Natural Selection on Social Signals: Signal Efficacy and the Evolution of Chameleon Display Coloration

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ABSTRACT: Whether general patterns of signal evolution can be explained by selection for signal efficacy (detectability) has yet to be established. To establish the importance of signal efficacy requires evidence that both signals and their detectability to receivers have evolved in response to habitat shifts in a predictable fashion. Here, we test whether habitat structure has predictable effects on the evolution of male and female display coloration in 21 lineages of African dwarf chameleon (*Bradypodion*), based on a phylogenetic comparative analysis. We used quantitative measures of display coloration and estimated signal detectability as the contrast of those colors among body regions or against the background vegetation as perceived by the chameleon visual system. Both male and female display colors varied predictably with different aspects of habitat structure. In several (but not all) instances, habitat-associated shifts in display coloration resulted in habitat-associated variation in detectability. While males exhibit a remarkable variety of colors and patterns, female display coloration is highly conserved, consisting in all populations of contrasting dark and light elements. This color pattern may maximize detectability across all habitat types, potentially explaining female conservatism. Overall, our results support the view that selection for signal efficacy plays an important role in the evolution of animal signals.

Keywords: detectability, visual signals, phylogenetic comparative methods, phylogenetic signal, sensory drive.

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The evolution of animal signals results from the interaction between natural and sexual selection. Geographic or microhabitat variation in one of these selective pressures or in the nature of their interaction can lead to phenotypic divergence and speciation (Endler 1983; Price 1998; van Doorn et al. 1998; Boughman 2002). Traditionally, the role of natural selection has been examined in terms of habitat-related variation in predation risk (Endler 1980). However, there has been growing interest in how the environment shapes sexual signals by influencing signal efficacy or detectability (Endler 1992; Endler and Basolo 1998; Espmark et al. 2000; Leal and Fleishman 2004). For the sensory system of any given receiver, signal detectability will be affected by numerous environmental factors, including ambient light, properties of the medium through which it must be transmitted (e.g., air or water), and the visual background (Endler 1992; Endler and Basolo 1998). The ability of animals to effectively signal to conspecifics influences both male-male interactions and mate-choice decisions, potentially leading to divergence in signaling traits (Marchetti 1993; Boughman 2001; Fuller et al. 2005). This view has been formalized as the sensory drive hypothesis, which proposes that when populations diverge in habitat preferences, the interaction between signal efficacy and sexual selection can promote reproductive isolation (Endler and Basolo 1998; Boughman 2002).

For visual signals, evidence that selection for signal efficacy is an important factor driving the evolution of signaling traits comes from two types of study. The first type of study searches for general correlations between habitat type or the associated light environment and the colors of sexual ornaments, based on a priori predictions about the kinds of colors that should be conspicuous in a given habitat (Marchetti 1993; Fleishman 2000; Fuller 2002; McNaught and Owens 2002; Gomez and Théry 2004). For instance, in terrestrial environments, colors that have high reflectance over wavelengths in which ambient light is relatively rich are expected to be more conspicuous (Endler 1990). Colors should also be more conspicuous when rich

in wavelengths that are reflected poorly by the background (Endler 1990). Because the conspicuousness of a color, or its contrast against the background, is a combined function of ambient light and background reflectance, such qualitative predictions are not always straightforward (but see Fleishman 2000 for quantitative predictions). For instance, ambient light in closed-forest habitats is relatively UV poor, suggesting that UV signals may be less effective; yet UV signals should be highly contrasting against a dark background of bark and leaves because these have next to no UV reflectance (Fleishman 2000). Detailed inference regarding selection for signal efficacy requires quantitative measures of contrast against the visual background, preferably incorporating information on the visual system of the receiver (Endler 1992; Endler and Basolo 1998).

Consequently, the second type of study has focused on quantifying differences in the contrast of colors against the background for sympatric or allopatric populations differing in their habitat characteristics and signaling traits (Macedonia 2001; Leal and Fleishman 2002, 2004; Heindl and Winkler 2003*a*, 2003*b*; Doucet et al. 2007; Gomez and Théry 2007). Some of these studies provide evidence for habitat-associated differences in signal detectability, as perceived by the receiver (Heindl and Winkler 2003*b*; Leal and Fleishman 2004; Endler et al. 2005; Doucet et al. 2007; Gomez and Théry 2007). For example, sympatric species of manakin place their leks at a position in the vertical gradient of ambient light in tropical forest that increases the contrast of their color signals to other birds (Heindl and Winkler 2003*b*). Similarly, allopatric populations of an *Anolis* lizard occupying mesic and xeric habitats have diverged in the spectral characteristics of their dewlaps (throat fans) in a way that influences detectability to conspecifics in their respective habitats (Leal and Fleishman 2004). Although not specifically concerned with the influence of habitat variation, Endler et al. (2005) also recently showed that selection for signal efficacy has influenced the evolution of bowerbird plumage and bower ornaments. Empirical evidence, however, currently lags far behind our theoretical understanding of signal efficacy. We have little evidence that selection for signal efficacy can explain general patterns of signal evolution (but see Doucet et al. 2007; Gomez and Théry 2007). Moreover, we still have a limited understanding of how different aspects of vegetation structure (e.g., canopy cover, understory density, background complexity) influence signal detectability. Testing for such general relationships is essential to assess the importance of selection for signal efficacy in the evolution of animal signals.

Here, we combine a comparative approach with quantitative estimates of chameleon display coloration to investigate how habitat structure has influenced the evolution of display signals for 21 populations (divergent lineages) of southern African dwarf chameleon (*Bradypodion*). We first test whether display colors per se, independent of the background or the ambient light under which they are viewed, have evolved predictably in response to habitat shifts. Next, we test whether these evolutionary shifts in display coloration have resulted in habitat-associated shifts in the detectability of those signals. We assume that detectability is a function of simple measures of achromatic (brightness) and chromatic contrast of display colors against the background vegetation and among body regions. For both analyses, we employ a phylogenetic comparative approach that allows us to examine the relative influences of adaptive process and phylogenetic constraint or inertia on the evolution of chameleon display coloration.

Dwarf chameleons occupy a wide variety of habitats, including montane and lowland rain forest, grasslands, montane and lowland Mediterranean heath, and shrubby thicket (Branch 1998). Although morphologically conserved, they show great variation in male display coloration. Chameleons appear cryptic most of the time (shades of green, brown, and gray), but when they encounter a conspecific, they show striking color change (Nečas 2001). Male dwarf chameleons exhibit very different species-specific display colorations, while female display coloration appears to be remarkably conserved. Females show a characteristic aggressive rejection display coloration (Stuart-Fox and Whiting 2005) that, in all species, consists of a contrasting light and dark color pattern. The display colors of both males and females clearly function exclusively for intraspecific communication because these color patterns are shown in response to another chameleon and, unlike in *Anolis* lizards and bowerbirds, all species are allopatric, which argues against a species recognition function for signaling traits. Several aspects of chameleon biology, such as their high visual acuity, morphological specialization (e.g., projectile tongues used for prey capture), and restricted mobility, suggest that chameleons are likely to be almost exclusively reliant on visual signals for intraspecific communication (Nečas 2001) and consequently that selection for signal efficacy may be important. This, combined with variation in both habitat preferences and signaling traits and with the contrast between male and female display coloration, makes dwarf chameleons an excellent system in which to examine the relationship between display coloration and the signaling environment.

Methods

Study System

Dwarf chameleons (genus *Bradypodion* sensu stricto) are endemic to southern Africa. 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. Tolley, and W. R. Branch, unpublished manuscript). We collected data for 21 populations (table 1), which include all currently described species except *Bradypodion karooicum*, which is a local variant of *Bradypodion ventrale*, phylogenetically nested within the latter (Tolley et al. 2004). In addition to described species, the 21 populations include morphologically distinct, genetically divergent lineages identified by Tolley et al. (2004) and in recent phylogeographic work on the *Bradypodion transvaalense* complex (T. Townsend, unpublished data).

Dwarf chameleons are small (50–110-mm snout-vent length), viviparous lizards with reversed sexual size dimorphism (Branch 1998). Males are intolerant of other males and readily display, with contests often escalating to physical combat (Stuart-Fox 2006; Stuart-Fox et al. 2006*b*). When confronted with another male chameleon, males begin by displaying bright coloration with a lateral aggressive display (fig. A1 in the online edition of the *American Naturalist*) or head shakes. Often, one male retreats immediately after the opponent initiates with one of these behaviors. Contests that involve mutual display often escalate further to aggressive displays with open-mouth threat and chasing followed by biting and/or jaw locking (Stuart-Fox 2006; Stuart-Fox et al. 2006*b*). Males assess female receptivity and willingness to mate with characteristic courtship displays, and females generally respond with aggressive rejection displays, which include rapid, violent swaying, gaping (open-mouthed threat display), chasing, and biting (Stuart-Fox and Whiting 2005). In all species, such rejection displays are associated with mottled or striped contrasting coloration (fig. A2 in the online edition of the *American Naturalist*).

Chameleon Display Coloration

We captured chameleons by hand at night and kept them in cloth bags with branches. Over the next 2 days, we conducted trials within the natural habitat, between 1000 and 1500 hours, when chameleons are naturally active. We placed chameleons on a perch (a natural branch) and presented each focal individual (male or female) with a male. To control for variation in the signaling environment, we used the same branch and location for all trials. As soon as the chameleon showed clear aggressive behaviors (male: head shake, lateral display, chase; female: gape, sway, chase)

Table 1: Sampling localities and sample sizes for display coloration for each *Bradypodion* population

Population	Locality	Sample size	
		Male	Female
B. sp. 1	Swartberg Pass, WC	7	4
B. sp. 2	Dhlinza Forest, Eshowe, KZN	7	6
B. sp. 3	Ngome Forest Reserve, KZN	3	7
B. caffrum	Port St. Johns, EC	9	7
B. damaranum	Between George and Knysna, WC	7	7
B. dracomontanum	Royal Natal National Park, KZN	1	4
B. gutterale	Anysberg Nature Reserve, WC	5	2
B. kentanicum	Vicinity of Kentani, EC	4	5
B. melanocephalum	Kennethstainbank Nature Reserve, Durban, KZN	4	3
B. nemorale	Nkandla Forest Reserve, KZN	2	4
B. occidentale	Paternoster, WC	10	3
B. pumilum	Stellenbosch, WC	6	4
B. pumilum	Vogelgat Nature Reserve, WC	2	2
B. setaroi	St. Lucia, KZN	10	7
B. taeniabronchum	Lady's Slipper, EC	4	4
B. thamnobates	Bulwer, KZN	4	4
B. transvaalense	Barberton, MP	5	5
B. transvaalense	Tullach Moor Nature Reserve (Eland's Valley), MP	7	4
B. transvaalense	Vicinity of Graskop, MP	7	8
B. transvaalense	Woodbush Forest, LP	8	10
B. ventrale	Vicinity of Grahamstown, EC	4	4

Note: Province abbreviations: EC = Eastern Cape, WC = Western Cape, MP = Mpumalanga, LP = Limpopo, KZN = KwaZulu Natal.

associated with color change, we took reflectance measurements (figs. A1, A2).

We took measurements using a probe at the end of a 1.2-m bifurcated fiber-optic cable connected to a spectrometer (SD2000, Ocean Optics, Dunedin, FL) and a light source (PX2, Ocean Optics). Readings were from an oval area 3.5 mm × 5 mm, at a constant distance of 0.5 cm from the surface. Illumination was at 45° relative to the surface, and reflectance was measured at the same angle, following established protocols (Endler 1990; Stuart-Fox et al. 2003). Measurements were expressed relative to a certified 99% diffuse white reflectance standard. We took dark current and white standard measurements before measuring each lizard. For males, we took reflectance measurements for three body regions (top, middle, and bottom flank; fig. A1). For females, where possible, we took measurements of light and dark patches on the top, middle, and bottom flank. However, not all species show both light and dark patches on all three body regions, so for comparative purposes, we restrict our analysis to the dark top-flank patch and the light middle-flank patch, which are consistently evident in all species and represent the extremes of the light and dark pattern elements (fig. A2). The order in which the body regions were measured was randomized to prevent any systematic bias in color measurements due to handling. Usually, measurements for only one or two body regions could be taken before the chameleon would start to change color. We then returned the chameleon to the perch, allowed it to settle, presented it with the stimulus male again, and took readings for the remaining body region(s). After behavioral trials, we released the chameleons at their site of capture (recorded with GPS data and/or marked with flagging tape).

Background Reflectance and Habitat Light

To quantify background colors, we took reflectance readings of the leaves, branches, grass, or vines on which chameleons were caught and those in the immediate vicinity of the perch where experiments were conducted. These backgrounds can be classified into four types of colors: (1) dark brown branches or twigs; (2) light brown grass heads or stems, dry vines, or twigs; (3) the top side of leaves; and (4) the underside of leaves and lichens (fig. 1*A*). All four types were not necessarily encountered in each habitat. Thus, we designated the most common type of background color as the primary background and used the median of the primary background color for each population. This measure of background represents the color against which a chameleon would be most likely to view a conspecific. Assuming a uniform background (rather than taking an average across multiple background types)

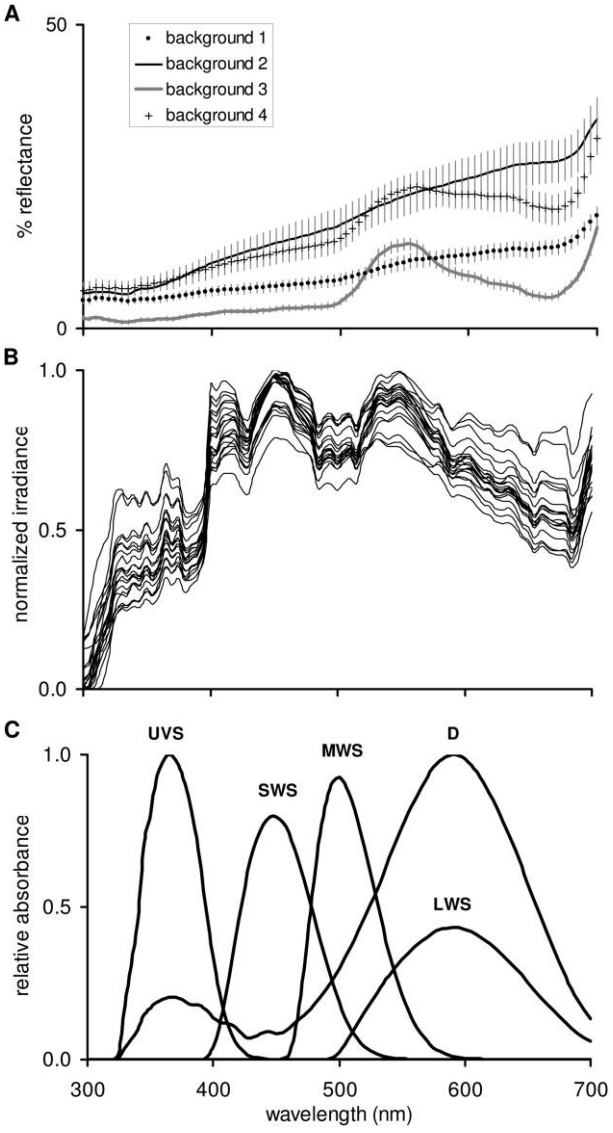

Figure 1: *A*, Mean and standard error of reflectance for the four types of background color for *Bradypodion damaranum*. For this population, background 3 is the primary background (see text for details). *B*, Sidewelling irradiance for the 21 populations. All spectra are normalized to a maximum of 1. Spectra differ primarily in the amount of UV and blue relative to green and longer wavelengths. *C*, Visual-pigment relative absorbances corrected for ocular media transmission and oil droplet absorbance. *UVS* = ultraviolet-sensitive; *SWS* = short-wavelength-sensitive; *MWS* = medium-wavelength-sensitive; *LWS* = long-wavelength-sensitive; *D* = double cone. Absorbance spectra of the single cones have been normalized to equal area under the curve (see text for further details).

is appropriate for close viewing distances, prevalent in intraspecific interactions.

We measured irradiance with an SD2000 spectrometer and a calibrated, cosine-corrected irradiance probe (CC-

3-DA, Ocean Optics), under fine conditions in the shade, between 1000 and 1100 hours, in the same conditions under which the behavioral experiments were conducted (fig. 1*B*). We measured side-welling (parallel to the ground) rather than down-welling irradiance because it is a more accurate measure of the light illuminating a chameleon's flank during lateral displays.

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: (1) canopy height, (2) percentage canopy cover, (3) percentage vine cover, (4) number of trees more than 5 m tall, (5) number of shrubs (between 1 and 5 m tall), (6) mean shrub height, (7) mean shrub width, (8) number of stems or potential perches at 0.5–1 m within a 50 × 50 × 50-cm cube, and (9) number of perches at 1.5–2 m within a 50 × 50 × 50-cm cube. Canopy height was visually estimated as 0–5, 5–10, 10–15, 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 understories or open shrublands. The number of perches at 0.5–1 or 1.5–2 m was measured as the mean number of perches within five 50 × 50 × 50-cm cubes placed randomly within the plot at those heights. Continuous variables were log transformed. To summarize the nine habitat variables, we extracted the first three principal components (PCs) from a principal components analysis and used these axes in subsequent phylogenetic comparative analyses.

Chameleon Visual System

We used data on the visual system of one dwarf chameleon species, *Bradypodion pumilum*, derived from microspectrophotometry (E. Loew and L. J. Fleishman, unpublished data). The visual-pigment spectral sensitivities of the five chameleon species (representing three genera) examined to date are highly conserved (Bowmaker et al. 2005; E. Loew, personal communication), suggesting that the use of data from *B. pumilum* to represent all members of the genus is reasonable. Chameleons have pure-cone retinas with four types of single cone as well as double cones (Bowmaker et al. 2005; E. Loew, personal communication). In many animals, including lizards, perception of the chromatic aspect of color is thought to be a function of single cones (Kelber et al. 2003). Perception of luminance, or brightness, is still poorly understood but may be an additive combination of receptor types that are also used for color vision (e.g., in primates) or by a single, separate receptor type (e.g., in birds; Osorio and Vorobyev 2005). In general, however, most animals use the output of a single photoreceptor type for luminance perception, which is important for tasks such as motion detection (Osorio and Vorobyev 2005). The photoreceptors used in luminance perception are generally the most abundant type in the retina (excluding rods; Osorio and Vorobyev 2005). Lizards (including chameleons), like birds and fish, have double cones, which are the most abundant type of photoreceptor and, as in birds and fish, are probably used for luminance perception (Osorio and Vorobyev 2005). We therefore assume that the four single cones are used for discrimination of chromatic variation while the double cones are used for achromatic (brightness) discrimination.

Absorbance curves for the visual pigments within each cone type were generated using the following maximum absorbance (λ_{max}) values: ultraviolet-sensitive (UVS; pigment A1), 365 nm; short-wavelength-sensitive (SWS; pigment A2), 443 nm; medium-wavelength-sensitive (MWS; A1), 483 nm; and long-wavelength-sensitive (LWS; A1 and A2), 571 nm for A1 and 619 nm for A2. We also used the visual-pigment templates of Govardovskii et al. (2000) for rhodopsins (A1) and porphyropsins (A2). Because the LWS cone may contain two pigment types (A1 and A2), we used an average of the two absorbance curves. The double cones also contain these LWS photopigments. Visual-pigment absorbance curves were multiplied by the transmission spectra of their respective oil droplets and the ocular media (lens and cornea) and then normalized to equal area (Endler and Mielke 2005). The oil droplets associated with the UVS, SWS, MWS, and LWS cones were transparent, clear ($\lambda_{cut} = 410.5$ nm), yellow ($\lambda_{cut} = 475$ nm), and yellow ($\lambda_{cut} = 506$ nm), respectively, where λ_{cut} is the wavelength below which effectively no light is transmitted by the oil droplet (Hart and Vorobyev 2005). The principal member of the double cone was associated with a pale oil droplet similar to that recorded by Bowmaker et al. (2005).

Receptor Quantum Catches

First, we averaged reflectance spectra over 5 nm using a kernel-smoothing function in the statistical package R (Ihaka and Gentleman 1996). We calculated receptor quantum catches Q_i by multiplying visual-pigment spectral sensitivities (fig. 1*C*) by radiance spectra (the product of

reflectance and irradiance spectra), then taking the sum to derive receptor quantum catches for each cone type (Vorobyev and Osorio 1998; Vorobyev et al. 2001; Endler and Mielke 2005):

$$Q_i = \int_{\lambda_{300}}^{\lambda_{700}} R_i(\lambda)S(\lambda)I(\lambda)d\lambda, \quad (1)$$

where λ represents wavelength, R_i is the spectral sensitivity of cone type i, $S(\lambda)$ is the reflectance of the color patch, and $I(\lambda)$ is the irradiance on the color patch, integrated over the visible spectrum (300–700 nm). Visual-pigment spectral sensitivities were normalized to equal area to satisfy the assumption that all four cones are stimulated equally by white light (Fleishman and Persons 2001; Endler and Mielke 2005). Quantum catches of the four single cones were converted to relative quantum catches by dividing the quantum catch of each single cone by the sum of the quantum catches for all four cones:

$$U = \frac{Q_{\text{u/vs}}}{\sum Q_i},$$

$$S = \frac{Q_{\text{sws}}}{\sum Q_i},$$

$$M = \frac{Q_{\text{mws}}}{\sum Q_i},$$

$$L = \frac{Q_{\text{lws}}}{\sum Q_i}, \quad (2)$$

for the ultraviolet- or violet-sensitive (U/VS), SWS, MWS, and LWS cones, respectively.

Contrast against the Background and among Body Regions

Signal detectability depends on both the light in which it is viewed and the background against which it is viewed (i.e., adjacent colors). Thus, we calculated contrast of chameleon display colors against the background and among body regions using population-specific side-welling irradiance spectra. We assumed that the chromatic contrast (Δ_{T}) of two colors is a function of the Euclidean distance between them in four-dimensional color space (based on the quantum catches of the four single cones; Fleishman and Persons 2001):

$$\Delta_{\text{T}} = \sqrt{(U_a - U_b)^2 + (S_a - S_b)^2 + (M_a - M_b)^2 + (L_a - L_b)^2}, \quad (3)$$

where U_a, S_a, M_a, and L_a are the single-cone relative quantum catches of color a (e.g., the chameleon) and U_b, S_b, M_b, and L_b) are the relative quantum catches of color b (e.g., a different body region or the background).

Brightness contrast (chameleon vs. background or contrast among body regions) was calculated as the difference in the double-cone quantum catches (Q_{D}) of the two colors divided by their sum (Osorio et al. 2004):

$$C_{\text{L}} = \frac{Q_{\text{D}_a} - Q_{\text{D}_b}}{Q_{\text{D}_a} + Q_{\text{D}_b}}. \quad (4)$$

These measures of chromatic and brightness contrast assume that the greater the difference in the relative stimulation of the four single cones or the double cone, the more different they will appear to the receiver (Fleishman and Persons 2001). The measure of chromatic contrast makes several implicit assumptions about color perception, the most important of which is that all four cones contribute to color perception equally. In reality, however, color perception is likely to be influenced by the relative proportion and distribution of cone types within the retina, which can vary even among closely related species (Hart 2001*a*). Moreover, this measure ignores opponency mechanisms (comparison of outputs of different cone types) known to be important for color discrimination (Kelber et al. 2003). Other, more complex models that do take these factors into account have been developed for some taxa (e.g., Vorobyev and Osorio 1998); however, these require additional data that are not available for chameleons, and they predict discrimination between similar colors rather than how different two colors appear to a receiver. In the absence of information on how the chameleon retina and brain processes photoreceptor quantum catches, the simple model we employ is reasonable and accurately predicts signal detectability in the lizard *Anolis cristatellus* (Fleishman and Persons 2001).

Phylogeny

We derived a phylogeny (fig. 2) based on mitochondrial 16S and ND2 sequences from GenBank (table B1 in the online edition of the *American Naturalist*; Tolley et al. 2004, 2006), with four additional ND2 sequences kindly provided by T. Townsend (unpublished data) for the four populations of "*B. transvaalense*." When they were available, we included two representatives per species/lineage from different localities in the phylogenetic analysis. The complete data set used for phylogenetic analysis comprised sequences for 38 individuals (including two outgroup taxa). This data set included the 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), so we are confident

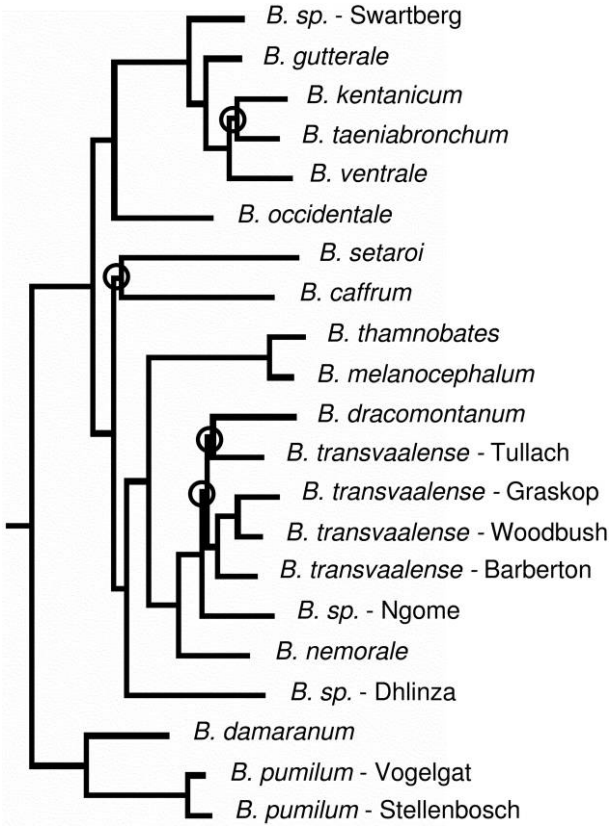

Figure 2: Phylogenetic relationships of the 21 lineages of dwarf chameleon. Nodes with less than 0.9 Bayesian posterior probability are circled. The four genetically divergent and morphologically distinct lineages of *Bradypodion transvaalense* are denoted by the species name followed by the locality, and divergent lineages that are yet to be described are denoted as *Bradypodion* sp. followed by the locality.

that these sequences are representative of the genetic relationships (based on mtDNA) among our study populations.

For phylogenetic analysis, we used MrBayes, version 3.1.1 (Ronquist and Huelsenbeck 2003). We used a single, combined data set such that each data set was parameterized separately but linked with regard to branch length estimation. We ran four simultaneous, independent runs, each comprising four chains, sampling every 100 generations. The most general model (GTR + I + G) was used because it was identified as the best Akaike model of DNA substitution (Akaike Information Criterion weight = 0.8724, 0.9716, and 0.997 for 16S, ND2, and the combined data set, respectively) with MrModelTest (Nylander 2004). The four independent runs converged to a stationary distribution at approximately 300,000 generations (standard deviation of split frequency < 0.01). Burn-in period was 50,000 generations. All four runs recovered the same tree with good congruence (average potential scale reduction factor for taxon bipartitions < 1.007, SE < 0.001). To derive a phylogeny with branch lengths of our 21 populations, we pruned the consensus tree from the four runs of MrBayes to only those 21 populations used in our study (fig. 2), using Mesquite, version 1.11 (Maddison and Maddison 2006).

Comparative Analysis

We used phylogenetic generalized least squares (PGLS; Martins and Hansen 1997), which 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 and King 2004; Hansen and Orzack 2005). PGLS (as implemented in Compare 4.06) assumes an Ornstein-Uhlenbeck (OU) model of phenotypic evolution, which includes both drift and selection (Hansen 1997; Martins and Hansen 1997; Butler and King 2004). The Brownian motion (BM) model of phenotypic evolution assumed by most comparative methods, such as Felsenstein's independent contrasts (FIC; Felsenstein 1985), is a pure-drift process that constitutes a special case of the OU model (Butler and King 2004). Thus, when the parameter α is set to 0, PGLS produces results identical to those of 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).

We used PGLS, as implemented in Compare 4.06 (Martins 2004), for three reasons. First, it allows comparison among methods (PGLS with maximum likelihood estimate of α, with α at 0 [FIC] or with large α [TIPs]). Second, it can incorporate intraspecific variation using standard errors of population means. Third, the parameter α provides a measure of phylogenetic inertia or constraint, similar to Lynch's H^2 (Lynch 1991; Housworth et al. 2004) or Pagel's λ (Pagel 1999; Freckleton et al. 2002), which differ from α in assuming a BM process of phenotypic evolution.

First, we tested whether chameleon coloration per se, independent of the habitat, has evolved in response to habitat shifts. For this analysis, we used the relative receptor quantum catches of the four single cones and the quantum catch of the double cones. Here we were interested in display coloration independent of habitat (i.e., independent of background and ambient light), so we used a constant irradiance (broadband and flat) for all populations to calculate receptor quantum catches. Second, we tested whether the habitat-associated evolutionary changes in display coloration have resulted in changes in signal detectability. For this analysis, we calculated receptor

quantum catches using our population-specific irradiance measures and then calculated chromatic and achromatic contrast against the background and among body regions, which we used as measures of signal detectability. We used population means and standard errors for all analyses. We began by doing multiple regressions of each dependent variable (color measures) on our independent variables (habitat measures). We then reran regressions, sequentially removing variables that did not contribute significantly. Because some branches in our phylogeny were weakly supported, we reran all analyses on a phylogeny with branches with less than 0.9 Bayesian posterior probability collapsed (fig. 2), that is, treating these nodes as polytomies. Results were qualitatively the same for both trees; therefore we present only those for the fully resolved tree.

Table 2: Principal components analysis of habitat variation

	Component loadings		
Variable	Axis 1	Axis 2	Axis 3
Canopy cover	**.432**	.119	.004
Canopy height	**.387**	.245	−.241
No. trees	**.393**	.154	−.301
Vine cover	**.344**	.349	−.047
No. shrubs	.205	−.358	**−.523**
Shrub height	**.379**	−.303	.290
Shrub width	.283	−.385	**.548**
Stem density at .5–1 m	−.283	**.448**	.082
Stem density at 1.5–2 m	.212	**.459**	.429
Variance explained (%)	53.8	15.2	13

Note: The highest loadings for each variable are highlighted in boldface.

Results

Habitat Structure

The first three principal components explained 82% of the variation in the nine habitat variables (table 2). Because additional PCs each explained less than 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. We refer to this axis as "forest cover." The second PC is positively associated with perch density at both heights. Thus, high values of PC2 indicate habitats with high perch density below 2 m (e.g., grasslands or habitats with a dense herb or shrub understory), while low values of PC2 indicate habitats with a sparse understory. We refer to this axis as "understory density." 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, instead dominated by few, wide shrubs. We refer to this axis as "shrub structure." Correlations among the original habitat variables are given in table C1 in the online edition of the *American Naturalist*.

Relationship between Display Coloration and Habitat

Habitat structure consistently and strongly predicted variation in several aspects of both male and female display coloration, explaining 17%–65% of variance in color traits (tables 3, 4). PGLS tended to be less conservative than FIC, and consequently several patterns that were significant under PGLS were not significant under FIC but not vice versa.

In more closed, forested habitats, male display colors have a higher relative UV component and lower relative medium- and short-wavelength components (table 3). In addition, in these habitats the quantum catch of the double cone (which we refer to as "brightness" for simplicity) of the top and middle flanks was lower (negative relationship with forest cover). The top flank of males also had a higher relative UV component and lower relative medium- and long-wavelength components, as well as lower overall brightness in habitats with a dense understory.

As in males, the light middle flank of females had higher relative UV and short-wavelength components and lower relative medium- and long-wavelength components as well as lower overall brightness in more closed, forested habitats. The dark top flank of females showed lower brightness (i.e., was darker) in habitats with higher perch density in the understory.

Relationship between Detectability and Habitat

In more closed, forested habitats, males had higher brightness contrast against the background (middle and bottom flanks; table 4). Male top flanks were more chromatically contrasting against the background in habitats dominated by few, large shrubs (positive relationship with shrub structure; table 4). Female dark top flanks contrasted less in brightness against the background in more closed, forested habitats but contrasted more in habitats with higher stem density. Female top flanks were also more chromatically contrasting against the background in more open habitats.

Brightness and chromatic contrast among body regions was unrelated to habitat in males (table 4). Females showed lower brightness contrast among body regions in more closed, forested habitats.

Phylogenetic Signal

In general, α was large, suggesting little phylogenetic constraint on the evolution of chameleon display coloration.

Table 3: Relationship of male and female display colorations to one or more of the three habitat axes

Sex, body region, and dependent variable	Independent variable(s)	Model α	Model R^2 (%)	Slope	Slope SE
Male:					
Top flank:					
U	Forest cover, understory density	15.5	51.31	.49, .86	.15,[a] .3[a]
S	…	…	…	…	…
M	Forest cover, understory density	15.5	49.1	−.13, −.37	.05,[a] .11[a,b]
L	Forest cover, understory density	15.5	39.15	−.46, −.84	.18,[a] .37[a]
D	Forest cover, understory density	11.84	38.43	−7.49, −18.32	3.45,[a] 7.09[a,b]
Middle flank:					
U	Forest cover	15.5	19.13	.67	.32[a]
S	…	…	…	…	…
M	Forest cover	6.06	16.95	−.68	.34[a]
L	Forest cover	15.5	20.18	−.64	.29[a]
D	Forest cover	15.5	38.38	−12.09	3.51[a]
Bottom flank:					
U	Forest cover	15.5	18.49	.73	.35[a]
S	Forest cover	3.2	20.31	−.91	.42[a,b]
M	…	…	…	…	…
L	…	…	…	…	…
D	…	…	…	…	…
Female:					
Top, dark:					
U	…	…	…	…	…
S	…	…	…	…	…
M	…	…	…	…	…
L	…	…	…	…	…
D	Understory density	4	22.09	−3.25	1.4[a,b]
Middle, light:					
U	Forest cover	15.5	49.4	.66	.15[a,b]
S	Forest cover	15.5	18.47	.19	.09[a,b]
M	Forest cover	15.5	38.08	−.18	.05[a,b]
L	Forest cover	15.5	46.01	−.67	.17[a,b]
D	Forest cover	15.5	38.79	−10.31	2.97[a,b]

Note: Results are of multiple regressions of the three habitat axes (independent variables) with each color measure (dependent variable). *U*, *S*, *M*, *L*, and *D* refer to the quantum catches for the ultraviolet-sensitive, short-wavelength-sensitive, medium-wavelength-sensitive, long-wavelength-sensitive, and double cones, respectively. When the 95% confidence intervals around the slope (1.96 × SE) do not incorporate 0, the slope can be considered significant. Only variables with significant slopes under phylogenetic generalized least squares (PGLS) or Felsenstein's independent contrasts (FIC) were retained in the final multiple-regression models. Model α refers to PGLS maximum likelihood estimate of α, and model R^2 percentages and slopes are based on PGLS.

[a] Variables significant assuming no phylogenetic constraint.

[b] Variables significant under FIC, that is, when $\alpha = 0$.

Only medium-wavelength capture of the middle flank, relative short-wavelength capture of the bottom flank, and brightness contrast against the background for males, as well as brightness of the top flank for both sexes, showed α values less than the maximum of 15.5. As a consequence of large α values, all results using PGLS were also significant under TIPs (tables 3, 4). Nonphylogenetic (TIPs) correlations among the nine original habitat variables and each of the color variables are given in table C2 in the online edition of the *American Naturalist*.

Discussion

Vegetation structure can dramatically affect the detectability of signals, yet we still know little about whether the signaling environment has predictable effects on the color

Table 4: Relationship between habitat structure and chromatic (C_C) and brightness (C_L) contrasts of male and female display coloration against the background for each body region as well as among body regions

Sex, body region, and dependent variable	Independent variable(s)	Model α	Model R^2 (%)	Slope	Slope SE
Male:					
Top flank:					
C_L	Forest cover	14.2	12.06	2.4	1.48[a]
C_C	Shrub structure	15.5	23.11	7.67	3.21[a,b]
Middle flank:					
C_L	Forest cover	12.01	36.71	3.68	1.11[a,b]
C_C	…	…	…	…	…
Bottom flank:					
C_L	Forest cover	9.34	39.48	5.47	1.55[a,b]
C_C	…	…	…	…	…
Among body regions:					
C_L	…	…	…	…	…
C_C	…	…	…	…	…
Female:					
Top, dark:					
C_L	Forest cover, understory density	15.5	32.7	−2.23, 4.86	1.1,[b] 2.26[a,b]
C_C	Forest cover	15.5	68.31	−3.81	.6[b]
Middle, light:					
C_L	…	…	…	…	…
C_C	Forest cover	15.5	14.63	−4.42	2.45[a]
Among body regions:					
C_L	…	…	…	…	…
C_C	Forest cover	15.5	29.60	−4.15	1.47[a,b]

Note: Results are of multiple regressions of the three habitat axes (independent variables) with each color measure (dependent variable). When the 95% confidence intervals around the slope (1.96 × SE) do not incorporate 0, the slope can be considered significant. Only variables with significant slopes under phylogenetic generalized least squares (PGLS) or Felsenstein's independent contrasts (FIC) were retained in the final multiple regression models. Model α refers to PGLS maximum likelihood estimate of α, and model R^2 percentages and slopes are based on PGLS.

[a] Variables significant under FIC, that is, when $\alpha = 0$.

[b] Variables significant assuming no phylogenetic constraint.

patterns used by terrestrial animals for intraspecific communication (but see Leal and Fleishman 2004; Gomez and Théry 2007). Our results show several strong relationships among three axes describing quantitative aspects of habitat structure and the spectral qualities of chameleon display colors as perceived by a conspecific. This suggests that selection for signal efficacy has played a role in the evolution of chameleon display coloration.

Both male and female display colors consistently had a higher relative UV component and lower relative medium- and long-wavelength components in more closed, forested habitats. In these habitats, many male display colors have secondary UV peaks, which are usually absent in species occupying more open habitats (fig. A1). These secondary peaks are likely to be associated with structural coloration in the case of UV-blues or UV-greens but may also be associated with carotenoid-based coloration in the case of UV-yellows and UV-oranges (Bleiweiss 2005). In dwarf chameleons, the UV component of display colors is likely to primarily have a signaling function because it is only apparent during displays (D. Stuart-Fox, unpublished data).

Ambient light in closed forest is relatively UV poor (Endler 1993*a*); however, forest species of dwarf chameleon prefer gaps and edges (Reisinger et al. 2006). Thus, the irradiance spectra in all habitats we measured had a moderate relative UV component (fig. 1*B*), indicating that UV signals are detectable. In addition, the background reflectance in closed habitats (e.g., the dark green leaves in forest) is UV poor but rich in medium wavelengths. Together, these observations suggest that display colors that are relatively UV rich (and concomitantly, medium- to long-wavelength poor) will be conspicuous in forested habitats. Based on quantitative models of detectability for *Anolis* lizard dewlaps under differing signaling conditions (full shade, partial shade and no shade), Fleishman (2000) showed that high UV reflection increases detectability in full and partial shade environments but not in open (no

shade) habitats. He found little match between these predictions and the UV reflectance of the dewlaps of 17 *Anolis* species and hypothesized that the UV component of *Anolis* dewlaps may instead be associated with selection for species recognition. Dwarf chameleon display colors are unlikely to function in species recognition (all are allopatric) and match Fleishman's predictions in that display colors of species occupying more shaded environments have a relatively higher UV component. In contrast to that in *Anolis* lizards, therefore, the UV component of chameleon display colors is likely to reflect selection for signal detectability.

Brightness was also consistently lower in more closed, forested habitats for all body regions of both sexes. However, because males and females have very different kinds of display colors, variation in chromatic and brightness contrast to the background and among body regions in relation to habitat structure differed greatly between the sexes. In spite of being less bright in closed habitats, males consistently contrasted more in brightness against the background in these habitats (all three body regions), while females did not. Several comparative studies on birds have examined the relationship between brightness (but not brightness contrast) and habitat; these have produced mixed results. Marchetti (1993) found that species inhabiting closed habitats had brighter plumage, in terms of both the number of patches and total reflectance. In contrast, McNaught and Owens (2002) found that species in more open habitats tend to be brighter, and Gomez and Théry (2004) found that canopy foragers tend to have brighter plumage than understory foragers. Our results support the findings of the latter studies insofar as species occupying more open habitats had higher absolute brightness. However, our results also suggest that species in more closed habitats use display colors that have high brightness contrast against the dark background. This highlights the importance of quantifying contrast as well as absolute spectral properties of signals.

In several cases, relationships between contrast and habitat structure do not appear to be the result of evolutionary shifts in chameleon display colors. For example, chameleon display colors were unrelated to shrub width or density, yet the chromatic contrast of male top flanks was significantly correlated with this component of habitat structure. Similarly, receptor quantum catches for female top flanks were unrelated to canopy cover, yet brightness and chromatic contrast against the background was significantly greater in more closed, forested habitats. These relationships between contrast and habitat structure are therefore primarily due to variation in background reflectance and ambient light and do not reflect evolutionary responses of chameleons to selection for signal efficacy.

Conversely, consistent habitat-associated shifts in chameleon display coloration did not always result in a corresponding relationship between habitat structure and signal conspicuousness. For instance, relative quantum catches of the single cones are associated with canopy cover in both males (all three body regions) and females (pale middle-flank patch), yet this resulted in habitat-associated shifts in chromatic contrast (and thus, presumably, detectability) only for females. In more closed, forested habitats, females showed less chromatic contrast against the background as well as less chromatic contrast among body regions. Similarly, the negative association between quantum catches for the male top flank and density of understory perches did not correspond to differences in brightness or chromatic contrast. In most cases, this is because the background colors vary in the same direction. Thus, in spite of consistent evolutionary shifts in male display coloration in response to habitat shifts, and substantial variation in both male display coloration and habitat, the chromatic contrast of signals was unrelated to habitat structure. There are two possible explanations for this. First, quantum catches of the single cones, all of which influence chromatic contrast, may be related to habitat structure in different ways. For instance, in closed habitats, male display colors had a higher relative UV component but lower relative medium- and short-wavelength components. This could explain why overall chromatic contrast of male display colors was unrelated to habitat openness. Second, selection for signal efficacy may be similar among habitat types. If all populations evolve toward an "optimal" level of conspicuousness, a similar level of contrast or detectability (and therefore no relationship) is expected across habitats.

In addition to selection for signal efficacy, selection for crypsis could play a role in the evolution of chameleon display colors. Animal color patterns will represent a tradeoff between selection for conspicuousness for signaling functions and selection for crypsis (Endler 1983, 1993*b*). In this system, however, the habitat-associated shifts in display coloration are unlikely to be due primarily to selection for crypsis because conspicuous colors are displayed only briefly during intraspecific communication. The great majority of the time, chameleon coloration closely matches the background (Stuart-Fox et al. 2006*a*). In addition, contrast as measured here is relative to conspecific receivers rather than predators. Nevertheless, colors conspicuous to a chameleon will also be conspicuous to an avian predator because the visual system of birds is similar to that of chameleons (Hart 2001*b*; Kelber et al. 2003). Consequently, chameleon display colors may represent a compromise between the need to be conspicuous and the need not to be too conspicuous. This view is supported by our finding that males in more closed habitats had display colors with higher brightness contrast

against the background but lower absolute brightness. Similarly, in habitats with higher density of understory perches, female dark top flanks showed greater brightness contrast against the background but nevertheless had lower absolute brightness. It is therefore possible that display coloration evolves to maintain a level of conspicuousness that represents an optimal balance between selection for crypsis and selection for signal efficacy. Data on relative predation pressure are needed to test whether selection for crypsis differs or is similar among habitat types and whether it is associated with signal detectability.

Although both male and female display colorations vary consistently with habitat structure, they use very different color patterns. In most systems, male and female colorations are correlated, as a result of either genetic correlation between the sexes or sexual selection acting directly on female traits (Amundsen 2000; Ord and Stuart-Fox 2006). In chameleons, male and female colorations resemble each other to some degree when the animals are not displaying, but display colorations differ dramatically. Female coloration in most sexually dichromatic species also tends to be more cryptic than that of males, but in dwarf chameleons, this is not necessarily the case. Female display coloration has higher brightness contrast against the background and among body regions than that of males but shows less chromatic contrast. Females of all species use contrasting light and dark color patterns during aggressive rejection displays, whereas males show a great variety of colors and patterns. Why are female color patterns so conserved? One possible explanation is that by maximizing brightness contrast among body regions, rather than contrast against the background, female display colors are detectable (and conspicuous) in all habitat types. Additionally, during aggressive displays, females sway rapidly and vigorously from side to side (Stuart-Fox and Whiting 2005), whereas males present themselves laterally with little body movement (Stuart-Fox et al. 2006*b*). Brightness contrast is more important than color contrast for motion detection (Persons et al. 1999; Kelber et al. 2003; Osorio and Vorobyev 2005), which reinforces the view that signals with high brightness contrast among body regions may maximize signal detectability for females across all habitat types. In addition, highly contrasting color patterns may also provide effective disruptive camouflage in all habitat types. This, perhaps combined with limited sexual selection acting directly on female color patterns, may explain why female display color patterns are so much more conserved than those of males. Subtle differences in female display coloration were nevertheless associated with habitat structure. Overall, females occupying more closed habitats had less contrasting display color patterns (among body regions and against the background) than females in more open habitats, suggesting that, despite overall conservatism of female display colors, natural selection has influenced the evolution of female coloration.

Our results suggest that chameleon display colors are highly evolutionarily labile. Phylogenetic constraint, as estimated using the PGLS parameter α, was generally low (i.e., high values of α) for all regression models. This confirms growing evidence that color patterns may evolve readily in response to environmental shifts (discussed in Endler et al. 2005). Dwarf chameleons have radiated relatively recently in response to climatic and associated vegetation changes in southern Africa (Tolley et al. 2006), and our results suggest that display coloration has evolved in response to these environmental shifts. Recent evidence suggests that behavioral traits exhibit more evolutionary lability than body size or morphological, life-history, or physiological traits (Blomberg et al. 2003; Martins et al. 2004; Ord and Martins 2006). Like the behavioral traits examined in these studies, chameleon display colors are exhibited only during intraspecific communication. Thus, it is possible that morphological or behavioral signals used for intraspecific communication evolve particularly rapidly in response to natural and/or sexual selection (Ord and Martins 2006). Indeed, in *Sceloporus* lizards, color patches used in displays are even more evolutionarily labile than display behavior (Wiens 2000).

Chameleons are unusual among vertebrates because they have the ability to rapidly change color (Nečas 2001), making quantifying color challenging. Our measurements may be an underestimate of the full range of chameleon display coloration. Nevertheless, because all animals were measured under similar conditions, interpretation of relative differences among populations is possible. In analyzing chameleon display colors, we have assumed that signal detectability can be approximated by simple measures of contrast in two visual system channels, chromatic and achromatic (brightness). These measures of contrast make several implicit assumptions about color perception (see "Methods"), and their adequacy in predicting behaviorally relevant differences in signal detectability can be assessed only via behavioral experiments. Nevertheless, chromatic contrast as calculated in this study has been shown to accurately predict signal detectability in other lizards (Fleishman and Persons 2001) and represents an advance in human-oriented measures of color or the analysis of spectral data without reference to the receiver's visual system.

Conclusions

The detectability of signals used for intraspecific communication can influence both male-male interactions and mate-choice decisions (Marchetti 1993; Boughman 2001; Fuller et al. 2005), with different potential consequences

for signal evolution (Boughman 2002). When environmental shifts result in reduced efficacy of a particular signal, sexual selection may act to increase its conspicuousness. Alternatively, the signal may be lost (e.g., Scott 2001), and females may instead make mating decisions or males may assess rivals based on alternative male traits. Both mechanisms potentially result in divergence of signaling traits. We have shown that the spectral properties of chameleon signals vary predictably with habitat structure, and for several signal components, this is likely to be influenced by selection for signal efficacy. The interaction between selection for signal efficacy and sexual selection may explain the remarkable diversity of male display coloration in this otherwise morphologically and behaviorally conserved group.

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A male dwarf chameleon *Bradypodion transvaalense* displays to a female. Photograph by Adnan Moussalli.