



Habitat light, colour variation, and ultraviolet reflectance in the Grand Cayman anole, *Anolis conspersus*

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Received 22 November 2000; accepted for publication 2 April 2001

Data from a diversity of sources are consistent with the hypothesis that the Grand Cayman anole, *Anolis conspersus*, is descended directly from *Anolis grahami* of Jamaica. Although the two species have remained morphologically similar, coloration in *A. conspersus* has changed considerably from that of its ancestor. The most dramatic difference is seen in dewlap colour, where *A. conspersus* has evolved a blue and highly UV-reflective dewlap from the ancestral orange-and-yellow colour state. In addition, variation in normal (non-metachrosis) dorsum coloration in *A. grahami* populations is limited to shades of green (olive, emerald, teal), whereas in *A. conspersus* dorsum coloration varies from green to blue and to brown. This increased colour variation occurs despite Grand Cayman being a small, relatively featureless island only 35 km in length. Results of this study suggest that ambient light differences associated with precipitation-related vegetation structure may have played an important role in the evolution of *A. conspersus* body colour variation. Evidence is presented to show how geological, ecological, and physiological factors could have interacted to select for a short wavelength-reflective dewlap from a long wavelength-reflective precursor following the colonization of Grand Cayman from Jamaica by *A. grahami* between 2 and 3 Mya.

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ADDITIONAL KEY WORDS: *Anolis* lizards – visual signals – colour evolution – dewlap – ultraviolet – colour segment classification – principal components analysis – habitat light.

INTRODUCTION

Signal evolution is driven by details of signal perceivers' sensory systems and characteristics of the environment that enhance or diminish signal transmission (e.g. Endler, 1991, 1992). For visual signals, relevant ecological variables include the ambient light spectrum in which a signal is viewed and features of the visual background from which the signal must be discriminated. Studies of guppies (e.g. Endler, 1991) and birds (Endler & Thery, 1996) have been important in demonstrating the influence of habitat light and contrast on colour signal evolution. Moreover, Endler's (1978, 1980, 1987, 1991) work on guppies has shown how differences in spectral sensitivity between a signalling species and its predators can select for colour

patterns that minimize predator detection while remaining conspicuous to the species in which the signal has evolved.

FOREST LIGHT HABITATS AND THEIR CONSEQUENCES FOR ANIMAL COLOUR SIGNALS

Endler (1992, 1993) has shown that, under sunny skies, four types of structural light habitats occur in forests that are a result of differences in forest geometry. *Forest shade* occurs under a closed canopy where virtually all of the ambient light has been filtered through and reflected from the foliage. This light is strongest in the middle wavelengths (green, yellowish-green) of the visible spectrum. *Woodland shade* occurs under a discontinuous canopy where little or no light comes directly from the sun, light is transmitted through and reflected from leaves, and short wavelength skylight (blue, violet, and UV) dominates the spectrum. *Small gaps* in the canopy allow shafts of long-wavelength light (yellow, orange, red) to penetrate the forest when the sun is overhead. Sunlight is orders

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of magnitude brighter than forest shade or even a blue sky, and it dominates the irradiance spectrum in the location of the sunbeam. *Large gaps* in the canopy allow light both from the sun and the sky to invade, resulting in the same whitish light that occurs in open areas and under cloudy skies.

For a colour pattern to be conspicuous in forest habitats it should take advantage of the strongest region of wavelengths in the irradiance spectrum, but must also contrast with tree bark and leaves. For example, in the yellow-green light of forest shade the most reflective colour patch would be yellow-green because it most closely resembles the ambient spectrum (e.g. Endler, 1993). Nevertheless, a leaf-coloured signal could be highly reflective in forest shade and yet inconspicuous against the visual background of the leaves themselves. The most effective colour signal in forest shade therefore might be yellow or gold (yellow-orange), because these wavelengths would be bright while also contrasting with green leaves. Note that although a violet colour patch would exhibit even greater colour contrast with green leaves than would yellow or gold, light intensity at very short wavelengths is too weak in forest shade to provide sufficient reflectivity for a violet colour patch to be very bright. In the short wavelength-biased light of woodland shade, however, a violet colour patch would be highly reflective, as would be blue and ultraviolet. In forest gaps and in open areas, yellow, orange, and red would all be highly effective colours for signalling.

Chroma, or colour saturation, also affects how colours appear in forest light habitats. Whereas unsaturated colours vary considerably in colour and brightness under different ambient spectra, saturated colours vary much less (e.g. Endler, 1997: fig. 14.3). Where colour patches are used for signalling saturated colours should be selected because they retain their spectral integrity across a variety of light habitats. In contrast, colour patches used in crypsis can be unsaturated because their reflectance spectra will change with changing light conditions, making them harder to recognize and track (Endler, 1993).

THE ANOLIS DEWLAP AS A COLOUR SIGNAL

Animal colour signals evolve as a tradeoff between the benefit to reproductive success through male–male competition and female choice, and the cost of being detected by predators (e.g. Endler, 1991, 1992; Ortolani, 1999). In nearly all species of *Anolis* lizards adult males possess extensible throat fans, termed ‘dewlaps’, that frequently are large and colourful (Fitch & Hillis, 1984; Losos & Chu, 1998). Males use these display organs to broadcast their whereabouts to conspecifics for the purpose of maintaining a territorial presence and attracting conspecific females (e.g. Crews

& Williams, 1977; Williams & Rand, 1977), and even for signalling to predators (e.g. Leal, 1999). The ability to conceal the dewlap colour signal when not in use provides the advantage of reducing the bearer’s probability of detection by predators.

A hallmark of *Anolis* dewlap coloration is its tremendous diversity. With roughly 400 described species in the Caribbean and Central and South America, virtually every colour in the visible spectrum can be found (e.g. Schwartz & Henderson, 1985) as well as ultraviolet colour patterns (Fleishman, Loew & Leal, 1993; Macedonia *et al.*, 2000; Stoehr & McGraw, 2001). Traditionally, the function ascribed to dewlap colour has been one of species recognition and reproductive isolation. This argument has been based largely upon observations of colour diversity in relatively large *Anolis* communities (e.g. Rand & Williams, 1970; Williams & Rand, 1977). Perhaps the most compelling observational evidence for a reproductive isolating function has been the character displacement in dewlap colour observed in three sibling species distributed sequentially along the west coast of Haiti (Webster & Burns, 1973). In other Hispaniolan locations, however, dewlap colour has been insufficient to prevent high rates of hybridization between the morphologically-similar *A. brevirostris* and *A. distichus* (Williams & Case, 1986). Experimental evidence for a species recognition function for dewlap colour is particularly scant (e.g. Losos, 1985; Macedonia & Stamps, 1994) and more work is needed in this area.

There has been some suggestion that dewlap colour is related to climatic variation (e.g. Crews & Williams, 1977; Fitch & Hillis, 1984), and it seems likely that differences in light habitats stemming from different vegetational biomes underlie some of the clinal variation observed. Fleishman (1992) pointed out that for anoles living in particularly dark or particularly bright environments, dewlap colour options will be limited by the need to produce brightness contrast with the visual background. Indeed, for those species documented, anoles that inhabit dark forest environments exhibit dewlaps that may be white or yellow, but which are never orange or red (Fleishman, 1992). Nevertheless, a sufficient amount of colour variation should be possible even in the most complex *Anolis* communities, through selection for species-specific colour patterns on the dewlap (e.g. contrasting borders, central spots, colour combinations) as well as differences in body coloration (Williams & Rand, 1970).

CRYPTIC AND CONSPICUOUS BODY COLORATION IN ANOLES

Given the signalling function of the dewlap, body coloration rarely has been considered in discussions of *Anolis* colour signals. Moreover, both sexes in many

Anolis species possess body colour patterns that appear cryptic, usually by resembling tree bark to varying degrees. Yet, there are a number of reasons why male body coloration may serve a signalling function in some species of anoles.

First, in a number of *Anolis* species body coloration in adult males is distinct from that of females. Where this sexual dichromatism is exhibited males always are the more brightly-coloured sex (e.g. Lazell, 1964, 1972). Second, females in many species of anoles exhibit a dorsal stripe or chevron pattern (e.g. Lazell, 1964; Schoener & Schoener, 1976) that almost certainly serves a disruptive coloration function (Cott, 1940; Endler, 1981). Third, juvenile males typically are indistinguishable in colour pattern from females, suggesting that acquisition of the adult male colour state is a transition away from a cryptic colour pattern to a more conspicuous one. Fourth, many *Anolis* species possess the ability to change rapidly from a more conspicuous to a more cryptic coloration. This is achieved by mobilizing melanin granules into the termina of melanophore extensions that extend over the top of the chromatophore (see Bagnara & Hadley, 1973). Anoles possessing this capacity, termed metachrosis, exhibit it in response to stress hormones and to cold (e.g. Cooper & Greenberg, 1992). Metachrosis turns the lizard some shade of brown, rendering it less conspicuous through reduction of contrast with dark tree bark. In addition, males in some species of anoles exhibit an almost female-like barring or chevron pattern that only appears during metachrosis. Importantly, males of many *Anolis* species that typically perch head-down on tree trunks usually exhibit their bright colour when in this location (e.g. Trivers, 1976), despite the fact that metachrosis coloration would reduce their contrast with the bark. In sum, although the dewlap of *Anolis* unquestionably has evolved as a signalling organ, normal (non-metachrosis) male body coloration in some species of anoles likely serves a signal function as well.

COLOUR VARIATION IN MALE *ANOLIS CONSPERSUS*

Fleishman and colleagues (e.g. Fleishman, 1986, 1988a, b, 1992; Fleishman *et al.*, 1993; Hertz, Fleishman & Armsby, 1994; Fleishman, Marshall & Hertz, 1995; Fleishman *et al.*, 1997; Persons *et al.*, 1999) have contributed most of what currently is known about the effects of the visual system and habitat light on the evolution of *Anolis* motion and colour displays. In this report I extend research on *Anolis* colour signals to a new case: a species having evolved a short wavelength-reflective dewlap from an ancestor possessing a long wavelength-reflective dewlap. The dewlap of *Anolis conspersus* reflects light most strongly in the near ultraviolet (peak reflectance approx. 40% at 340 nm),

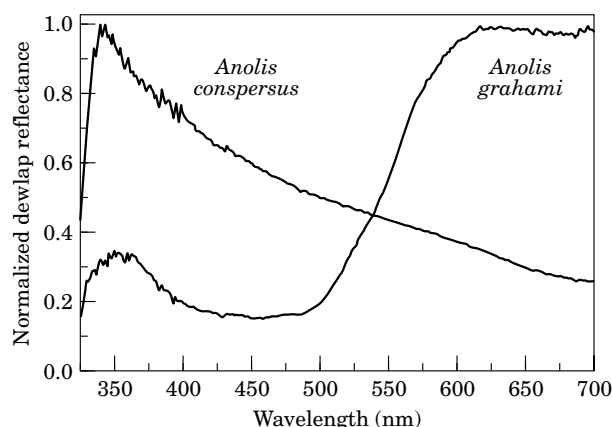


Figure 1. Normalized representative dewlap reflectance spectra for *Anolis grahami* and *Anolis conspersus*.

and its blue appearance to humans belies its true nature as an ultraviolet signal (Fig. 1). In contrast, the direct ancestor of *A. conspersus*, *Anolis grahami*, possesses a bright orange dewlap with a yellow rim (Fig. 1). Arguments supporting an ancestor-descendant relationship of *A. grahami* and *A. conspersus* are presented elsewhere (Macedonia & Clark, 2001; Jackman, Irschick, de Querioz, Losos & Larson, unpub. data). Regardless, because all other close relatives of *A. conspersus* (i.e. the remaining members of the 'grahami group' of anoles – *Anolis opalinus* and *Anolis garmani*; Hedges & Burnell, 1990) possess long wavelength-reflecting dewlaps, the transition to a short wavelength-reflective dewlap in *A. conspersus* is not contingent upon *A. grahami* being its direct ancestor.

An interesting case of body colour variation exists in *A. conspersus*, as three colour forms occur on Grand Cayman: a 'green morph' with a yellowish head (*A. c. conspersus*), a 'brown morph' with brown or bluish legs (*A. conspersus lewisi*), and a taxonomically unrecognized turquoise 'blue morph'. These distinctions apply to sexually mature males; females and juveniles are muted shades of grey or brown. As quantities of pteridine pigments in the dewlap and body skin are very similar among the three colour morphs (Macedonia *et al.*, 2000), colour differences are likely due to relative amounts of carotenoid and melanin present (see Bagnara & Hadley, 1973 for a schematic illustration of an *Anolis* chromatophore). Differences in the size and spacing of purine platelets in iridophores also have been shown, however, to affect colour in some lizard taxa (e.g. *Sceloporus*: Morrison, Rand & Frost-Mason, 1995).

In this paper I document colour variation in adult male *A. conspersus* as it relates to the light habitats and natural backgrounds of the three colour morphs. I also consider the conditions in which male body

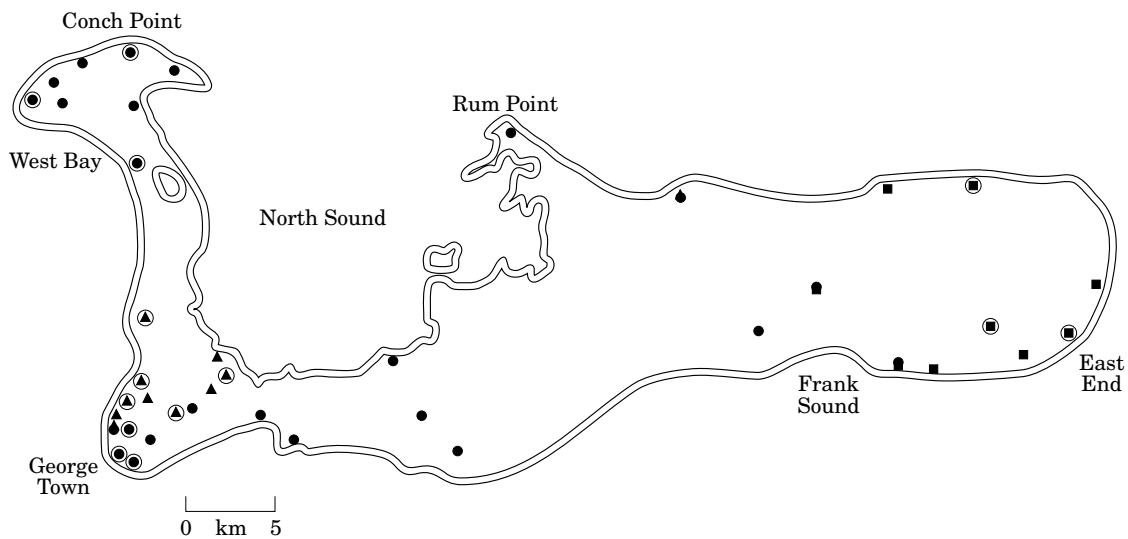


Figure 2. Areas on Grand Cayman surveyed for *Anolis* in June 1997 and 1998. Triangles = green morph sites, circles = blue morph sites, squares = brown morph sites. Symbols surrounded by open circles indicate sites at which habitat light spectra were gathered.

coloration may be considered conspicuous or cryptic. Finally, I bring geological, ecological, and physiological evidence to bear on speculation about the evolutionary context that could give rise to a blue and UV-bright dewlap in this species.

MATERIAL AND METHODS

SAMPLING LOCATIONS

From 2–11 June 1998 spectral measurements were obtained for adult male *A. conspersus* and of the habitats in which they were found on Grand Cayman. Over 40 sites distributed along the coast and inland were examined (Fig. 2). Areas were chosen by driving main and secondary roads and stopping at locations where vegetation appeared adequate to support lizard populations. In these areas a variety of data were gathered, including location on the road map, GPS coordinates, topographic description, dominant plant species, colour morph(s) present and number of lizards seen. Adult male *A. conspersus* were most often observed on tree trunks, typically in a head-down posture with forelimbs outstretched, and at perch heights from 1 to 3 m above the ground (e.g. Avery, 1988; Losos, Marks & Schoener, 1993). Lizards were captured with a pole and noose, and by hand. Individuals were maintained in paper lunch bags marked with the collecting locality, and were taken to a housing facility where spectral readings of their colours were obtained. Lizards not transported subsequently to the USA were returned to the precise location of their capture and released.

COLOUR MORPHS

The green morph of *A. conspersus* appears to be restricted primarily to the George Town area in the southwest corner of Grand Cayman (Fig. 2). This is the tourist centre and the location of greatest rainfall (Burton, 1994; Ng & Beswick, 1994). The increased precipitation in this part of the island stems from convection currents that rise from a large (approx. 3500 hectares) central mangrove that abuts the eastern edge of the North Sound. The moisture condenses as it rises and cools to form clouds that drift over George Town and out to sea (Burton, 1994, and pers. comm.). The few plots of undisturbed habitat that can be found in this area are comparatively lush.

The brown morph occurs to the east of a longitudinal line running roughly from Frank Sound to the north coast (Fig. 2). The lower rainfall in this region, exacerbated by a highly porous exposed limestone substrate, results in vegetation ranging from woodland to semi-xeric habitat, although mangrove is present in some areas (e.g. Johnston, 1975).

The blue morph is the most widespread colour variant. It occurs throughout the island to the west of the brown morph's distribution with the exception of areas in the southwest that contain only the green morph. 'Typical' blue morph individuals are (1) turquoise with light dots (not vermiculations), (2) exhibit a brownish wash on the dorsum, and (3) have turquoise or blue legs. This population also is the most variable in coloration, both within and among geographic locations. Adult males with yellow-green snouts are fairly common, and although there may be a greenish cast to

the body they still can be identified as 'blue morph'. Population genetic studies have yet to be conducted on *A. conspersus* so nothing is known about the blue (or any other) morph's genetic integrity. Nevertheless, because the colour variations observed in the green or brown morphs do not encompass those of the blue morph, it is considered its own entity in the present work.

MEASURING MALE *ANOLIS CONSPERSUS* COLOUR VARIATION

Spectral data were acquired from six body regions: head (dorsal, anterior to parietal eye), dewlap (centre), dorsum (midpoint along vertebral column), ventrum (centre), leg (outer, upper thigh), and tail (dorsal, slightly distal to base). Lizards were restrained during measurements by securing the feet and the end of the snout with black tape. A subject was laid on its side on a non-glaring black rubber pad, and the edge of its outstretched dewlap was taped to the pad. Unlike some other *Anolis* species, adult male *A. conspersus* typically responded to restraint by initiating metachrosis but only partly completed the colour change, followed by returning to normal coloration in two to three minutes. If a subject did not begin to return to normal coloration by five minutes post-restraint, spectral readings were not gathered for that individual. Radiance measurements of skin coloration were obtained at right angles (approximate) relative to the skin surface through a fibre optic cable (400 μ m) fitted with a collimating lens (Ocean Optics 74-UV, 4° acceptance angle) and interfaced with an Ocean Optics S2000 portable spectrometer. The light spectrum was digitized with a 100 kHz A/D card (National Instruments DAQCard-700) using a Compaq Armada 1130 laptop computer. Data were displayed with OOIBASE software (v 1.5, Ocean Optics, Inc.). A Whiteport Optolon 2 matte reflectance standard (>97% reflectance from 300–1100 nm, ANCAL Inc.) was used to calculate skin reflectance. A reading of the standard was obtained for each subject. A dark current reading also was taken for each subject and subtracted from that subject's radiance spectra.

MEASURING HABITAT LIGHT

A hemispherical cosine receptor (ANCAL COS-7, 180° acceptance angle) was used to measure ambient light in lizard habitats. Calibration of the COS-7 was performed with the aid of a calibrated light source (LS-1-CAL) and cosine receptor (CC-3-UV) from Ocean Optics, Inc. The resulting calibration file was used to correct irradiance data at the analysis stage.

Habitat light data collection was restricted to times when the sky was more than 1/3 blue and the sun was not obscured by clouds (e.g. Fleishman *et al.*, 1997).

Downwelling irradiance was measured underneath trees by orienting the lens of the cosine receptor directly upward at the location where an adult male lizard had been perched. Radiance readings (using the collimating lens) were gathered for tree bark and leaves, which are the primary elements making up the visual background of arboreal anoles.

All spectral readings in the field were obtained outdoors during periods of relatively clear sky conditions, although high-altitude haze sometimes was present. If low-altitude clouds were present, readings were not taken when a cloud was near to or obscuring the sun. Spectral data were gathered at a resolution of 0.37 nm increments (approx.). Over the region of interest (325–700 nm) this resulted in 1085 data points per reading. In the year prior (1997) subjects had been collected in the field and transported to Indiana University where skin reflectance was measured outdoors in exactly the same manner, but only on very clear days in the absence of high-altitude haze.

MULTIVARIATE STATISTICAL ANALYSIS

To summarize spectral data statistically, data first were normalized to a common area under the curve (=1) to equalize brightness among all spectra (e.g. Grill & Moore, 1998). Data points then were grouped into 10 nm bins and averaged, resulting in 38 summary values per spectrum. Principal components analyses were conducted on the lizard reflectance data, grouped by colour morph, in two ways. First, a single PCA was run on all 228 spectral segment means (38 values \times 6 body regions). Second, a PCA was run for each of the six body regions. Following these analyses a PCA was run on the 38 spectral segment means of the habitat irradiance data (see Cuthill *et al.*, 1999 for a detailed discussion of the application of PCA to spectral data). Next, one-way ANOVAs were used to detect differences among the population means of components generated for lizard coloration and for their habitats. Where differences were significant in the overall ANOVA, Bonferroni-protected pairwise tests were used to determine which pairs of colour morphs and habitats differed significantly from each other.

The spectral distinctiveness of the *A. conspersus* colour morphs and of their habitats was examined using one additional technique: stepwise discriminant function analysis (DFA). DFA requires data to be normally distributed; thus, PCA component scores were used as input data rather than the original spectral segment means. The SPSS (v 6.1 for Macintosh) default values were used for variable entry and retention (F -to-enter=3.4; F -to-remove=2.7). The discriminant functions that were generated then classified the component scores according to colour morph in a 'blind' fashion.

COLOUR SEGMENTS AND COLOUR SPACE

Reflectance spectra of the lizards and their natural backgrounds were summarized graphically in several ways. Endler (1990) developed a simple means to classify animal colour patterns and the backgrounds of their habitats. This 'segment classification' method presumes only the presence of a typical opponency system of colour vision that compares the outputs of receptors sensitive to non-adjacent portions of the visible spectrum, i.e. red-green, and yellow-blue in humans. The technique provides a graphical summary of differences in hue and chroma among spectra. In this paper 'hue' refers to colour in the everyday sense (e.g. red, green, blue) and is defined by the shape of the spectral curve, particularly by its dominant wavelength. 'Chroma' refers to a colour's saturation, and is a function of the magnitude of the dominant wavelength slope. 'Brightness' refers to a spectrum's total intensity, and is measured as the area under the spectral curve (e.g. Endler, 1990).

Extending the segment classification method to include wavelengths in the near ultraviolet range, each 1085-point spectrum from 325–700 nm was partitioned into five, 75 nm colour segments containing 217 points each. These segments correspond roughly to ultraviolet (325–400 nm), violet-to-blue (400–475 nm), green (475–550 nm), yellow-to-orange (550–625 nm), and red (625–700 nm). Each colour segment was summed, producing one value per segment, then each of the five values was divided by the sum of the unsegmented spectrum, resulting in five final values.

By subtracting non-opposing pairs of colour segment sums (i.e. red minus green, yellow minus blue, green minus UV), three final 'colour scores' summarizing each spectrum were plotted in a two-dimensional colour space. Note that creation of a green-UV axis does not require colour opponency between UV-sensitive and middle-wavelength sensitive photoreceptors, but serves the same heuristic function as the red-green and blue-yellow axes. Hue is indicated by the angle of a colour score relative to the top-centre (i.e. 0°) of the graph, and chroma increases with the distance of a colour score from the origin. Whether a lizard colour scores falls within or outside the colour space occupied by the backgrounds can be visualized by plotting both types of spectra on the same graph. The further a lizard's colour score falls from the region of colour space occupied by the visual backgrounds, the greater the colour contrast and the more conspicuous that body region should appear.

A recent study (Grill & Rush, 1999) compared Endler's (1990) colour segment method with PCA as spectral data analysis techniques. The authors concluded that although both methods possess strengths and weaknesses, either technique is far superior to more widely-used treatments (e.g. human subjective

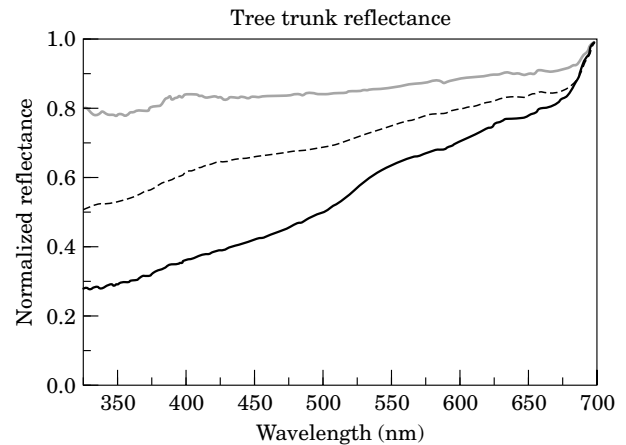


Figure 3. Normalized tree trunk reflectance from *A. conspersus* colour morph habitats. Black line=green morph ($n=10$), dashed line=blue morph ($n=7$), grey line=brown morph ($n=6$).

ratings, Munsell colour chips) in the assessment of animal coloration. For the purposes of the present study, colour segment classification and PCA provide complimentary benefits. Thus, both methods are employed herein.

CONTRAST WITH VISUAL BACKGROUNDS IN HABITAT LIGHT

Effects of habitat light on colour contrast and brightness contrast between the lizards and their natural backgrounds were determined as follows. Mean reflectance spectra of lizards, bark, and leaves were first converted to radiance spectra by multiplying them by the mean irradiance spectrum (normalized) from their own habitat. Because tree trunk reflectance differed somewhat among colour morph habitats (Fig. 3), contrast calculations utilized habitat-specific bark averages (normalized). Leaf spectra were very similar among colour morph habitats and were pooled in these calculations.

To determine colour contrast between a lizard body region and a visual background, the mean radiance spectrum of a colour morph's body region and the mean background radiance (bark or leaves) first were equalized relative to each other for total brightness (i.e. area under the curve 325–700 nm). A 'difference spectrum' then was calculated between the two spectra, and the square root was taken of this difference spectrum's sum (Endler, 1990: formula 20). This calculation provides a Euclidean distance measure of the difference in colour (hue and chroma combined) between the colour patch and the background.

Brightness contrast between a lizard body region and a visual background was calculated as the difference

between the mean radiance spectrum of a colour morph's body region and mean background radiance (bark or leaves) in that colour morph's habitat, divided by the sum of the same two quantities. This operation produces a symmetrical index between 1 and -1, where lizard colour patches that are lighter than the background have positive values, and colour patches that are darker than the background have negative values.

RESULTS

ANOLIS CONSPERSUS REFLECTANCE SPECTRA

The reflectance curves of the *A. conspersus* colour morphs revealed several patterns that are relatively consistent both within and among morphs (Fig. 4). Dewlap reflectance was similar for all three colour morphs, peaking at 340 nm (mean = 339.5, SD = 2.5, $n = 22$) and decreasing monotonically with increasing wavelengths. On the whole the brown morph was the brightest of the three colour morphs (excluding the dorsum) but exhibited comparatively weak chroma (excluding the ventrum). Reflectance was strongest in the long wavelengths on the head and dorsum and was (marginally) strongest in the middle wavelengths for most other body regions in the brown morph (Fig. 4). Notably, this colour morph was unique in exhibiting strong short wavelength and UV reflectance in certain body regions, particularly the head, legs and tail.

Excluding the dorsum, the green morph was not as bright as the brown morph but commonly exhibited strong chroma (Fig. 4). The head (and to some degree the ventrum) peaked in the 'yellow' part of the spectrum, whereas other body regions (excluding the dewlap) peaked in the 'leaf-green' middle wavelengths (leaf mean = 552.6 nm, SD = 2.2, $n = 20$).

The blue morph exhibited both low brightness and low chroma (Fig. 4). Overall, its reflectance spectra appeared intermediate to the other two colour morphs.

STATISTICAL ANALYSIS OF COLOUR VARIATION

From 228 spectral segment means a PCA created 17 factors with eigenvalues >1.0 that accounted for 98.3% of the variance in the original variables. The first two factors explained 52.4% of the variation (Fig. 5). The green morph exhibited no overlap with the brown morph and virtually no overlap (one individual) with the blue morph in component space. In contrast, the blue morph distribution all but completely encompassed the distribution of the brown morph (Fig. 5).

The contribution of each body region to the PCA was determined by running separate PCAs on these locations. Results showed for each body region that only the first three of 17 factors exhibited eigenvalues

>1.0, accounting for a mean variance of 97.3% (range: 96.6–98.4%). Some body regions were more colour morph-distinctive than others (Fig. 6). For example, excluding dewlap and leg reflectance there was virtually no overlap between the green and brown colour morph distributions in component space for head, dorsum, ventrum, and tail reflectance. Likewise, the brown and blue morphs exhibited no overlap in head and back reflectance, and overlapped with only a single individual in leg reflectance. Thus, similar spectral reflectance for belly, tail, and dewlap of the brown and blue morphs (and smaller within-group colour variance in the brown morph) accounts for the brown morph falling within the component space of the blue morph when all six body regions were analysed together.

The PC coefficients reveal how the first three principle components were correlated with each body region. Because brightness was equalized prior to analysis (e.g. Grill & Moore, 1998; Cuthill *et al.*, 1999), the PC coefficients represent chroma and hue (Fig. 7). Statistical results of one-way ANOVAs on the PC scores (Table 1) bear out the distribution patterns observed in component space (Fig. 6). On PC1, for example, all body regions other than the dewlap differed significantly between the green and brown morph and between the green and blue morph, but none differed between the blue and brown morph (Table 1). Many of the differences observed between the brown and blue colour morphs (Fig. 6) are statistically significant, nevertheless, in ANOVAs of the less influential PC2s (Table 1).

Finally, the PC scores were subjected to stepwise discriminant function analysis (DFA). With the 17 PC factors (eigenvalues >1.0) from the PCA of 228 spectral variables available ('combined' analysis: Table 2), only the first three factors were used by the analysis to create two discriminant functions. These functions correctly classified over 90.38% (47 of 52) of the subjects to the 'correct' colour morph. Only a marginal improvement in classification accuracy was achieved (94.23%; 49 of 52) when 18 PC factors (i.e. three factors from each of six body regions) were available to create the two discriminant functions ('separate' analysis: Table 2). In sum, body coloration in *A. conspersus* varies sufficiently across Grand Cayman such that three colour morphs can be distinguished with regularity in most of the statistical procedures utilized here.

COLOUR SPACE

Within the colour space of Endler (1990) most regions on the lizards' bodies do not overlap with the backgrounds of tree bark (reddish-brown polygon) or leaves (green polygon) against which they are viewed in the natural habitat (Fig. 8). Three body regions common to both plots stand out against the background (Fig. 8A, B): the dewlap (solid triangles), head (open squares), and tail

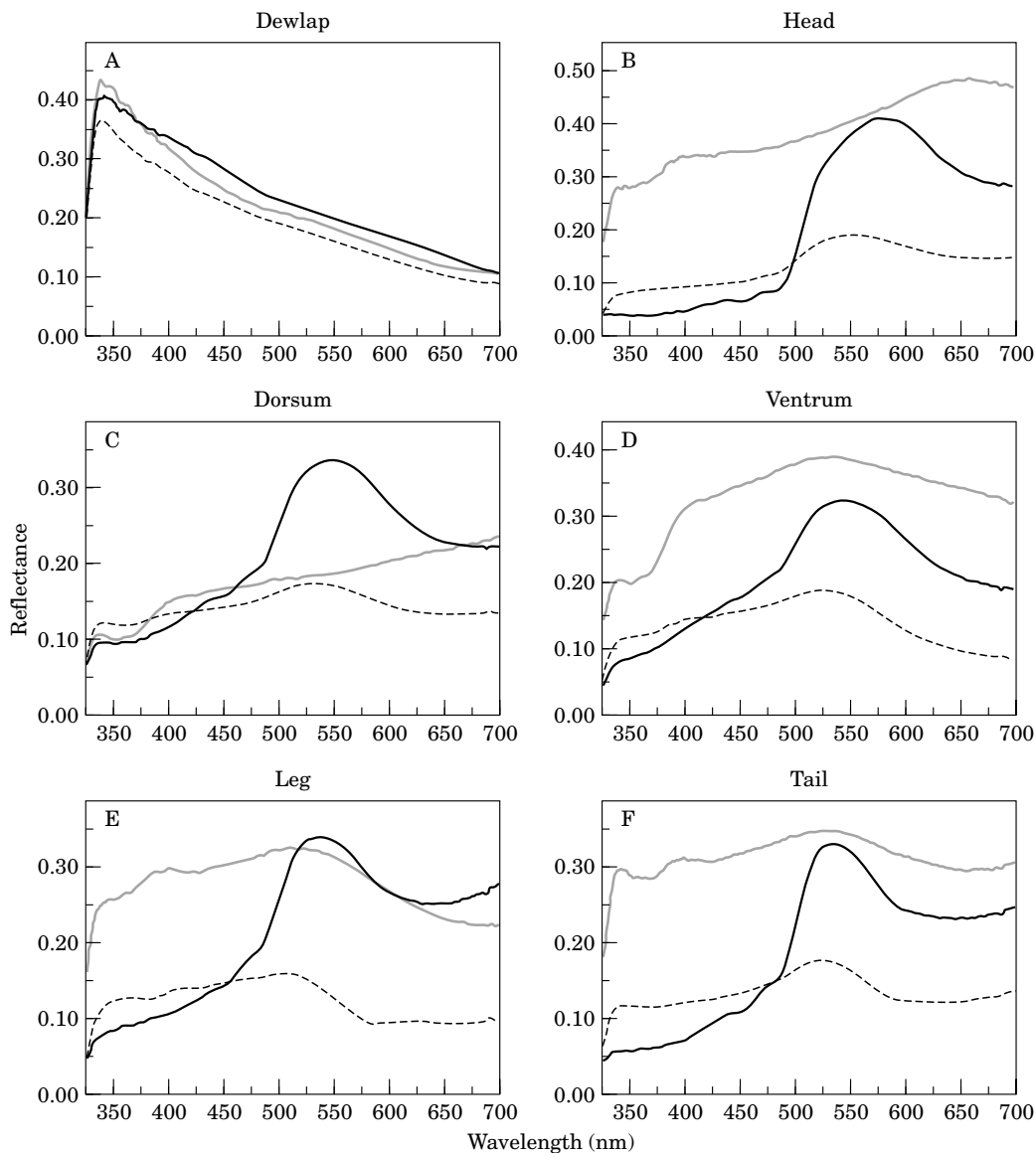


Figure 4. Mean reflectance spectra from the six body regions measured. Colour morphs: black lines = green morph ($n=9$), dashed lines = blue morph ($n=9$), grey lines = brown morph ($n=5$).

(open triangles). Given that all points in the colour space (including the backgrounds) have the same brightness, contrast of the ventrum against bark and leaves (Fig. 8A) seems unlikely to be an example of adaptive countershading. Rather, the difference in chroma and hue against the background probably renders the lizards conspicuous when seen from below – a view most likely to be witnessed during display and territorial patrolling.

When using a red-green colour axis, body regions that lacked colour contrast with the background included the dorsum and head of most brown morph subjects against tree bark and the dorsum from several green and blue morph subjects against leaves (Fig.

8A). When using a UV-green colour axis the dorsum reflectance of most subjects fell within the bark or leaf polygons, as did the legs and tails of some individuals. Colour space statistics (Table 3) indicate for each colour morph which body regions were significantly different from the background of bark and leaves combined.

STATISTICAL ANALYSIS OF LIGHT HABITATS

Three primary differences in irradiance spectra were found in the shade of the colour morph-specific sites: (1) wavelengths in the blue to blue-green region of the spectrum were proportionally stronger in the blue

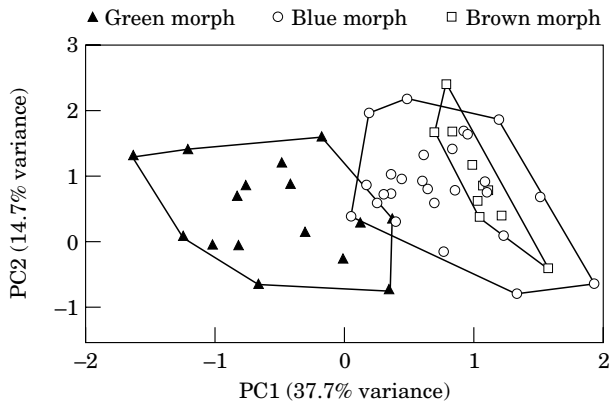


Figure 5. Results of principal components analysis of 228 skin reflectance measures (six body region variables \times 38 spectral segments of 10 nm each) for *A. conspersus*. Morphs: (\blacktriangle) green, $n = 16$; (\circ) blue, $n = 26$; (\square) brown, $n = 10$.

morph sites, (2) long wavelengths (yellow to red: 570–610 nm) were proportionally stronger in the brown morph sites, and (3) although the middle wavelengths (green) were strongest both in the green and blue morphs' sites, the irradiance spectrum was narrowest in the green morph sites (Fig. 9).

A PCA run on the 38 mean values of the 10 nm-wide spectral segments from 330–700 nm produced three factors that explained 97% of the variance. The first factor accounted for most of this variance (82.1%), with the second and third factors adding 8.5% and 6.4% respectively. One-way ANOVAs on these three derived variables revealed that the first factor did not differ significantly among the colour morphs, whereas the second and third factors were significant (Table 4). Finally, a stepwise DFA used these PC factors to create three discriminant functions which then classified the PC scores from the individual habitat light samples as to which habitat they originated from. Only one of the 25 samples were misclassified, resulting in overall classification accuracy of 96% (Table 5). These results suggest that although ambient lighting in the habitats of the three colour morphs exhibits more similarities than differences, consistent habitat-specific differences nevertheless exist.

INTERACTIONS BETWEEN AMBIENT LIGHT AND REFLECTANCE SPECTRA

The appearance of each colour morphs' colour patterns in ambient light (i.e. radiance) was approximated by multiplying their reflectance spectra by the (normalized) irradiance spectra from their own habitats. Comparing the calculated radiance of the colour morphs' body regions (Fig. 10) with their reflectance

(Fig. 4) revealed two particularly interesting findings. First, although the dewlap was among the more strongly reflective regions of the body at peak reflectance (Fig. 4A), it was only moderately radiant in the light habitats where these lizards live. This difference stems from the fact that, within each colour morphs' habitat, middle wavelengths in the region of 525–575 nm are the most intense, followed by middle-long (575–625 nm) wavelengths (Fig. 10). Second, the brown morph, which exhibited the weakest chroma in its body coloration (Fig. 4) was most strongly affected by habitat light (Fig. 10). This morph's body coloration therefore should vary more with changing light conditions than that of the other colour morphs.

Calculations of lizard (brightness-equalized) colour contrast against vegetation in their habitats (Fig. 11A, B) revealed patterns similar to those of spectra plotted in Endler's colour space (Fig. 8). For example, the dewlap exhibited greater colour contrast with leaves and bark than did any other body region. Were more short wavelength light present in the colour morphs habitats, dewlap colour contrast with the background vegetation would be even stronger. For other body regions, the green morph generally exhibited the strongest colour contrast with bark and the weakest with leaves, the brown morph exhibited the opposite pattern, and the blue morph most frequently exhibited colour contrast intermediate to the other colour morphs (Fig. 11A, B).

Analysis of brightness contrast revealed all body regions of the three colour morphs to be darker than leaves and tree bark (Fig. 11C, D). Within a colour morph, all body regions for the green and blue morphs, including the dewlap, exhibited similar brightness contrast with the background vegetation. Among colour morphs the blue morph was much darker against its bark and leaf backgrounds than was the green morph. The brown morph exhibited a different pattern, where some body regions exhibited strong brightness contrast with bark and leaves (dewlap, dorsum), and other regions exhibited moderate (ventrum, leg, tail) or weak (head) contrast.

DISCUSSION

Spectral readings from different body regions of *A. conspersus* reveal a signature reflectance pattern for each colour morph. The brown morph is a high brightness/low chroma lizard that reflects long wavelengths from the head and dorsum most intensely but which otherwise exhibits strong short wavelength reflectance – particularly in the UV. The green morph is somewhat less bright but exhibits very high chroma in the green and yellow regions of the spectrum. The blue morph is, like the brown morph, a weakly-coloured form, but it is dark rather than being bright.

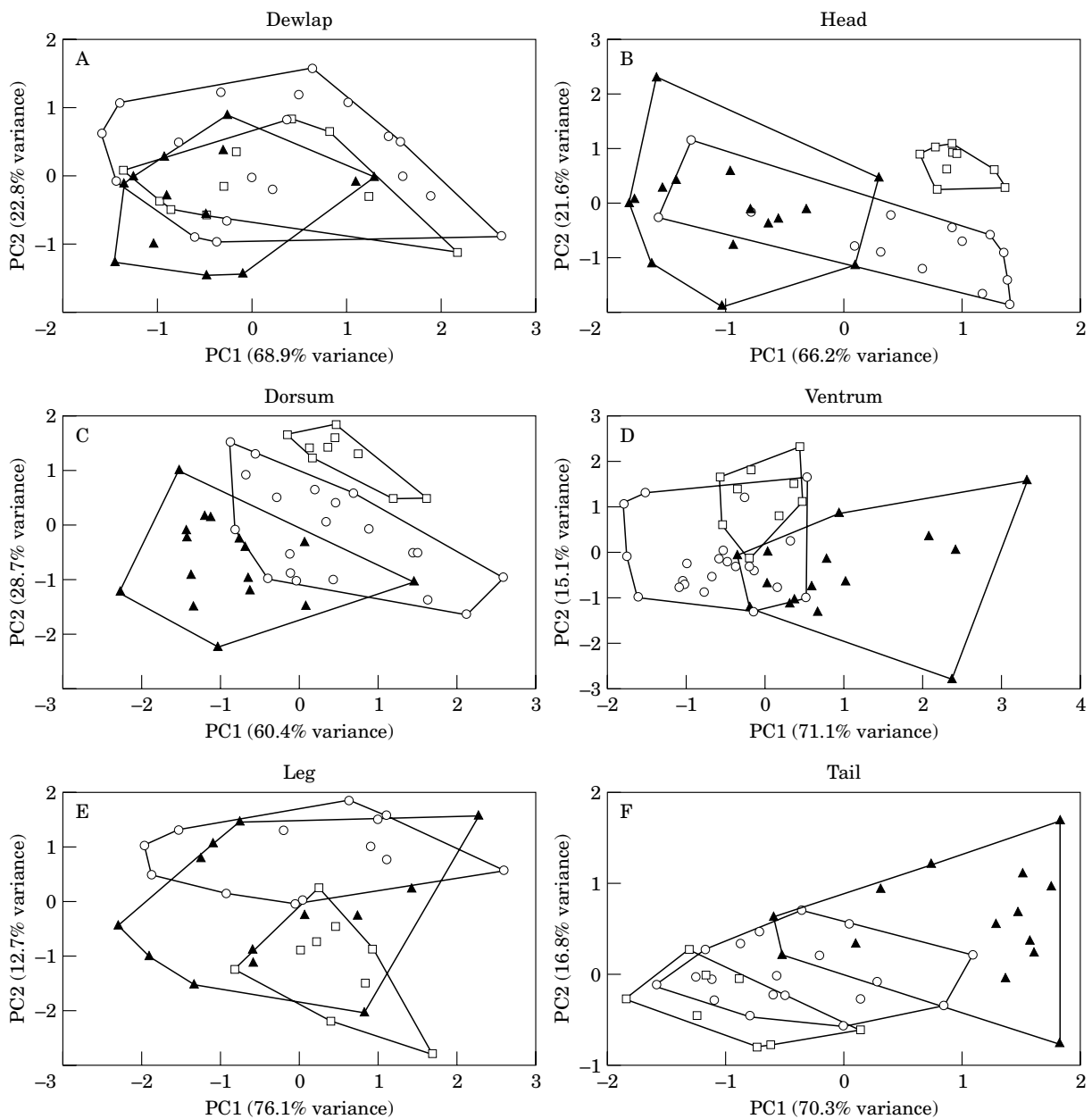


Figure 6. (A–F) Results of separate principal components analyses of individual body regions (38 spectral segments of 10 mn each in each analysis) for *A. conspersus*. Legend as in Fig. 5.

SPECTRAL DISTINCTIVENESS OF *ANOLIS CONSPERSUS* COLOUR MORPHS

PCA showed that, when considering all body regions together, the green and brown morph exhibited no overlap in component space (Fig. 5). This result suggests that these two morphs are completely distinctive in overall reflectance spectra. Although only one blue morph subject fell well within green morph component space, all but one brown morph subject fell within blue morph component space (Fig. 5). Thus, when

considering all the measured body regions together, the PCA suggests that brown morph coloration constitutes a subset of colour variation present in the blue morph.

By examining results of PCAs run on each body region independently it can be determined if the brown and blue morph differ in any respects. These plots (Fig. 6) show that head and dorsum reflectance of the brown and blue morph are distinctive in component space, but that they exhibit considerable overlap in

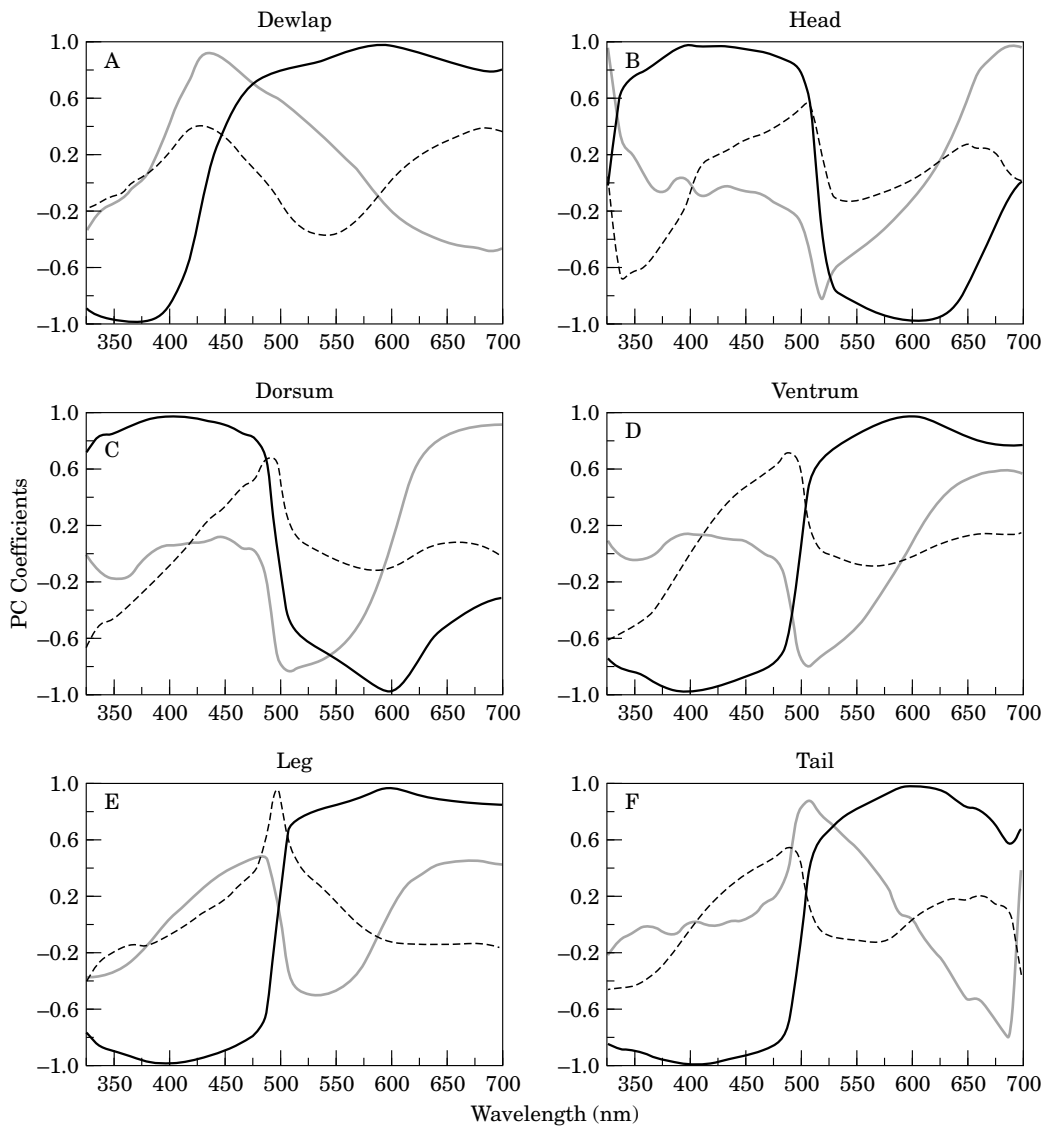


Figure 7. PC coefficients for each analysis shown in Fig. 6. The coefficients, or 'loadings' show the spectral weightings of the first three principal components for the six body regions. Black lines = PC1, grey lines = PC2, dashed lines = PC3.

ventrum leg, and tail (and, of course, dewlap) coloration. Note also that conducting PCAs on the separate body regions provides a generally different view of which colour morphs exhibit the greatest overlap: in the analyses of separate body regions the blue morph exhibited overlap with the green morph in *every* plot, often quite extensively (Fig. 6).

The overall results of the PCAs indicate that the blue morph is not consistently distinctive in colour pattern from either the green or the brown morph. On the other hand, the blue morph does command regions of component space (Figs 5, 6) that are not occupied by the other two morphs. Moreover, DFA constructed

functions that had no more difficulty assigning blue morph subjects 'correctly' than brown or green morph subjects. If sufficient coloration differences did not exist in the blue morph to distinguish it from the other two morphs, the extraordinary success rate in the discriminant analyses would not have been possible.

Taking all of this (sometimes conflicting) information together underscores the fact that the blue morph is comparatively variable in coloration, where some individuals and body regions are distinctive but others are not. This greater colour variation in the blue morph could be an indication that it lives in more heterogeneous light habitats than do the other two colour

Table 1. One-way ANOVA on principal components of reflectance spectra among the three *Anolis conspersus* colour morphs¹

Region	<i>F</i> -ratio PC1	Significant pairs	<i>F</i> -ratio PC2	Significant pairs	<i>F</i> -ratio PC3	Significant pairs
Dewlap	1.940	none	1.318	none	0.996	none
Head	26.758***	BL-GR, BN-GR	3.187*	BL-BN	3.203*	BN-GR
Dorsum	12.664***	BL-GR, BN-GR	15.997***	BL-BN, BN-GR	2.860	none
Ventrum	16.052***	BL-GR, BN-GR	11.429***	BL-BN, BN-GR	1.364	none
Leg	16.979***	BL-GR, BN-GR	1.453	none	12.082	BL-BN, BN-GR
Tail	17.288***	BL-GR, BN-GR	3.518*	none	3.567*	BL-GR

¹ All PCs had eigenvalues >1.0. Degrees of freedom are 2, 49 in all analyses. Colour morphs: GR=green, BL=blue, BN=brown. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.0001$. Alpha for significance in Bonferroni-protected pairwise comparisons = 0.05.

Table 2. Stepwise DFA (canonical) classification assignments for principal components scores of skin reflectance from the three *A. conspersus* colour morphs

Body region grouping	Actual colour morph	<i>n</i>	Predicted colour morph		
			Green	Brown	Blue
Combined ¹	Green	16	14	0	2
		%	87.5%	0.0%	12.5%
	Brown	10	1	9	0
		%	10.0%	90.0%	0.0%
	Blue	26	1	1	24
		%	3.8%	3.8%	92.3%
Separate ²	Green	16	15	0	1
		%	93.8%	0.0%	6.3%
	Brown	10	2	8	0
		%	20.0%	80.0%	0.0%
	Blue	26	0	0	26
		%	0.0%	0.0%	100.0%

¹ Combined = all 38 spectral segments from each of six body region being entered into a PCA together. The stepwise DFA used three of 17 PCs with eigenvalues >1.0 to create two discriminant functions. ² Separate = separate PCAs for each body region. The stepwise DFA used six of 18 PCs with eigenvalues >1.0 to create two discriminant functions. Correct classification percentages are in bold type.

morphs, and/or that gene flow may be occurring where the blue morph comes into contact with the green and brown morphs.

COLOUR SPACE

Plots of colour scores in the colour space of Endler (1990) facilitate visualization of colour contrast (hue and chroma) among different colour patches on the lizards as well as between the lizards and their visual

backgrounds (bark and leaves). When using blue-to-yellow and green-to-red colour opponent axes (Fig. 8A) it is seen that most body locations exhibit sufficient colour contrast with the backgrounds as to be distinguishable from them. The primary exceptions are the head and dorsum colour scores of the brown morph falling within the tree bark polygon, and several dorsal and leg colour scores of the green morph falling within the leaves polygon (Fig. 8A). Dewlap and head reflectance, however, reside in opposite quadrants of the colour space. This is more prominently seen when replacing the green-to-red axis with a UV-to-green axis (Fig. 8B), and occurs for all three *A. conspersus* colour morphs. Strong colour contrast between two adjacent colour patches is one means to maximize conspicuousness (Endler, 1992). Moreover, the head and the dewlap are the two body parts that are in motion during the headbob display, and tails in many lizard species contrast with the rest of the body, functioning to draw the attention of predators away from the more vulnerable body parts. Anoles often wiggle their tails when cornered or caught by predators, and do so as well during contests that have escalated to the point of physical contact (pers. obs.).

The green morph appears to have taken colour contrast to an extreme in three ways. First, its head colour scores always fell outside those of the visual background. Second, the yellowish-green colour of the head and the blue-UV colour of the dewlap are 'complementary colours' (i.e. they have few strong wavelengths in common). Third, one of these colours (yellow-green) has a cut-off frequency in the region where ambient light is most intense in the habitat (see Endler, 1992 and below).

LIGHT HABITAT CHARACTERISTICS

Irradiance spectra recorded in this study were not nearly as distinctive as some published examples of

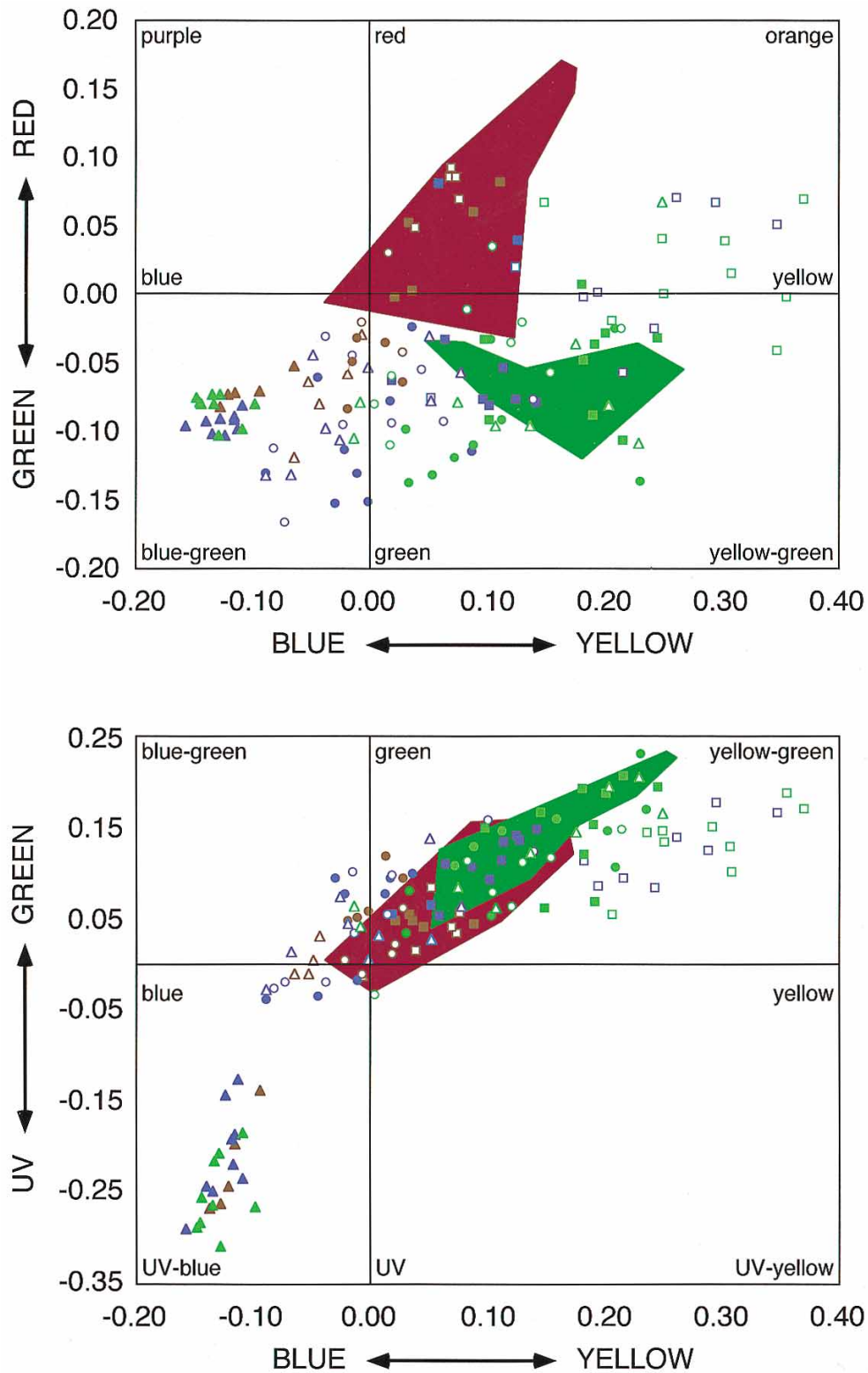


Figure 8. Colour segments of *A. conspersus*, tree bark, and leaf reflectance spectra plotted in the 'colour space' of Endler (1990). Colour morphs: green ($n=9$), blue ($n=9$), brown ($n=5$). Solid squares = dorsum; solid circles = ventrum; solid triangles = dewlap; open squares = head; open circles = leg; open triangles = tail. Green polygon encloses leaf sample ($n=11$); reddish-brown polygon encloses tree trunk bark sample ($n=23$).

Table 3. Differences among *Anolis conspersus* colour morphs and their backgrounds¹ in colour space

Axis: red-green												
	Dewlap		Head		Dorsum		Ventrums		Leg		Tail	
morph ²	U ³	P ⁴	U	P	U	P	U	P	U	P	U	P
green	13.5	0.000	144.0	0.7881	69.0	0.0121	69.0	0.0121	78.0	0.0251	42.0	0.0009
brown	13.0	0.0025	47.5	0.1151	61.0	0.3133	33.0	0.0289	46.0	0.2953	16.0	0.0134
blue	10.0	0.0000	129.5	0.4829	85.0	0.0423	19.5	0.0000	149.0	0.0019	36.0	0.0005
Axis: yellow-blue												
	Dewlap		Head		Dorsum		Ventrums		Leg		Tail	
morph	U	P	U	P	U	P	U	P	U	P	U	P
green	0.0	0.000	10.0	0.0000	41.0	0.0008	144.5	0.7997	147.5	0.8696	109.5	0.1940
brown	0.0	0.0004	71.5	0.5706	56.0	0.2231	12.5	0.0023	11.5	0.0072	1.0	0.0014
blue	0.0	0.0000	43.0	0.0010	150.5	0.9405	34.0	0.0004	58.0	0.0046	35.5	0.0005
Axis: green-UV												
	Dewlap		Head		Dorsum		Ventrums		Leg		Tail	
morph	U	P	U	P	U	P	U	P	U	P	U	P
green	0.0	0.000	77.5	0.0242	61.0	0.0060	106.5	0.1650	147.5	0.8696	97.5	0.0975
brown	0.0	0.0004	42.5	0.0742	64.5	0.3891	74.5	0.6591	22.5	0.0304	0.0	0.0050
blue	0.0	0.0000	106.0	0.1605	114.0	0.2443	112.0	0.2209	121.5	0.3470	82.0	0.0340

¹ Background = tree bark + leaves ($n=36$); ² green morph: $n=9$, blue morph: $n=9$, brown morph: $n=5$; ³ Mann-Whitney U-test, P -values corrected for ties; ⁴ alpha used for significance = 0.008 due to use of same 'backgrounds' data set in six pairwise comparisons (per colour axis). Significant differences are in bold type.

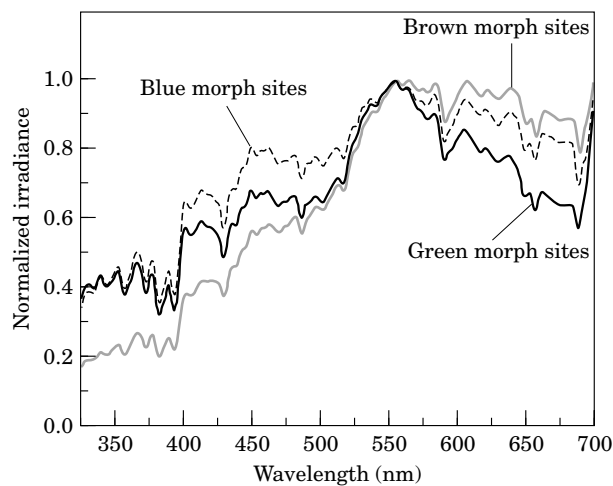


Figure 9. Normalized mean downwelling irradiance spectra from sites demarcated in Fig. 2. Black line = green morph: nine samples from five sites; dashed line = blue morph: eight samples from six sites; grey line = brown morph: six samples from three sites.

Table 4. One-way ANOVA on principal components of irradiance spectra from habitats of the three *Anolis conspersus* colour morphs

PC	F-ratio	Significant pairs
1	0.530	none
2	6.761**	BL-BN, BN-GR
3	46.072***	BL-BN, BL-GR

Degrees of freedom = 2, 22 in each case. Legend as in Table 1.

different forest light environments (e.g. Endler, 1992, 1993). Nevertheless, mean ambient spectra exhibited regions of intensity that were correlated with body coloration in each colour morph: the 'greenest' light (middle wavelengths) occurred in green morph habitats, the 'bluest' in light (short wavelengths) in blue morph habitats, and the 'brownest' light (long wavelengths) in brown morph habitats (Fig. 9). The causes of these differences in habitat light spectra seem straightforward. Green morph habitat was largely

Table 5. Stepwise DFA (canonical) classification assignments for principal components scores of habitat light from the three *A. conspersus* colour morph habitats¹

Actual colour morph habitat	n	Predicted colour morph habitat		
		Green	Brown	Blue
Green	10	10	0	0
	%	100.0%	0.0%	0.0%
Brown	6	1	5	0
	%	16.7%	83.3%	0.0%
Blue	9	0	0	9
	%	0.0%	0.0%	100.0%

¹The stepwise DFA used three PCs with eigenvalues >1.0, constructed from 38 spectral segments that were 10 nm in width, to create three discriminant functions. Correct classification percentages are in bold type.

closed canopy forest, and most of the ambient light was filtered through and reflected from green foliage. Blue morph habitat exhibited a more broken canopy, and skylight contributed more to the irradiance spectrum than in green morph habitat. Brown morph habitat was similar to blue morph habitat but was drier and more open, and trees appeared to be more thinly-leaved. Consequently, although dry brown vegetation made a contribution, direct sunlight probably exerted the strongest influence on the shape of irradiance spectra in brown morph habitats (Fig. 9).

IS MALE *ANOLIS CONSPERSUS* BODY COLORATION CONSPICUOUS OR CRYPTIC?

Whether or not males of each colour morph appear conspicuous or cryptic depends upon (a) the ambient light in their habitats, (b) the hue, chroma, and brightness of the lizards and of their backgrounds, (c) the colour contrast and brightness contrast between the lizards and their backgrounds, and (d) the spectral sensitivity of the organism that is viewing them. Given that adult male *A. conspersus* spend much of their time perched on tree trunks relatively close to the ground (e.g. 1–3 m), tree bark may be the most important background against which they are viewed by conspecifics and predators alike. Regardless of coloration, males of all three colour morphs may be less visible among the leaves simply due to the increased complexity and obscuring qualities of that visual environment. The following discussion therefore is limited to consideration of colour morph appearance against tree trunks.

Body coloration of the green morph exhibits only

moderate brightness contrast with the visual background, and brightness contrast is the primary visual mechanism by which most animals (including anoles) detect moving objects (e.g. Persons *et al.*, 1999). In addition, avian predators of *A. conspersus* (smooth-billed ani: *Crotophaga ani*, Greater Antillean grackle: *Quiscalus niger*, loggerhead kingbird: *Tyrannus caudifasciatus* – Johnston, 1975) as well as the relatively arboreal, lizard-eating Grand Cayman racer: *Alsophis cantherigeris caymanus* (Grant, 1940; J. Gillingham, pers. comm.; pers. obs.) are unlikely to possess visual ‘feature extraction’ capabilities similar to those of humans (Fleishman, 1992) that would allow them to detect motionless lizards. Nevertheless, the green morph maximally exploits the ambient light of its habitat for reflectance, exhibits good colour contrast with tree bark (Fig. 11), and the strong chroma of the body coloration (Fig. 4) ensures minimal colour variance with changing light conditions (Fig. 10). Moreover, the yellowish head of this colour morph (Fig. 4) is similar to the yellow dewlap found in many forest shade anoles (e.g. Fleishman, 1992; Macedonia *et al.*, 2000) and should be exceptionally eye-catching during a headbob display on a tree trunk perch.

The blue morph exhibited the most straightforward pattern of body colour adaptation: brightness contrast (Fig. 11). Like the green morph it should be relatively safe from the roving eyes of predators – as long as it remains still. However, once it moves most vertebrate visual systems should find it to be the most readily detectable of the colour morphs.

Although brown morph body coloration exploits the long wavelength-biased irradiance in its habitat, this colour morph exhibits poor colour contrast and variable brightness contrast with tree bark (Fig. 11). Moreover, brown morph body colour is almost uniformly low in chroma, which will cause the reflected colour patterns to vary considerably with lighting conditions (Fig. 10). Interestingly, present data on habitat-specific tree bark coloration revealed that average bark colour in brown morph habitat exhibits weak-chroma and comparatively strong-UV reflectance (Fig. 3) that is similar to that of brown morph body coloration (Fig. 4) – a relationship that should enhance crypsis. In sum, it can be conjectured that in the more arid and more open habitat of this colour morph, increased predation pressure might have selected for a more cryptic appearance in the brown morph as compared to its conspecifics in more closed habitats.

THE ENIGMATIC BLUE-UV DEWLAP OF *ANOLIS CONSPERSUS*

Why should three populations of *A. conspersus* differ dramatically in body colours and yet possess very

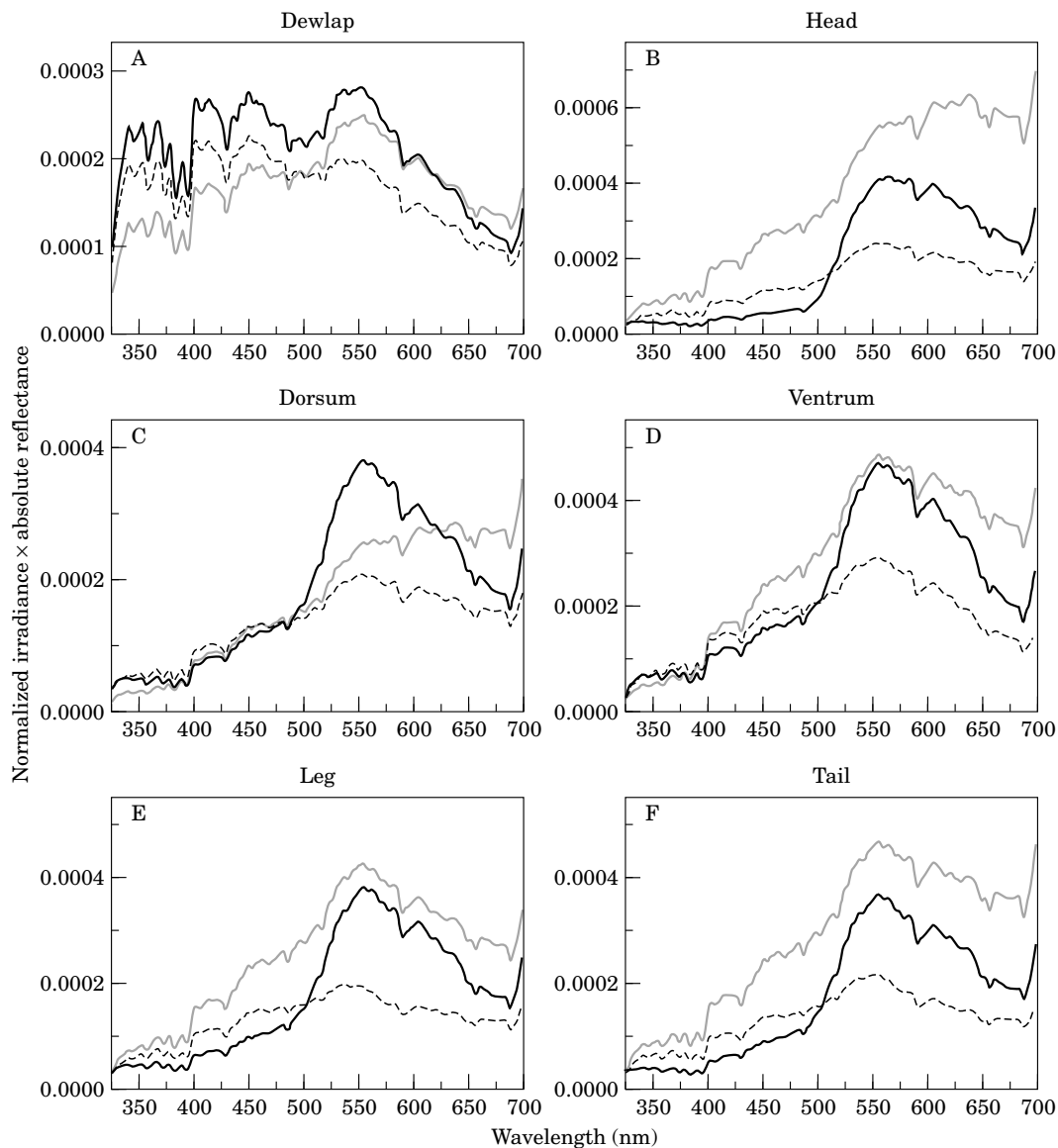


Figure 10. Calculated radiance spectra from the six body regions of the colour morphs. Mean irradiance spectra first were equalized in brightness such that the area under each curve = 1. These 'normalized' irradiance spectra then were multiplied by the reflectance spectra shown in Fig. 4. Legend as in Fig. 4.

similar dewlap coloration? Furthermore, what factors might have selected for a blue and UV-bright dewlap in this species, given that its closest phylogenetic relatives possess long wavelength-reflective dewlaps? Answers to these questions can be approached by examining (a) the possibility of a sensory bias in the *A. conspersus* visual system that has 'driven' the evolution of this dewlap colour, (b) current potential benefits of a blue-UV dewlap for signaling on Grand Cayman, and (c) past potential benefits accruing in an ecological context no longer present on the island.

Sensory bias, visual photopigments, and ultraviolet perception

The most fundamental necessity for perceiving an ultraviolet signal is a visual system that is sensitive to the UV part of the spectrum. All *Anolis* species examined to date, including all species of the Jamaican radiation, have a UV-sensitive visual photopigment (E. Loew, pers. comm.). The UV and short wavelength photoreceptor pigment peaks in *A. conspersus* and *A. grahami* are identical, and the medium and long

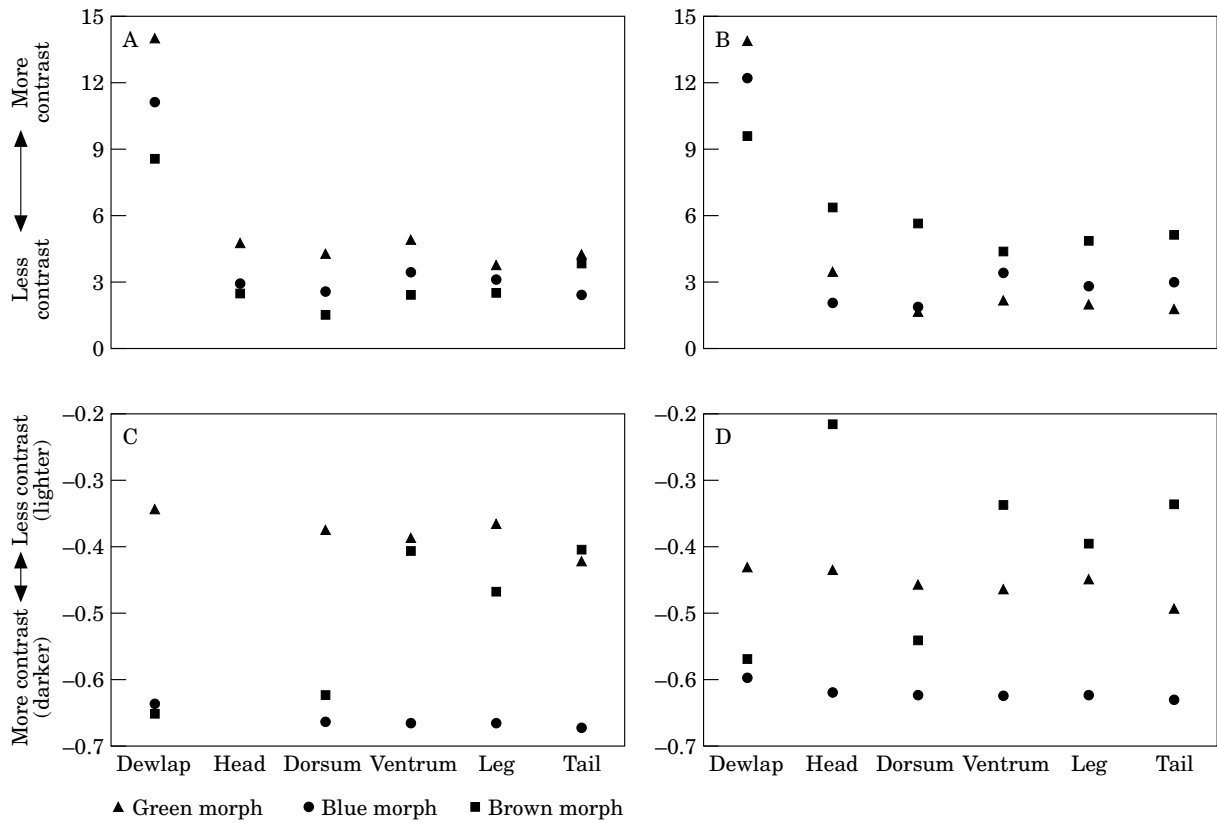


Figure 11. Colour contrast (A, B) and brightness contrast (C, D) between *A. conspersus* colour morphs and the natural backgrounds of tree trunks (A, C) and leaves (B, D). Reflectance of lizard body regions and backgrounds was converted to radiance prior to contrast calculations by multiplying these quantities by colour morph-specific habitat irradiance spectra.

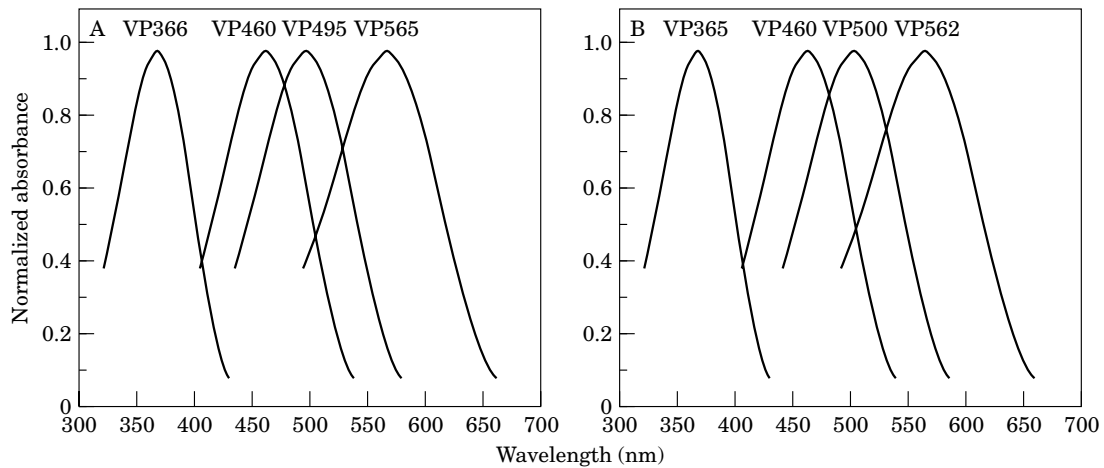


Figure 12. Normalized visual pigment absorption spectra for (A) *A. grahami* and (B) *A. conspersus*. VP=visual pigment; numbers indicate peak absorbance value for each class of photoreceptor. Carotenoid-pigmented oil droplets (not shown) act as effective long-pass filters for the middle- and long-wavelength-absorbing photopigments, such that wavelengths below the following values (approx.) are not absorbed by the photopigments: *A. grahami*: VP565, cut-off = 478 nm; VP495, cut-off = 503 nm; *A. conspersus*: VP562, cut-off = 472 nm; VP500m cut-off = 512 nm. Data courtesy of Ellis Loew, Cornell University.

wavelength peaks are within 5 nm of each other (Fig. 12). Thus, although anoles are (like many other animals) 'pre-adapted' to make use of ultraviolet visual signals (e.g. Fleishman *et al.*, 1993), there is nothing in the peripheral visual system of *A. conspersus* – at least in terms of photopigments – that would suggest a superior ability to perceive UV light.

Dewlap signal efficacy

Unlike body coloration, which can serve to advertise or to conceal, the anoline dewlap has evolved exclusively as a signalling organ that is hidden at other times. Sexual selection therefore should favour a dewlap colour that takes advantage of the ambient spectrum in which it most frequently is displayed, as well contrasting with the visual background against which it is viewed. Addressing this latter point first, results showed that the *A. conspersus* dewlap contrasts strongly with the backgrounds of tree bark and leaves, as this vegetation absorbs the very wavelengths that the dewlap reflects. Nevertheless, contrast will matter little if sufficient ambient light energy is very weak in the wavelengths that the dewlap has been designed by selection to reflect.

Endler's (1992, 1993) woodland shade habitat provides the ideal ambient spectrum for maximizing reflectance from the *A. conspersus* dewlap. It therefore is curious that none of the ambient spectra measured in this study closely resemble that light habitat. The only light habitat documented in this study where a blue-UV dewlap should be a moderately effective signal is that of the blue morph (Fig. 9), but even in this case there would seem to be better choices for dewlap colour. For example, were one to design dewlap colours to take full advantage of the ambient spectra in the three colour morphs' habitats, the green morph might have a yellow dewlap, the blue morph an orange and blue-violet dewlap, and the brown morph an orange-red dewlap. Yet, none of these colour patterns are found in *A. conspersus* dewlaps.

Thus, an answer for why *A. conspersus* has evolved a blue-UV dewlap with little long wavelength reflectance remains elusive when considering factors like visual pigments and habitat light on contemporary Grand Cayman. Current ecological conditions on the island, however, may not represent those in which the blue-UV dewlap evolved. By bringing together factual information from the geological record, physiology, and the characteristics of light habitats, a speculative yet logical scenario emerges that provides a clear selective advantage for the *A. conspersus* blue-UV dewlap. Moreover, this scenario leads to predictions about the phylogeographic relationships of the colour morphs that can be tested with molecular techniques.

DEWLAP COLOUR EVOLUTION IN *ANOLIS* *CONSPERSUS*: SCENARIO AND PREDICTIONS

Scenario

Grand Cayman is a flat, relatively featureless island, most of which is less than 4 m above sea level (Ng & Beswick, 1994). Geological data suggest that the eastern end of the island, which reaches elevations of up to 17 m, has been continuously above water for approximately 2 Myr (F. Burton, pers. comm.). Molecular clock dating of mtDNA sequences suggests that *A. conspersus* arose from *A. grahami* about 2.8 Mya (Jackman *et al.*, unpub. data). Thus, *A. grahami* probably colonized Grand Cayman soon after the island's final emergence from the Caribbean Sea 2–3 Mya. Today, the eastern end of the island is drier than the west (Fig. 2) because (a) it takes the westerly winds directly, (b) much of the ground is porous limestone with poor soil to none at all, and (c) it does not have the benefit of the central mangroves which provide convection-based rainfall to the west. During eastern Grand Cayman's early emergence above sea level it must have been a small mound of largely bare coral containing only low-stature vegetation.

How did the *A. grahami* colonists from Jamaica survive in such an inhospitable environment? *Anolis grahami* is heliophilic and hardy (Wingate, 1965; Rand, 1967; Schoener, 1970; Schoener & Schoener, 1971; Lolis, 1996; pers. obs.), but meeting thermoregulation and water balance requirements still would have been a formidable challenge. Anoles reduce evaporative water loss (EWL) by decreasing skin permeability through the deposition of lipids at the epidermis (e.g. Kobayashi, Mautz & Nagy, 1983; Kattan & Lillywhite, 1989). Nevertheless, EWL increases with increasing temperature and decreasing humidity, and conditions on emergent Grand Cayman must have been sun-baked with little fresh water available. The most direct way to reduce EWL in such an environment would have been to maintain a lower body temperature. This could only be achieved by remaining *in the shade* whenever possible. Notably, *A. conspersus* is a shade species that cannot withstand high temperatures like those preferred by *A. grahami* (e.g. Schoener, 1967; Losos *et al.*, 1993; pers. obs.).

The prospect that EWL was a primary factor in the evolution of a shade-dwelling 'proto-*conspersus*' from the *A. grahami* colonists could be examined experimentally. Hertz *et al.* (1994) used a laboratory apparatus in which light intensity and operative temperature were uncoupled to demonstrate that the behaviorally-thermoregulating *Anolis cristatellus* used light intensity as a direct cue for selecting thermal microhabitats of appropriate temperatures. An experiment in which light, heat, and humidity were independently controlled could determine how EWL

affects thermoregulatory behavior in *A. grahami* and *A. conspersus*, and provide an empirical assessment of the ‘shade-seeking’ hypothesis of dewlap colour change proposed here.

The shade on the emergent Grand Cayman would have been woodland shade to a fault – much like the blue-UV spectrum in the shade of a desert boulder. It therefore may be no coincidence that the world’s only blue iguana (*Cyclura nubila lewisi*), whose skin actually reflects most strongly in the ultraviolet (pers. obs.), is another endemic saurian of Grand Cayman. In contrast, the orange dewlap of the heliophilic *A. grahami* is a long wavelength reflector (Fig. 1), ideal for signalling in sunlight but ill-suited for the blue-UV skylight of woodland/desert shade. If the *A. grahami* colonists spent much time in the shade to reduce EWL, they would have done so at the price of dramatically reducing dewlap signal effectiveness. Selection therefore should have favoured mutations that interfered with deposition of short wavelength-absorbing pigments in the dewlap. It is conceivable that such mutations could spread rapidly through an initially small and localized population.

Initially, the reduction of short wavelength-absorbing pigments would have produced an *all*-wavelength reflector. A whitish dewlap would have been superior to an orange dewlap in short wavelength-biased shade, as at least it would have reflected short wavelengths rather than absorbing them, but would have carried at least two disadvantages: (1) the dewlap colour would covary with changes in ambient lighting conditions, and (2) it would be difficult to detect against bright backgrounds. The evolutionary solution appears to have been the addition of a melanin layer directly above the silvery fascia in the dewlap – a trait that is unique to *A. conspersus* in the *grahami* series anoles (Macedonia *et al.*, 2000). Given that the coloration of the *A. conspersus* dewlap is the product of short wavelength-reflecting iridophores plus melanin, its long wavelength-transmittance spectrum is the virtual opposite of its reflectance spectrum and contrasts strongly with the bright sky (Fig. 13).

Although the elevation of Grand Cayman above the sea floor has been stable for at least the past 0.5 Myr (Vezina, Jones & Ford, 1999), sea levels have fluctuated. Wave-cut notches indicate that the most significant highstand occurred 125 k years ago when the Caribbean Sea was 6 m higher than at present (Jones & Hunter, 1990). The only significant portion of the island remaining above water appears (very roughly) to be about a 40 km² area in the east (estimated from map in Jones & Hunter, 1990).

Predictions

Sea levels began to recede for the last time about 125 k years ago (Jones & Hunter, 1990), and only since this

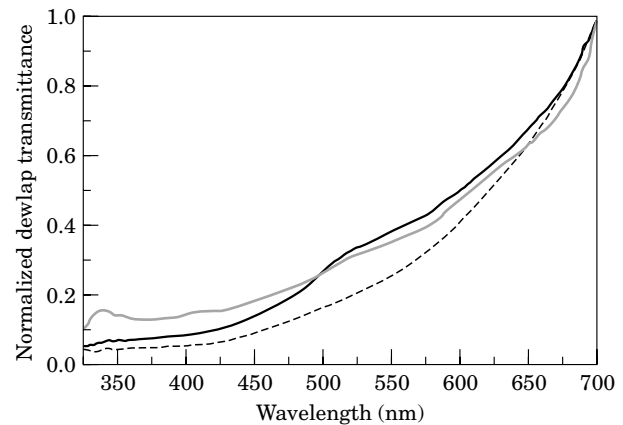


Figure 13. Normalized dewlap transmittance spectrum of *A. conspersus*. Black line: green morph ($n=12$), dashed line: blue morph ($n=9$), grey line: brown morph ($n=7$).

time period could the extensive central mangroves have formed permanently on the island and altered the botanical make-up of western Grand Cayman, especially the southwest, where the green morph occurs. A prediction that follows from these geological and biotic events is that the green morph (*A. c. conspersus*) is a far more recently derived colour form than is the brown morph (*A. c. lewisi*).

A second prediction concerns the blue morph and stems from spectral reflectance data in the present study, and from the literature. The distribution of the brown and blue morphs is contiguous, and the blue morph distribution bypasses that of the green morph along the southwest coast of Grand Cayman as it extends into the northwest corner of the island. Curiously, island-wide observations of *A. conspersus* made in the 1930s only hint at bluish coloration, but solely within the colour description of the brown morph in eastern Grand Cayman (Grant, 1940: 25). In addition, *A. conspersus* from West Bay (Fig. 2) were stated as being ‘yellow-green’ in colour (Grant, 1940: 25). Given that southwestern and western Grand Cayman have undergone enormous development over the past half-century, it is possible that the brown morph’s range has expanded via the coastal highway, with individuals becoming less brown and more blue as they moved ever westward. Between the 1940s and today this range expansion appears to have resulted in the displacement of yellow-green individuals from West Bay, as the ‘green shade’ of closed-canopy forest gave way to the ‘blue shade’ of residential and commercial development (see Endler, 1997). It therefore is predicted that the blue morph in western Grand Cayman is more similar genetically to the brown morph (*A. c. lewisi*) at the opposite end of the island that it is to the green morph (*A. c. conspersus*) which it surrounds.

Population genetics research using modern molecular methods should be able to explicitly test these predictions.

CONCLUSIONS

The primary purpose of this study was twofold: (1) to assess the spectral distinctiveness of the Grand Cayman anole's three colour forms and their light habitats, and (2) to determine if adult male coloration in each colour morph was conspicuous or cryptic. Results of statistical analyses reinforced the differences in coloration between the green and brown morph, as these two forms showed virtually no overlap on any measure. Blue morph reflectance overlapped that of one or the other morphs on nearly all measures. Nevertheless, attributes of blue morph coloration occupied locations in colour space and principle component space that were unique, and discriminant analysis had no difficulty in creating functions that could single out the blue morph from the green and brown morphs. One conclusion drawn from these findings is that the blue morph's greater colour variation may indicate that it lives in more heterogeneous light habitats than do either of the other two colour morphs. A larger sample of irradiance spectra from the habitats of all three colour morphs will be required to test this possibility. Alternatively, given that the blue morph distribution comes into contact with the distributions of the allopatric green and brown morphs, some degree of gene flow may be occurring in the blue morph that is not occurring between the green and brown morphs. This possibility could be examined in a study of *A. conspersus* population genetics.

Results from spectral analysis of the colour morphs' light habitats suggested that body coloration has been selected to take advantage of wavelength biases in each habitat. In addition, analyses of spectral contrast showed that whereas some body regions (typically dorsum and legs) were relatively inconspicuous against the visual backgrounds of bark or leaves, other locations – especially those that are in motion during headbobbing displays – contrasted strongly with the background vegetation. In general, the green morph exhibited strong chroma and good colour contrast with tree trunks but not leaves, the brown morph exhibited weak chroma and good colour contrast with leaves but not tree trunks, and the blue morph showed intermediate chroma and colour contrast but very strong brightness contrast with bark and leaves.

Although the dewlap exhibited the greatest contrast against the visual background, with the exception of blue morph habitat, ambient light was not particularly strong in the wavelengths that would best illuminate this display organ. It seems conceivable that dewlap colour has not kept pace with body colour evolution as

A. conspersus has colonized new habitats. The proposed once-beneficial loss of short wavelength-absorbing pigments from the dewlap might represent a permanent change that has become a workable yet imperfect solution in the contemporary environments of Grand Cayman.

ACKNOWLEDGEMENTS

The following people helped to bring this project about. D. Veale assisted with the collection of *A. conspersus* in 1997, and S. Echternacht provided invaluable field assistance and logistical support in 1998. Glen Gerber corresponded at length about *A. conspersus* colour variation, and Dave Clark provided housing and maintenance for lizards following the completion of data collection. Export of *A. conspersus* was authorized by A. Benjamin, Chief Veterinary Officer, Dept. of Agriculture, Cayman Islands. I thank G. Ebanks Petrie, Dept. of the Environment, for permission to conduct this study, and F. Burton and P. Clifford (1997) for housing arrangements and hospitality. M. Rowe calibrated the irradiance receptor and, along with J. Phillips and L. Fleishman, provided insights on theoretical as well as practical issues regarding the collection and interpretation of spectral data. A. Buerkle kindly wrote a macro to compute colour scores from raw spectral data. This manuscript was improved by comments from G. Burghardt, S. Echternacht and two anonymous reviewers.

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