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Differences in Visual Signal Design and Detectability between Allopatric Populations of *Anolis* Lizards

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ABSTRACT: We tested the prediction of the sensory drive hypothesis using four allopatric populations of the lizard *Anolis cristatellus* from two distinct environments (i.e., mesic and xeric conditions). For each population, we measured habitat light characteristics and quantified signal design by measuring the spectral and total reflectance and transmittance of the dewlap. We used these data to calculate dewlap detectability using an empirically based model of signal detection probability. We found that populations from mesic and xeric conditions occupy two distinct habitats with respect to light intensity and spectral quality and that dewlap design has diverged between populations in a way that increases signal detectability in each habitat. The major difference in dewlap design was in total reflectance and transmittance, making dewlaps from xeric habitats darker and dewlaps from mesic habitats brighter. Furthermore, dewlap detection decreased significantly when a dewlap from a xeric habitat is detected under the spectral conditions of a mesic habitat. The converse is true for a dewlap from a mesic habitat. We propose that sensory drive has promoted divergence in dewlap design in distinct habitat light conditions, and we discuss the possibility that selection might promote early stages of reproductive isolation as a by-product of selection on dewlap design to distinct habitat light conditions.

Keywords: Anolis, sensory drive, speciation, natural selection, signal detectability, population divergence.

Animals communicate with an amazing variety of signals, and even closely related species often exhibit great signal diversity. A number of studies suggest that divergence in communication signals is one factor that can promote speciation (reviewed in Boughman 2002). Moreover, it has been suggested that in genera where rapid and extensive speciation has taken place, signal diversification may have played an important role in promoting species richness. For example, the high rate of speciation among African cichlids has been partially attributed to diversity of body color patterns (Seehausen et al. 1997).

In the last decade, the sensory drive hypothesis has received considerable attention as a mechanism promoting signal diversity between closely related species (Endler and McLelland 1988; Endler 1992; Endler and Basolo 1998; see also Ryan 1990). Sensory drive assumes that there is natural selection for signals to effectively stimulate the receiver sensory system and that the nature of the most effective signal design depends on habitat conditions. Under this scenario, signal diversity evolves because species or populations come to occupy different habitat conditions where selection for effective communication promotes divergence in signal designs. This may occur because differences in habitat conditions favor differences in sensory systems, which in turn select for differences in signal design. Alternatively, differences in habitat noise and transmission properties may favor differences in signal design even if no change occurs in the sensory system (Marchetti 1993).

Under the sensory drive hypothesis, reproductive isolation may evolve as a by-product of selection favoring adaptations for efficiency of communication to distinct ecological conditions, a process that is in accordance with the predictions of ecological speciation (Endler 1977; Schluter 1998, 2000; references therein). Sensory drive can promote early stages of reproductive isolation, which may lead to speciation in at least two ways. First, adaptation for signal detectability in one habitat might reduce signal detectability in another. For example, a male whose territorial displays are adapted to one habitat might be unable to effectively establish and/or defend a territory in another habitat because of a reduction in signal detectability, favoring a possible reduction in gene flow between habitats (e.g., Marchetti 1993). Second, if sensory drive selects for a change in signal design in an aspect of the signal that

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is important for mate choice or species recognition, an individual adapted for one habitat might be unsuccessful at attracting a mate in the other habitat because of a breakdown in recognition (Paterson 1985).

In studies of visual communication, two types of evidence have been collected to infer the role of sensory drive in promoting signal divergence and possibly speciation. First, in a number of instances, it has been shown that visual signal design differences among different species are consistent with the idea that selection has favored more effective visual system stimulation that differs under differing habitat conditions (Marchetti 1993; Endler and Théry 1996; Fleishman 2000; Marshall 2000; Leal and Fleishman 2002). These studies, however, do not directly demonstrate a role of sensory drive in the process of speciation. It is possible that reproductive isolation occurred first and that signal differences arose only after gene flow among populations was largely eliminated (Boughman 2002). Second, in a limited number of cases, it has been shown that signals have diverged between allopatric populations of fishes that occupy distinct habitat conditions (Endler 1980; McDonald and Hawryshyn 1995; Boughman 2001; Fuller 2002). These studies provide the strongest support for sensory drive as a process leading to signal divergence and, possibly, speciation. However, the spectral properties of aquatic systems are quite different than terrestrial systems. Water, unlike air, has a color that causes dramatic differences in visual signal transmission properties (Lythgoe 1979; Lythgoe and Partridge 1989; Chiao et al. 2000). These differences tend to be much more dramatic than the differences that are found in terrestrial systems (see Fleishman et al. 1997; Chiao et al. 2000). Recent studies of habitat light in terrestrial systems have revealed that, except for extreme habitats (see Leal and Fleishman 2002), the spectral quality of terrestrial habitats is composed of a few basic components that are found in nearly all (Endler 1993; Fleishman et al. 1997; Chiao et al. 2000). Furthermore, comparative studies of visual system characteristics of terrestrial animals have revealed that they tend to be extremely conservative, with related species from different habitats exhibiting little or no differences (Fleishman et al. 1997; Briscoe and Chittka 2001; Loew et al. 2002; references therein). Thus, to assess the potential role of sensory drive in the speciation process in terrestrial systems, it is crucial to ascertain whether modest differences in habitat conditions, such as those exhibited by most terrestrial habitats, are sufficient to promote signal divergence between populations that occupied distinct habitats and whether this can occur in the absence of differences in sensory tuning of individuals from different populations.

West Indian *Anolis* lizards have become a model system in evolutionary ecology because of their high species richness, diversity of ecological niches, and what appears to be a high speciation rate (Williams 1983; Losos 1994; Losos and Schluter 2000). Anoles rely almost exclusively on visual cues for social communication (Fleishman 1992). Territorial males frequently signal spontaneously from conspicuous perches throughout their ranges using visual displays that consist of motion patterns of the head, body, and a colorful throat fan called the dewlap. The displays serve to advertise position, to repel other males, and to attract potential female mates (Jenssen 1977; Fitch and Hillis 1984; Tokarz 1995). There is a great deal of variation among species in the color and pattern of the dewlap. Two nonexclusive explanations have been offered for this variation. First, there is evidence that color pattern differences among sympatric species have been selected for by the need for rapid unambiguous identification of species by conspecifics (i.e., species recognition; Rand and Williams 1970; Williams and Rand 1977; Losos 1985; Macedonia and Stamps 1994; Fleishman 2000; Leal and Fleishman 2002). Second, there is evidence that differences in habitat light conditions have selected for different color patterns in different microhabitats (i.e., selection through the process of sensory drive; Fleishman et al. 1993; Fleishman 2000; Macedonia 2001; Leal and Fleishman 2002). However, recent studies have demonstrated that their visual systems are highly conserved across most habitat types (Loew et al. 2002).

In this study, we test whether the process of sensory drive can take place at the population level of a single species: *Anolis cristatellus* from the island of Puerto Rico. *Anolis cristatellus* exhibits a continuous distribution throughout the coastal plains of Puerto Rico, where it occupies two distinct habitat types (Heatwole 1976). Populations inhabiting the southwest coastal plains occupy a dry, sparsely vegetated, xeric habitat, whereas populations inhabiting the northern coastal plains occupy a moist, more vegetated, mesic habitat. The differences in vegetation profile between xeric and mesic habitat are expected to result in differences in the habitat light conditions. Heatwole (1976) noticed some minor differences in overall dewlap coloration between populations from the southwest and those from the north. Throughout its range, *A. cristatellus* has a broad thermal niche and exploits a wide range of structural niches (Heatwole 1976; Huey and Webster 1976). The visual physiology of *A. cristatellus* has been studied previously, and no measurable differences between populations from xeric and mesic habitats have been found (Fleishman et al. 1997; Leal and Fleishman 2002; Loew et al. 2002; M. Leal, unpublished data; E. Loew, unpublished data).

A number of models of the effects of color on signal visibility for animal visual systems have been presented (Endler 1991; Neumeyer 1992; Chittka 1996; Vorobyev and

Osorio 1998), but there is no consensus on which model is most appropriate. However, for *A. cristatellus*, an empirically based model has been developed for assessing the relative visibility of different dewlap designs (Persons et al. 1999; Fleishman and Persons 2001; see "Methods" for a detailed discussion of the model). This empirically based model provides a mechanism for predicting the relative effectiveness with which different signal designs will draw the visual attention of conspecific lizards, which we refer to as that signal's detectability. While signal colors may serve a variety of functions, a signal is useless if it is not initially detected by an intended receiver. Thus, detectability is a critical feature of a visual signal design, no matter what function the signal serves (Dawkins and Guilford 1997; Fleishman 2000).

Anolis cristatellus provides an excellent opportunity to test whether it is possible for sensory drive to operate at the population level within a single species. First, there are populations of *A. cristatellus* that occupy different habitat light conditions. Second, an empirically derived and tested model has been developed to predict the relative detectability of different signal designs under different habitat light conditions. Finally, because we can model dewlap detectability for any known light conditions, we can test whether selection for an increase in detectability in one type of habitat results in reduced detectability in another.

We sampled two populations from mesic habitats in the south and two from xeric habitats in the north and collected two kinds of information. First, we measured the total intensity and spectral quality of the light at locations occupied by individuals of each population. We then collected males from each locality and measured the spectral transmission and reflectance properties of their dewlaps and the spectral properties of their bodies. Second, we modeled the relative visibility of the dewlap design from each population under the light conditions found at each site. If dewlap detectability is a target of natural selection, we predicted that in each habitat the dewlap design of individuals from that habitat should be more detectable than the dewlap design of individuals from other habitats, since the dewlap design should diverge in a way that enhanced detectability in each habitat.

Methods

This study was conducted at two xeric sites, Guanica Dry Forest Reserve (Guanica) and Aguirre Forest Reserve (Guayama), located in the south coastal region of Puerto Rico, and two mesic sites, Cambalache Forest Reserve (Cambalache) and La Vega Forest Reserve (La Vega), located in the northeast coastal region of Puerto Rico. The exact location of these four sites on the island of Puerto Rico is illustrated in figure A1 in the online edition of the *American Naturalist*. The xeric sites lie within Holdridge's Subtropical Dry Forest life zones, whereas the mesic sites lie within Holdridge's Subtropical Moist Forest life zones (Ewel and Whitmore 1973).

Habitat Light

We measured the habitat light environment at each of the four sites. Habitat light data was collected May 10–23, 2001, between 0900 and 1700 hours. We took data over a 2-d period at each of the sites. Data was taken on 31 male lizards per site. We only collected data during sunny days, in which there was 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. 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. The proportion of displaying to nondisplaying lizards at each site was as follows: Guayama, 16 : 15; Guanica, 27 : 4; La Vega, 24 : 7; Cambalache, 26 : 5.

Habitat light data was measured with an Ocean Optics PS1000 portable spectroradiometer. Two types of data were collected at each location where a lizard had been observed perching and/or displaying. First, we measured spectral irradiance (μmol m^{-2} s^{-1} nm^{-1}) using a 180° acceptance angle cosine-corrected probe attached to the end of the input fiber optic. The center of the probe was oriented parallel to the ground. Measurements were taken in two opposite directions to measure light striking the dewlap from each side. The irradiance probe was then replaced with a radiance probe, and radiance (μmol m^{-2} s^{-1} nm^{-1} sr^{-1}, where sr refers to 1 steridian of solid angle) 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 measures the background against which the displaying lizard's dewlap would be seen by another individual looking toward the perch. For a detailed discussion of the purpose of the radiance and irradiance measurements, see Leal and Fleishman (2002).

Data was initially collected over the range 300–800 nm and was later interpolated to 2-nm intervals and converted to appropriate units for radiance and irradiance on the basis of calibration of the spectroradiometer with a Li-Cor 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 (for a detailed discussion of PCA analysis of spectral data, see Cuthill et al. 1999). Before 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 analyzed 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 Endler 1990) in order to factor out total intensity so that we could compare the shape of the spectra, and we carried out PCA analysis on the corrected data. For statistical analyses, we considered only principal components (PC) that had an eigenvalue higher than 1.0. Principal component scores were analyzed using ANOVA. All statistical tests were carried out in Statview 5.0 (SAS Institute 1999).

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

Dewlap Spectral Characteristics

We collected five males from each of the sites and brought them back to our laboratory in order to measure reflectance and transmission properties of the dewlaps. Lizards were maintained in the laboratory in small individual cages on a 12L : 12D schedule. They were fed vitamin-supplemented crickets daily and watered twice daily. We took dewlap spectral data on five individuals from Cambalache, Guayama, and Guanica and on four individuals from La Vega. 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 mounted on a modified vertically mounted microscope stage-type manipulator, allowing us to hold the dewlap in a natural fully extended position.

Dewlap reflection and transmission characteristics are dependent on the geometry of illumination. In order to approximate natural light conditions, we directed a diverging beam from a 300-W xenon arc lamp onto a large sheet of tracing paper (transmissive at all relevant wavelengths) to create a broad circle of diffuse light to illuminate the dewlap. The diffuse illuminating circle was 30 cm diameter. The dewlap was positioned at the center of this circle at a distance of 20 cm. Under these conditions, the radiance probe could be pointed almost directly at the dewlap without any artifacts caused by specular reflectance. The radiance probe of the Ocean Optics PS1000 spectroradiometer was positioned at an angle of 70° with respect to the plane of the dewlap. This angle approximates the view of a conspecific looking nearly directly at the dewlap without blocking the direct rays from the brightest part of the illumination source. For each individual, we took both reflectance and transmission measurements. Before we took each measurement, a positioning light was passed out through the sampling fiber optic in order to precisely determine the recording area. The positioning light was turned off before sampling. Measurements were taken at the center and bottom edges of each dewlap, which differ slightly in color. After each set of dewlap radiance measurements was completed, we measured the spectral irradiance of the light striking the front of the dewlap using a cosine-corrected irradiance probe placed at the position where the dewlap was placed during the measurements. Radiance and irradiance measurements were converted to appropriate values in 2-nm intervals.

For each reflectance and transmission spectrum, we divided the radiance value at each wavelength by the irradiance value for each wavelength of the light illuminating the dewlap to produce a set of values of the radiance-irradiance ratio. This ratio was calculated for two purposes. First, when plotted against wavelength, this ratio gives a curve that is identical in shape to a percent reflectance curve (the standard method of presenting reflectance data) and can also be used to produce an equivalent curve for the transmission spectrum. This plot can be thought of as the radiance of a dewlap when illuminated with light whose irradiance has a value of 1.0 at all wavelengths. Second, this ratio can be used to calculate dewlap radiance for any known habitat irradiance striking the dewlap, simply by multiplying the habitat irradiance spectrum times the radiance-irradiance ratio. This method was used to calculate dewlap radiances under light conditions measured in the field.

We also measured the reflectance characteristics of the body of lizards from each population at a spot located directly over the front limb. Measurements were taken following the same methodology described for the dewlaps.

Modeling Signal Detectability

Persons et al. (1999) and Fleishman and Persons (2001) carried out experiments in which a colored stimulus flag was positioned in the visual periphery of male *Anolis cristatellus*. The flag was briefly moved in then out of view of the animal (or alternatively moved up and down while consistently in view). Detection was assessed by whether or not the viewing animal shifted its gaze toward the stimulus. The probability of detection was then quantified as a function of the contrast in spectral quality and intensity between the stimulus and the background against which

it was viewed. Detection probability was shown to be an additive function of brightness contrast (the difference in perceived intensity between stimulus and background) and chromatic contrast (the difference in spectral quality independent of intensity) between stimulus and background and could be predicted with the following equation:

$$p = 0.40[\mathrm{ABS}(C_B)] + 0.43(C_C) + 0.16,$$

where p = probability of detection and $\mathrm{ABS}(C_B)$ = the absolute value of brightness contrast. Brightness contrast is defined as $(B_s - B_b)/(B_s + B_b)$, where B_s = stimulus brightness and B_b = background brightness. Brightness values were determined by multiplying the spectral radiance of the stimulus or background times the spectral sensitivity over the range 450–700 nm (shorter wavelengths were shown not to contribute to the brightness component of detection). The spectral sensitivity was determined using electroretinographic flicker photometry (for details, see Fleishman et al. 1997; Fleishman and Persons 2001). Note that brightness contrast (C_B) is negative when the stimulus is darker than the background and positive when the stimulus is brighter than the background. Chromatic contrast (C_C) is a quantity based on the lizard's perceived difference in spectral quality, independent of brightness, between the stimulus and background. The details of this calculation are presented in Fleishman and Persons (2001). In short, C_C is an estimate of the difference in relative stimulation of each of the four classes of cone photoreceptors from the *A. cristatellus* retina. The spectral absorption function for each of four known cone classes, corrected for the absorption of their most common oil droplet filters, was normalized to a total value of 1.0. This function was multiplied by each spectrum (e.g., the dewlap spectral radiance or the background spectral radiance). The value for each cone class was then divided by the sum of all four classes to yield a set of relative stimulation values. The relative stimulation of each cone class can be thought of as a point in a four-dimensional space. The chromatic contrast is then defined as the Euclidian distance in this space between the stimulus spectrum and the background spectrum. The data on spectral sensitivity of the four cone classes is based on data from microspectrophotometric analysis of the retina (E. R. Loew, unpublished data; also see Loew et al. 2002). We have also shown elsewhere that there are no measurable differences in the cone photoreceptors or in the spectral sensitivity of anoles from xeric versus mesic habitats (Fleishman et al. 1997; Leal and Fleishman 2002; M. Leal, unpublished data).

The equation above gives the probability of detection under a rather specific set of laboratory conditions (e.g., fixed viewing distance). It is not expected that these probabilities would be precisely the same under field conditions. This calculation will nonetheless provide an accurate prediction of the relative probability of the likelihood of different signals being detected under any given set of light conditions. In this article, we calculated the radiance spectrum of different dewlaps under each measured set of habitat light conditions and then calculated the probability of detection for each dewlap on the basis of the equation shown above. These probabilities are best thought of as a relative index of detection for different signals at any given location rather than as a true probability. In this article, statistical inferences in the comparison of different population dewlaps at each site are only based on the relative value of each population's dewlap at each location measured: the probability of detection value of each lizard at each site was divided by the mean value of the four lizards measured at each site.

As noted above, at each sampling site, the irradiance striking the dewlap from each side was measured as well as the radiance forming the visual background behind each dewlap. From this, we could calculate detection probability for a viewer on either side of the dewlap. To do this, first, the viewer was assumed to be on one side of the dewlap. Second, the irradiance values from the opposite side of the viewer were multiplied for each wavelength by the I/R ratio for dewlap transmittance. Third, the irradiance values from the same side as the viewer were multiplied by the I/R ratio at each wavelength for dewlap reflectance, and the values were added for each wavelength to yield a total dewlap spectral radiance. Fourth, the background radiance from the side opposite the viewer was then used in the detection probability calculation. Fifth, the calculation was then repeated for a viewer on the opposite side of the dewlap.

For the habitat light data from each sampling location, in each population's site, the detection probability was calculated for average dewlaps from each of the four populations. Thus, the data allow us to compare the relative detectability of each of the four dewlap designs at every location. These calculations included the dewlap from the population actually inhabiting that site as well as the dewlaps of the populations from each of the other sites.

The effect of habitat light conditions on dewlap detection probability was determined by calculating the dewlap detection probability for each of the populations under each of the four habitat conditions, using the detection probability model described. The detection probability model gave a detection value for both a right-side viewer and a left-side viewer. We averaged the value between both sides as the detection probability. For statistical analysis, we normalized the detection probability at each measurement location by dividing each value of dewlap detection probability by the mean value for detection probability at

that location. This resulted in a relative detection probability for each dewlap design at each location. In other words, for each measurement location, the dewlap design from each population was given a value (=relative detection value) compared with a mean value set equal to 1.0. We performed ANOVA on these corrected values to test for significant differences in relative detection probability between populations.

Results

Habitat Light

Initially, we tested for differences between display and nondisplay sites within each population and found no significant difference 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 of the populations.

The habitat light conditions for the four sites (populations) are summarized in figure 1. Figure 1*A* shows the uncorrected irradiance spectra of the four populations. For all the populations, the spectrum was broad, with a relative small peak at approximately 550 nm. However, the intensity was greater across all wavelengths for xeric habitats. The uncorrected radiance data (fig. 1*B*) show a similar pattern of greater intensity across all wavelengths in the xeric habitats, but the shape of the spectrum differs between habitats. The radiance spectrum of the mesic habitats is disproportionately more rich in long (570–650 nm) wavelengths. However, for all habitats, the radiance spectrum exhibits a clear peak at 550 nm, which dominates the spectral background.

The PCA for the uncorrected irradiance measurements resulted in a single PC accounting for 95% of the total variation. When the coefficients of this PC were plotted against wavelength, it was a nearly straight line, indicating that it is a measure of total intensity. This PC was significantly different between xeric and mesic habitats, indicating than the light environment of xeric habitats was significantly more intense than mesic habitats (one-way ANOVA; $F = 32.53$, df $= 3, 120$, $P < .001$). Within xeric habitats, total light intensity for the Guayama population was significantly greater than for the Guanica population ($P < .05$; pairwise post hoc analyses, using Bonferroni correction), but there was no difference within mesic habitats. The PCA for the uncorrected radiance measurements also resulted in a single PC accounting for 92% of the total variation. As in the case of the irradiance, a plot of the coefficients of this PC was also nearly a straight line. This PC was also significantly different between xeric and mesic habitats ($F = 18.60$, df $= 3, 120$, $P < .001$). However, unlike irradiance, there were no significant differences within xeric or mesic habitats ($P > .05$; pairwise post hoc analyses, using Bonferroni correction).

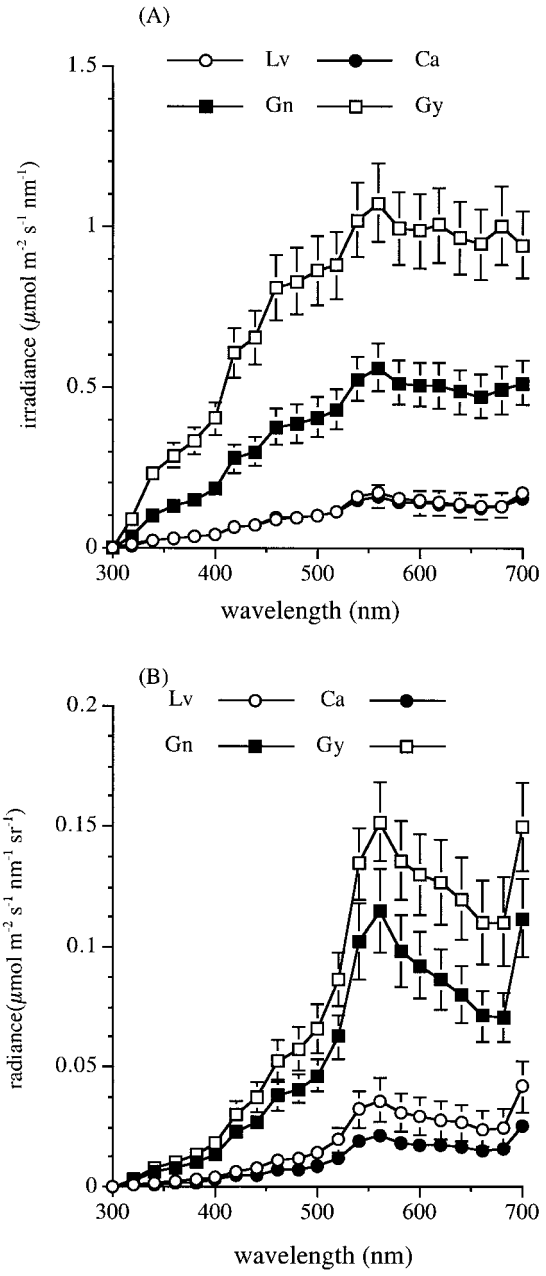

Figure 1: Average spectra of the habitat of populations of *Anolis cristatellus*. *A*, Irradiance spectra. *B*, Radiance spectra. Population abbreviations: *Ca* = Cambalache, *Gn* = Guanica, *Gy* = Guayama, and *Lv* = La Vega. $N = 31$ for each of the sites. Bars indicate ±SE.

In order to test for differences in spectral shape independent of total intensity, we carried out PCA on the data after correcting for total intensity. For irradiance, PC1 and PC2 combined account for 80% of the observed variation.

The PC1 correlates positively with the short wavelength section of the spectra (350–475 nm) and negatively with the long wavelength region (580–660 nm). There were significant differences between xeric and mesic habitats in the scores of PC1 ($F = 12.81$, df $= 3, 120$, $P < .001$). Xeric habitats score significantly higher than mesic habitats in the short wavelength region, while mesic habitats score significantly higher than xeric habitats in the long wavelength region. Therefore, the proportion of short wavelength was significantly higher in xeric habitats, whereas the proportion of long wavelength was significantly higher in mesic habitat. The PC2 correlates negatively in the middle wavelength region (500–570 nm), with a peak value at 550 nm. There were no significant differences between xeric and mesic habitats in PC2 ($F = 0.99$, df $= 3, 120$, $P > .05$). For radiance, PC1, PC2, and PC3 combined account for 90% of the observed variation. In terms of spectral shape, the shape of PC1 and PC2 was the same as the one for the irradiance data. However, there were no significant differences between xeric and mesic habitats in either of the PC's (PC1: $F = 0.76$, df $= 3, 120$, $P > .05$; PC2: $F = 0.76$, df $= 3, 120$, $P > .05$). The PC3 correlates positively with the long wavelengths (580–660 nm), with a peak at 630 nm, and was significantly different between xeric and mesic habitats ($F = 75.67$, df $= 3, 120$, $P < .001$). Mesic habitats exhibited a proportionally greater amount of long wavelength light than xeric habitats.

In summary, for both irradiance and radiance, xeric habitats have greater total intensity than mesic habitats. In overall shape, the spectra from xeric and mesic habitats are quite similar (fig. 1), with a strong peak at 550 nm. There are, however, some subtle differences: the irradiance of the xeric habitats is relatively richer in short wavelengths (UV and blue), while the radiance for the mesic populations is relatively richer in long wavelengths.

Dewlap and Body Spectral Properties

Spectral properties of the center region of the dewlaps are shown in figure 2. The main difference in dewlap reflectance between xeric and mesic populations is in total intensity (fig. 2*A*). Dewlaps from mesic populations reflect more light across all wavelengths than dewlaps from xeric populations. Furthermore, within mesic populations, dewlaps from Cambalache lizards reflect more light than dewlaps from La Vega lizards.

Figure 2*E* shows the dewlap reflectance spectra, corrected for intensity by making the total area under each spectrum (320–700 nm) equal to 1.0, for each of the populations. This reveals differences in the shape of the reflectance spectrum independent of intensity. Dewlaps from mesic populations reflect proportionately more ultraviolet than either dewlap from xeric populations. There are also differences in the wavelength cut-on (the wavelength at which reflectance moves rapidly from very low to very high) and in saturation. The position of the cut-on wavelength is shifted slightly to a longer wavelength in the xeric dewlaps.

The dewlap transmission properties differ dramatically between xeric and mesic populations (fig. 2*B*). Dewlaps from mesic populations are more transmissive across all wavelengths. The corrected transmission spectra for each of the populations are shown in figure 2*F*. Interestingly, the graph reveals no differences between populations in spectral shape.

The same pattern described for the center region was also found at the edge region of the dewlap (fig. 2*C*, 2*D*). However, in the edge region, the differences in reflectance were less pronounced between xeric and mesic populations. In particular, the difference in the cut on wavelengths was less evident. However, the differences in transmission were as dramatic for the edge region as described for the center region.

Unlike the case for the dewlap coloration, there were no clear differences between xeric and mesic populations in body coloration (see fig. A2 in the online edition of the *American Naturalist*). This indicates that differences between populations in dewlap darkness are not simply the result of overall differences in darkness of the body.

Signal Detection

The relative detection probability of the dewlap design of each population was affected by the habitat light conditions under which a dewlap display was viewed. Dewlaps from xeric populations (i.e., Guanica and Guayama) exhibited a higher relative detection probability under xeric habitat conditions, whereas dewlaps from mesic populations (i.e., Cambalache and La Vega) exhibited a higher relative detection probability under mesic habitat light conditions (fig. 3). Furthermore, the relative detection probability of dewlaps from xeric populations decreased when detected under mesic habitat light conditions. The converse pattern is also true for the detection probability of dewlaps from mesic populations. The effect of habitat light conditions on dewlap relative detection probability was confirmed by a significant interaction between habitat light conditions and dewlap design in a two-way ANOVA (center region: $F = 2.38$, df $= 9, 480$, $P = .01$; edge region: $F = 3.45$, df $= 9, 480$, $P < .01$). The same pattern is observed if the mesic and xeric populations are combined for the analysis (center region: $F = 6.53$, df $= 3, 488$, $P < .001$; edge region: $F = 9.56$, df $= 3, 488$, $P < .001$).

Since there were some differences in habitat light conditions among the two mesic habitats and among the two xeric habitats, we tested to see whether there were de-

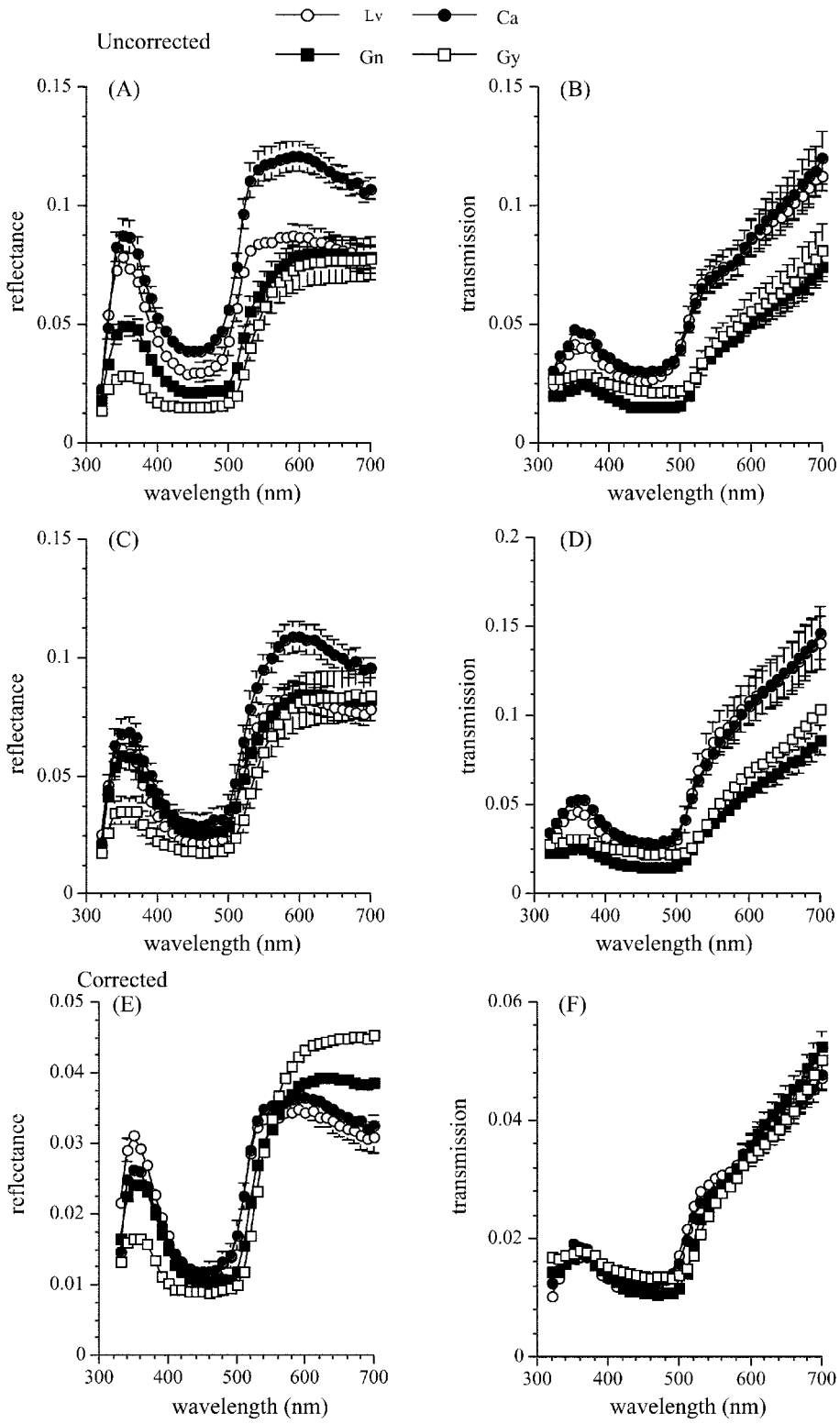

Figure 2: Comparison of the reflectance and transmission spectra for the center and edge region of the dewlap of populations of *Anolis cristatellus*. Uncorrected: (*A*) center reflectance; (*B*) center transmission; (*C*) edge reflectance; (*D*) edge transmission. Corrected: (*E*) center reflectance; (*F*) center transmission. Population abbreviations: *Ca* = Cambalache, *Gn* = Guanica, *Gy* = Guayama, and *Lv* = La Vega. $N = 5$ for Guanica, Guayama, and Cambalache; $N = 4$ for La Vega. The units of the *Y*-axis for corrected and uncorrected reflectance and transmission are radiance/irradiance ratios (see "Methods" for details). Bars indicate $\pm$SE.

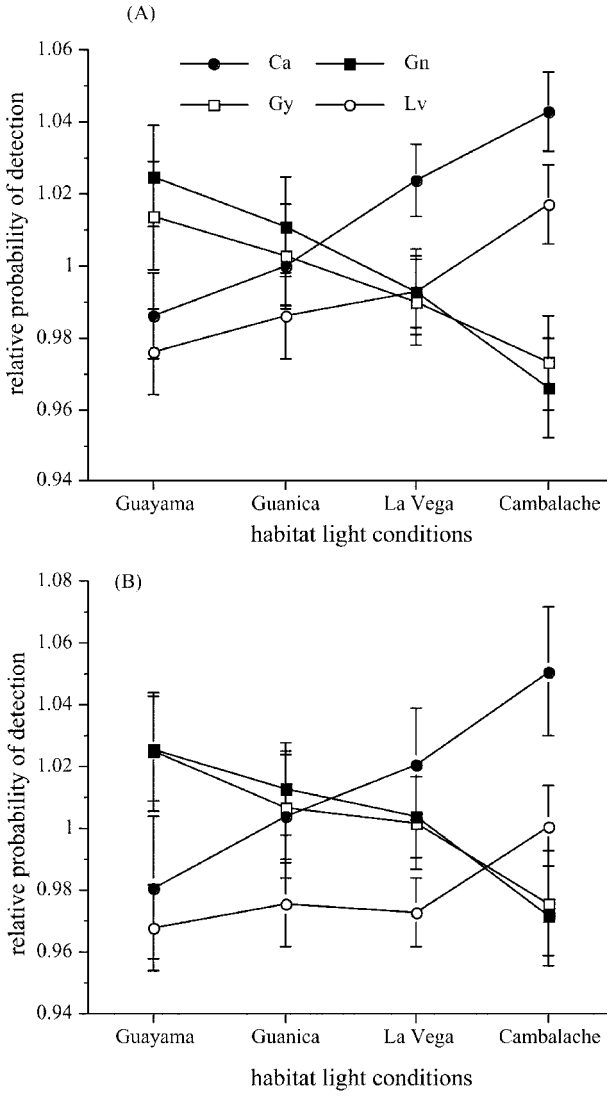

Figure 3: Dewlap relative detection probability for each population of *Anolis cristatellus* as a function of habitat light conditions. *A*, Edge region of the dewlap. *B*, Center region of the dewlap. Habitats are presented in decreasing order of total light intensity. Population abbreviations: *Ca* = Cambalache, *Gn* = Guanica, *Gy* = Guayama, and *Lv* = La Vega. Bars indicate ±SE.

tectability differences for the populations within each habitat type. We tested this possibility by performing a one-way ANOVA for each of the habitats, followed by a post hoc analyses to test for significant pairwise differences with Bonferroni correction. There was no significant difference between dewlaps from xeric populations (i.e., Guanica and Guayama) under any of the habitat light conditions ($P > .05$). In the case of mesic populations (i.e., Cambalache and La Vega), dewlaps from Cambalache exhibited a significantly higher relative detection probability than dewlaps from La Vega at both of the mesic habitats ($P < .05$) but did not differ at xeric habitats ($P > .05$). Thus, we do not see evidence of signal divergence toward increased detectability within mesic habitat or within xeric habitat.

A closer evaluation of the results of the detection model revealed that, although both the chromatic and brightness contrast component of the dewlap design contributed to dewlap detection probability, the significant differences in dewlap detection are primarily the result of the differences in brightness contrast due to habitat conditions. In fact, dewlaps from mesic or xeric populations produce very similar chromatic contrast under all habitat conditions (fig. 4). In the case of brightness contrast, the dewlaps from xeric populations, on average, produce a negative contrast under xeric habitats conditions (fig. 4*B*, 4*D*), whereas the dewlaps from mesic populations, on average, produce a positive contrast under mesic habitat conditions (fig. 4*F*, 4*H*). Because the model for detection probability gives equal weight to positive or negative brightness contrasts, a higher detection probability can be achieved either by being brighter than the background, as in the case of the mesic dewlaps, or by being darker than the background, as is the case with the xeric dewlaps.

Discussion

One of the main factors that has been proposed for generating the great species richness among West Indian *Anolis* is the extensive diversity of dewlap designs (Rand and Williams 1970; Williams and Rand 1977). However, the mechanisms that have favored the evolution of dewlap diversity are poorly understood. Our results suggest that sensory drive may be an important mechanism favoring the evolution of diversity in *Anolis* dewlap designs. Sensory drive predicts that adaptations for efficacy of communication in one environment come at a cost of a decrease in efficacy in another environment (Endler 1992). Our results demonstrate such a trade-off in dewlap detection probability for different populations of *Anolis cristatellus* as a function of habitat light conditions under which the dewlap are observed. To our knowledge, this is the first example showing a habitat-based difference in signal detectability among allopatric populations that occupy distinct habitat conditions in a terrestrial environment.

Light Environment and Signal Detectability

Habitat light characteristics can strongly influence signal efficacy (Marchetti 1993; Endler and Théry 1996; Seehausen et al. 1997; Fleishman 2000). Our results indicate that mesic (i.e., Cambalache and La Vega) and xeric (i.e., Guanica and Guayama) populations of *A. cristatellus* occupy

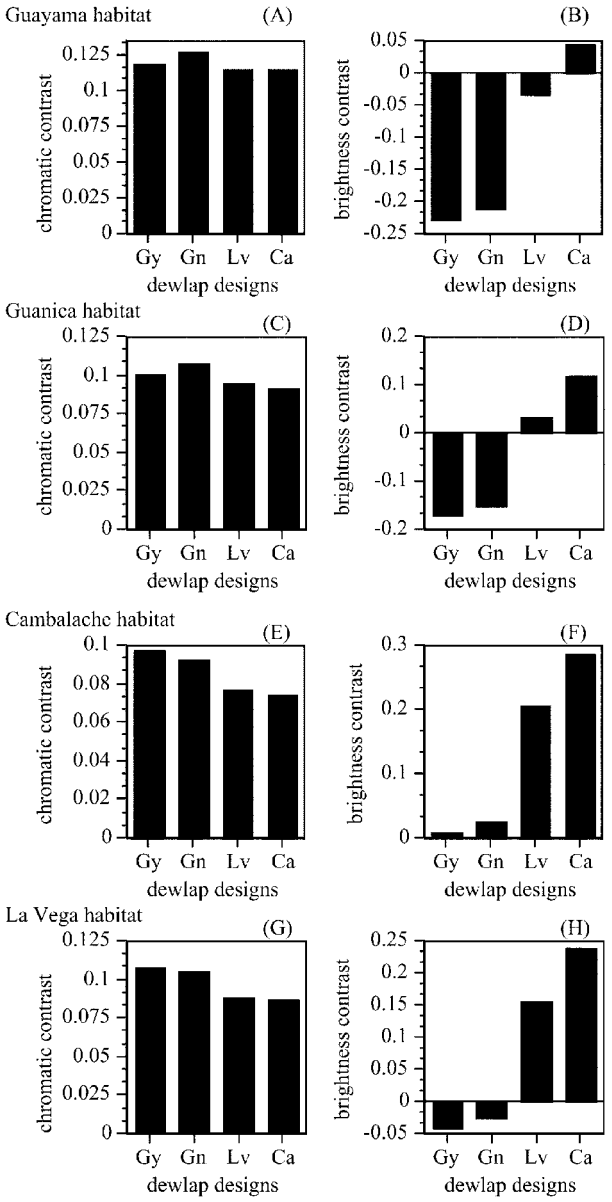

Figure 4: Chromatic and brightness contrasts of the dewlap designs under each of the habitat light conditions. Bars are median values. Population abbreviations: *Ca* = Cambalache, *Gn* = Guanica, *Gy* = Guayama, and *Lv* = La Vega. $N = 31$ for each population.

two distinct environments with regard to habitat light intensity and spectral quality (fig. 1).

The dewlap designs of our four populations fell into two distinct groups. The xeric dewlaps were very similar in total reflectance and transmission (fig. 2*A*–2*D*). They differed only in the ultraviolet range, with the Guanica dewlaps exhibiting greater ultraviolet reflectance. The mesic dewlaps were essentially identical in transmission (fig. 2*B*, 2*D*). In reflectance, the two mesic dewlaps were very similar except that the Cambalache dewlaps exhibited higher total reflectance above 500 nm (fig. 2*A*, 2*C*). The two mesic dewlaps exhibited much greater total transmission at all wavelengths than did the two xeric dewlaps.

Figure 2*E* shows the reflectance spectra for the center region of the dewlaps normalized to the same total intensity. This shows that xeric and mesic dewlaps also exhibited differences in spectral shape. The xeric dewlaps have relatively low UV reflectance, and the cut-on wavelength occurs at a longer wavelength. Under equal lighting conditions, the xeric dewlaps will appear darker and slightly redder (and, to a UV-sensitive animal, relatively lacking in UV) than the mesic dewlaps.

The results of the detection probability model indicated that the light conditions under which a dewlap is displayed had a significant effect on probability of detection (fig. 3). We had predicted that if sensory drive was an important force in selection for dewlap design, each population's dewlap would be most visible at its own site. When we compared xeric and mesic habitat types, the predictions of sensory drive were supported. Overall, the mesic dewlaps are more detectable in the mesic sites, and the xeric dewlaps are more detectable at the xeric sites (fig. 3). Clearly, the differences are most dramatic at Guayama and Cambalache, but the same pattern is observed at the two intermediate sites (La Vega and Guanica). On a broad scale (xeric vs. mesic) then, there are clear differences in dewlap design, and these are consistent with selection for increased detectability under differing habitat light conditions. It is apparent that a lizard migrating from one habitat type to the other (e.g., from Cambalache to Guayama) will be at a competitive disadvantage with local residents because its dewlap would be, on average, harder to detect.

Within habitat type, the predictions of sensory drive were not supported. The dewlaps from the two xeric sites were essentially equal in their detectability at all sites (fig. 3). For the two mesic populations, the Cambalache dewlaps were more detectable than were the La Vega dewlaps at mesic sites including La Vega and were essentially equal in their detectability at the two xeric sites (fig. 3). Thus, within habitat type (mesic or xeric), we did not see evidence for selection to the light condition, perhaps because the differences in light conditions are too subtle to allow this to occur.

The detection model shows that the relative detection probability is determined by two components: brightness and chromatic contrast. In figure 4, these values are plotted for each dewlap in each habitat. This shows that the significant differences in dewlap detection probability are mainly due to differences in dewlap brightness (i.e., total transmission and reflection) between populations. Populations from xeric habitats (i.e., Guanica and Guayama)

have evolved dark dewlaps with relatively low transmission and reflectance at all wavelengths. This design makes them highly detectable in xeric habitats where the background radiance is relatively high, because they form a high negative contrast (i.e., will appear darker than the overall brightness of the background) to the background (fig. 4*B*, 4*D*). The mesic populations have evolved bright dewlaps because of their relatively high reflection and transmission at all wavelengths. This design makes them more detectable in mesic habitats where the background (radiance) habitat light intensity is relatively dark. They tend to be illuminated by downwelling light and show up against the dark background by being brightly lit, especially with transmitted light (fig. 4*F*, 4*H*; see app. B in the online edition of the *American Naturalist* for movie clip illustrating this phenomena). Thus, the major difference in dewlap design that impacts detectability is the overall brightness of the dewlap. There were differences in chromatic contrast between the populations, but these consistently favored the xeric dewlaps. This is because the spectral shape of the background radiance was quite similar in both types of sites, which in both cases were dominated by green vegetation.

We have documented differences in habitat light conditions and dewlap designs in mesic versus xeric habitats, and we have shown that these differences are consistent with the hypothesis that they arose as the result of natural selection for enhanced signal detectability under different habitat conditions. However, we certainly cannot rule out the possibility that the difference in dewlap design originated through some other mechanism, such as genetic drift, or as a pleiotropic effect of selection for some unknown feature (see Schluter 1998, 2000; Boughman 2002). It is also possible that the differences we observed are environmentally induced (Pigliucci 2001), for example, as a result of dietary differences. Although common garden rearing experiments are necessary to test for phenotypic plasticity, it should be mentioned that lizards that we have maintained in the laboratory under common feeding and light conditions for up to 1 yr still exhibit the characteristic differences in dewlap coloration observed in the field populations.

Thus, we cannot say with certainty that the observed differences in dewlap design are the result of natural selection for increased detectability. Nevertheless, we feel these results are important for two reasons. First, we have shown for the first time for a terrestrial system that modest differences in visual signal design can result in significant differences in signal detectability such that individuals are more detectable under the light conditions of their own habitat. Second, if efficient detection by conspecifics in either a mating or territorial defense context is important, then we would expect the observed differences in dewlap design—no matter what their origin—to reduce gene flow between populations, because lizards from one habitat type will experience reduced signaling efficiency when moving to the other habitat type.

Implications for Speciation

The debate about adaptations to divergence in ecological conditions leading to speciation centers around the possible role of natural selection in promoting the early stages of reproductive isolation as a by-product of selection (Endler 1977, 1986; Price 1998; Grant et al. 2000; Rundle et al. 2000; Schluter 2000, 2001). Natural selection as a mechanism promoting speciation should have its strongest impact when the trait that is the target of selection is directly involved in reproductive success (Endler 1986; Schluter and Price 1993; Schluter 2000, 2001).

We propose two nonexclusive mechanisms by which the changes in dewlap pattern could lead to genetic isolation between populations of *A. cristatellus*. First, a decrease in dewlap detectability can decrease the ability of males to successfully reproduce if they migrate to habitats in which the habitat light conditions are different from the ones to which their dewlaps are adapted. Male anoles are highly territorial, and dewlap displays are constantly used to establish and to maintain boundaries of the territory; it has been suggested that mating success might be directly correlated to territory size because females are also territorial and their territories are within the male territory (Rand 1967; Trivers 1976; Stamps 1977; Schoener and Schoener 1982). If a signal has lower detection probability, the lizard will have to display more frequently, increasing energy expenditure and predation risk, or it will face a reduction in territory size. While this mechanism would work only on males, in a number of anoline species it has been demonstrated that most dispersal is by males and that females tend to exhibit a great deal of site fidelity (Rand 1967; Stamps 1977; Andrews and Rand 1983).

Selection for signal detectability might also lead to reproductive isolation through the disruption of the species-specific content of the dewlap. Under this scenario, reproductive isolation could evolve because females or males might be unable to recognize a migrant individual as a conspecific during courtship displays or at least mate preferentially with males exhibiting the more familiar pattern (Paterson 1985; Grant and Grant 2002; Shaw and Parsons 2002). The chromatic content of a signal is likely to be most important for species recognition. We found two differences in the chromatic design of the center of xeric versus mesic dewlaps: a change in long wavelength cut-on and a change in ultraviolet coloration (fig. 2*A*, 2*E*). The observed differences in chromatic content might have arisen as an indirect consequence of selection for differ-

ences in dewlap transmission and/or reflectance. A simple mechanism that could cause the observed differences in total dewlap transmission and reflection would be through differences in the density of a short wavelength absorbing pigment such as a carotenoid. Increasing density of such a pigment would not only cause a darker dewlap, it would also shift the long wavelength cut-on to a larger value (e.g., increased density of a yellow carotenoid pigment tends to cause reddening). Such a change might also tend to mask an underlying ultraviolet-reflecting component causing the observed changes in relative ultraviolet. Differences in carotenoids content is one of the factors causing interspecific differences in dewlap reflectance spectra (Macedonia et al. 2000).

The amount of UV reflectance has been suggested to play a role in the species recognition function of the dewlap (Fleishman et al. 1993; Leal and Fleishman 2002), and UV reflectance pattern has also been suggested to play a role in assortative mating between populations of the lizard *Gallotia galloti* (Thorpe and Richard 2001). Several 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). Disruption in the species recognition complex due to adaptations to ecological conditions leading to reproductive isolation has been suggested for African cichlids (Seehausen et al. 1997), greenish warblers (*Phylloscopus trochiloides*; Irwin et al. 2001), and Darwin finches (Podos 2001; see also Grant and Grant 2002).

Conclusions

The diversity of overall dewlap patterns has been suggested to play an important role in promoting species diversity in anolines. The finding that selection for dewlap detectability may favor signal divergence in allopatric populations of *Anolis cristatellus* in the absence of divergence of the perceptual system suggests that sensory drive may be an important mechanism in the dynamics of the speciation process in *Anolis*. The high species richness of West Indian anoles might be the outcome of the interactions between selection for dewlap detectability and the ability of anoles to exploit a great diversity of habitat conditions that tend to exhibit differences in the habitat light conditions. A diversity of habitat light conditions would provide the opportunity for the sensory drive process to promote dewlap divergence between incipient species occupying different habitats and possibly speciation as a by-product of natural selection favoring adaptations of the dewlap design to a diverse ecological conditions. Finally, selection for signal detectability might prove to be a critical factor in promoting visual signal diversity in terrestrial environments.

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