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ORIGINAL PAPER

Habitat light and dewlap color diversity in four species of Puerto Rican anoline lizards

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Abstract Closely related species often have signals that differ dramatically in design. The evolution of such differences may be important in the process of speciation. Selection for signal detectability under different habitat conditions has been proposed as a mechanism leading to the evolution of signal diversity. We examined dewlap color in four closely related species of *Anolis* lizards that occupy habitats with different light conditions. Initially, we tested the hypothesis that lizards choose specific light conditions within each habitat in which to signal. We rejected this hypothesis for all four species. We next calculated the detectability of the dewlap color of all four species at display locations in each habitat. If selection for detectability under the different light conditions explained the divergence in signal design, the occupant of a given habitat was predicted to have the highest signal detectability in that habitat. However, the rank order of detectability of the four dewlap colors was nearly the same in all four habitats. We concluded that divergent selection for signal detectability does not, by itself, explain the evolution of dewlap color diversity. We hypothesize that the evolution of dewlap color diversity results from simultaneous selection for multiple functions of dewlap color.

Keywords *Anolis* · Vision · Visual signal design · Color · Communication

Abbreviation

SD Standard deviation

Introduction

Animal signals are highly diverse, and even closely related species often exhibit a great deal of signal diversity. Understanding the forces that give rise to this diversity is of great interest because the evolution and maintenance of signal diversity is believed to be critical to the process of speciation and maintenance of species diversity (Boughman 2001, 2002; Rundle and Nosil 2005). In the past few decades neuroethologists and evolutionary biologists have focused on the role that sensory responses have played in the evolution of signal diversity (for reviews see Bradbury and Veherencamp 1998; Johnston 1997; Dangles et al. 2009). Before a signal can serve a function or transmit information, it must be detected by a receiver. The detectability of a signal is highly dependent on the environmental conditions in which the signal occurs. Habitat noise and transmission characteristics will interact with sensory filter properties to determine the relative detectability of different signal designs. If two different populations, or species, occupy different habitats, the properties that most effectively stimulate the sensory system may differ and selection for detectability may drive the signal design of each species

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in a different direction. Thus, selection for signal detectability under disparate habitat conditions might, to at least some degree, explain the evolution of signal diversity among related animal groups. This hypothesis is known as "sensory drive" (Endler and McLellan 1988; Endler and Basolo 1998; Seehausen et al. 2008).

Anolis is an extremely diverse genus of small lizards, with over 300 species that have radiated extensively into a variety of very different habitats. In this paper, we present a study of the influence of signal detectability on the evolution of diversity in the colors of dewlaps of anoline lizards. The dewlap is an expandable throat fan used in a variety of visual displays. The precise functions of the dewlap are not well understood. It is employed during social interactions, including long-range displays and in close-range agonistic and courtship interactions. Some possible functions include stimulating females to become reproductively active (Crews 1977), signaling quality during male–male agonistic interactions (Lailvaux and Irschick 2007), keeping other males away from, and attracting females to the territory (Fleishman 1992). Dewlap color and pattern is widely believed to play a role in species recognition in locations where multiple species are found sympatrically (Williams and Rand 1977; Fitch and Hillis 1984; Losos 1985; Fleishman 2000; Vanhooydonck et al. 2009). It has been speculated that dewlap color plays a role in female mate choice, but this has not been demonstrated experimentally (Tokarz et al. 2005).

The most common use of the dewlap is in so-called "assertion" displays, in which territorial males move about their home range and give spontaneous visual displays from conspicuous perches (Carpenter 1967; Jenssen 1977; Fleishman 1988a, 1992; Stamps 1977). Since the intended receivers of the assertion display are often not close at hand, and typically not attentive to the displaying individual, there should be strong selection on the components of the display to enhance detectability. Assertion displays have been shown to include movement patterns that are particularly effective at eliciting attention at long distances in the presence of habitat noise (Fleishman 1986, 1988b, 1992; Ord et al. 2007; Ord and Stamps 2008).

Light conditions vary temporally and spatially within many habitats. Mobile animals can strongly influence the detectability of their signals by choosing where and when they signal (e.g., Endler and Théry 1996). Anoline lizards are easy to observe as they move about and display frequently. In this study, we were able to record light conditions at the precise times and locations where displays were given, and compare these to randomly selected locations in order to test whether or not individuals actively select specific light conditions in which to display.

The main focus of this study was to examine the role of selection for detectability on the evolution of dewlap color patterns in four closely related species of *Anolis* from Puerto Rico. We tested the hypothesis that selection for signal detectability under distinct light conditions, accounts for the evolution of signal-color diversity. *Anolis* is an excellent group for this test for several reasons. The different species are microhabitat specialists that have diverged into distinctly different habitats with different light conditions (Rand 1964; Fleishman et al. 1995, 1997; Macedonia et al. 2000; Macedonia 2001; Leal and Fleishman 2002) and the evolutionary relationships among the species are well known (Jackman et al. 1999; Nicholson et al. 2005; Losos et al. 2006). Finally, dewlap appearance and detectability can be accurately calculated based on field-collected light data and our detailed knowledge of visual physiology and behavioral response to visual stimuli (Fleishman and Persons 2001; Loew et al. 2002; Leal and Fleishman 2004; Fleishman et al. 2006).

Methods

The four species of Puerto Rican anoles used in this study come from the monophyletic clade shown in Fig. 1, and are all descendents of a single ancestor that colonized Puerto Rico. *Anolis krugi* and *Anolis pulchellus* are sister taxa and *Anolis gundlachi* is one node removed. These species are separated by one node from a cluster of very closely related species with similar body forms and dewlap colors that have only very recently radiated (Rodríguez-Robles et al. 2007; Glor et al. 2009). The most common and widespread of these is *A. cristatellus* (used in this study). A simplified cladogram showing the relationship of the four species in this study is shown in Fig. 2 along with their habitat preferences and dewlap colors. The habitats differ greatly in spectral quality, and the total intensity of light varies by two orders of magnitude from the heavy shade species to the open habitat species (Fleishman et al. 1995, 1997).

Among this group of four species, the two most closely related species, *A. krugi* and *A. pulchellus* have the most different dewlaps in terms of total brightness, chroma and spectral shape. The dewlaps of the other two species fall in between the first two in each of these variables. Thus, within this group of four species there is no evidence that phylogenetic history has constrained dewlap color. Throughout the genus the body colors and overall morphology of anoline lizards have evolved to closely match their habitat, regardless of phylogenetic position, suggesting that body colors evolve quickly. It has been argued that animal colors, in general, tend to evolve rapidly in response to habitat variation (Endler et al. 2005; Stuart-Fox et al. 2007). A recent study of dewlap colors of 140 species of anoles found no evidence for a phylogenetic signal in the evolution of dewlap coloration (Nicholson et al. 2007).

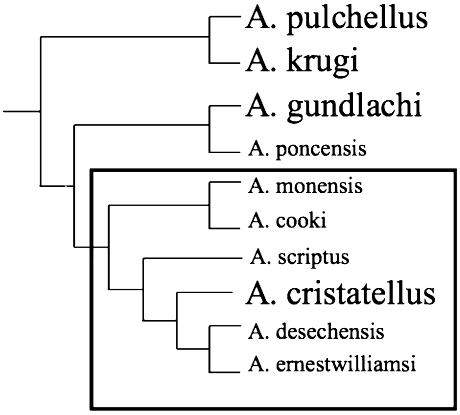


Fig. 1 A diagram of the monophyletic clade that includes all of the four species used in this study based on Nicholson et al. (2005). The species used in this study are shown in *bold* type. The *rectangular box* shows the recently radiated cluster of similar species that includes *Anolis cristatellus*

Thus, these four species have diverged from a common ancestor, and now occupy distinctly different habitats. Each species appears to have occupied its current habitat long enough to have adapted to the point where there is little or no phylogenetic signal for dewlap color within the comparison group. This means that, with respect to dewlap color, we can treat these four species as though they have diverged independently from a single common ancestor.

This allows us to carry out a critical test of the hypothesis that selection for signal detectability in different habitats has accounted for much of the observed difference in dewlap color among the four species. If we calculate the detectability of the dewlap color of all four species in each of the four habitats, the hypothesis predicts that the species that actually occupies a given habitat should have a dewlap that is more detectable than that of its related species under the light conditions of that habitat. In other words, if the

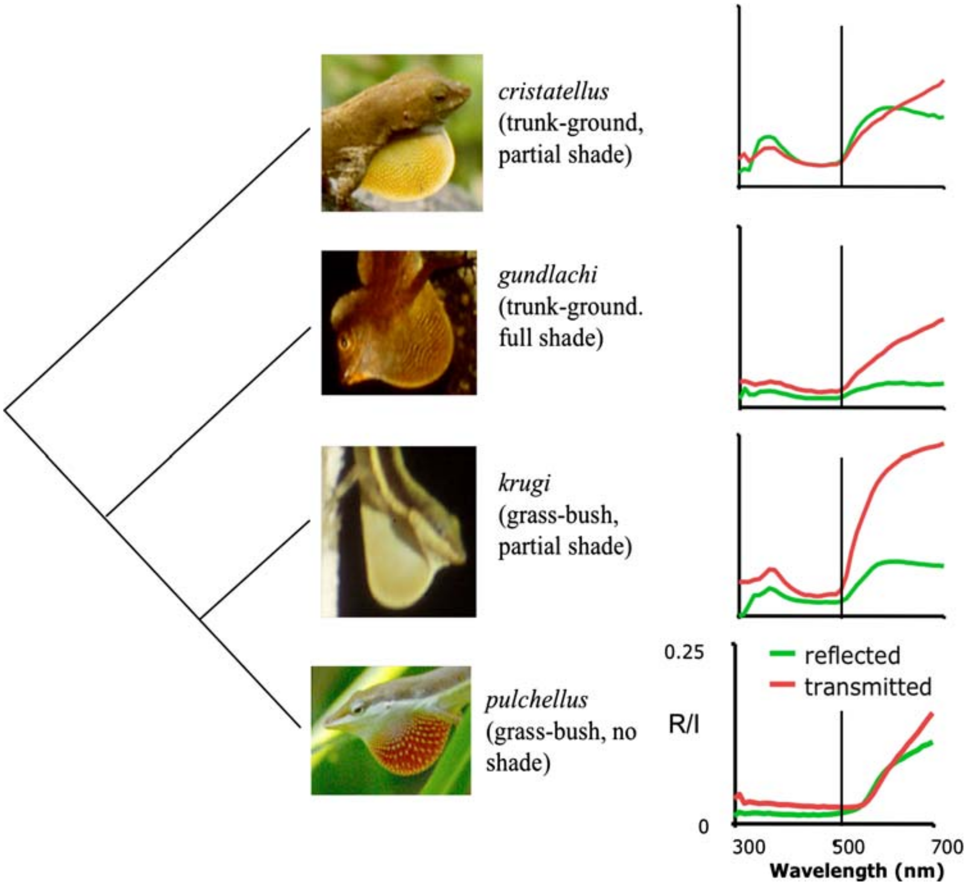


Fig. 2 A cladogram showing the evolutionary relationships of the four species of Puerto Rican *Anolis* lizards (based on Nicholson et al. 2005) used in this study. The dewlaps of adult males are shown along with the typical habitat light conditions and their typical habitat substrate. Dewlap transmission and reflection spectra are also shown in units of radiance/irradiance ratio. This yields spectral shapes that are equivalent to reflectance or transmittance (see text). In each graph there is a vertical line drawn at 500 nm to facilitate comparison. *A. krugi* and *A. cristatellus* have dewlaps with fairly high overall transmission and reflection at wavelengths of 500 nm and longer, making them appear *yellowish*. *Anolis gundlachi* has a spectrally broad dewlap with relatively low reflection and transmission, making it appear *dark brown*. The *Anolis pulchellus* dewlap reflects strongly at long wavelengths (550 nm and longer) and absorbs short wavelengths and therefore appears red, with low overall reflection and transmission

reason that the dewlap colors of the four species are different is that the species have diverged in their habitat preference, and each dewlap has evolved to become more detectable in its habitat, then the dewlap that evolved in a given habitat should be more detectable than any dewlap that evolved in a different habitat. If, alternatively, we find that the dewlap color for each species is not the most detectable in its own habitat, we must conclude that selection for detectability is not sufficient to explain the diversity in dewlap color among these four species.

Animals and field sites

The field data for this study were collected over a 12-day period in August 1997. For each species we selected a sampling habitat in which that species was particularly common. We sampled *A. pulchellus* in two small fields approximately 2 miles N of the El Verde field station located in the Luquillo Experimental Forest in northeastern Puerto Rico. We sampled for *A. gundlachi* in the understory of the closed-canopy rain forest of the Luquillo National Forest adjacent to the El Verde field station. We sampled for *A. krugi*, typically found at forest edges or in medium-sized forest light gaps, near the El Verde field station along a small road and on a plot of privately owned partially cleared forest land. We sampled *A. cristatellus* within the Cambalache Forest Reserve, Barrio Garrochales, Arecibo, located in Northwestern Puerto Rico. This protected forest is dryer and has a lower, more open, canopy than the Luquillo rainforest (Leal and Fleishman 2004).

Sampling of habitat light

For clarity in the explanation that follows we refer to the general area in which we sampled for a given species as a "habitat" (e.g., *A. gundlachi* habitat). We refer to the precise location within a habitat where a light measurement was made as a "location." As detailed below, we sampled from three types of locations: (1) where lizards were observed to display ("display"), (2) where lizards were observed, but did not display ("no display"), and (3) randomly chosen locations ("random").

We sampled throughout the day between 0800 and 1700 hours. In the case of *A. pulchellus* we did not sample midday (1100–1400 hours) because a prior study has shown this to be a period of very low activity (Gorman and Harwood 1977). We sampled under a full range of sky conditions from full sun to full overcast. We did not sample in the rain. We sampled all species approximately half the time under blue sky and half under full or partial overcast. We devoted approximately equal sampling effort to each of the four species. Individuals of some species were easier to locate than others so that our sample sizes differ among the four species (see Table 1).

Light sampling was carried out by two investigators. We walked slowly through the chosen habitat until a lizard was spotted from a distance of at least 3 m. We observed the lizard for up to 10 min. If the lizard gave a dewlap display we immediately moved to the lizard's location and measured light conditions. If the lizard did not display after 10 min we measured light conditions at the location it was first sighted. After measuring the light at the lizard's location, we used a random number table to generate a distance (1–20 paces), direction (one of eight compass points), and height (0–2 m). We moved to this randomly selected location and repeated our measurements. This scheme created the three types of light measurement location: "display", "no display" and "random." The four species chosen spend most of their time within 2 m of the ground. Lizards spotted higher above the ground than 2 m were not used in the study.

We made light measurements with an Ocean Optics PS1000 fiber optic spectroradiometer. At each location we recorded the irradiance of the light striking the dewlap plane, which is perpendicular to the ground, by orienting a 180° cosine-corrected irradiance probe parallel to the ground. We measured in two directions arbitrarily defined by the position of the experimenter as "right" and "left." We then removed the irradiance probe and replaced it with a 4° acceptance angle radiance probe. We measured radiance of the background with the detector oriented parallel to the ground to the right and to the left (we refer to these measurements as "radiance"). We also measured radiance in each direction with the probe pointed upward at 45°, which we refer to as "radiance-up." This represents the background view that would be seen by a lizard below the displaying animal and off to one side, which is relevant because females generally perch lower to the ground than males.

All radiance and irradiance measurements were later converted to quantal units, based on a calibration of the spectroradiometer (once before and once after the field

Table 1 Sample sizes for measurements at "display", "no display" and "random" locations within each habitat

Habitat	Display	No display	Random
A. pulchellus	16	5	21
A. krugi	12	8	20
A. cristatellus	20	8	30[a]
A. gundlachi	10	4	14

[a] The number of random displays exceeds display plus no display because two samples had to be discarded due to equipment malfunctions

work—no change occurred) using a Li-Cor standard irradiance/radiance source. Once converted to appropriate units, spectra were interpolated to three wavelength scales: 2, 10 and 20 nm intervals by taking the median value of the appropriate interval above and below the recorded wavelengths. All graphs of spectra in this paper show 10 nm intervals, and this interval was used in our calculations of signal detectability. For principal components analysis we used 20 nm intervals.

For intensity analyses the area under each curve from 300 to 700 nm was determined to yield total intensity in appropriate units of either irradiance or radiance. For analyses of wavelength spectral distribution, independent of intensity, each spectrum was normalized to an area under each curve equal to 1.0 (as in Endler 1990).

Measurement of dewlaps

Dewlaps were measured in our laboratory in Schenectady, NY after the field study was completed. Five individuals of each species were captured in the field and returned to the laboratory. Each animal was secured in a small holder. The head and nose were held securely in place and the front of the hyoid bone was carefully grasped with the tips of a pair of forceps controlled by a set screw, which were mounted on a two-axis microscope-type motion stage. The dewlap was gently pulled down and away from the animal and held in a natural fully open position. The dewlap was positioned at the center of a 30 cm circle of diffuse white light at a distance of 20 cm. The light was created with a 300 W xenon arc lamp whose beam was allowed to expand and project onto a 1 m square piece of tracing paper. The dewlap was measured with a radiance probe attached to the Ocean Optics PS1000 positioned 10 cm from the dewlap and oriented at an angle of 70° to the dewlap plane. This angle was a compromise—steep enough to represent the view of an animal looking directly at the dewlap, but at enough of an angle to avoid blocking the light illuminating the dewlap. Measurements were made on the same side of the dewlap (reflected light) and on the side of the dewlap opposite the source (transmitted light). Immediately after each set of measurements the animal was removed and spectral irradiance of the source was measured at the former position of the dewlap. Measurements were carried out on five individuals of each species and average values were calculated for use in this study. The variance in these measurements was quite small, and we have demonstrated elsewhere (Leal and Fleishman 2002) that individual variation within populations of these species is quite low.

For each dewlap we determined a radiance/irradiance (*R*/*I*) ratio for each wavelength in 10 nm steps for both reflected and transmitted light. This ratio is useful because it can be multiplied by any known irradiance (e.g., from field measurements) to estimate the radiance of the dewlap for a given light condition. Fleishman et al. (2006) showed that this method produces a good estimate of dewlap radiance under a variety of habitat light conditions, although there is some error for habitat conditions in which the majority of the light is highly directional and located behind the dewlap.

We measured each dewlap at its approximate center and at a point 2 mm proximal to the lower leading edge. In two species (*A. gundalchi* and *A. krugi*) there was no difference between the edge and center. For the other two species (*A. cristatellus* and *A. pulchellus*) the edge consistently yielded higher detectability values than the center, and it is the edge which is viewed in contrast with the background as the dewlap opens or moves. We, therefore, used the dewlap-edge spectra for the analyses we present here for all four species. For comparisons of center and edges of dewlaps see Leal and Fleishman (2004).

Comparison of locations and habitats

The first aim of this study was to test for differences among location types (i.e., display, no display, random) within habitats and for differences between habitats in each measure of light condition. Since two directions of measurement were taken for each variable at each location, we started by randomly selecting either right or left for each location in order to avoid overestimating sample size. For each habitat we tested the hypothesis that there were differences between display, no display and random locations. We compared four measures of light intensity: total irradiance, total radiance, total radiance-up, and radiance/irradiance (*R*/*I*) ratio. *R*/*I* ratio is a measure that quantifies the geometrical arrangement of light intensity. For example, in a habitat where there is proportionally more downwelling light and a background that is relatively dark, the *R*/*I* ratio will be relatively low because the side-welling irradiance includes downwelling light as well as light from the side. In a more uniformly illuminated habitat we would expect a higher *R*/*I* ratio. The radiance and irradiance values were log transformed prior to statistical testing. In order to test for effects of location within each habitat we carried out a one-factor ANOVA for each light intensity variable in each of the four habitats.

We also tested for differences in the wavelength spectrum among the three different location types within each habitat, for the three types of light measurement (radiance, radiance-up and irradiance). We normalized each spectrum and analyzed it using principle components analysis. For details see Leal and Fleishman (2004). For statistical analysis we considered only the first three PC's that had an eigenvalue higher than 1.0. We ran a separate one-factor ANOVA on principle component scores for each PC for radiance, radiance-up and irradiance from each habitat.

After establishing that the three types of location did not differ significantly for any variable (see "Results"), we combined the display, no display, and random locations within each habitat and compared the four different habitats using the same set of measures as described above. For each measure of light intensity (radiance, radiance-up, and irradiance) we carried out a one-factor ANOVA with habitats as treatments. We also compared each of the first three PC's from the PCA analysis by carrying out a one-factor ANOVA on each PC for each of the measures of habitat light.

For each of the ANOVA tests described above, where significant differences were found, we made pairwise post hoc comparisons. Since sample sizes for each treatment were unequal, we used the Scheffe *F*-test, which is not sensitive to unequal sample sizes Zar (1999). Statistical tests were carried out in Statview 5.0 (SAS Institute).

Testing for relative detectability

Fleishman and Persons (2001) demonstrated that the probability of detection of a small moving stimulus presented in the visual periphery is determined by the radiance contrast between the stimulus and the background. Chromatic (i.e., difference in perceived color) and brightness (i.e., difference in perceived intensity) contrast contribute additively to the detection probability.

In order to determine the relative detectability of each dewlap at each location we used a procedure described in detail in Leal and Fleishman (2004). As described above, transmission and reflection radiance/irradiance ratio spectra were determined for the dewlap of each species. For every location we calculated the radiance of the dewlap of all four species (i.e., the dewlap of the species native to a habitat as well as the dewlaps of the three species that occupy the other habitats) for each of two possible viewing directions. Irradiance from the opposite side (away from the viewer) was multiplied by the transmitted dewlap radiance/irradiance ratio. Irradiance striking the dewlap on the same side as the viewer was multiplied by the reflected dewlap radiance/irradiance ratio. These two values were added to yield an estimate of dewlap radiance. This was repeated for a viewer on the opposite side. We then determined the contrast between the calculated dewlap radiance and measured background radiances (level radiance and angle-up) in order to calculate detectability (see below). Detectability was calculated for the average dewlap of each of the four species at every location in all four habitats.

Fleishman and Persons (2001) determined, based on a series of laboratory behavior experiments, that the probability of detection for a moving "dewlap-like" stimulus) can be accurately estimated by the following equation:

$$P(d) = 0.40[\mathrm{ABS}(C_\mathrm{B})] + 0.43(C_\mathrm{C}) + 0.16 \qquad (1)$$

where $P(d)$ probability of detection and $[\mathrm{ABS}(C_\mathrm{B})]$ the absolute value of brightness contrast, defined as $(B_\mathrm{s} - \mathrm{B}_\mathrm{b})/(B_\mathrm{s} + B_\mathrm{b})$, where B_s stimulus brightness and B_b background brightness. Brightness was determined by multiplying the spectral radiance of the stimulus (or background) from 450 to 700 nm (the range of wavelengths that was shown to influence perceived brightness) times the spectral sensitivity of the species of lizard whose dewlap was being tested (Fleishman and Persons 2001). Spectral sensitivity for each of the four species was based on data from electroretinographic flicker photometry (Fleishman et al. 1997). Note that C_B is positive when the stimulus is brighter than the background and negative when the stimulus is darker than the background.

Chromatic contrast (C_c) is an estimate of the perceived difference in spectral quality between stimulus and background, independent of brightness. The details and justification for this calculation are described in Fleishman and Persons (2001) and Leal and Fleishman (2004). Color vision in anoles is mediated by cones with four classes of pigment: UV (ultraviolet), S (short wavelength), M (middle wavelength) and L (long wavelength). Each cone contains an oil droplet that acts as an optical filter. The absorption maxima and spectra for cones and oil droplets of all the species used in this paper are described in Loew et al. (2002). We determined spectral sensitivities for the four cone classes for each species using pigment and oil droplet data from Loew et al. (2002). We used the average maximum absorption values ($\lambda_{\max}$) to calculate an absorption spectrum utilizing Lamb's photopigment template (Mansfield 1985; Lamb 1995), and we multiplied the absorption spectrum times the spectrum of oil droplet usually found in that cone type, normalized to a maximum value of one, following the procedure described in Loew et al. (2002).

Prior to calculating chromatic contrast we corrected for the effects of chromatic adaptation. We used the average side-welling irradiance from each habitat as the typical adapting stimulus. This value was multiplied by the spectral sensitivity of each cone/oil droplet combination (i) to yield a factor k_i. In the subsequent calculations of chromatic contrast the output of each cone class (i) was multiplied by $1/k_i$. This correction assumes that a white stimulus viewed under any average irradiance conditions will yield an equal response from each cone class. This correction, known as von Kries adaptation, introduces chromatic adaptation into our model, which is an

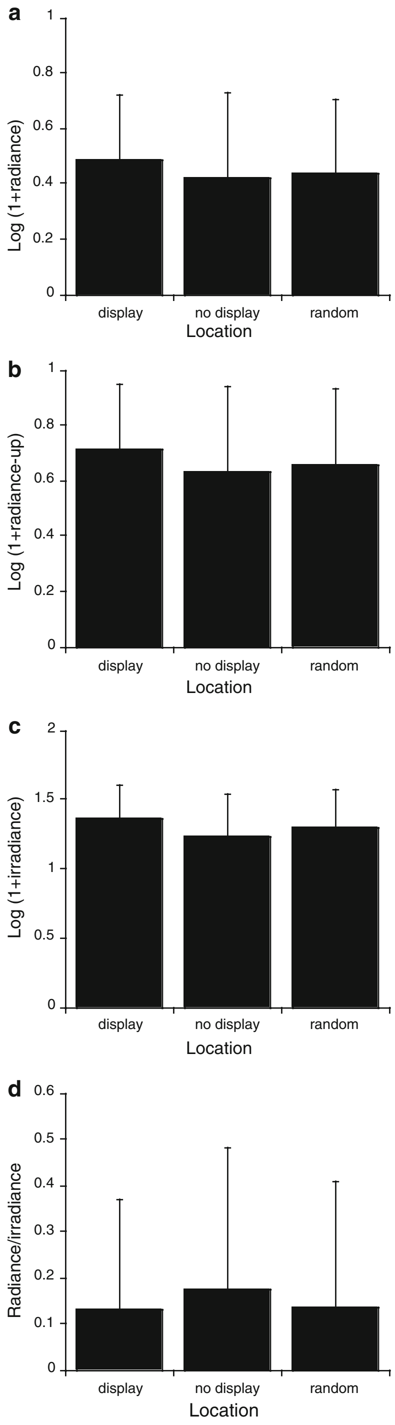


Fig. 3 A comparison of total light intensity for the three different location types for *Anolis krugi*. The location types are “display”, “no display” and “random.” The units for radiance are µmol $\mathrm{m}^{-2}\,\mathrm{s}^{-1}\,\mathrm{sr}^{-1}$ over the spectral range 300–700 nm. The units for irradiance are µmol $\mathrm{m}^{-2}\,\mathrm{s}^{-1}$. In the first three plots the intensity data are log transformed as indicated. *Error bars* indicate 1 SD. **a** Radiance measured parallel to the ground. **b** Radiance-up: radiance measured at an upward angle of 45°. **c** Irradiance. **d** The ratio of radiance (parallel to the ground) to irradiance. Data is shown only for *A. krugi* but the results were very similar for all four species in that there was little or no difference in the intensity of the different location types

important feature of most animal vision systems (Foster and Nascimento 1994; Siddiqi et al. 2004).

To calculate chromatic contrast (C_c) for a given dewlap against a given background, we used the photoreceptor spectral sensitivities for the species whose dewlap we were measuring. We multiplied the dewlap radiance spectrum by each of the chromatically adapted photoreceptor spectral sensitivities. The output from each cone was then expressed as that value divided by the sum of the outputs of the four photoreceptor classes. This created a value between 0 and 1 for each of the four cone types. We repeated this measurement for the background radiance spectrum. Thus, background and dewlap spectral radiance were each represented by a point in a four-dimensional space, where relative stimulation of each cone class is one axis. Chromatic contrast, C_c, is then defined as the Euclidian distance between these two points. Note, because the four cone output values add to one, it is possible to plot these points in a three dimensional, tetrahedral space (e.g., see Endler and Mielke 2005). The two methods are mathematically equivalent (see Fleishman and Persons 2001). There are other, more sophisticated models of chromatic contrast in the literature (e.g., see Vorobyev 2003), but these are designed to calculate chromatic discrimination thresholds and do not provide an estimate of detection probability for chromatic stimuli well above threshold. The advantage of the model presented here is simply that it has been shown, empirically, to provide an accurate estimate of detection probability in anoline lizards (Fleishman and Persons 2001).

For each location we calculated dewlap radiance, and then calculated brightness and chromatic contrast using four different background radiances created by four possible viewing directions: right and left, and radiance-up to the right and left. We used these values to calculate the probability of detection ($P(d)$) for the dewlap of each species at every measurement location. For each species, at each location we used an average of the detection probability for the right and left viewing directions to avoid inflation of sample size. For statistical analysis of probability of detection ($P(d)$) values we carried out an arcsine transformation ($P'(d) = \arcsin \sqrt{(P(d))}$) to better approximate a normal distribution of the data (Zar 1999). We then tested for significant differences in $P'(d)$ of the different species in each habitat with a repeated-measures ANOVA. For each location, the four $P(d)$ values (one for each species) represent a block, and we tested for a significant effect of species. Where significant effects were found based on the omnibus ANOVA test, we made pairwise comparisons using the Tukey test (Zar 1999).

Table 2 *P* values for single factor ANOVA tests for comparisons of "display", "no display" and "random" locations as treatments for the habitat of each species

Habitat	Radiance	Radiance-up	Irradiance	Radiance/irradiance
A. pulchellus	0.82 (2,39,0.20)	0.72 (2,39,0.33)	0.94 (2,39,0.95)	0.62 (2,39,0.48)
A. krugi	0.83 (2,37,0.19)	0.90 (2,37,0.10)	0.92 (2,37,0.08)	0.82 (2,37,0.20)
A. cristatellus	0.60 (2,55,0.52)	0.59 (2,55,0.53)	0.68 (2,55,0.38)	0.39 (2,55,0.96)
A. gundlachi	0.93 (2,25,0.07)	0.60 (2,25,0.517)	0.58 (2,25,0.55)	0.66 (2,25,0.42)

Four measures of intensity were tested. For the habitat of each species, and for each measure of total light intensity a single ANOVA was carried out to test for the effect of location type on the measured light value. For radiance, radiance-up and irradiance values were converted to $\mathrm{Log}_{10}(1 + \text{intensity})$ and then tested for effect of location type. Each value is the outcome of one a single factor ANOVA. Degrees of freedom and *F* value (groups *df*, error *df*, *F*) are included in parentheses under each *P* value

Results

Do lizards seek specific light conditions in which to display?

For all four species we compared "display" to "non-display" to "random" locations for all measures of light intensity and spectral quality. Sample sizes are summarized in Table 1. Typical results are illustrated for one species (*A. krugi*) in Fig. 3. No significant effect of location type was found for any of the intensity variables. Statistical results for all four species are summarized in Table 2. The results presented for *A. krugi* in Fig. 3 are typical of the results for all four species. In no case did we find any significant effect of location type.

We then compared normalized spectral shape across location types. Average normalized spectra (shifted along the *y* axis for clarity of presentation) are shown for *A. krugi* in Fig. 4. There were no differences across location types. These results were typical for all four species. We used principal components analysis to test for effects of location type on normalized spectral shape. The full results are summarized in Table 3. We analyzed irradiance spectra, background radiance spectra and radiance-up spectra for all four species. A significant effect of location type was found in only one case; *A. cristatellus*, radiance-up, PC2. However, this result does not appear to be biologically meaningful. The average spectra for each location type for *A. cristatellus* radiance-up are shown in Fig. 5 and they are very similar in shape, and case pairwise testing of PC2 revealed no significant difference between any two pairs of location types (Scheffe *F*-test). Given the similarity in appearance of the spectra, the lack of significance in pairwise testing, and the fact that no significant effect was found for irradiance or level spectra we believe that the lone significant effect is a statistical anomaly.

Comparisons across habitats

Since we found no evidence of active choice of display sites, we combined display, no display, and random locations from each habitat for subsequent analysis. Results for intensity measures are plotted in Fig. 6. There were significant differences among the four habitats in total irradiance [$P < 0.0001$, $df = (3,164)$, $F = 70$], radiance [$P < 0.0001$, $df = (3,164)$, $F = 34$], and radiance-up [$P < 0.0001$, $df = (3,164)$, $F = 40$]. Pairwise comparisons (Scheffe *F*-test) revealed that there were significant differences between *A. gundlachi* habitat and the other three, and between *A. pulchellus* habitat and the other three for all three intensity measures. There were no significant differences between *A. krugi* and *A. cristatellus* habitat for any of the measurements. There was no significant difference among the habitats in radiance/irradiance ratio (Fig. 6).

In Fig. 7, the data from the normalized habitat spectra are plotted. The PCA analysis for these data is summarized in Tables 4 and 5. There were significant differences in at least two of the three PCs for the three measures: radiance, radiance-up and irradiance. However, as can be seen in Fig. 7 the differences in spectral radiance were very subtle, and unlikely to be of biological significance (also see Fleishman et al. 1997). There were much more substantial differences among the habitats in the irradiance and radiance-up spectra. In more open the habitat, the shape of the spectral curve for average irradiance and radiance-up was broader.

Signal detectability

We determined the detectability of the dewlap of all four species in all four habitats. Since there were essentially no differences in light spectra, intensity or *R*/*I* ratio among display, no display and random locations, we combined these locations within each habitat in order to increase effective sample size.

At every location, in each habitat, we calculated the detection probability ($P(d)$) of each of the four dewlaps when viewed by the visual system of the species whose dewlap we were testing for radiance and radiance-up backgrounds. The average $P(d)$ of the dewlap of each species in each habitat is summarized for the radiance (Fig. 8), and radiance-up (Fig. 9) backgrounds.

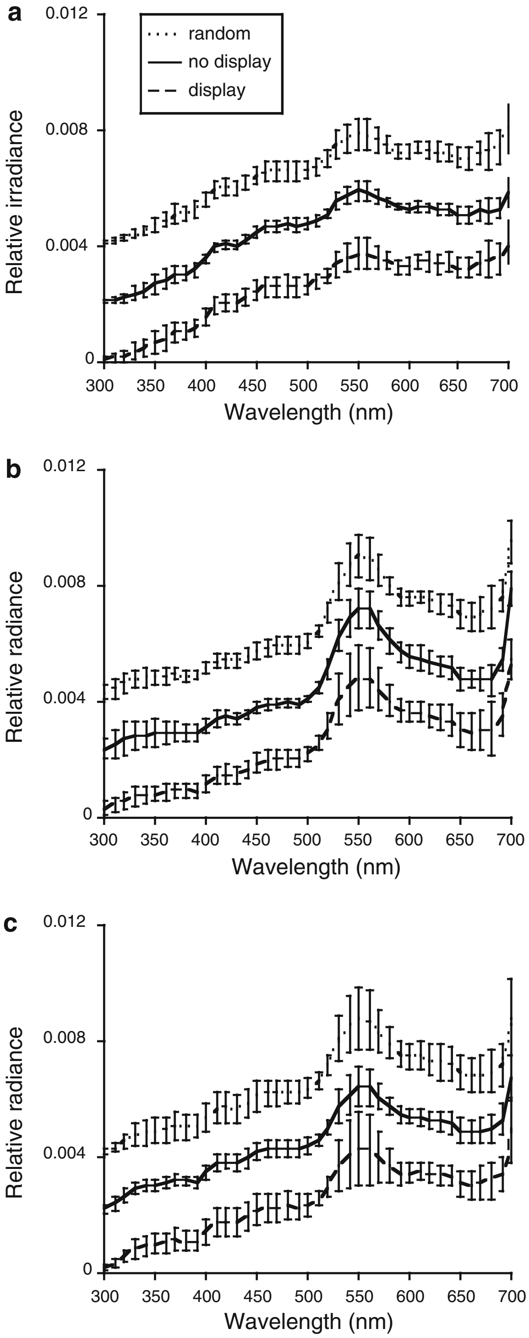


Fig. 4 Comparisons of normalized radiance and irradiance spectra (300–700 nm) from the different location types ("display", "no display", and "random") for the three types of light measurement (radiance, radiance-up and irradiance) for *A. krugi.* Spectra were normalized to a total area of 1.0 under the curve and then averaged. *Error bars* indicate ±1 SD. Within each graph the spectra from the different location types are shifted along the *y* axis for clarity of comparison. The *y* axis units are relative intensity. Plots show **a** irradiance, **b** radiance and **c** radiance-up. The results for *A. krugi* were typical of those for all four species: there was very little difference between location types

We had hypothesized that if selection for signal detectability were responsible for the evolution of among-species differences in dewlap color each species would be most detectable in its own habitat. It is clear from Figs. 8, 9 that this was not the case. For the level radiance background *A. pulchellus* and *A. krugi* were tied (i.e., no significant difference) for the highest detectability across all four species. *A. gundlachi* and *A. cristatellus* had a consistently lower *P*(*d*) than the other two species, across all habitats. There was a significant difference between these two only in the *krugi* habitat (Fig. 8b). For the radiance-up condition *A. pulchellus* had the highest detectability across all four habitats, and *A. gundlachi* was the second most detectable dewlap for all habitats. The overall rank order of the detection probabilities of the different species changed little with habitat.

The data underlying calculations of detection probability are summarized in Fig. 10, which shows the median chromatic and brightness contrast for each dewlap under each habitat condition. *A. pulchellus* consistently had the highest chromatic contrast. Against the level radiance *A. krugi* was consistently brighter than the background, followed by *A. cristatellus*, and the magnitude of the average brightness contrast was greater than that for *A. gundlachi* and *A. pulchellus*, which, for most cases had negative contrast. When viewed against the radiance-up background the darker, less transmissive dewlaps of *A. gundlachi* and *A. pulchellus* had a high negative brightness contrast, while the brighter dewlaps (*A. cristatellus* and *A. krugi*) had a lower negative contrast, with the exception of *A. krugi* which, in its own habitat, had a small positive contrast.

In summary there was little effect of habitat on the rank order of detectability of the different dewlaps. When measured against a level radiance the dewlaps of *A. pulchellus* and *A. krugi* were consistently more detectable than those of the other two species. This was largely due to high chromatic contrast of the bright orange/red *A. pulchellus* dewlap and the very high positive brightness contrast of the *A. krugi* dewlap, which is spectrally broad and highly transmissive and reflective (see Fig. 2). When viewed against radiance-up, the *A. pulchellus* dewlap was consistently the most detectable by virtue of its high chromatic contrast and high negative brightness contrast, while there were no consistent differences among the other three species. The dewlap of *A. gundlachi* also tended to stand out well against the radiance-up background because it is dark and exhibited a high negative brightness contrast with the background.

Table 3 Summary of within-habitat comparisons of different location types for habitat light spectra

Habitat (and *df*)	Location	PC1		PC2		PC3	
		Proportion of variance	*P* (*F*)	Proportion of variance	*P* (*F*)	Proportion of variance	*P* (*F*)
A. gundlachi (2,25)	radiance	0.42	0.70 (0.36)	0.28	0.93 (0.07)	0.22	0.96 (0.04)
	Radiance-up	0.75	0.57 (0.58)	0.15	0.78 (0.35)	0.070	0.51 (0.69)
	Irradiance	0.43	0.99 (0.00046)	0.34	0.79 (0.24)	0.17	0.19 (1.80)
A. cristatellus (2,55)	Radiance	0.45	0.75 (0.29)	0.32	0.08 (2.66)	0.17	0.34 (1.11)
	Radiance-up	0.69	0.60 (0.52)	0.20	0.03* (3.67)	0.081	0.18 (1.78)
	Irradiance	0.42	0.94 (0.06)	0.35	0.96 (0.041)	0.19	0.59 (0.54)
A. krugi (2,37)	Radiance	0.44	0.80 (0.22)	0.29	0.70 (0.36)	0.23	0.60 (0.53)
	Radiance-up	0.62	0.69 (0.37)	0.27	0.50 (0.70)	0.093	0.51 (0.69)
	Irradiance	0.40	0.64 (0.47)	0.32	0.79 (0.24)	0.25	0.50 (0.71)
A. pulchellus (2,38)	Radiance	0.55	0.85 (0.17)	0.26	0.84 (0.17)	0.15	0.23 (1.5)
	Radiance-up	0.70	0.36 (1.06)	0.18	0.09 (2.58)	0.098	0.16 (1.95)
	Irradiance	0.47	0.76 (0.28)	0.35	0.78 (0.24)	0.13	0.54 (0.63)

The results of ANOVA testing for an effect of location type on the normalized spectrum within each habitat using PCA are shown. Each of the first three PC's were tested for each habitat with a single factor ANOVA. A significant effect (indicated by *) was found in only one case: PC2 for "radiance-up" in *A. cristatellus* habitat. Degrees of freedom are the same for all tests on each species and are indicated in parentheses under the species name. *F* values are listed in parentheses after each *P* value

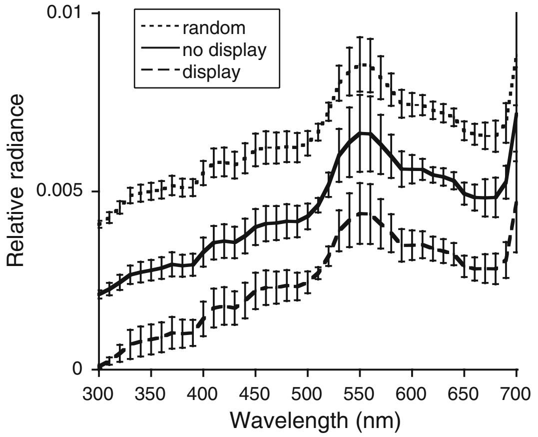


Fig. 5 Normalized spectra from *Anolis cristatellus* for the three different location types for "radiance-up." *Error bars* indicate ±SD. The spectra from the different locations are shifted along the *y* axis for clarity

Discussion

In this study, we asked two key questions regarding the role of habitat light conditions in the evolution of signal-color diversity in anoline lizards. First, do individual lizards actively seek display sites that are a non-random subset of the available light environments within a habitat in order to display? Second, are species differences in dewlap color the outcome of divergent selection for high detectability under the different habitat light conditions? We found that within each species, display locations were random with respect to available habitat light. We did not find evidence to support the idea that selection for high detectability in different habitat light conditions was mainly responsible for the observed diversity in dewlap colors.

A key feature of visual signaling systems in which sensory drive has been previously tested is that the displaying individuals choose locations and/or times which improve the detectability of their signals. For example, in various species of lekking birds, males choose sites with specific habitat light conditions to enhance the effectiveness of their signals (Endler and Théry 1996; Heindl and Winkler 2003; Uy and Endler 2004), bower birds orient and decorate their display courts so that the sunlight falls on their decorations in a way that enhances overall detectability (Endler et al. 2005), and male guppies display preferentially at times of day that enhance visibility of their signal colors (Endler 1991). In the four species of anoline lizards tested here, displays occurred randomly with respect to available light conditions. The fact that anoline lizards do not choose specific light conditions in which to display may be explained by the nature of their social structure. Male anoles are highly territorial and move throughout their territories displaying regularly (Fleishman 1992; Jenssen 1977; Lovern and Jenssen 2003) in order to prevent encroachment by neighbors. If male anoles are obligated to display throughout their territory and throughout the day, and if there is considerable fine-scale variation in the light conditions, they may not have the option of choosing specific display locations within the territory. This is not the case for lekking birds, bower birds

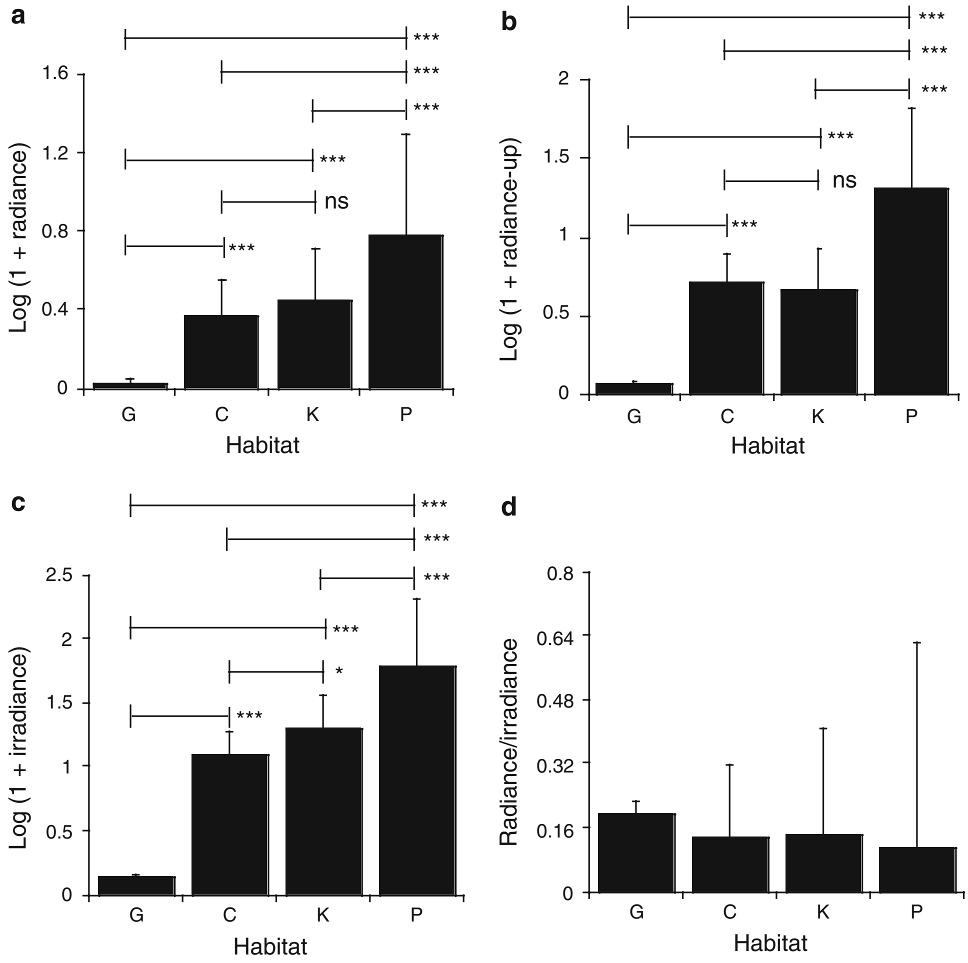


Fig. 6 A comparison of the measures of intensity across the different habitats. In the first three graphs the intensity has been log transformed. *Error bars* indicate 1 SD. Results of pairwise statistical tests are indicated to the right of the *horizontal lines* connecting pairs of means (Scheffe *F*-test): $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, and *ns* no significant difference. The plots are **a** radiance, **b** radiance-up, **c** irradiance and **d** radiance/irradiance ratio. In **d** there was not a significant difference across habitats, so no pairwise comparisons are shown. The species are indicated by letters as follows: *P pulchellus*, *K krugi*, *C cristatellus* and *G gundlachi*

or guppies whose displays are directed only at potential mates, and are not used for territorial defense. Unlike anoles, these animals can display in specific places and/or times.

In the second part of this study, we tested the hypothesis that selection for increased signal detectability in different habitats explains the evolution of the observed diversity of dewlap colors. We predicted that if the dewlap colors of these four related species have diverged primarily due to selection for increased detectability in each habitat, then each species' dewlap should be, on average, more detectable than the other three under its own habitat light conditions. Examination of Figs. 8 and 9 reveals that our results did not support this prediction. The relative ranking of probability of detection of the dewlaps of the different species showed little change when tested under the light conditions of the different habitats.

The first question that this result raises is: why is there little change in the relative detectability of the dewlaps across habitats? The answer appears to relate to the nature of the differences in habitat light, and the critical factors that determine dewlap detectability. Detection probability is a function of contrast between stimulus and background and, over the range of intensities that anoles are active, does not depend on total light intensity (Persons et al. 1999; Fleishman and Persons 2001). Leal and Fleishman (2004) showed that if irradiance striking the dewlap is high relative to background radiance, highly reflective and transmissive dewlaps (i.e., "bright dewlaps") are more detectable, because they achieve high positive brightness contrast against the relatively dark background. If background radiance is relatively high compared to irradiance, dark dewlaps (i.e., with low reflection and transmission properties) are favored because they create a strong negative brightness contrast with the relatively bright background. The key variable which determines which of these two possibilities will be favored is the ratio of the background radiance to the irradiance striking the dewlap (radiance/irradiance ratio). In Fig. 3, we see that although light intensity changes dramatically across habitats, the irradiance and background radiance scale together resulting in the outcome, shown in Fig. 3d: the *R*/*I* ratio is equivalent

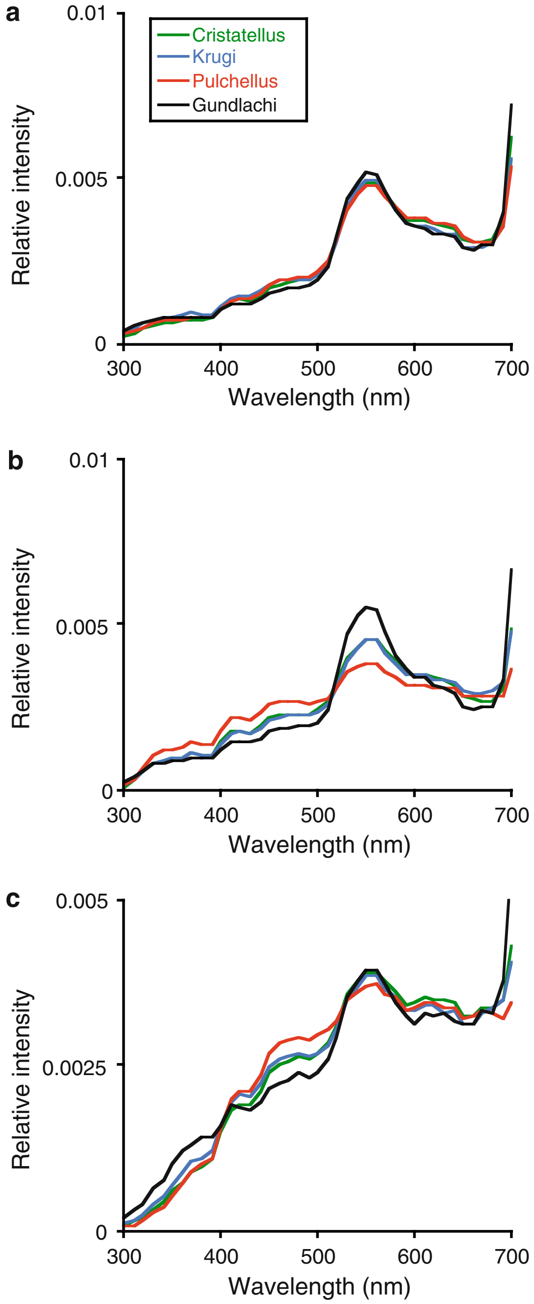


Fig. 7 Comparisons of normalized spectra from the four different habitats. All locations were combined for each habitat: **a** radiance, **b** radiance-up, **c** irradiance

across the four habitats. The consequence of this can be seen in Fig. 10. As we move across habitats the relative brightness contrast of the dewlaps of the different species shows little change.

The second factor that influences signal detectability is chromatic contrast. The shapes of habitat spectra are summarized in Fig. 7. The most dramatic difference is that the irradiance spectrum broadens as one moves from shaded to open habitat. However, visual systems are designed to correct for the spectral quality of the illuminant (Foster and Nascimento 1994; Siddiqi et al. 2004), since without such a correction object appearances would change dramatically with illuminating light conditions. The average side-welling irradiance spectrum in each habitat represents a weighted sum of the background radiances that stimulate the lizard's eye as the gaze shifts from location to location. Since the eyes adapt chromatically to the prevailing irradiance spectrum in each habitat, differences in the irradiance spectrum across habitats will have little or no impact on the chromatic appearance of the dewlap. For this reason, chromatic contrast is determined largely by the difference between dewlap and background spectral radiance. The background radiance measured parallel to the ground (Fig. 7a) is quite similar across all four habitats. There was a greater among-habitat difference for radiance-up measurements, but the difference was not sufficient to shift the relative chromatic contrast of the different dewlap colors. The fact that the relative magnitude of chromatic contrast of the different dewlaps does not change very much across habitats can be seen in Fig. 10.

Taking together the fact that visual systems correct for the illuminating irradiance spectrum, the similarity in the background radiance spectra of the different habitats, and the conservation of the *R*/*I* ratio across habitats, we see that these four habitats are, on average, fairly similar in terms of the variables that are critical in determining signal detectability, even though they differ dramatically in vegetative structure, level of shade and irradiance spectrum.

The results of this study are surprising in light of some earlier findings.

Leal and Fleishman (2004) compared dewlap color in different populations of *A. cristatellus*, from xeric versus mesic habitats and found that subtle dewlap color divergence in the different populations resulted in enhanced detectability for each population in its own habitat. The lack of evidence found here for similar divergence among different species occupying habitats that differ more dramatically was unexpected. The difference in the conclusions may have to do with a fundamental difference in the nature of the habitat variation in the two studies. The different populations of *A. cristatellus* studied by Leal and Fleishman (2004) lived in habitats that differed substantially in average annual rainfall. This wet-to-dry axis of habitat variation resulted in distinct differences in the light geometry of the habitats (specifically, it altered the *R*/*I* ratio) and a change in the background radiance spectra arising from differences in vegetation types. Dry habitats had a larger *R*/*I* ratio, and a broader background radiance spectrum than did wet habitats. These factors caused different dewlap designs to differ significantly in detectability for the different populations. The present study involved

Table 4 Tests for significant effects of habitat on each of the three measurements of normalized habitat light spectra

Measurement	PC1		PC2		PC3	
	Proportion of variation	*P*	Proportion of variation	*P*	Proportion of variation	*P*
Radiance	0.51	<0.0001* (7.9)	0.25	0.21 (1.5)	0.18	<0.0001* (11.5)
Radiance-up	0.52	<0.0001* (8.0)	0.26	<0.0001* (7.8)	0.11	<0.0001* (10.1)
Irradiance	0.41	<0.0001* (9.5)	0.33	<0.0001* (22.1)	0.20	0.96 (0.09)

The three types of location (display, no display, random) are combined for each habitat. The table shows the proportion of variance accounted for by each principal component and the probability results of the single factor ANOVA test for effect of habitat on each PC. Degrees of freedom for each of these tests was (3,164). The *F* value for each test is shown in parentheses under the *P* value. Statistical significance is indicated by *

Table 5 Probability values for pairwise comparisons based on the Scheffe *F*-test for the first three principal components from the normalized habitat spectra measurements described in the previous table

Measurement	Pairwise comparison	PC1	PC2	PC3
Radiance	P versus K	0.0072*	NS	0.58
	P versus C	0.99	NS	0.50
	P versus G	0.02*	NS	0.0018*
	K versus C	0.006*	NS	0.012*
	K versus G	0.96	NS	<0.0001*
	C versus G	0.019*	NS	0.048*
Radiance-up	P versus K	0.0002*	0.0033*	0.058
	P versus C	0.0029*	0.072	0.0015*
	P versus G	<0.0001*	0.96	<0.0001*
	K versus C	0.27	0.56	0.81
	K versus G	0.33	0.0019*	0.069
	C versus G	0.043*	0.037*	0.27
Irradiance	P versus K	0.096	0.43	NS
	P versus C	0.45	0.90	NS
	P versus G	<0.0001*	0.0009*	NS
	K versus C	0.012*	0.096	NS
	K versus G	0.0097*	0.081	NS
	C versus G	<0.0001*	<0.0001*	NS

Significant differences are indicated by an *. In cases where the ANOVA (Table 4) did not indicate a significant effect, no *P* value was calculated. These are indicated with the abbreviation NS

comparisons of habitats that differed greatly in level of shade, resulting in large differences in total intensity, but not in rainfall levels. The light geometry (*R*/*I* ratio) and background spectra of the habitats compared did not differ by a great amount. Thus, with respect to the variables that critically determine dewlap detectability, the habitats compared in this study actually varied much less than did those that were compared in Leal and Fleishman (2004). It appears that some kinds of habitat variation (e.g., a difference between wet to dry conditions) may lead to divergent selection for detectability while others may not (e.g., differences in shade level of wet habitats).

This suggests that selection for visibility in different habitats can explain divergence in dewlap color in some species, whose populations occupy habitats that differ in certain ways (e.g., wet vs. dry), but not in others. However, the results of the current study cast doubt on this process as the most important general mechanism for driving the evolution of dewlap color divergence in the genus as a whole, since dewlap color diversity is found throughout the genus in all kinds of habitats. There must be other processes that account for the evolution of dewlap color diversity. Indeed, VanHooydonck et al. (2009) reported divergence in dewlap color patterns in isolated populations of *A. sagrei* that did not appear to be related to habitat light differences.

A second reason why we were surprised by the results of the present study is that some broad surveys of dewlap color and habitat light have revealed relationships between habitat light and dewlap color. Fleishman (1992) looked at the frequency of occurrence of different dewlap colors in different habitat types and found that species with yellow and white dewlaps are most common in heavily shaded areas, whereas species with red, orange, and blue dewlaps are more common in less shaded habitats. Similarly, Fitch and Hillis (1984) had found that pale white and/or yellow dewlaps were more common in rain forest and cloud forest habitats, while darker red, orange and blue colors were more common in open, more seasonal, habitats. Before carrying out the present study, we had thought that these patterns could be largely by explained by differences in detectability under different habitat light conditions, but the results here do not support this idea.

If selection for signal detectability does not account for dewlap color diversity among most of the Puerto Rican anoline species, then what does? Making the signal more detectable is only one function of dewlap color. There is a body of evidence that suggests that another important function of dewlap color is to facilitate rapid and unambiguous species recognition (Rand and Williams 1970; Williams and Rand 1977; Losos 1985; Fleishman 2000; Leal and Fleishman 2002, 2004; Nicholson et al. 2007;

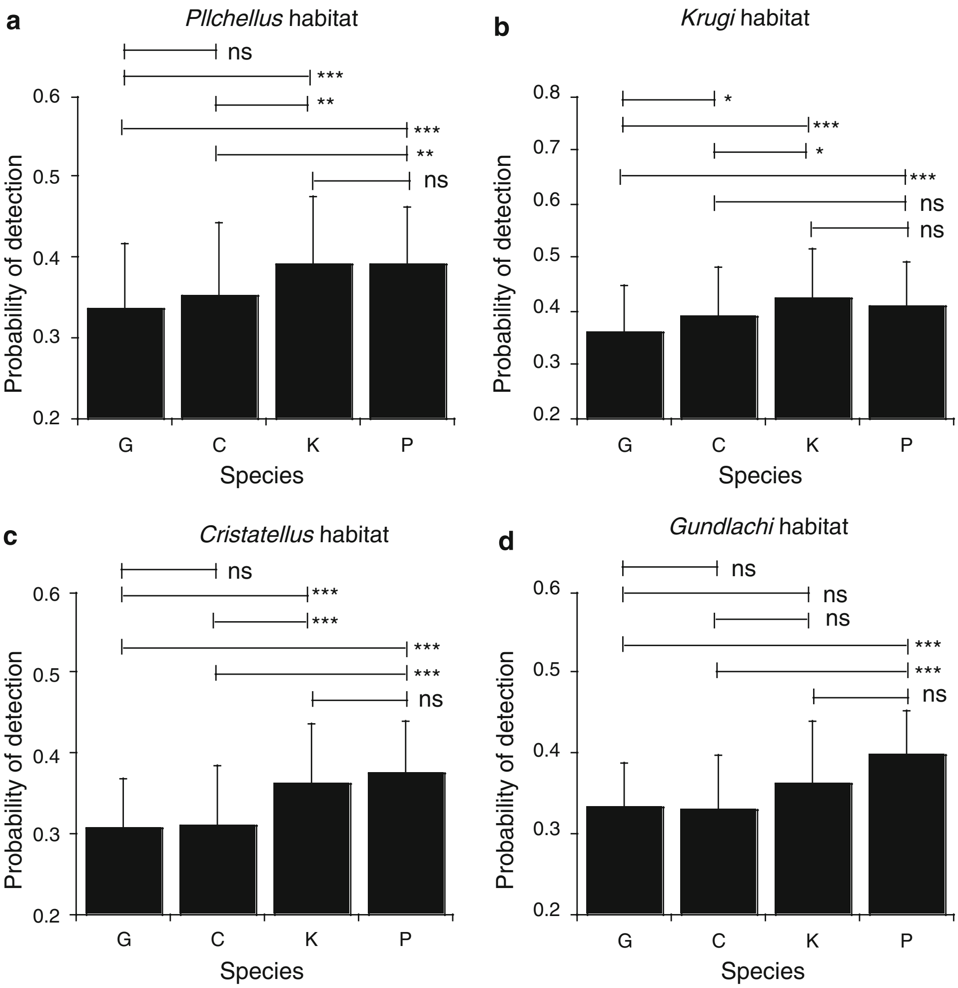


Fig. 8 The probability of detection ($P(d)$) for the dewlap of each species determined at every location in each habitat with radiance measured parallel to the ground as the background. *Error bars* indicate 1 SD. Results were analyzed using a repeated-measures ANOVA on the log transformed probabilities. In all four cases the difference among the means was highly significant ($P < 0.0001$). Results of pairwise statistical tests are indicated to the right of the *horizontal lines* connecting pairs of means (Tukey test): $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, and *ns* no significant difference. Habitats shown are **a** *A. pulchellus,* **b** *A. krugi*, **c** *A. cristatellus* and **d** *A. gundlachi*

Vanhooydonck et al. 2009). A number of recent studies have suggested that selection for effective communication of signal content may result in signal designs that are more diverse than can be explained by selection for detectability alone, and may at times result in less than optimal detectability (Schaefer and Schmidt 2004; Doucet et al. 2007; Schaeffer et al. 2007). A male anole displaying in a complex environment where a number of sympatric species are present will be at a selective advantage if inattentive conspecifics are easily made aware of his presence and can easily and quickly identify him as a conspecific. Indeed, there are a number of examples where closely related sympatric anoline species with similar body shapes have dramatically different dewlap colors (Fleishman 2000; Leal and Fleishman 2002). An example of such a pair are the sympatric grass-dwelling species *A. pulchellus* and *A. krugi* (Fig 2).

Selection for species identity (i.e., signal content) may explain why dewlap colors differ among species, but it cannot, by itself, cannot explain why there is a relationship between habitat light and dewlap color (e.g., more white and yellow dewlaps in shaded habitats). However, the efficiency and reliability with which content can be transmitted is dependent on the response patterns of the visual system, and on habitat light as well (Grether et al. 2004; Rowe et al. 2004). It is possible that habitat light conditions may influence dewlap color evolution by influencing the effectiveness with which different colors can reliably convey information about species identity. In order to be an effective signal of species identity the dewlap color must be distinct in perceptual color space from the color of other dewlaps. In heavily shaded, dimly lit environments, two different colors that reflect and transmit relatively few photons may be difficult to distinguish even if both can be detected, because color discrimination thresholds become elevated in low light (Wyszecki and Stiles 1982; Vorobyev 2003; Osorio et al. 2004). In such conditions darker, high chroma colors (e.g., red, blue, orange) may be less effective than brighter colors that reflect a greater total number of photons (e.g., white, yellow), simply because darker colors tend to converge in appearance in dim light. Darker colors may be detectable, but it may be difficult to tell them

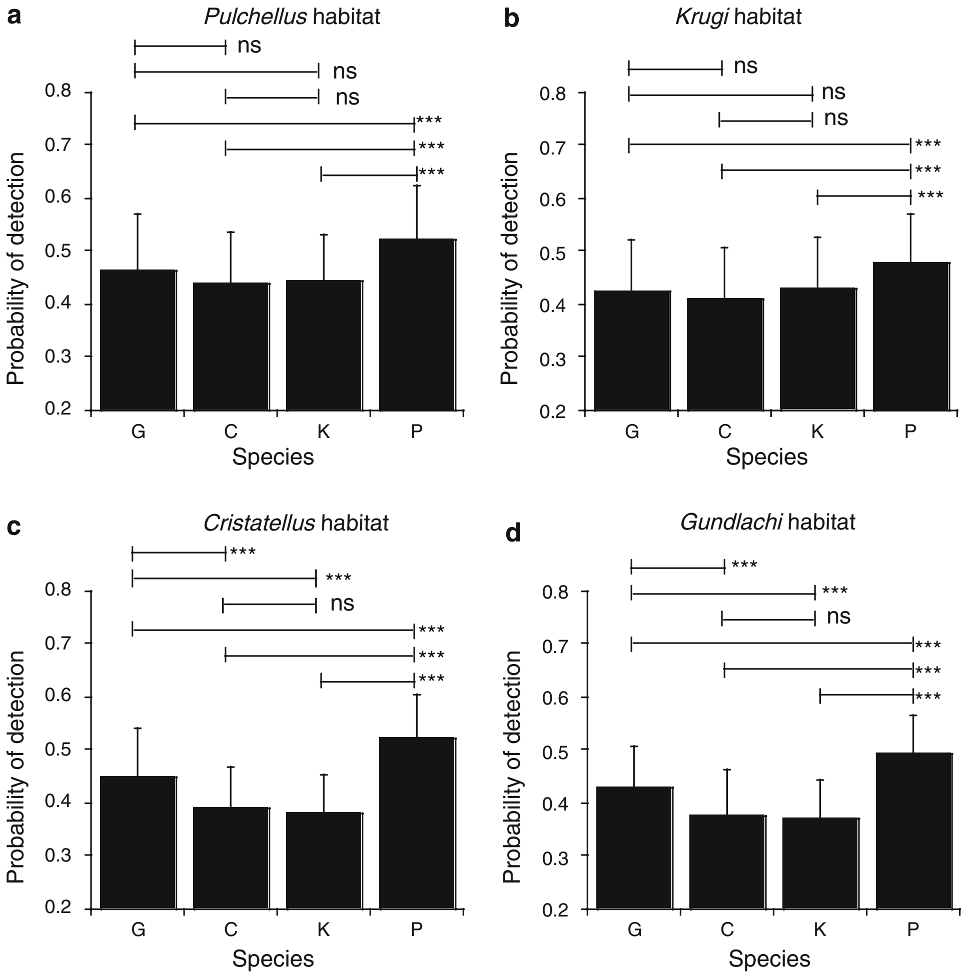
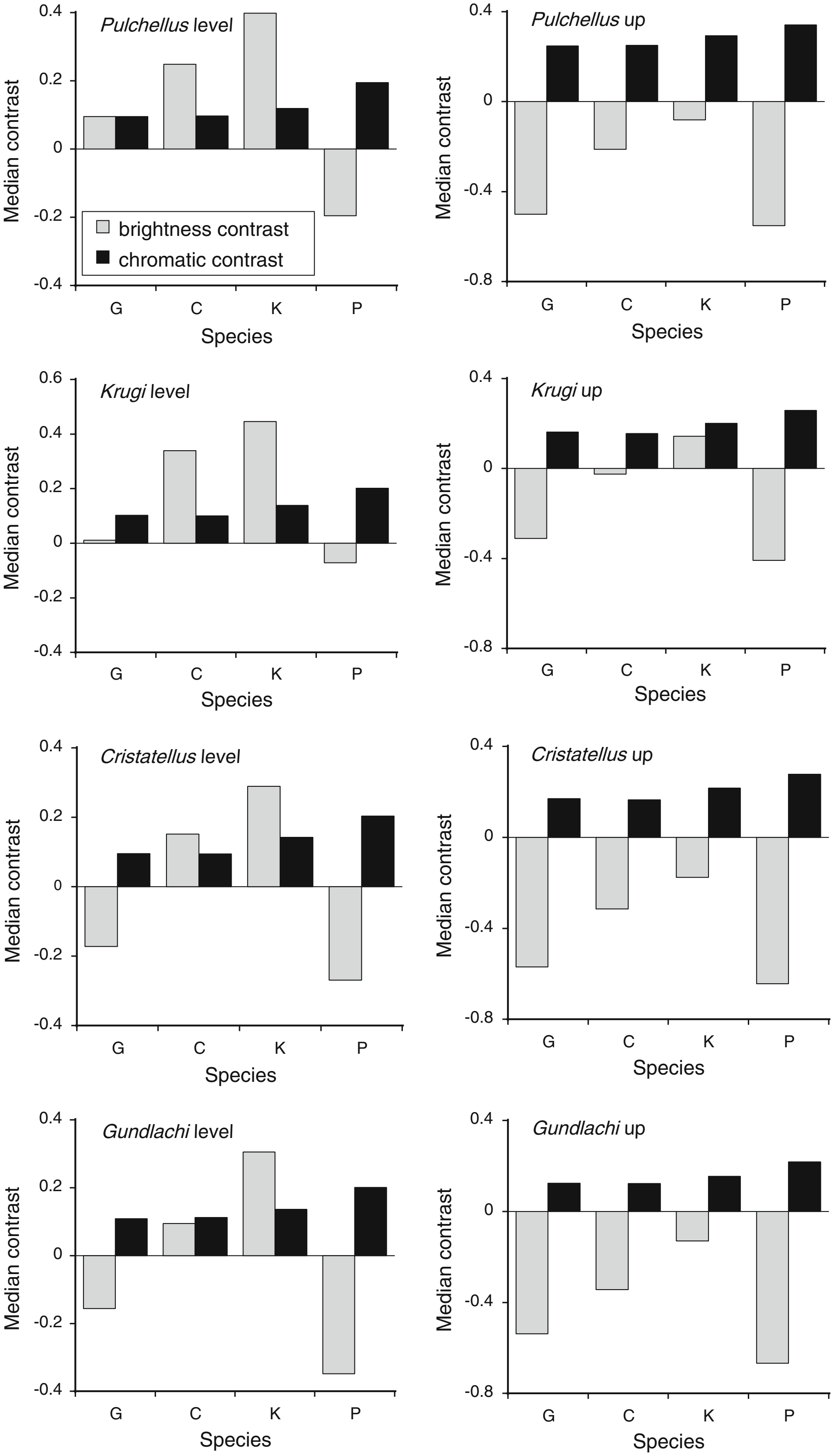


Fig. 9 As in Fig. 8, but here the background is formed by the "radiance-up" measurements. Results were analyzed using a repeated-measures ANOVA on the log transformed probabilities. In all four cases the difference among the means was highly significant ($P < 0.0001$). The results of pairwise statistical tests (Tukey test) are shown in each plot as in Fig. 8

apart. It is possible that under very dark habitat conditions color discrimination may be too limited to allow chromatic cues to be used for species discrimination. Interestingly, there are a few cases where anoles from heavily shaded forest have very dark, low-chroma dewlaps (Fleishman 1992). *A. gundlachi* is one such example. It may be that in dim light the perceptual color space is too limited to allow chromatic differences to be reliable as a species recognition cue. In this case it is possible that animals may rely on large differences in brightness as a recognition cue (e.g., Cummings 2007). While brightness in general is a much less reliable recognition cue than color, very dark dewlaps can presumably be reliably distinguished from very bright ones. Indeed, *A. gundlachi* sometimes shares trees with another species—*Anolis evermanni*—that has a very bright yellow dewlap.

At present our best hypothesis for the mechanism underlying the evolution of diversity of colors among anoline dewlaps is that a number of different selective factors are at work. First, selection for detectability sets broad limits on the possible colors that will be effective (Fleishman 2000). Second, selection for detectability can lead to color differences for some types of habitat difference (e.g., mesic vs. xeric habitat) but not others (Leal and Fleishman 2004). Third, there is selection for dewlap colors to diverge in perceptual color space from colors of the dewlaps of other species (and possibly other colored objects) in the habitat. Fourth, total habitat light intensity may influence the nature of the available perceptual space which can be filled with dewlap colors, and thereby constrain the range of colors available for species discrimination. Finally, other factors, such as counter-selection from visual predators or limitations on what sorts of pigments can be obtained and/or synthesized are also likely to play a role. A coherent analysis of the evolutionary factors accounting for the diversity in anoline dewlap colors will require an understanding of the relationship between each different function served by the dewlap color, how the sensory system processes this information, and the influence of habitat light variables on this processing (see, e.g., Fleishman 2000). Additionally we will have to consider each anoline community as a whole, since it appears that dewlap colors of different species tend to diverge in the available perceptual color space.

Fig. 10 The values for chromatic contrast and brightness contrast for radiance measured level and up as background. Values are shown for each dewlap in each habitat



Our findings differ from studies of some other systems in which habitat light appears to play a more direct role in driving the evolution of signal divergence. For example, Lall et al. (1980) found that fireflies that signal early in the evening use yellow flashes that stand out from the green background vegetation, while those that signal later in the evening, when background vegetation is not visible, use green light. A number of studies have found that signal colors of different fish species have diverged due to differences in the transmission properties of water (e.g., Mann et al. 2006; Seehausen et al. 2008).

Our results appear to be more consistent with a number of recent studies of the influence of habitat light on signal-color evolution in terrestrial habitats, which suggest that selection for detectability in differing habitat conditions is only one factor in the evolution of color diversity. For example, Gomez and Théry (2004, 2007) studied colors in rainforest birds and found broad overall differences between canopy and understory species that were consistent with selection for signal visibility. However, among the species within each habitat light environment, there was a great deal of additional diversity. Stuart-Fox et al. (2007) studied color pattern evolution in African dwarf chameleons and found that only some of the differences could be attributed to evolution towards increased detectability in different habitats. Thus, while selection undoubtedly favors signals that can be efficiently detected by relevant viewers, and this can be influenced by habitat conditions, for many systems this appears to be only one of a suite of factors that contribute to the evolution of signal diversity.

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