THE ROYAL SOCIETY

Received 13 September 2001
Accepted 30 October 2001
Published online 11 February 2002

Evidence for habitat partitioning based on adaptation to environmental light in a pair of sympatric lizard species

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Terrestrial habitats exhibit a variety of light environments. If species exhibit evolutionary adaptations of their visual system or signals to habitat light conditions, then these conditions can directly influence the structure of communities. We evaluated habitat light characteristics and visual-signal design in a pair of sympatric species of lizards: *Anolis cooki* and *Anolis cristatellus*. We found that each species occupies a distinct microhabitat with respect to light intensity and spectral quality. We measured the relative retinal spectral sensitivity and found significant differences between the species that correlate with differences in habitat spectral quality. We measured the spectral reflectance of the dewlaps (colourful throat fans used in communication), and found that the *A. cooki* dewlap reflects little ultraviolet (UV), while that of *A. cristatellus* reflects strongly in the UV. For both species downwelling light (irradiance) is rich in UV. However the background light (radiance) is rich in UV for *A. cooki*, but low in UV for *A. cristatellus*. Thus, the dewlap of each species creates a high contrast with the background in the UV. Our findings strongly suggest that these two species are partitioning their habitat through specializations of the visual system and signal design to microhabitat light conditions.

Keywords: *Anolis*; competition; habitat spectral characteristics; signal design; spectral sensitivity; visual ecology

1. INTRODUCTION

Complex habitats, such as coral reefs or forests, are made up of numerous microhabitats which have distinctly different light environments characterized by differences in spectral quality, intensity and geometry of illumination and backlighting (Endler 1993; Marshall 2000). There is evidence that some animals make specialized use of specific light environments. This suggests that the nature and distribution of distinct light environments within an area may influence its community structure and species diversity (Seehausen *et al.* 1997). There are two main ways that diurnally active animals have been shown to specialize according to habitat light. First, the visual system may exhibit adaptations that make it able to function most effectively under certain conditions. For example, it has been shown that in the threespine stickleback (*Gasterosteus aculeatus*), there is a correlation between the spectral sensitivity and the spectral quality of habitat light (McDonald & Hawryshyn 1995). Second, there may be adaptations of animals' signalling systems to maximize their efficiency under very specific light conditions (e.g. Marchetti 1993; Endler & Théry 1996). If an animal can signal with great effectiveness in particular light conditions it can presumably attract mates and defend its territory more efficiently, allowing it to devote more time and energy to other activities, thereby making it an effective competitor in the appropriate microhabitat. If resources are limiting, specializations to habitat conditions can allow species to coexist sympatrically by effectively using different areas of the habitat.

In aquatic systems there are a number of examples of diurnally active species whose visual systems and signalling behaviour are specialized for specific habitat light conditions (e.g. Lythgoe 1979; Endler 1992; McDonald & Hawryshyn 1995; Marshall 2000), and there is some evidence that sympatric species diversity correlates positively with diversity of the habitat light environment (Seehausen *et al.* 1997). In terrestrial systems, Endler & Théry (1996) have demonstrated that rainforest birds in Guyana make use of specific, distinct light environments for signalling. However, to our knowledge there are no known examples where two or more diurnally active terrestrial vertebrate species have been shown to partition a habitat based, primarily, on the light environment. In terrestrial systems heterogeneity of the light environment can be directly correlated with heterogeneity of the vegetation profile (Endler 1993). Therefore, communities composed of highly visual organisms, in which the vegetation profile exhibits a great diversity, should be probable candidates to evaluate the possibility of niche partitioning due to the microhabitat light environment.

Anolis lizards are the most conspicuous, abundant, and diverse diurnal vertebrates that inhabit terrestrial ecosystems on the islands of the West Indies. Anoles have a highly acute visual system, and they rely on vision almost exclusively for social communication, and detection of prey and predators (Underwood 1970; Fleishman 1992). During social interactions anoles communicate exclusively using visual signals, based on motion patterns of the head, and the colourful, expandable throat fan or dewlap (Jenssen 1977). Males display spontaneously, and frequently, from conspicuous perches throughout their territories with motion patterns of the head and dewlap. These displays serve to repel other males from the territory and

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probably help to attract females from some distance away (Fleishman 1992).

West Indian *Anolis* lizards have been extensively used as a model system to study factors affecting community structure. As a general rule anoles are able to occur sympatrically by minimizing species interactions along three main axes: (i) the structural niche, which is characterized by type, height and diameter of preferred perches; (ii) the thermal niche, which is characterized by the range of body temperatures maintained during periods of high activity; and (iii) prey size, which is highly correlated with lizard body size (Hertz & Huey (1981); Losos (1994); Leal *et al.* (1998, and references therein)).

In this paper we study an example that appears, upon first examination, to represent an exception to this general rule. *Anolis cristatellus* is found throughout the island of Puerto Rico. In the dry coastal forests of southwestern Puerto Rico it is found sympatrically with *Anolis cooki*. The habitat in this region grades from dense xeric vegetation inland to small isolated patches of xeric vegetation surrounded by rocky outcrops or sandy areas at the coast. The two species are so similar in appearance that until non-morphological data were collected (i.e. karotype) they were considered a single species (Gorman *et al.* 1968). They have nearly the same body shape and coloration, and the colour of their dewlap is very similar to the human observer. Jenssen *et al.* (1984) quantified the structural niche of the two species in the areas of allopatry and sympatry and found no significant differences between species in the areas of allopatry. However, in the areas of sympatry *A. cristatellus* perched on significantly wider perches than *A. cooki*. However, there was no significant difference in perch height between species. Huey & Webster (1976) observed that *A. cooki* tends to perch in more exposed (i.e. less shaded and less densely vegetated) locations and hypothesized that it occupied a different thermal niche to that of *A. cristatellus*. However, Hertz (1992) tested this idea and found no significant differences between their thermal niches. Although found in microhabitats differing in the amount of shade, both species achieve the same body temperatures through behavioural thermoregulation. Thus this species pair appears to coexist without clear niche differentiation. Due to the lack of clear evidence supporting niche partitioning, Jenssen *et al.* (1984) proposed that this species pair represents an example of competitive interference, in which *A. cooki* has been displaced by *A. cristatellus* to less vegetated, and presumably less optimal, regions of the habitat.

In this paper we explore a different possibility. We hypothesize that *A. cooki* and *A. cristatellus* are dividing the habitat based on differences in the 'light environment' of their respective microhabitats. It is known that differences in vegetation structure result in distinct differences in the spectral quality and intensity of ambient and background light (Endler 1993; Fleishman *et al.* 1997). We propose that *A. cooki* has become specialized to the light conditions characteristic of localities of low vegetation density in which it is normally found.

In order to explore the idea that *A. cooki* and *A. cristatellus* may be coexisting by specializing in different local light environments we examined three aspects of their visual ecology. First, we carefully measured the total intensity and spectral quality of light at locations occupied by individuals of each species (i.e. microhabitat light conditions) to look for evidence of differences. Second, we made electrophysiological measurements of the spectral sensitivity of each species (i.e. visual physiology) to look for evidence of evolutionary specializations of the visual systems to the differences in the spectral quality of habitat light. Third, we measured the spectral reflectance of the dewlaps of males of each species (i.e. signal design) in order to look for evidence that their visual signals showed adaptations for high signalling efficiency under specific microhabitat light conditions.

2. MATERIAL AND METHODS

(a) *Definitions of terms*

In the description that follows we use certain terms that have specific meanings in the context of visual ecology. We define 'intensity' as an objective measure of light measured in units of μmol, where 1 μmol = 6.02×10^{17} photons. 'Brightness' refers to the perceived intensity of an object or scene, and is a function of the intensity and spectral quality of the stimulus, and spectral sensitivity of the observer. We made two kinds of measurements of habitat light. *Irradiance* is a measurement of all the light impinging on a flat surface measured over a hemisphere centred on the surface. This was measured with a cosine-corrected irradiance probe. The probe was always oriented parallel to the ground (i.e. not pointed upward as is more commonly done), so that it measured all the light striking a surface facing out to the side (for example, an extended dewlap, or one eye of an animal looking straight out along the ground). *Radiance* refers to the measurement of light over a small solid visual angle, and is typically used to measure the light emanating or reflecting from a source. We measured radiance with a radiance detector probe, which sampled light over a 4° acceptance angle, directed parallel to the ground. Radiance is used to measure the visual background against which any object is to be detected (e.g. a conspecific dewlap, or a prey item). *Spectral radiance* (or *irradiance*) refers to measurement over a defined range of wavelengths, while *total radiance* (or *irradiance*) refers to the total area under the spectral curve over a defined wavelength range. The units of spectral irradiance are $\mu mol\ m^{-2}\ s^{-1}\ nm^{-1}$, while units of spectral radiance are $\mu mol\ m^{-2}\ s^{-1}\ nm^{-1}\ sr^{-1}$, where sr refers to 1 steridian of solid angle.

(b) *Habitat light*

We sampled lizards at two sites on the southwest coast of Puerto Rico: Bahia Ballena and at the Guanica Dry Forest Reserve, which is located directly across Bahia Ballena. The two species are found sympatrically at both sites. The data were originally collected as part of a study of male signalling behaviour so only male lizards were used in this study. Microhabitat light data were collected on 28–30 July 1997. Data collection was carried out between 08.00 and 18.00 over the two days. Both were sunny days with a nearly clear blue sky, and only occasional clouds. At each site we walked through the habitat slowly looking for lizards. We only took measurements when the lizard we spotted was 2 m or more away and did not appear disturbed by our presence. We observed each lizard until it displayed (any display involving full expansion of the dewlap), or until 10 min had passed without a display occurring. During this time we took careful note of its location and orientation. At the end of each observation we went to the location where the lizard had displayed, or, in the case of no display, to its final location, and

measured light conditions. Data were recorded on 23 *A. cooki* lizards and 20 *A. cristatellu*s lizards. After each observation the lizard was captured (by hand or with a small noose) and its species identity confirmed by inspection of the scale pattern.

Habitat light data were measured with an Ocean Optics PS1000 portable spectroradiometer. Two measurements were taken at each location where a lizard had been observed perching and/or displaying. First we measured spectral irradiance using a 180° acceptance angle cosine-corrected probe attached to the end of the input fibre-optic. Measurements were taken in two opposite directions to measure light striking each eye, or the light striking the dewlap from each side. The irradiance probe was then replaced with a radiance probe and radiance was measured in two opposite directions with the probe pointed parallel to the ground at the approximate position where the lizard's head had been. This measurement was designed to measure the background against which any object would be seen by a lizard looking straight ahead from its perch, or by another individual looking toward the perched lizard.

Data were initially collected over the range 300–800 nm, and were later interpolated to 2 nm intervals and converted to appropriate units for radiance and irradiance based on calibration of the spectroradiometer with a Li-Cor (model 1800-02) radiance and irradiance calibration lamp. Principal components analysis (PCA) was performed on the data, which reduces the number of correlated variables (i.e. intensity at each wavelength) into a small number of orthogonal variables that summarize most of the variation (see Cuthill *et al.* (1999) for a detailed discussion of PCA analysis of spectral data). Prior to PCA analysis we reduced the number of data points for each spectrum by calculating the median value at 20 nm intervals from 300 to 700 nm. We analysed these data in two ways. First we carried out PCA on the original 'uncorrected' data. We then corrected each spectrum for intensity by making the total area under each curve (300–700 nm) equal to 1.0 (method followed that of Endler (1990)) in order to factor out total intensity so that we could compare the shape of the spectra, and carry out PCA analysis on the corrected data. For statistical analyses we considered only PCs that had an eigenvalue higher than 1.0. Principal component scores were analysed using ANOVA.

We originally made measurements for each value in two directions at each site. However, for the PCA analysis we randomly selected one measurement direction from each locale since the measurements in two directions at each site are not independent (this direction was selected independently for both types of light measurement).

(c) *Spectral sensitivity*

We measured spectral sensitivity between 19 January and 3 February 2001 in our laboratory, using lizards collected on 28 December 2000 at the same localities where field data were collected. Lizards were maintained in the laboratory in small individual cages on a 12 L : 12 D schedule. They were fed vitamin-supplemented crickets daily and watered twice daily.

Spectral sensitivity was determined using electroretinographic (ERG) flicker photometry. The technique is described briefly as follows. (For a detailed description, see Jacobs *et al.* (1996) and Fleishman *et al.* (1997).) In this technique an electrical response from the retina is recorded with an electrode placed at the surface of the cornea. The magnitude of this response is proportional to the brightness (perceived intensity) of the stimulus light. A coloured stimulus light is flashed alternately with a broadband white control, the intensity of which is kept constant. The intensity of the coloured stimulus light is adjusted until the response to the coloured stimulus flash exactly matches the response to the white control flash. In this way the relative sensitivity to each wavelength is determined by measuring the intensity required to evoke a response equal to that of the control. Spectral sensitivity was measured in three male *A. cristatellus* and three male *A. cooki*.

At the beginning of each experiment the lizard was anaesthetized with an intramuscular injection of nembutal (0.01 mg g^{-1}) and immobilized with an intramuscular injection of tubocurarine chloride (0.03 mg g^{-1}). The lizard was positioned on its side and respired artificially with a small-rodent respirator through a small plastic tube positioned at the tip of the trachea. The lower eyelid of the eye facing upward was held open with a drop of cyanoacrylate adhesive and a thin film of 2% xylocaine gel (Astra) was spread on the surface of the eye. ERGs were recorded differentially. The active electrode consisted of a small stainless steel tube mounted at the end of a fibre-optic cable through which the stimulus light was delivered, which was brought into direct contact with the surface of the cornea. The indifferent electrode consisted of a stainless steel pin electrode placed in a small slit in the gular region after local application of xylocaine. At the end of the experiment the electrodes were removed, the eye and gular area were rinsed with a sterile saline solution and the eyelid was gently pulled shut. The lizard remained on the respirator until fully recovered from the effects of anaesthesia.

The stimulus to the eye was delivered through the single end of a bifurcated fibre-optic cable. The light passed directly through the small stainless steel tube placed at its end, which also served as the active electrode. The coloured stimuli were created by passing the focused output from a 300 W xenon arc lamp through a 1/8 m monochrometer resulting in monochromatic stimuli (10 nm-1/2 energy passband). The coloured light was collimated, passed through a linearly variable optical density neutral density filter, through a rotating chopper wheel, and was focused into one input end of the bifurcated fibre-optic. A dim control light from a 50 W QTH fibre-optic illuminator passed through a neutral density filter, passed through the chopper wheel and into the other input end of the bifurcated fibre-optic. The two inputs to the fibre-optic were positioned such that the chopper wheel created regularly timed alternate flashes of the coloured stimulus and control at a rate of 7 Hz. At each test the wavelength intensity of the coloured stimulus was adjusted with the variable neutral density filter in steps of 0.1 optical density until the responses to control and coloured light were matched (see Fleishman *et al.* (1997) for details of how this match is determined). The intensity required to achieve this match was determined in 10 nm intervals from 370 to 700 nm. These data were converted to sensitivity (1/[intensity at criterion]) and normalized by dividing all values by the maximum response to produce the relative sensitivity.

(d) *Dewlap spectral reflectance*

In May 2001, five males of *A. cooki* and of *A. cristatellus* were collected from the field sites and brought back to our laboratory in order to measure reflectance properties of the dewlaps. Laboratory care for these animals was as described in the previous section. Each individual was placed in a specially designed holder, which held the head and body steady. The hyoid bone was gently pinched with a pair of fine forceps, whose opening was controlled by a small set screw, mounted on a modified vertically-mounted microscope stage-type manipulator. The

dewlap extended to a natural fully extended position by extension of the hyoid bone. The dewlap was illuminated with light from a 300 W xenon arc lamp passed through a sheet of tracing paper acting as a diffuser. The radiance probe of the Ocean Optics PS1000 spectroradiometer was positioned at an angle of 5° toward the dewlap (we tested, and found there to be no effect of the detector probe angle on reflectance). Prior to taking each measurement a light was passed out through the sampling fibre-optic in order to determine the precise recording area and was turned off before sampling. We took measurements at the centre and bottom edge of each dewlap, which differ slightly in colour. After each measurement was completed the lizard was removed and a calibrated white reflectance standard was placed at the same position and measured. Reflectance was determined by dividing the radiance value at each wavelength for the dewlap by the value at the same wavelength for the white standard.

Data were initially collected over the range 300–800 nm, and were later interpolated to 2 nm intervals. For statistical analysis we determined the reflectance value at four wavelengths: 360, 450, 550, and 650 nm, which can be used to distinguish the spectral characteristics of the dewlaps of the different species. We compared these values for the different species using non-parametric statistics.

Statistical analyses were performed with StatView (v. 5.0.1, SAS Institute Inc., Cary, NC). All probabilities are two-tailed and the significance level for all tests was 0.05. The statistical values for non-parametric tests are corrected for ties.

3. RESULTS

(a) *Habitat light*

Initially, we tested for differences between display and non-display sites within species (as described below), and found no significant difference for either species for any of the habitat light measurements taken. In the analysis that follows, the data for the two types of sites are combined for each species.

The light conditions in the locations at which lizards were observed are summarized in figure 1. Figure 1*a* shows the uncorrected irradiance spectra for both species. For both species the spectrum was fairly broad with no obvious peaks. The intensity was greater across all wavelengths in the *A. cooki* locations. The uncorrected radiance data (figure 1*b*) show a similar pattern of greater intensity across all wavelengths in the *A. cooki* locations, but the shape of the spectrum differs between species. The *A. cristatellus* locations show a clear peak at *ca.* 550 nm, while the *A. cooki* locations show a gradual increase in intensity across all wavelengths. As the *A. cooki* spectrum is fairly broad (i.e. not peaked), while the *A. cristatellus* spectrum peaks at 550 nm, the *A. cooki* radiance is disproportionately more intense in short (300–450 nm) and long (570–650 nm) wavelengths.

PCA for the uncorrected data resulted in a single PC accounting for 92% of the total variation. When the coefficients of this PC were plotted against wavelength, a nearly straight line resulted, indicating that this PC is a measure of total intensity. This PC was significantly different between *A. cristatellus* and *A. cooki* for both irradiance and radiance (table 1).

In order to test for the differences in spectral shape independent of total intensity, we carried out a PCA on the data after correcting for total intensity. For radiance and irradiance two PCs (which we refer to as PC1 and PC2) combined accounted for 85% or more of the observed variation. PC1 correlates positively in the short wavelength section of the spectra (350–475 nm) while PC2 correlates positively in the middle wavelength region (500–570 nm) with a peak value at 550 nm, and negatively in the long wavelength region (570–650 nm). For both irradiance and radiance measurements, *A. cooki* perch sites exhibited significantly greater scores of PC1, whereas *A. cristatellus* perch sites exhibited significantly greater scores of PC2 (table 1).

In summary, radiances in *A. cooki* perch sites have greater total intensity and exhibit a broadband spectrum relatively richer than that of *A. cristatellus* in short and long wavelengths, and without any pronounced peak in the middle wavelengths. *Anolis cristatellus* perch sites tend to

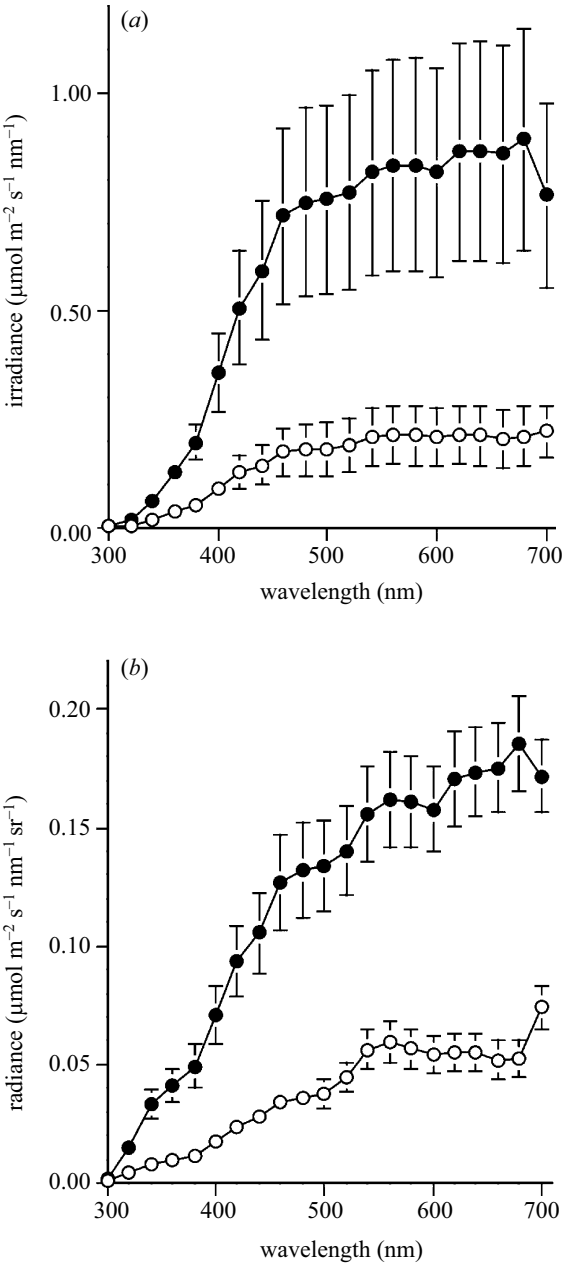

Figure 1. Average spectra from field localities where *A. cooki* (filled circles) and *A. cristatellus* (open circles) were found perching. (*a*) Irradiance spectra; (*b*) radiance spectra. *A. cooki*, $n = 23$; *A. cristatellus*, $n = 20$. Bars indicate ± s.e.

Table 1. Results of one-way ANOVAs for the comparison of the PCA scores from the habitat light measurements of *A. cooki* and *A. cristatellus* habitats.

measurement	d.f.	*F*	*p*
uncorrected data (PC = light intensity)			
irradiance	1,41	7.60	0.008
radiance	1,41	22.79	<0.001
corrected data (PC1 = short wavelengths; UV and blue)			
irradiance	1,41	4.46	0.04
radiance	1,41	5.29	0.03
(PC2 = middle wavelengths; green)			
irradiance	1,41	42.29	<0.001
radiance	1,41	14.95	<0.001

show a peak close to 550 nm. The same pattern occurs with irradiance but the difference in spectral shape is much less pronounced.

(b) *Spectral sensitivity*

The spectral sensitivity measurements based on ERG flicker photometry are summarized in figure 2. The curve for *A. cristatellus* exhibits two small peaks at 380 nm and at 420 nm, followed by a region of increasing sensitivity from 450 to 560 nm, where there is a clear peak in sensitivity. Beyond 560 nm sensitivity declines steadily. The curve for *A. cooki* is quite different. Although there is a measurable sensitivity below 450 nm, the relative sensitivity is less than was seen in *A. cristatellus* and clear peaks cannot be distinguished. Sensitivity rises steadily from 450 nm, but does not exhibit a sharp peak. There is a plateau region from 550 to 600 nm, and the decrease in sensitivity does not begin until 610 nm. At their respective peaks of sensitivity, there are significant differences between *A. cristatellus* and *A. cooki*. At 560 nm *A. cristatellus* is significantly more sensitive (unpaired *t*-test, $t = -2.83$, $p = 0.047$, $n = 6$), whereas at 600 nm *A. cooki* is significantly more sensitive (unpaired *t*-test, $t = 3.17$, $p = 0.034$, $n = 6$). Thus the peak region of the *A. cooki* curve is broader and shifted to longer wavelengths in comparison with *A. cristatellus*.

Figure 2*b* shows the short wavelength portion of the spectrum at greater magnification. While both species exhibit UV (360–400 nm) and short wavelength (400–430 nm) sensitivity, sensitivity appears to be lower in *A. cooki*. However, the differences were not significant at 380 nm (unpaired *t*-test, $t = -0.67$, $p = 0.5$, $n = 6$) or 420 nm (unpaired *t*-test, $t = -2.13$, $p = 0.1$, $n = 6$).

(c) *Dewlap spectral reflectance*

The reflectance spectra for *A. cooki* and *A. cristatellus* dewlaps are shown in figure 3. The dewlaps differ dramatically in the UV (360–380 nm). There are also more subtle differences at longer wavelengths. The long wavelength 'cut-on' (the wavelength at which per cent reflectance moves rapidly from very low to very high) is slightly shifted to a longer wavelength in *A. cooki*. Overall the *A. cooki* dewlap is slightly darker and 'redder' and reflects much less UV. This conclusion is supported by statistical comparison (Mann–Whitney *U*-test in each case, $n = 10$ for each test). There are significant differences between species at both the centre and the edge at 360 nm (centre: $Z = -2.61$, $p < 0.01$; edge: $Z = -2.61$, $p < 0.01$), due to the greater UV reflectance of *A. cristatellus*. At 450 nm there was a significant difference at the edge ($Z = -2.61$, $p < 0.01$) but not at the centre ($Z = -1.57$, $p = 0.1$). For both centre and edge the *A. cristatellus* dewlap showed significantly higher reflectance at 550 nm (centre: $Z = -2.61$, $p < 0.01$; edge: $Z = -2.61$, $p < 0.01$), due to the shorter position of the cut-on wavelength. At 650 nm there was no significant difference at either the centre ($Z = -1.15$, $p = 0.3$) or the edge ($Z = -0.5$, $p = 0.6$).

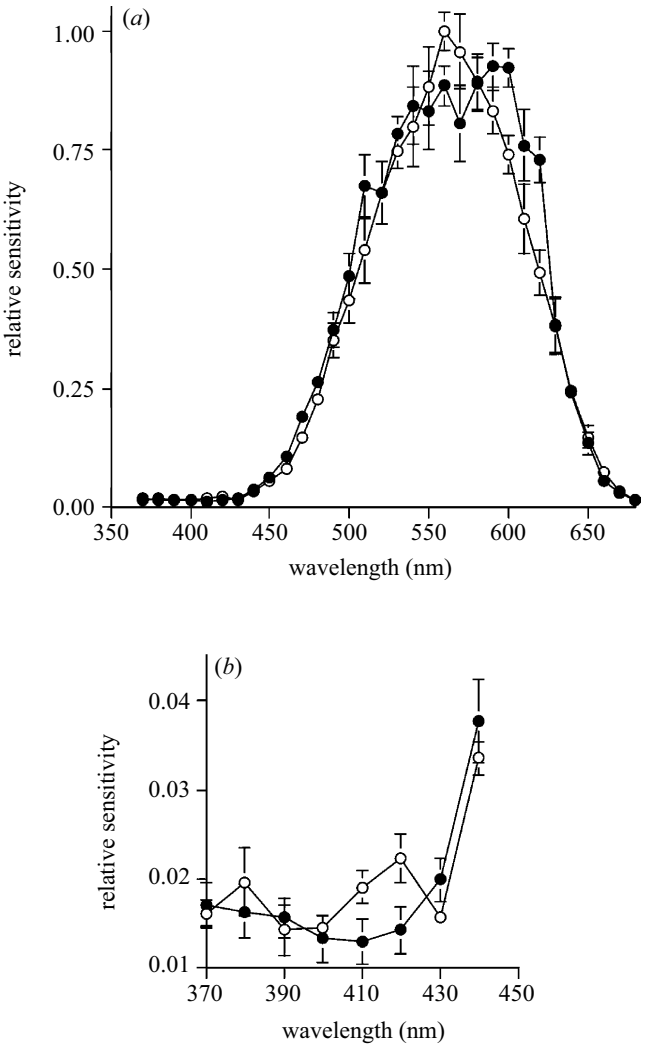

Figure 2. Average spectral sensitivity functions for *A. cooki* (filled circles) and *A. cristatellus* (open circles). (*a*) Spectral sensitivity function from 370 to 700 nm; (*b*) spectral sensitivity from 370 to 440 nm, illustrating the sensitivities at the shorter wavelength. Spectral sensitivity functions are based on three individuals of each species and bars indicate ± s.e.

4. DISCUSSION

West Indian *Anolis* have emerged as a classic example of an adaptive radiation. A primary factor responsible for this radiation has been the ability of anoles to adapt morphologically and physiologically to different features of the environment, and by subdividing the habitat into microhabitats in which each species competes most effectively, as many as 20 species can coexist sympatrically.

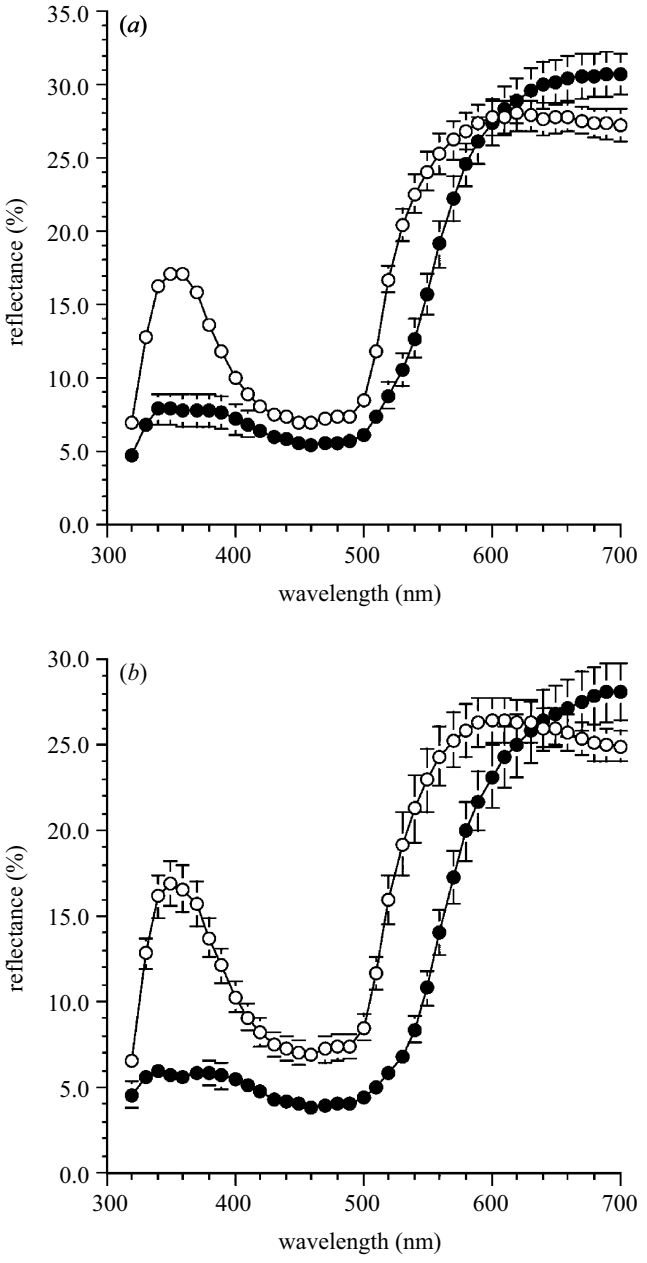

Figure 3. Comparison of the dewlap reflectance spectra of *A. cooki* (filled circles) and *A. cristatellus* (open circles). (*a*) Spectra from the central region of the dewlap; (*b*) spectra from the edge region of the dewlap. The spectra are the average ± s.e. from five individuals per species.

Previous studies have indicated that this partitioning has occurred along three primary axes: structural niche, thermal niche, and prey size. Here we raise the distinct possibility that coexistence may be facilitated by partitioning along a fourth axis—environmental light—resulting from adaptations of signal design and/or sensory system to the microhabitat light environment (i.e. light niche).

Anolis cooki and *A. cristatellus* occupy two distinct microhabitats with regard to habitat light intensity and spectral quality. For irradiance and radiance *A. cooki* microhabitat has a higher intensity (figure 1). *Anolis cooki* occupies a microhabitat in which both irradiance and radiance are spectrally broad. Compared with *A. cristatellus,* the radiance in the *A. cooki* habitat is significantly richer in short and longer wavelengths (represented by PC1, table 1). These differences are due to the relative absence of green vegetation cover at the perching sites of *A. cooki.* There is more direct exposure to blue sky and sunlight and the background radiance is dominated by sand and rocky outcrops, both of which reflect short and long wavelengths effectively. On the other hand, *A. cristatellus* tends to occupy partially open perches that are surrounded by vegetation: in particular, bushes and trees. Because green leaves tend to absorb short wavelengths, in particular UV, and long wavelengths while reflecting maximally at 550 nm (Endler 1993), the microhabitat light environment for *A. cristatellus* (particularly the background radiance) is low in UV but rich in the green region of the spectrum (represented by PC2, table 1).

Anoles rely very heavily on visual motion detection for most aspects of their daily activities (Fleishman 1992). Extensive work on motion sensitivity in many invertebrates and vertebrates has shown that motion detection depends heavily on differences in brightness (i.e. perceived intensity) between the moving stimulus and the background (see Srinivasan 1985; Fleishman *et al.* 1997; Persons *et al.* 1999). Theory suggests that optimal detection will occur when the brightness function (i.e. the spectral sensitivity) matches the spectral shape of the background (Lythgoe 1979; Fleishman *et al.* 1997). If we compare the spectral sensitivity of *A. cristatellus* with the average background radiance we see that both peak at 550 nm (figure 1*b*). The background radiance for *A. cooki* microhabitat is spectrally broader and peaks at a longer wavelength. The spectral sensitivity peak of *A. cooki* is similarly broader and its peak is shifted towards longer wavelengths. Thus there is a clear difference in the spectral sensitivity of these two species, which correlates with differences in the habitat radiance.

Since radiance in *A. cooki* habitat is richer in short wavelengths one might expect to see greater relative sensitivity in *A. cooki* in this range. However, short wavelength photoreceptors (i.e. cones with peak sensitivity at UV and blue) in anoles and other terrestrial vertebrates do not contribute directly to the brightness visual channel involved in motion detection (Fleishman & Persons 2001), and it is this brightness channel that should match the background. The short wavelength photoreceptors are involved in chromatic analysis (i.e. colour vision) independent of brightness (Fleishman & Persons 2001). The apparent reduction in UV and blue sensitivity in *A. cooki* may be due to the fact that in its very intense habitat fewer of these photoreceptors are required to contribute to chromatic sensation, because of the high absolute rate of short wavelength photon flux in the habitat.

A clear difference in spectral sensitivity between *A. cristatellus* and *A. cooki* is, in fact, a surprising finding. Fleishman *et al.* (1997) examined spectral sensitivity in six species of Puerto Rican anoles (including *A. cristatellus* and five other species that are more distantly related to *A. cristatellus* than is *A. cooki* (T. Jackman, unpublished data)), from a variety of different habitats, and found them all to have nearly identical spectral sensitivity functions. They proposed two possible hypotheses for this similarity in spectral sensitivity. First, it is possible that the visual system has been very conservative over evolutionary time, and anoles simply share the same basic visual system regardless of habitat light conditions (i.e. phylogenetic

constraint). Second, although the spectral irradiance and total intensity in the different habitats were quite different, the spectral radiance—i.e. the light quality of the background—was very similar in all six species: dominated by green vegetation. If optimal detection of objects against the visual background is a strong selective force on the spectral sensitivity function, then one might expect the sensitivity functions to be similar for any species from a habitat dominated by green vegetation. Fleishman *et al.* (1997) predicted that if their second hypothesis was true, species from a much more desert-like habitat should have a different spectral sensitivity. The results here seem to support that prediction.

The importance of background radiance as a selection force on spectral sensitivity may help to explain another phenomenon in visual ecology. In aquatic systems there are a number of examples of adaptation of spectral sensitivity (either of specific classes of photoreceptors or of overall sensitivity) to habitat light. In contrast, to our knowledge, this is the first example showing that two closely related terrestrial species have differences in spectral sensitivity that correlate with differences in habitat light (reviewed in Fleishman *et al.* 1997; Briscoe & Chittka 2001). In aquatic systems water colour varies greatly in different habitats and because light must travel through this coloured water the background radiances in aquatic systems tend to differ dramatically (Lythgoe 1979; Marshall 2000). However, in terrestrial systems air is largely transparent. Most terrestrial habitats have a background dominated by green vegetation. There may be much less diversity in background radiance in terrestrial habitats than in aquatic habitats (Chiao *et al.* 2000). A clear prediction from this line of logic is that animals from desert locales where green vegetation is rare should have spectral sensitivities that differ from those occupying greener habitats. The difference we have found between these two closely related species supports this idea.

The underlying basis for the difference between *A. cooki* and *A. cristatellus* in spectral sensitivity is not known at this time. ERG-flicker photometry measures response at the level of the retina. Differences in overall spectral sensitivity could be due to any of the following: (i) pre-retinal filtering by the lens or cornea; (ii) differences in the visual pigments within the photoreceptors; (iii) differences in the photoreceptor oil droplets, which filter the light entering each photoreceptor; or (iv) differences in the relative numbers of different types of photoreceptors or oil droplets. A preliminary analysis of the eye and retina using microspectrophotometry (E. R. Loew, personal communication) has been carried out, and it appears that there is no pre-retinal filtering involved (i.e. the lens and cornea of both species are clear over the wavelengths measured) but there was evidence of each of the other possibilities. There appear to be differences in the relative numbers of different photoreceptor classes (in particular there appear to be fewer UV and short-wavelength-sensitive cones in *A. cooki*), differences in absorption characteristics of oil droplets, and some differences in the absorption characteristics of pigments found in different photoreceptors.

The dewlaps of *A. cristatellus* and *A. cooki* are so similar in appearance to a human observer that they cannot be used reliably to tell the species apart. However, our reflectance measurements show that they are, in fact, quite different. The dewlap of *A. cristatellus* is highly reflective in the UV while that of *A. cooki* is highly absorbing (figure 3). Previous studies have suggested that UV in anoline dewlaps is important for social communication (Fleishman *et al.* 1993). Two non-exclusive hypotheses might account for the evolution of differences in UV reflectance between *A. cooki* and *A. cristatellus*. First, the difference in dewlap coloration might have evolved due to character displacement: in order for *A. cristatellus* and *A. cooki* to occur sympatrically natural selection favours the evolution of differences in dewlap design to facilitate rapid and unambiguous species recognition. Second, the difference in UV reflectance is also consistent with the prediction that selection should favour the evolution of signal components that effectively increase signal detection in the microhabitat in which the signals are commonly given (Endler 1992). The background radiance in the *A. cooki* microhabitat is richer in UV than is the *A. cristatellus* microhabitat (figure 1*b*). A dewlap that absorbs in the UV will contrast effectively with the background. In the *A. cristatellus* microhabitat the background is dominated by green vegetation that tends to absorb UV, and therefore a UV reflective dewlap will stand out well. The use of UV (or lack of UV) to increase signal contrast has been reported for the agamid lizard *Ctenophorus ornatus* (LeBas & Marshall 2000) and for the blue tit *Parus caeruleus* (Anderson *et al.* 1998). Several recent studies have documented the use of UV signals during sexual selection (e.g. mate choice in birds, Bennett *et al.* (1996); Sheldon *et al.* (1999)), and UV signals might also play a role in assortative mating between populations of the lizard *Gallotia galloti* (Thorpe & Richard 2001).

In contrast to previous studies on structural or thermal niche which found no clear differences between the niches of *A. cristatellus* and *A. cooki*, this study demonstrates that habitat spectral characteristics are dramatically different between the microhabitats of *A. cristatellus* and *A. cooki*. Moreover, the interspecific differences found in both visual system and signal design appear to be adaptations to the habitat spectral characteristics present at each microhabitat. Previous research suggested that competition between *A. cristatellus* and *A. cooki* is responsible for the present distribution of *A. cooki* (Ortiz & Jenssen 1982; Jenssen *et al.* 1984). However, there is no clear empirical evidence demonstrating competitive exclusion between *A. cooki* and *A. cristatellus* in the wild. The strongest evidence for competition comes from a study of interspecific agonistic encounters carried out in cages under artificial lighting lacking UV (Ortiz & Jenssen 1982). Under these conditions the most obvious difference in the dewlaps of the two species, the difference in UV reflectance, would not have been visible to the lizards, and the high levels of aggression observed might be artificially elevated because heterospecifics might be mistaken for conspecifics.

We propose that rather than being forced into the occupation of a less heavily vegetated microhabitat by competition with *A. cristatellus*, *A. cooki* is specialized to the light conditions in these microhabitats, and that these adaptations are facilitating resource partitioning along the light environment axis. For example, *A. cooki* might be more effective in detecting movements (e.g. prey items or conspecifics' signals) in its own habitat than in a more vegetated habitat (i.e. *A. cristatellus* habitat) because opti-

mal detection should occur when spectral sensitivity matches the spectral shape of the background. While we have by no means proven that *A. cristatellus* and *A. cooki* are partitioning the habitat based primarily on the light environment, we have shown that the light environments in the microhabitats used by these two species differ significantly and that there are differences in visual physiology and in signal design that should increase the fitness of each species in its own light environment. Moreover the species are closely related, which strongly suggests that the differences between them represent adaptations to their different microhabitats. Under this scenario the distribution of *A. cooki* is limited by its adaptations to highly open microhabitats. However, competition between *A. cristatellus* and *A. cooki* can still occur, and further work is required to sort out the relative contribution of adaptations to habitat light environment versus competition in limiting the distribution of *A. cooki*. In fish communities the light environment axis seems to play an important role in resource partitioning (Marshall 2000). The importance of the light environment axis in terrestrial communities is currently unknown, but the data presented here demonstrate that habitat light can potentially be a very important factor in structuring terrestrial animal communities. Furthermore, because the spectral quality of light in terrestrial communities depends directly on the vegetation profile, the light niche might be particularly vulnerable to habitat disturbance. In the case of *A. cooki,* which has a very limited range and is therefore a species of concern to conservation officials, excessive growth of vegetation, for example by artificial watering, may well threaten its ability to compete effectively and therefore exist sympatrically with *A. cristatellus*.

The authors thank E. R. Loew for providing unpublished data on *A. cooki* retinal composition and three anonymous referees for valuable suggestions. M. H. Persons and M. Canals offered invaluable field assistance. The authors are very grateful to the Departemento de Recursos Naturales y Ambientales of Puerto Rico, which allowed them to work with *A. cooki*. The authors followed the Recommendations for the Care of Amphibians and Reptiles (Pough 1991) in the treatment of all animals used in this study. The research presented here was described in Animal Research Protocol no. 1056 by the Institutional Animal Care and Use Committee of Union College, Schenectady. The research presented here was partially supported by the National Science Foundation (DBI 0001982 and IBN 9902323) to M.L.

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