *et al.*, 2003) and shape (Butler & Losos, 2002; Losos *et al.*, 2003). Additional studies that examine sex-specific ecomorphological variation and the evolutionary consequences for sexual dimorphism are needed to evaluate the generality of these patterns.

Here, we examine the relationship between habitat structure and both male and female morphology, and sexual dimorphism in both size and shape for 21 populations of dwarf chameleon (genus *Bradypodion*). Specifically, we examine the manner and extent to which the sexes differ in ecomorphological relationships, to elucidate environmental constraints on the evolution of sexual dimorphism. Chameleons are a particularly interesting group for examining ecomorphological variation because of their highly specialized morphology, including dorso-laterally compressed body, prehensile tails and zygodactylus feet (toes fused into two opposable pads; Nečas, 2001). Despite this specialization in body form, dwarf chameleons exhibit substantial morphological diversity in body size and shape and occur in a wide range of habitats, including montane and lowland rain forest, grasslands, montane and lowland Mediterranean heath and shrubby thicket (Branch, 1998).

We tested whether male and female morphology varies predictably with quantitative, multivariate aspects of habitat structure, using a modern phylogenetic comparative framework. We hypothesized that structural aspects of the habitat such as canopy cover, the density of vines and shrubs and the density of perches should exert strong selection on the morphology of dwarf chameleons because these habitat features influence both visibility (which may influence intraspecific signalling and the opportunity for sexual selection), as well as mobility (perch availability or ease of movement through dense grass or twigs). We explored the relationship between habitat structure, and body size, tail length, head dimensions, limb and toe lengths because these morphological traits show significant variation in relation to ecology in other lizard groups. Next, we tested whether sexual dimorphism in body size and shape varies with habitat structure. Such a relationship results when ecomorphological associations are apparent in one sex only or occur in both sexes but differ in magnitude (slope). Identifying patterns of sex-specific ecomorphological variation, using modern phylogenetic comparative methods, provides the basis for further mechanistic studies of how natural selection influences the evolution of sexual dimorphism (Losos *et al.*, 2003). Finally, we examined the influence of phylogenetic constraint or

inertia on the evolution of chameleon morphology and sexual dimorphism.

Materials and methods

Study system

Dwarf chameleons (genus *Bradypodion sensu stricto*) are small [50–110 mm snout-to-vent length (SVL)], viviparous lizards, endemic to southern Africa (Branch, 1998). Fifteen species are currently recognized, although based on recent phylogenetic work (Tolley *et al.*, 2004, 2006), several others are in the process of being described (C. Tilbury, K.A. Tolley and W.R. Branch, in prep.). We collected data for 21 populations (Table 1), which include all currently described species except *Bradypodion karooicum*, which appears to be a local variant of *B. ventrale* and is phylogenetically nested within the latter (Tolley *et al.*, 2004). In addition to described species, the 21 populations include three divergent lineages identified in Tolley *et al.* (2004, currently being described), as well as four divergent lineages identified by recent phylogeographic work on the *B. transvaalense* complex (T. Townsend, unpublished), which previous morphological work suggested comprises several distinct species (Jacobsen, 1989). Due to the taxonomic state of flux in this group, we refer to the 21 populations we studied as 'populations' rather than species or taxa. No species or divergent lineages of dwarf chameleon occur sympatrically. Thus, ecological competition between species and selection for species recognition, both of which can potentially influence the evolution of sexual dimorphism (discussed in Butler *et al.*, 2000; Butler & Losos, 2002; Losos *et al.*, 2003), are unlikely to be important in dwarf chameleons.

Morphology

We captured as many sexually mature, adult chameleons as possible (5–50 individuals of each sex, Table 1) by hand from each of the 21 populations and took morphometric measurements. Individuals were subsequently released at their site of capture, marked with GPS or flagging tape. We measured the following traits: SVL (nearest mm), tail length (cloaca to tail tip; nearest mm), jaw length (angle of the jaw to the tip of the snout), head width (width at the widest point), casque height (angle of the jaw to the highest point of the casque); front and hind-limb length (length of radius and tibia respectively measured with elbow/knee and wrist/ankle bent at right angles); front and hind toe length (middle toe from fold between medial and lateral pads). All traits except SVL and tail length were measured to the nearest 0.1 mm and all (apart from SVL) were converted to size-free variables by taking the residuals of these variables regressed against SVL (across all populations simultaneously).

Table 1 Sampling localities, sample sizes (*N*) and MANOVA testing for differences between the sexes in morphological traits for each population.

Population	Locality	<i>N</i> (female)	<i>N</i> (male)	<i>F</i> _{d.f.}	<i>P</i>
<i>Bradypodion</i> sp.	Swartberg Pass, WC	21	12	11.38 _{9,22}	< 0.0001
<i>B. caffrum</i>	Port St Johns, EC	15	11	11.50 _{9,16}	< 0.0001
<i>B. damaranum</i>	George to Knysna, WC	24	7	7.84 _{9,21}	< 0.0001
<i>B. dracomontanum</i>	Royal Natal NP, KZN	16	19	8.40 _{9,20}	< 0.0001
<i>B. gutterale</i>	Anysberg NR, WC	10	10	3.29 _{9,10}	0.039
<i>B. kentanicum</i>	Vicinity of Kentani, EC	9	10	21.40 _{9,7}	< 0.001
<i>B. melanocephalum</i>	Kennethstainbank NR, KZN	9	6	6.91 _{9,5}	0.023
<i>B. nemorale</i>	Nkandla Forest Reserve, KZN	8	5	1.28 _{9,3}	0.467
<i>B. occidentale</i>	Paternoster, WC	14	12	12.13 _{9,16}	< 0.0001
<i>B. pumilum</i>	Stellenbosch, WC	51	32	26.65 _{9,72}	< 0.0001
<i>B. pumilum</i>	Vogelgat NR, WC	10	5	5.10 _{9,5}	0.044
<i>B. setaroi</i>	St Lucia, KZN	10	21	9.57 _{9,21}	< 0.0001
<i>Bradypodion</i> sp.	Dhlinza Forest, Eshowe, KZN	8	18	6.07 _{9,16}	< 0.001
<i>Bradypodion</i> sp.	Ngome Forest Reserve, KZN	20	11	11.25 _{9,21}	< 0.0001
<i>B. taeniabronchum</i>	Lady's Slipper, EC	15	14	15.48 _{9,19}	< 0.0001
<i>B. thamnobates</i>	Bulwer, KZN	8	15	2.34 _{9,13}	0.08
<i>B. transvaalense</i>	Barberton, MP	6	15	2.34 _{9,11}	0.093
<i>B. transvaalense</i>	Tullach Moor NR, MP	5	9	6.29 _{9,4}	0.046
<i>B. transvaalense</i>	Graskop area, MP	11	11	3.71 _{9,11}	0.022
<i>B. transvaalense</i>	Woodbush Forest, LP	24	14	9.89 _{9,28}	< 0.0001
<i>B. ventrale</i>	Grahamstown area, EC	10	10	3.34 _{9,9}	0.043

EC, Eastern Cape; WC, Western Cape; MP, Mpumalanga; LP, Limpopo; KZN, KwaZulu Natal; NR, Nature Reserve; NP, National Park.

First, we tested for differences between the sexes in morphological traits using multivariate analysis of variance (MANOVA). The sexes differed significantly in morphology for all populations except for *B. nemorale*, *B. thamnobates* and *B. transvaalense* from Barberton (Table 1). For populations in which the sexes differed significantly, univariate tests revealed that the sexes differed in all morphological traits measured for at least some populations (see Table S1 in Supplementary material), therefore for all subsequent analyses, we examined each sex separately.

We calculated sexual size dimorphism (SSD) for each population as the natural log of mean male size divided by mean female size (Smith, 1999). Similar ratio-based indices have been widely used in comparative studies of SSD in reptiles (Stamps *et al.*, 1997; Butler *et al.*, 2000; Ord *et al.*, 2001; Cox *et al.*, 2003; Stuart-Fox & Ord, 2004; Harmon *et al.*, 2005). We calculated sexual dimorphism of all other morphological traits as the difference in size-corrected trait values (residuals of the trait regressed on SVL) between males and females.

As several of the traits are correlated (Table S2) and functionally related (e.g. front and hind limbs or front and hind toes), we explored variable reduction techniques (principal components analysis, PCA). The first principal component (PC) explained approximately 50% of the variation but component loadings of all original variables (size-corrected morphological traits) on the first axis were weak (< 0.4 absolute value) and all of approximately equal magnitude. Additional PCs were similarly difficult to interpret. This was the case for both

sexes and for PCAs with and without the inclusion of body size. Interestingly, Bickel & Losos (2002) found similar patterns for PCA on morphological traits among several genera of chameleons. This suggests that all morphological traits vary among species and no subset of traits captures more of the variance than another subset. Thus, we conducted our analyses on the original morphological traits but include only one limb and toe measurement (hind limb and toe) as measurements for front and hind limbs and toes were highly correlated ($r > 0.8$, Table S2).

Habitat structure

For each population, we measured nine structural habitat variables within five representative 10 × 10 m plots in which chameleons had been found. The variables were as follows: (i) canopy height; (ii) percentage canopy cover; (iii) percentage vine cover; (iv) number of trees over 5 m tall; (v) number of shrubs (between 1 and 5 m tall); (vi) mean shrub height; (vii) mean shrub width; (viii) number of perches at 0.5–1 m within a 50 × 50 cm cube and (ix) number of perches at 1.5–2 m within a 50 × 50 cm cube. Canopy height was visually estimated as 0–5, 5–10, 10–15 m or > 15 m. Percentage canopy cover was measured with a spherical densiometer and percentage vine cover was approximated as one of four categories: 0–25%, 25–50%, 50–75% and 75–80% of the trees or shrubs in the plot that were covered with vines or lianas. Height and width of each shrub were estimated by eye, then averaged to obtain a mean value for the

plot. Mean shrub height and width were included as variables to distinguish between low, uniform shrubs that dominate Mediterranean heath environments and the structure of shrubs in forest understoreys or open shrublands. The number of perches at 0.5–1 or 1.5–2 m was measured as the mean number of perches (< 3 cm in diameter) within five 50 × 50 cm cubes placed randomly within the plot at those heights. To summarize the nine habitat variables, we extracted the first three principal components (PCs) from a PCA. Continuous variables were first log-transformed.

Phylogenetic comparative analysis

First, we derived a phylogeny (Fig. 1) of our 21 populations based on mitochondrial 16S and ND2 sequences from GenBank (Tolley *et al.*, 2004, 2006) with four additional ND2 sequences provided by T. Townsend (unpublished) for the four populations of *B. transvaalense*. The data set used for phylogenetic analysis comprised sequences for 36 individuals (plus two outgroup taxa), including sequences for individuals from all but four of the localities of our 21 study populations. For these four exceptions, sequences were available from localities close by (within 50 km). Phylogenetic reconstruction is based on Bayesian analysis with the consensus tree from four independent runs of MrBayes (Ronquist & Huelsenbeck, 2003) subsequently pruned to only those 21 populations used in our study.

For phylogenetic comparative analyses, we used phylogenetic generalized least squares (PGLS, Martins & Hansen, 1997) and Felsenstein's independent contrasts (FIC, Felsenstein, 1985). PGLS estimates a parameter (α) for each correlation or regression that can be interpreted as phylogenetic constraint on a phenotypic trait or a measure of phylogenetic inertia (Hansen, 1997; Martins *et al.*, 2002; Butler & King, 2004; Hansen & Orzack, 2005). When the parameter α is set to 0, PGLS produces results identical to FIC. When α is large, it is equivalent to ignoring phylogeny or assuming all species radiated simultaneously from a single common ancestor (TIPS) (Martins *et al.*, 2002, 2004). PGLS, as implemented in COMPARE 4.06 (Martins, 2004) has the additional, important advantage of being able to account for intraspecific variation (using standard errors of population means).

For phylogenetic regression analyses, we used population mean values and standard errors of male and female morphology and habitat PCs. Because sexual dimorphism was based on mean male and female measurements, no standard errors were available for these variables. We began by doing multiple regressions of each dependent variable (morphology or sexual dimorphism) on our independent variables (habitat PCs). We re-ran regressions sequentially removing variables that did not contribute significantly. For analyses of the relationship between sexual dimorphism and habitat, we included the log of the mean species SVL [(male SVL + female SVL)/2]

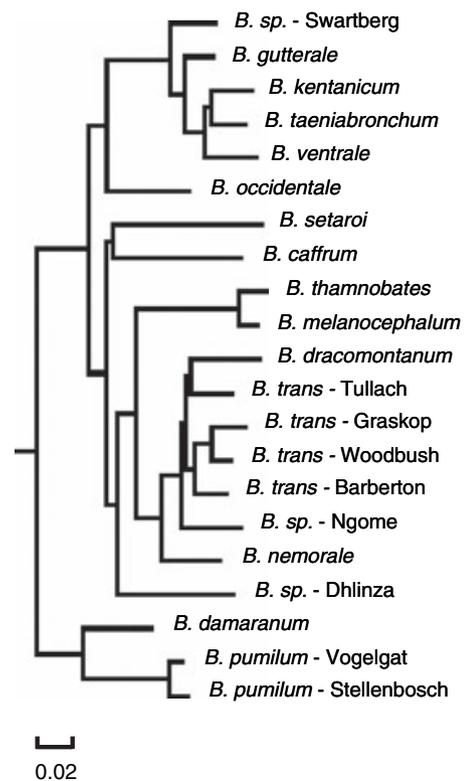


Fig. 1 Phylogenetic relationships of the 21 lineages of dwarf chameleon. The species name for *Bradypodion transvaalense* has been shortened to *B. trans*. Divergent lineages that are yet to be described are denoted as *B. sp.* followed by the locality.

as an independent variable to account for potential allometric effects. Relationships between habitat and sexual dimorphism may be an indirect consequence of a relationship between habitat and body size if sexual dimorphism increases allometrically with body size. Inclusion of body size as a covariate in regression models accounts for this potentially confounding effect as well as potential differences in age structure among populations (lizards have indeterminate growth so size is indicative of age).

Results

Habitat structure

The first three principal components (PCs) explained 82% of the variation in the nine habitat variables (Table 2). As each additional PC explained < 5% of the variance, we restricted analyses to the first three PCs. Based on component loadings (Table 2), the first PC is positively associated with canopy cover, canopy height, number of trees, vine cover and shrub height. Thus, high values of PC1 differentiate more closed, forested habitats from more open habitats. The second PC is positively

Table 2 Principal components analysis of habitat variation.

Component loadings	Principal component axes		
	1	2	3
Variable			
Canopy cover	0.432	0.119	0.004
Canopy height	0.387	0.245	-0.241
No. trees	0.393	0.154	-0.301
Vine cover	0.344	0.349	-0.047
No. shrubs	0.205	-0.358	-0.523
Shrub height	0.379	-0.303	0.290
Shrub width	0.283	-0.385	0.548
Perch density 0.5–1 m	-0.283	0.448	0.082
Perch density 1.5–2 m	0.212	0.459	0.429
% variance explained	53.8	15.2	13

The highest loadings for each axis are highlighted in bold.

associated with perch density at both heights. Thus, high values of PC2 indicate habitats with high density of grass stems or twigs below 2 m (e.g. grasslands or habitats with a dense herb or shrub understorey), whereas low values of PC2 indicate habitats with a sparse understorey. PC3 is negatively associated with number of shrubs and trees and positively associated with shrub width. High values of PC3 describe habitats with few trees over 5 m, instead dominated by few, wide shrubs (< 5 m).

Comparative analyses

Habitat structure consistently predicted variation in chameleon morphology and sexual dimorphism (Tables 3 and

4). Most results were consistent between the two types of phylogenetic comparative method (PGLS and FIC) because α was small. Although most of the patterns were evident regardless of the phylogenetic comparative method used, several relationships only became significant when phylogenetic signal had been taken into account (i.e. were nonsignificant under TIPS, Tables 3 and 4). We restrict our interpretation to those variables significant under both PGLS and FIC because results that are consistent between the two are likely to represent robust evolutionary patterns (Martins *et al.*, 2002, 2004; Ord & Martins, 2006).

Relationship of morphology to habitat

Both sexes of species occupying more closed, forested habitats (higher habitat PC1) had relatively higher casques, longer tails and relatively longer toes (Table 3). Males were also relatively larger in these habitats. Both sexes of species occupying habitats with high perch density (high habitat PC2) were smaller in size and had relatively smaller heads (jaw length and head width), but relatively longer tails. Males in these habitats also had longer toes. Finally, females of species in more shrubby environments (high habitat PC3) had relatively shorter jaws whereas males had relatively longer toes.

Relationship of sexual dimorphism to habitat

Sexual dimorphism was associated with all three aspects of habitat structure (Table 4). Species occupying more closed,

Table 3 Relationship of male and female morphology to habitat.

Sex	Dependent variable	Independent variable	Model α	Model % r^2	Slope	SE slope
Male	SVL	Habitat PC1	15.5	48.89	0.8	0.69*
		Habitat PC2			-5.64	1.42*†
	Casque height	Habitat PC1	15.5	20.06	0.2	0.09*†
		Habitat PC2	4.34	39.96	-0.32	0.09*†
	Jaw length	Habitat PC2	14.27	19.46	-0.2	0.09*†
		Habitat PC1	1.86	48.6	3.2	0.83*†
	Tail length	Habitat PC2			3.65	1.5*†
		Habitat PC1				
	Hind limb	-	-	-	-	-
	Hind toe	Habitat PC1	1.11	52.5	0.16	0.06*†
Habitat PC2				0.21	0.1*†	
Habitat PC3				0.32	0.13*†	
Female	SVL	Habitat PC2	15.5	48.31	-5.76	1.33*†
		Habitat PC1	15.5	37.34	0.25	0.07*†
	Casque height	Habitat PC2	15.5	49.12	-0.24	0.09*†
		Habitat PC3			-0.33	0.11*†
	Jaw length	Habitat PC2	3.99	12.64	-0.14	0.09*
		Habitat PC1	1.99	52.23	2.6	0.62*†
	Head width	Habitat PC1			2.91	1.13*†
		Habitat PC2				
	Tail length	Habitat PC1				
		Habitat PC2				
Hind limb	-	-	-	-	-	
Hind toe	Habitat PC1	2.01	39.59	0.2	0.06*†	

When the 95% confidence intervals around the slope ($1.96 \times SE$) do not incorporate 0, the slope can be considered significant. Only variables with significant slopes under PGLS or FIC were retained in the final multiple regression models. Model α refers to PGLS maximum likelihood estimate of α and model % r^2 and slopes are based on PGLS. Variables that are significant under Felsenstein's independent contrasts (FIC), i.e. when $\alpha = 0$, are marked with an asterisk (*) and variables significant assuming no phylogenetic constraint (TIPS) are marked with †.

Table 4 Relationship of sexual dimorphism to habitat.

Dependent variable	Independent variable	Model α	Model % r^2	Slope	SE slope
SVL	Habitat PC1	2.5	26.4	1.16	0.58*
	Habitat PC3			-2.59	1.32†
Casque height	-	-	-	-	-
Jaw length	Habitat PC2	2.97	36.91	-1.05	0.46*†
	Habitat PC3			1.19	0.43*†
	Body size			-15.2	7.64*
Head width	Habitat PC2	1.72	12.88	-0.82	0.41*†
Tail length	Habitat PC1	1.35	21.35	6.64	3.23*
	Habitat PC2			8.32	5.83*
Hind limb	Habitat PC1	14.52	45.24	-0.45	0.22*†
	Habitat PC3			2.1	0.62*†
Hind toe	Habitat PC1	8.37	43.28	-0.36	0.18*†
	Habitat PC3			1.38	0.43*†

When the 95% confidence intervals around the slope ($1.96 \times SE$) do not incorporate 0, the slope can be considered significant. Only variables with significant slopes under PGLS or FIC were retained in the final multiple regression models. Model α refers to PGLS maximum likelihood estimate of α and model % r^2 and slopes are based on PGLS. Variables that are significant under Felsenstein's independent contrasts (FIC), i.e. when $\alpha = 0$, are marked with an asterisk (*) and variables significant assuming no phylogenetic constraint (TIPS) are marked with †.

forested habitats (higher habitat PC1) were more sexually dimorphic in body size and tail length but less sexually dimorphic in leg and toe length. Species occupying habitats with high perch density (high habitat PC2) were more sexually dimorphic in tail length but less sexually dimorphic in head size (head width and jaw length). Finally, species in more shrubby environments (high habitat PC3) were more sexually dimorphic in jaw length as well as hind limb and toe length. Despite these consistent patterns, habitat structure generally explained less of the variance in sexual dimorphism compared with the variance in male or female traits. Only sexual dimorphism in jaw length showed positive allometry (Table 4).

Phylogenetic signal

Phylogenetic signal was generally weak (high values of α) for body size and head dimensions for both sexes (Table 3). By contrast, phylogenetic signal was strong (low values of α) for tail and toe lengths. Similarly, α values for regressions of trait sexual dimorphism with habitat were consistently low (Table 4), indicating strong phylogenetic constraint on the evolution of sexual dimorphism.

Discussion

Morphological variation in dwarf chameleons was strongly associated with quantitative aspects of habitat structure and relationships were generally congruent between the sexes. Nevertheless, sexual dimorphism was also consistently associated with habitat structure, even after taking allometric relationships into account. In spite of consistent patterns, the relationship of sexual dimorphism to habitat structure was generally weaker (in terms of variance explained) than the relationship of male or female morphology to habitat. This is consistent

with theoretical expectations; natural selection acts directly on morphological variation whereas the relationship between sexual dimorphism and habitat results from sex-specific ecomorphological adaptations as well as other sex-specific selection pressures such as fecundity selection on females and sexual selection acting more strongly on males (Shine, 1989).

Adaptive ecomorphological variation

The majority of ecomorphological relationships were congruent between males and females and are suggestive of morphological adaptation. For example, we found a consistent, negative relationship between body size and perch density for both sexes. Habitats with high perch density include grasslands and Mediterranean heaths, both of which experience much higher fire frequency than indigenous forests and open shrublands (Cowling *et al.*, 1997). High fire frequency may select for earlier maturation and smaller body size. Because both sexes are smaller in habitats with higher perch density, there was no relationship between perch density and SSD. Both sexes also have relatively smaller heads (head width and jaw length) in habitats with higher perch density. This may be an adaptation to moving through dense vegetation such as grass and Mediterranean heath and conforms to previous ecomorphological studies showing reduced relative head size in species that shelter in grass tussocks or semi-fossorial species that must move through a dense medium such as leaf litter (Pianka, 1969, 1986; Greer, 1989). Alternatively, reduction in body and head size in these habitats may be associated with selection for early maturation and paedomorphic features, although data on the allometry of head dimensions are required to test this hypothesis.

Other patterns are similarly suggestive of adaptive ecomorphological variation. For example, tail length was positively related to the first two habitat axes in both sexes. Chameleons with the shortest tails occur in Mediterranean heaths (fynbos), which are open habitats with moderate perch density (less than grasslands) and a high density of short, robust shrubs. These habitats have a high density of suitable perches (both horizontal and vertical perches strong enough to support a chameleon), potentially reducing the need for long tails needed to manoeuvre between more widely spaced perches. Similarly, both sexes had longer toes in more forested habitats, which may facilitate clinging to wider perches or a greater range of perch widths. In contrast to most other ecomorphological studies on lizards, we found no relationship between male limb length and habitat structure (e.g. Pounds, 1988; Losos, 1990a). In most lizards, longer hind limb length is associated with greater sprinting and jumping ability, which has potential fitness consequences, especially in terms of predator escape (Losos, 1990b; Garland & Losos, 1994; Irschick *et al.*, 2005). Chameleons have little leg musculature compared with other lizards and locomotor performance (e.g. sprinting and jumping ability) is less likely to be associated with fitness because chameleons rely primarily on camouflage and concealment (flipping to the other side of the twig or branch) to escape predators (Stuart-Fox *et al.*, 2006a).

Not all relationships between morphology and habitat are necessarily indicative of ecomorphological adaptation. For example, both sexes have higher casques in more closed, forested habitats. The casque has been shown to be an intra-sexually selected ornament in male Cape dwarf chameleons, *B. pumilum* (Stuart-Fox *et al.*, 2006b). The relative cost of sexually selected traits may differ among habitats if predation pressure varies with habitat structure (Endler, 1983). Thus, if predation risk is higher in more open habitats, this could potentially explain why species in more open habitats have reduced casques.

Habitat and sexual dimorphism

Several ecomorphological relationships were congruent between the sexes but result in a relationship between SSD and habitat structure because the sexes differ in the magnitude of the ecomorphological association. For example, both sexes have reduced jaw length and head width in habitats with higher grass or twig density but this relationship is stronger in males than females, resulting in an association between sexual dimorphism and habitat. Similarly, both sexes have longer tails and toes in more closed habitats, but male tail and toe length is disproportionately greater in these habitats. Not all patterns, however, were concordant between the sexes. Our results also provide evidence for sex-specific ecomorphological relationships, which result in a corresponding relationship

between habitat and sexual dimorphism. For example, only males are relatively larger in more closed, forested environments so SSD was greater in these habitats. Similarly, in open shrublands, females have relatively shorter jaws, and males have longer toes so there was a relationship between sexual dimorphism and the third habitat axis for both these traits.

There are three types of explanation for relationships between habitat structure and sexual dimorphism. First, females and males may occupy slightly different ecological niches (Shine, 1989). However, in dwarf chameleons, the magnitude of sexual dimorphism in size and shape is relatively small and there is no evidence of niche differentiation between the sexes (e.g. Burrage, 1973; Nečas, 2001); although information on the ecology of dwarf chameleons is limited. Secondly, selection on life-history traits will be different for each sex and may be associated with environmental gradients. For example, opportunities for thermoregulation, seasonality in rainfall and temperature, and fire frequency all vary with habitat type and exert strong selection on reproductive trade-offs (e.g. between offspring size and number, reviewed in Shine, 2005). This, in turn, will affect trade-offs in investment into growth versus reproduction, especially for females, potentially leading to habitat-associated variation in sexual dimorphism (Shine, 2005). The third explanation for an association between sexual dimorphism and habitat is that habitat structure influences the opportunity for sexual selection by affecting the detectability of conspecifics, population density and territoriality (discussed in Butler *et al.*, 2000; Butler & Losos, 2002; Perez-Barberia *et al.*, 2002; Losos *et al.*, 2003). Furthermore, if predation risk varies with habitat structure, then the trade-off between natural and sexual selection (i.e. the cost-benefit curve for sexually selected traits) may differ between habitat types, potentially leading to habitat-associated differences in sexual dimorphism. We provide evidence for habitat-associated selection on dwarf chameleon signalling traits (display coloration) in another study (D. Stuart-Fox, A. Moussalli & M. Whiting, unpublished) and similar selective pressures may be operating on morphological traits. The evolution of sexual dimorphism will reflect the interaction between these different selective pressures, the relative importance of which can only be determined via detailed field and experimental studies (e.g. Olsson *et al.*, 2002).

Phylogenetic constraint

Contrary to previous studies on *Anolis* (Butler *et al.*, 2000; Butler & Losos, 2002), we found that phylogenetic signal for the relationship between habitat and sexual dimorphism was strong in chameleons. There was also evidence of strong phylogenetic constraint on the relationship between habitat and both male and female tail, limb and toe dimensions. By contrast, relationships between head dimensions and habitat were more evolutionarily labile. Despite variability in the degree of phylogenetic constraint,

we found consistent ecomorphological associations for all morphological traits examined, suggesting that both historical and adaptive processes have contributed to the evolution of chameleon morphology. In dwarf chameleons, male and female display coloration evolves readily in response to environmental shifts (Stuart-Fox *et al.*, unpublished) suggesting that, in general, coloration is more evolutionarily labile than morphology in this group.

Conclusions

We have shown that both the size and shape of dwarf chameleons varies with habitat structure but that this variation differs between the sexes for some traits. Consequently, we detected a relationship between habitat structure and sexual dimorphism, which resulted from both differences in magnitude of ecomorphological relationships that were otherwise congruent between the sexes as well as sex-specific ecomorphological relationships. Several of the patterns we detected are suggestive of adaptation because they match functional expectations. However, as noted by Bickel & Losos (2002) detailed field and biomechanical studies on the functional and fitness consequences of morphological variation in chameleons are needed. Remarkably little is known about chameleon ecology and life history. In part, this is because chameleons are very difficult to find during the day and nighttime perch selection may not be a good indication of daytime habitat use. Nonetheless, in this study we have shown that sexual dimorphism is associated with structural features of the habitat. Our results confirm that natural selection plays an important role in the evolution of sexual dimorphism.

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Supplementary Material

The following supplementary material is available for this article:

Table S1 Morphological traits of male and female dwarf chameleons, sexual dimorphism shown.

Table S2 Correlation between 'size-corrected' morphological traits.

This material is available as part of the online article from <http://www.blackwell-synergy.com/doi/full/10.1111/j.1420-9101.2007.01295.x>

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