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The Evolution of Dewlap Color in Jamaican Anolis Lizards

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By

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ABSTRACT

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Within the animal kingdom, communication is of the utmost importance. As a general rule, these communicative signals must be highly efficient in stimulating the sensory system of the intended viewer. In this study we explored the signal diversity exhibited by the genus *Anolis*. This genus of lizard relies almost exclusively on visual signals for communication. Male anoles possess an expendable throat fan, referred to as a dewlap, which is used in visual displays within their habitat. Notably, this group as a whole exhibits extensive variation in dewlap coloration. Here we collected and analyzed spectral data for dewlap color and habitat light conditions for six species of anoles inhabiting the island of Jamaica. We investigated two distinct hypotheses for the driving force behind the evolution of dewlap color: (1) color evolved to enhance detectability and (2) color evolved for species recognition. We used spectral models and tetrahedral color space to assess our data in terms of both probability of detection and chromatic contrast, though we primarily focused on the latter. We found that chromatic contrast values between dewlap colors and habitats were frequently high and largely above random, whereas chromatic contrast values between the dewlaps of each species were low. The results exhibited support for our first hypothesis, but did not appear to support the second. We concluded that the dewlap diversity seen

in Jamaican anoles evolved largely as a function of detectability and was impacted minimally by a need to differentiate between sympatric species.

Within the natural world it is imperative that all species utilize communication in one form or another. Animals use signals that are often extremely complex and may serve multiple purposes including reproduction courtship, species recognition, survival, and simply socialization. Even closely related often species exhibit extensive signal diversity within sympatric and allopatric populations (Fleishman and Persons 2001; Leal and Fleishman 2004). One of the greatest goals within the study of animal communication is the understanding of the driving forces that lead to the evolution of this diversity (Fleishman and Persons 2001).

Natural selection should, in general favor signals that are often received by the intended viewer and done so in the most efficient way possible. Animal sensory systems evolve within each individual's distinct habitat to operate efficiently under the current conditions (Fleishman 1992). The sensory system therefore acts as a selection force on the signal, because the effectiveness of the signal relies on its ability to efficiently stimulate the sensory system of the receiver. It must be able to do this in accordance with the response parameters of the already evolved system as well as within the environmental conditions in which the signal is both presented and detected. It is these limitations that influence signal design (Endler 1992; Fleishman 1992; Fleishman 2000). This concept of sensory drive therefore assumes that the structure of the most effective signal is dependent on habitat conditions. Knowing that many related species occupy different habitats, one can hypothesize that signal diversity arises because of differing selective forces present in each locale. These forces can act in favoring

specific aspects of the sensory system and therefore promote the evolution of a signal that corresponds to the selected qualities. This in turn can lead to speciation because the most effective signal in one habitat may be less detectable in another (Leal and Fleishman 2004; Fleishman et al. 2009). Reduced detection ability can then further speciation in terms of reproductive success. If selective forces within one habitat have acted upon mating signals, a male that enters a foreign habitat may be unable to effectively attract a female, leading to reduced gene flow between the two populations.

There are however, cases in which conspecific species occupy habitats that have modest differences. This poses the question of whether detectability alone is a driving force and suggests that there is an inherent need for separate species to be able to identify one another. If two species occupy nearly the same habitat, there will then be a need for individuals of these species to be distinct from one another and thus have distinct, yet effective, signals. This necessity can, by itself be a selective force for signal differentiation as well. In such a case signal evolution would not be driven by habitat differences, but by the need for signals of different species to diverge. It is therefore important to be able to understand the evolution of signal design within groups of species that do not have differing visual systems but occupy varying habitats, some very different from one another and some very similar.

Anolis is a highly diverse genus of lizards, including close to 400 species. The genus exhibits vast ecological specialization, radiating into a number of

different habitats, and demonstrates rapid speciation. For this reason they are a very important model system for the study of the evolution of species diversity. Anoles are extremely visually oriented and appear to rely almost exclusively on visual displays for communication (Fleishman 1992; Leal and Fleishman 2009; Losos 2009). Along with high diurnal visual acuity, anoles also have relatively extensive color vision, which extends into the ultraviolet (Fleishman 2000; Fleishman and Persons 2001; Loew et al. 2002; Losos 2009). The anoline retina contains four classes of photoreceptors. Each cone contains visual pigments and oil droplets. A study by Lowe et al. (2002) determined that many species of anole do not differ in their visual pigments; most appear to be vitamin A1 derived. Oil droplets in turn vary more and act as filters for particular wavelengths of light thereby restricting the visual spectra (Lowe et al. 2002). Though these components appear relatively complex when coupled with the multiple possible light environments occupied by the genus, the anoline visual system has remained rather conservative. This suggests that evolution is not occurring within the visual system itself, but in the signals received by the system.

In almost all anole species males possess an expendable, colorful throat fan called a dewlap. They use this dewlap in displays that consist of body movements in an up and down bobbing fashion coupled with dewlap flashing. It is hypothesized that these structures and displays are used to target neighboring males in order to defend territory, attract proximal females for mating, and signal to predators to thwart an attack (Losos 2009). Though the precise functions of the

dewlap remain unknown, it is clear that there is extensive variation in dewlap color and pattern in the many species of anoles (Losos 2009).

In our research we set out to investigate the natural components that have driven the evolution of the color diversity seen in Jamaican anoles. We analyzed six different species, with overlapping, but distinct, light habitats: *Anolis grahami, A. garmani, A. lineatopus, A. opalinus, A. valencienni,* and *A. sagrei*. We aimed to determine and quantify the spectral intensity and quality of the light in each species' habitat so as to identify the different components that could be playing a role in the evolution of dewlap color. In order to fully understand this evolution it was also necessary for us to acquire spectral data for the light reflectance and transmission of the dewlap of each species. We hoped to quantify this data in terms of detection probability using Fleishman and Persons (2001) spectral model.

We aimed to use this data to assess two different hypotheses for the function of anoline dewlap color evolution: (1) color evolved to enhance detectability, i.e. to increase the possibility that an individual would be seen by any other targeted individual within the territory, and (2) color evolved for species recognition, i.e. to allow individuals to differentiate between others of the same species and individuals of other anoline species (congeners). The ability to rapidly and unambiguously identify the species identity of a displaying individual would be particularly important for females seeking mates. This is also important in male/male interactions. A potential intruder that detects the presence of a territorial male from a distance is likely to move away. If the signal is ambiguous,

the intruder might approach more closely, and this might lead to a potentially dangerous fight. In order to discuss these hypotheses efficiently, we have limited the scope with which we analyze both detectability and species recognition.

In order to assess the likely validity of the two hypotheses we assessed the habitat light data and dewlap spectral data in relation to randomly selected colors, each posed to represent a potential dewlap. To test the first hypothesis we predicted that the existing dewlap colors should, on average, be more detectable than a suite of randomly generated colors. If the second hypothesis – that dewlaps evolved to facilitate species discrimination- is true, we predicted that, on average dewlaps of species from the same community should have colors that are more distant in color space from each other, than the distance from random colors to the dewlaps in the community.

To illustrate our predictions we utilized a color space model similar to Stoddard and Prum (2011). Their study assessed avian plumage diversity using a color tetrahedron in which each apex represented one of the four avian retinal cones classes. Similarly, in this study we also used tetrahedral geometry to demonstrate the relative stimulation of each anoline retinal cone being that anoles, like birds, are also tetrachromats (Losos, 2009). When assessing visual communication among animals, it is of the utmost importance that each signal is evaluated with respect to the visual system of the receivers. Therefore our tetrahedron was restricted by the visual system of the *Anolis* lizard (Fig. 1) and modeled color as it would be seen by other anoles. For example, we can consider

the following: any color can be plotted within color space to illustrate relative cone stimulation and output. A color that stimulates each cone in a way that produces equal output will plot at a point equidistant from each apex (i.e. in the center of the tetrahedron). Stoddard and Prum (2011) demonstrated that different avian pigments stimulate different cones. One specific Prorphyrin pigment from the green throat of the *Pharomachrus mocinno* shows a reflectance peak between a wavelength of 500nm and 600nm, therefore primarily stimulating the middle wavelength cone. For this reason, the color plots relatively close to the middle cone apex within avian color space. This same plotted point would be nearly impossible to demonstrate within anoline color space. Due to the properties of the anoline visual system and the restrictions created by oil droplets located on each cone, the middle wavelength cone has a cutoff that causes great overlap between it and the long wavelength photoreceptor (as determined by Lowe et al 2002). This means that stimulation of the middle photoreceptor also results in stimulation of the long photoreceptor. Therefore a color, such as green, with a wavelength between 500nm and 600nm will not produce primary output from an anole's middle cone. In fact, no single color can produce primary output of this photoreceptor. For this reason, within the anoline tetrahedron no color can plot closer to the middle cone apex than to the long cone apex.

According to Fleishman and Persons (2001), detectability of a colored stimulus can be quantified as a function of brightness contrast and chromatic contrast. This was determined through experiments in which a flag was waved within sight of a male *A. cristatellus* and detection was assessed dependent on the

anole's recognition of the object. The probability of the detection was then quantified as the summation of brightness contrast (i.e. the difference in intensity between the stimulus and the background) and chromatic contrast (i.e. the difference in spectral quality between the stimulus and background measured as the distance between the two in color space). Using this model we were able to gain a prediction of the detectability of each species dewlap in each species' habitat. By using median spectra for each species dewlap, we assessed and compared relative detectability under each habitat light condition. Though we modeled probability of detection, for the sake of this study we focused primarily on the chromatic contrast values obtained from the data.

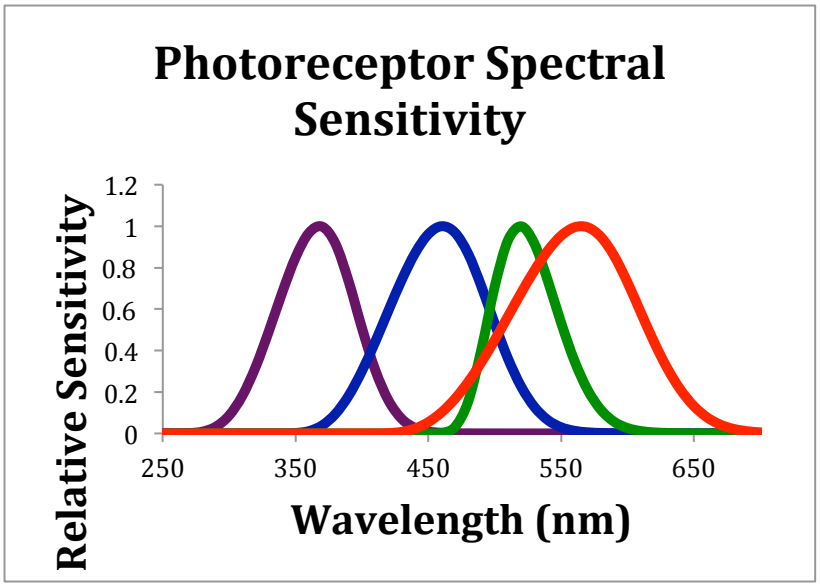

Figure 1. Anoline photoreceptor spectral sensitivity. The graph shows the relative sensitivity of the UV wavelength cone, the short wavelength cone, the middle wavelength cone, and the long wavelength cone as determined by the anoline retina physiology. Restrictions due to oil droplets located on each photoreceptor are represented; the most noticeable restriction is the overlap of the middle wavelength and long wavelength photoreceptors.

Methods

Field Sites

Spectrophotometric data was collected over the course of ten days in late June/early July in Jamaica. We were stationed near the northern coast of the island at two distinct field sites. The first was the area around a small set of guesthouses in Robin's Bay known as River Lodge as well as surrounding forests and roads leading to the site. Within this location, different light habitats were established for each species. *Anolis lineatopus* and *A. opalinus* were both found in much deeper forest under dense vegetation that created a very low light habitat. It is important to note that we found only one *A. opalinus* anole at River Lodge, though we suspect that more are present. *Anolis garmani* was also found in the forest, but was usually seen in the tops of large trees in spots where the sun penetrated. Because they are most likely a canopy species and because we lacked equipment that would allow us to sample in the canopy, it was very difficult to acquire accurate spectral data for this species. *Anolis valencienni* showed the most unusual habitat patterns of all six species. Though previous literature has cited it as a forest dwelling species, of the few sightings we had most were near forest edges in tree vines. For this reason the least data was collected for the species. *Anolis grahami* was found in habitat that consisted of partial shade and partial sun usually on the edge of forested areas. The only species that was found in completely open habitat was *A. sagrei*, for which data was sampled in mostly open fields and disturbed areas. The second study site was a planation called Circle B near the Discovery Bay area. At this locale

the same microhabitats were established for the varying species. The sample size for each species varied from day to day as well as from site to site. Because of this, our total sample size had varying numbers of data for each species dependent on the number of present individuals and out ability to find each.

Habitat Light Collection

We measured a large sample size for each established light habitat mentioned above. To do so we began our data collection at 7:30 A.M. and ended at 6:00 P.M. We would not continue sampling in the case of rain because we found few lizards to remain out of shelter in this condition. There was also a lull during the middle part of the day between in which sampling was minimal due to little anole activity. It required two individuals to collect data. We worked in two groups during each sample time. One pair would stay within the forest to collect data primarily for *A. lineatopus, A. opalinus,* and *A. garmani*. The other pair worked in more open habitat near forest edges to collect data primarily for *A. grahami,* and *A. sagrei*. Though the groups split to better cover the habitat variety, each was not limited to only the primary species. Whichever species a group found, they would record the data in that location so as to not reduce the sample size. It was not an unusual occurrence for one group to collect spectral data on at least one anole of each species due to the habitat overlap found in Jamaica. In a general area one can find all six species coexisting.

Each research pair walked through their selected habitat until an anole was seen. Once sighted, the team would remain at a distance of 2-3 meters so as to not

disturb or disrupt the anole. Each lizard was observed for up to ten minutes, or until it displayed with its dewlap. Each observation was either cut short when the anole displayed or ended at the ten-minute mark in the case of a "non-display". When a display occurred, the team immediately moved to the precise location where the lizard had expended its dewlap to measure the spectral data. If a display did not occur, the light data was collected at the anole's last seen location. In cases where the display or "non-display" site was unreachable, e.g. too high in a tree, light was measured at the closest point possible to the exact locality. This technique was used consistently for data on *A. garmani*, which could be considered the cause for any data inaccuracies for this species. Previous work by Fleishman (2009) showed that the differences between a display and a "non-display" site are negligible so for our current research we considered the spectral measurements in both cases equally useful and important. The spectral data collected from individual species constituted a distinct habitat. Therefore, we established a total of 6 separate light habitats, each which represented the irradiance and radiance spectra of the species measured. We referred to each habitat by the species the data was collected from (e.g. *A. garmani* habitat).

The spectral data was measured using an Ocean Optics Jaz spectroradiometer. Radiance readings were collected to the right and left of the display site covering an angle of 4 degrees visual angle. Focusing the optic fiber on and Ocean Optics diffuse white standard allowed us to collect irradiance data measuring light to the right, left, and upward directions of the display. This resulted in the measurements of the spectral quality of all light striking the flat

surface from a full hemisphere centered on the white standard. The three irradiance measurements together created a 360-degree total habitat surrounding the dewlap site. Later the irradiance readings for the upward direction were considered unnecessary for this study and discarded. Radiance was calibrated by recording the spectral radiance from a Li-Cor Li-1800 irradiance calibration lamp with a radiance attachment.

Dewlap Spectral Characteristics

At both locations we collected individuals of each species for further spectral assessment. Lizards were caught and brought back to each field station where they were placed in a custom-made holder that prevented the movement of their bodies and heads. The dewlap of each was extended manually using a pair of mounted forceps that pinched the hyoid bone allowing for a natural and full extension of the throat fan. While in this open position we measured reflectance and transmission characteristics using the Ocean Optics Jaz spectroradiometer for each individual. The dewlap was illuminated with an Ocean PX-2 pulsed xenon lamp delivered through a set of six single fused silica fibers. For transmission a fiber optic was placed 2 mm from the dewlap surface directly opposite the light source. Reflectance was recorded from a single fused silica fiber positioned in the center of the 6 illuminating fibers.. We also measured the reflectance characteristics of the bodies of some of the individuals. Measurements were either taken over the front limb of the individuals considered the shoulder area, or over the back limb on the portion of the abdomen considered the flank.

Data Calibration and Modeling

To establish the relationship between the data obtained from the spectroradiometer and quantal units, we used a Li-Cor-Li-1800 radiance calibration lamp. We combined the data from both field sites being that we found little difference between the two localities. Radiance spectra were converted into 10nm steps and a median of the points was used to produce final radiance spectra. We produced irradiance spectra by multiplying the radiance recorded off the diffuse white surface times pi. Our 82 randomly generated colors were produced using a Munsell color book and the Jaz spectroradiometer to measure the spectral properties of each color. The radiance spectra were corrected to have similar properties to dewlaps, such as ultraviolet characteristics.

According to Fleishman and Persons (2202), probability of detection can be defined by the equation P(d)= 0.40(CB) + 0.429(CC) + 0.156 where p(d) = the probability of detection, CB = brightness contrast, and CC = chromatic contrast. Brightness contrast can itself be quantified using the equation CB= (stimulus brightness – background brightness) / (stimulus brightness + background brightness). Each individual brightness value was obtained by multiplying the spectral radiance of the stimulus by the anoline photoreceptor spectral sensitivity, which was determined in a study of the anoline retina (Fig. 1; Lowe et al. 2002). Chromatic contrast was determined as the Euclidian distance in anoline color space using the relative stimulation of each photoreceptor in response to the stimulus. The stimulus and background spectral radiances were multiplied by the

photoreceptor spectral sensitivity to produce relative outputs of each cone class that constituted a number between 0 (no stimulation) and 1 (full stimulation). These values were then plotted as separate points within the color tetrahedron and the distance between each obtained to determine chromatic contrast.

Results

Within both field sites we collected habitat data from a total of 189 individuals. Sample distribution was not even among species, with the largest number consisting of *A. lineatopus* (Table 1). As previously stated, due to unusual habitat patterns the sample size for *A. valencienni* was extremely small and therefore data could not be considered completely accurate. With the data from both field sites combined, we considered the rest of our sample size large enough to produce accurate results. We used the median intensity at each wavelength to represent the typical irradiance (total illumination) and radiance (background lighting) spectrum for each habitat (Fig. 2). When plotted, all median habitat spectra plotted relatively close to the center of the color tetrahedron except that of the *A. sagrei* habitat (Fig. 3). This relatively equal output of each photoreceptor occurs because before calculating relative stimulation of each cone class, the average irradiance spectrum is assumed to produce equal stimulation for each cone class. This correction is based on the assumption that the eye exhibits chromatic adaptation to the natural lighting. This chromatic adaptation allows colors to look similar across different habitat.

Species	Location River Lodge	Circle B
Gar.	7	10
Gra.	35	11
Lin.	45	24
Opa.	1	31
Sag.	3	20
Val.	1	1

Table 1. Number of each anoline species for which habitat spectral data was collected. A total of 189 individuals were assessed in two separate locations. Species abbreviations: Gar = *A. garmani*, Gra = *A. graham*, Lin= *A. lineatopus*, Opa = *A. opalinus*, Sag = *A. sagrei*, and Val = *A. valencienni*.

Calculated photoreceptor outputs for individual species dewlaps, as well as bodies, produced similar plotting patterns in each species habitat (Fig. 3). Due to the nature of the dewlap of *A. lineatopus,* the dewlap was split into two separate colors, a white edge and yellow center, making a total of 7 plotted dewlap colors as opposed to 6. We plotted the other dewlaps based solely on the color that covered most of the dewlap. Body colors consistently plotted more closely to the habitat than any dewlap and remained in a small conglomeration. Similarly, dewlaps also plotted in what appeared to be a relatively constrained mass, with the exception of one dewlap, which expressed greater ultraviolet properties than the others. As a whole, this mass was located nearest the long photoreceptor apex, representing an overall greater stimulation of the long wavelength cone. Neither dewlaps nor bodies expressed high outputs from either the ultraviolet or short wavelength photoreceptor. Low output values for the middle wavelength photoreceptor were also obtained, but this was expected because of the overlapping sensitivity of the middle and long wavelength photoreceptors (as seen in Fig. 1).

Species	*grahami*	*lineatopus* (yellow)	*lineatopus* (white)	*opalinus*	*garmani*	*valencienni*	*sagrei*
***A. grahami* habitat**							
C chrom	**0.316942 58**	0.135006605	0.105091149	0.304841174	0.158802577	0.211461401	0.231807117
C bright	**0.047855 953**	0.244201338	0.550577518	0.015607 33	0.186288041	0.329784193	0.005746815
p(d)	**0.295919 413**	0.301683177	0.412267467	0.278179 402	0.288036247	0.366498238	0.245021573
***A. lineatopus* habitat**							
C chrom	0.3752601 58 -	**0.219305 728**	**0.209150 813**	0.356317 255 -	0.239950359 -	0.134280858 -	0.268611063 -
C bright	0.0445238 25	**0.157054 216**	**0.480036 498**	0.076944 288	0.268853853	0.416952869	0.100031779
p(d)	0.3179135 93	**0.300543 978**	**0.425674 924**	0.323304 617	0.353521685	0.370493491	0.297457137
***A. lineatopus* habitat**							
C chrom	0.3752601 58 -	**0.219305 728**	**0.209150 813**	0.356317 255 -	0.239950359 -	0.134280858 -	0.268611063 -
C bright	0.0445238 25	**0.157054 216**	**0.480036 498**	0.076944 288	0.268853853	0.416952869	0.100031779
p(d)	0.3179135 93	**0.300543 978**	**0.425674 924**	0.323304 617	0.353521685	0.370493491	0.297457137
***A. opalinus* habitat**							
C chrom	0.4397096 5	0.304775077	0.309995123	**0.41577 5575 -**	0.321574155 -	0.108318872 -	0.322365434 -
C bright	0.0073183 34	0.207404742	0.5194048	**0.02529 1843**	0.219843763	0.373001266	0.048414795
p(d)	0.3288111 94	0.354871928	0.481759969	**0.32642 6967**	0.366567165	0.342528055	0.298312092
***A. garmani* habitat**							
C chrom	0.3053437 25 -	0.120443211 -	0.066064103	0.297140991 -	**0.144162 157 -**	0.246153221	0.234291688 -
C bright	0.1984658 54	0.001868213	0.351616264	0.229309239	**0.413592 451**	0.531812571	- 0.249420233
p(d)	0.3515238 32	0.198924507	0.317072147	0.360580092	**0.373101 844**	0.461186317	0.343484768
***A. valencienni* habitat**							
C chrom	0.3245359 12 -	0.152265709 -	0.104651958	0.310403791 -	0.186396266 -	**0.208177827**	0.233199794 -
C bright	0.1394635 29	0.068577961	0.416805473	0.171780846	0.351364673	**0.48466642**	0.191243414
p(d)	0.3355997 76	0.238337468	0.358582972	0.342873854	0.365104376	**0.427137699**	0.319777283
***A. sagrei* habitat**							
C chrom	0.2936619 64 -	0.135099993 -	0.059190336	0.294999097 -	0.152125216 -	0.339510245	**0.261381762 -**
C bright	0.0505008 15	0.151553082	0.485841188	0.082570375	0.280148125	- 0.406809745	**0.101568872**
p(d)	0.2876651 11	0.264661233	0.368012601	0.301027789	0.322909336	0.448527996	**0.295180254**

Table 2. Relative chromatic contrast, brightness contrast and detectability values for dewlap of each species in relation to the six distinguished habitats. Six sets of all three values dependent on each habitat were calculated for the dewlaps of each species. The yellow and white portions of the dewlap of *A. lineatopus* were assessed as two separate colors. The bolded values of each set represent the habitat light spectra used for the set. The light spectrum of the A. lineatopus habitat was used for both represented *A. lineatopus* dewlap colors.

Randomly generated colors also appeared to primarily plot near to the center of the tetrahedron in all habitat cases (Fig. 3). Once the colors were plotted within the color space we were forced to discard 2 of the 82. These 2 specific colors produced outputs that were not consistent with the confines of the tetrahedron and thus plotted outside of the geometrical boundaries. The remaining 80 random colors were more dispersed throughout the color space than both the anoline dewlaps and bodies, but also showed relatively low outputs of the middle and short photoreceptors. They expressed greater ultraviolet output, which could be a product of our randomly integrated values to better model realistic dewlap properties. Noticeably the generated colors appeared to be much more similar to the habitat and body colors than to the dewlaps. The majority of the random colors congregated toward the center of the tetrahedron surrounding the body colors while fewer occupied the same space as the six species dewlaps.

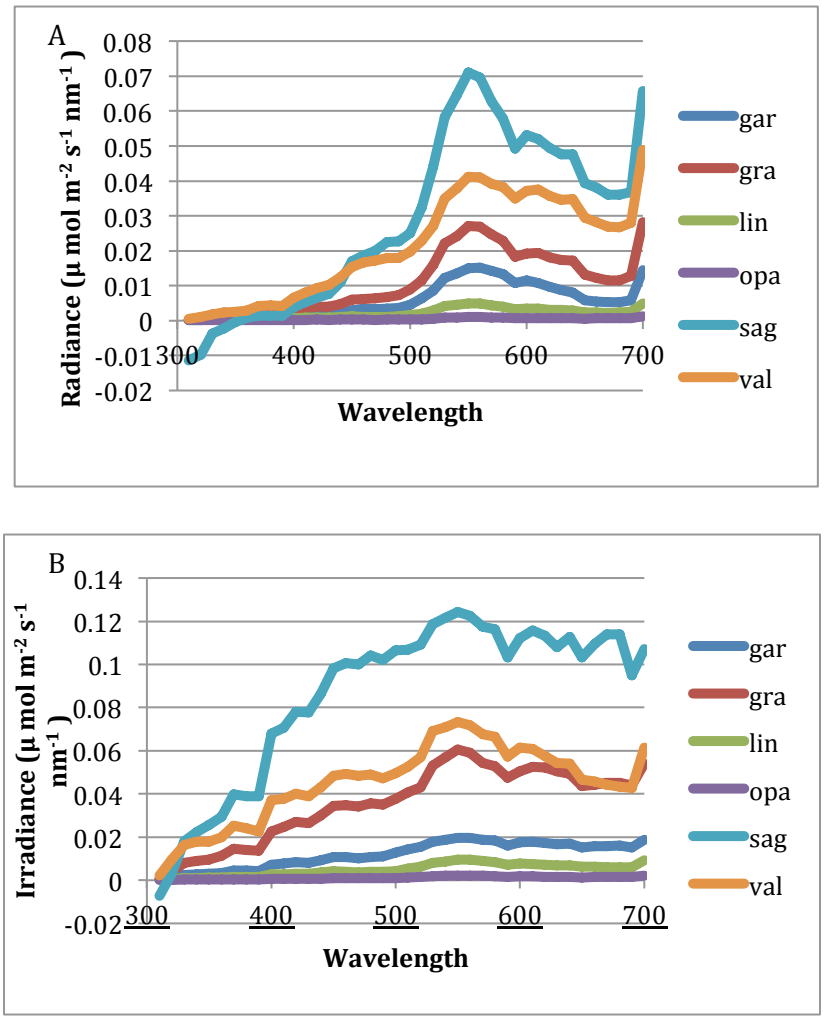

Figure 2. Compiled spectra of each six species-based habitats. Median intensities at each wavelength were taken from the complete data collection to produce typical irradiance and radiance spectrum for each habitat. A, Radiance spectra. B, Irradiance spectra. Habitat/Species abbreviations: gar = *A. garmani* habitat, gra = *A. grahami* habitat, lin = *A. lineatopus* habitat, opa = *A. opalinus* habitat, sag = *A. sagrei* habitat, and val = *A. valencienni* habitat.

The chromatic contrast, brightness contrast, and probability of detection values for each individual species dewlap in each habitat can been seen table 2. All relative probabilities ranged from 0.1989 to 0.4818. Chromatic contrast values ranged from 0.0592 to 0.4397. As previously hypothesized by Fleishman et al.

(2009), if signal detectability is responsible for driving the evolution of dewlap color then it should follow that each species should be most detectable in its own habitat. Though we didn't focus greatly on this hypothesis, we still considered it important to look at the comparative data, which can be seen in figure 4. Likewise to Fleishman et al. (2009) we found that though each species was not the least detectable in its own habitat, it was usually not the most. The two most detectable dewlaps appeared to be the white portion of *A. lineatopus* and *A. valencienni*. Interestingly enough, *A. lineatopus* was the most detectable in all habitats that were partly or mostly shaded (i.e. *graham, lineatopus,* and *opalinus* habitat) whereas *A. valencienni* was the most detectable in habitats that consisted of more sunlight. Similarly, each species did not have the greatest chromatic contrast to the background in its own habitat, though this varied more so than detectability (data not shown).

Chromatic contrast between dewlaps and randomly generated colors was done with respect to the primary species in each habitat. We ranked chromatic contrast between the dewlaps of existing species and the habitat to compare dewlaps and random colors. The ranks of the primary species in each of their habitats can be seen in table 3. The corresponding percentages further illustrate whether each individual ranked above or below random. *Anolis garmani* was the only species to rank below random, though *A. sagrei* was only slightly above random at 50.60 percent. Both the yellow and white colors that made up the *A. lineatopus* dewlap ranked similarly.

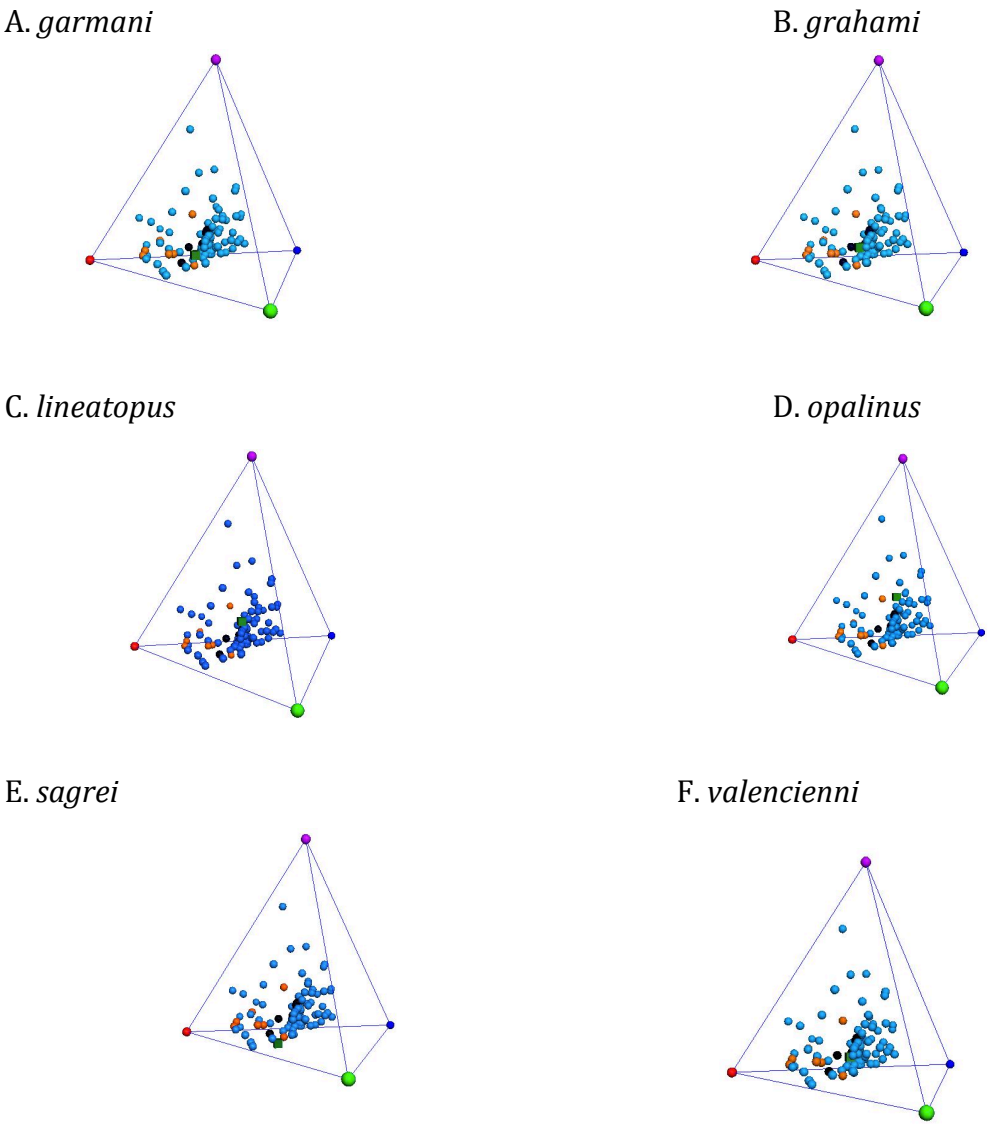

Figure 3. Anoline tetrahedral color space illustrating the relative stimulation of the four photoreceptors by each of the six median habitat spectra and body spectra of each species, dewlap spectra of each species, and the spectra of 80 randomly generated colors with respect to the corresponding habitat light conditions. A, *A. garmani* habitat. B, *A. grahami* habitat. C, *A. lineatopus* habitat. D, *A. opalinus* habitat. E, *A. sagrei* habitat. F, *A. valencienni* habitat. Purple apex of the tetrahedron represents the UV wavelength photoreceptor, blue apex represents the short wavelength photoreceptor, green apex represents the middle wavelength photoreceptor, and the red apex represents the long wavelength photoreceptor. Within the tetrahedron habitat

background is represented by a dark green cube, lizard bodies are represented by black spheres, dewlaps are represented by orange spheres, and random colors are represented by light blue spheres. Two separate spheres illustrate the dewlap of A. lineatopus–one sphere representing the white portion of the species' dewlap and another representing the yellow portion of the dewlap.

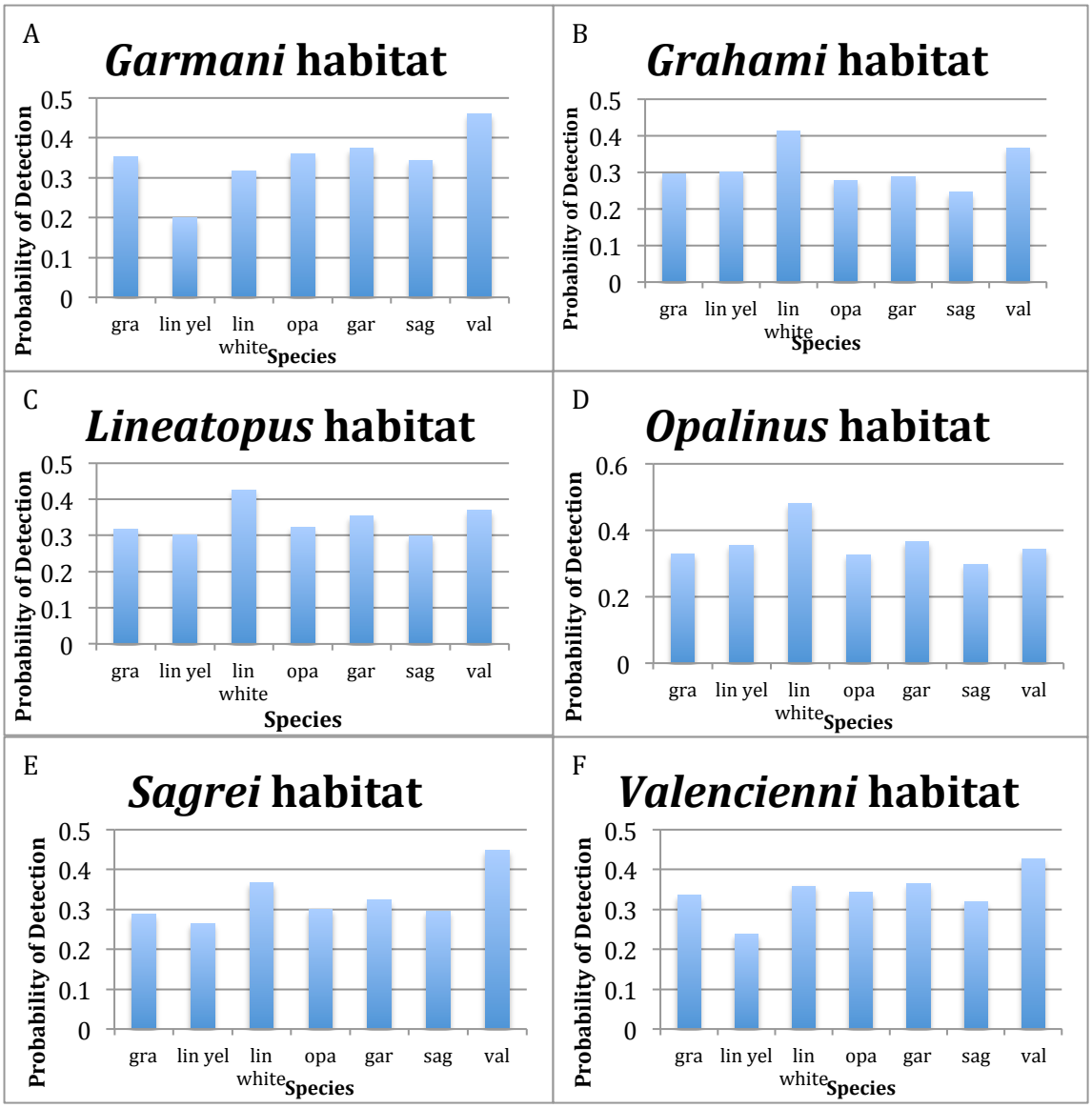

Figure 4. Probability of detection (p(d)) for the dewlap of each species as determined under the light conditions of each habitat. . The yellow and white portions of the dewlap of *A. lineatopus* were assessed as two separate colors *A*, *A. garma*ni habitat. B, *A. grahami* habitat. C, *A. lineatopus* habitat.

D, *A. opalinus* habitat. E, *A. sagrei* habitat. F, *A. valencienni* habitat. Species abbreviations: gra = grahami, lin yel = yellow portion of lineatopus, lin white = white portion of lineatopus, opa = opalinus, gar = garmani, sag = sagrei, and val = valencienni.

The distances in color space between the secondary species (i.e. the species not native to the habitat measured, but found nearby) and the primary species (Table 4) were also ranked against the distances between the secondary species dewlaps and random colors (Table 5). This provided an illustration of whether or not existing dewlaps had smaller chromatic contrast values with the dewlaps of other sympatric species, than that of dewlaps and randomly generated colors. The minimum-distance rank was relatively low for all species apart from *A. valencienni*. Similarly, the average contrast values, except for that of *A. valencienni*, ranked low and were either the same as or close to the rank of the corresponding minimum value.

Lizard	**Chromatic Contrast**	**Rank Based on Cc (out of 81)**	**Percentage**
A. garmani	0.144162157	33	39.76
A. grahami	0.31694258	67	80.72
A. lineatopus yellow	0.219305728	56	67.47
A. lineatopus white	0.209150813	53	63.86
A. opalinus	0.415775575	74	89.16
A. sagrei	0.261381762	42	50.60
A. valencienni	0.208177827	50	60.24

Table 3. Chromatic contrast (Cc) between the dewlap of each species and the corresponding habitat background. The values of each species are with respect to each species' own habitat light conditions. Chromatic contrast of the listed species was ranked based on the comparison between

the corresponding chromatic contrasts of 80 random colors and backgrounds in the same habitat. A percentage over 50 represented a chromatic contrast value that is above random.

Discussion

In this study, we set out to investigate the mechanisms behind dewlap diversity. We proposed two distinct hypotheses. First, dewlap color evolved to enhance detectability and second, dewlap color evolved for species recognition. In terms of probability of detection, we focused primarily on chromatic contrast. Though this component is only partially responsible for detectability, we found that in this study it was the most definitive. It was previously determined that detectability is proportional to the chromatic contrast between the background and dewlap color (Fleishman and Persons 2001) and thus we determined that if dewlap color is functioning for detectability, dewlaps of each species should have a greater chromatic contrast against the natural background than the randomly generated colors. We found that 5 of the 6 species had chromatic contrast values that ranked above random (Table 3). *Anolis garmani* appeared to be the only species with a dewlap that hasn't evolved to be very distinct from the background. Inspection of the dewlap showed green pigmentation, which could explain the similarity with and thus proximity to the habitat within the tetrahedron. The remaining species values suggest that dewlaps are evolving to be far enough apart from the background that they become more detectable. The restricted

distribution of the dewlaps within color space, as seen in figure 2, also suggest that the species are converging on characteristics that increase visibility.

Though we found evidence to support our first hypothesis through the evaluation of chromatic contrast, it is important to note that we did not find much support when examining probability of detection as a whole. It has previously been predicted that if dewlap design is evolving to increase detectability in each species' habitat, then each species' dewlap should be more detectable than the other species in their own habitat. Figure 4 shows that our results were not consistent with this notion of increased visibility. Instead, one species (*A. lineatopus*) dominated shady habitats and another (*A. valencienni*) dominated sunnier habitats. Though this would appear to suggest that the dewlaps of Jamaican anoles are not evolving to enhance detectability, we cannot say for sure. Our chromatic contrast data appears

	Chromatic Contrast
grahami	
lin y	0.185478666
lin w	0.297187069
opa	0.031334765
gar	0.187208902
val	0.365690623
sag	0.128327813
lineatopus yellow	
gra	0.179370008
lin w	0.127577338
opa	0.172339818
gar	0.049203252
val	0.259472686
sag	0.13202382
lineatopus white	
gra	0.286721908
lin y	0.127577338
opa	0.283766634
gar	0.156719275
val	0.294156515
sag	0.239598789
opalinus	
gra	0.03155302
lin y	0.172480247
lin w	0.284420764
gar	0.178720005
val	0.333773363
sag	0.096826975

to support this claim, but our brightness contrast data was much more inconclusive. Leal and Fleishman (2004) showed that brightness contributed to detectability in two significant ways. Very bright dewlaps (i.e. highly reflective and transmissive) are more visible when the irradiance of the dewlap is high in comparison to the radiance of the background due to their high brightness contrast with the background. Conversely, when the background radiance is relatively high in comparison with the irradiance of the dewlap, darker dewlaps tended to be more visible because of their negative brightness contrast. Essentially, bright dewlaps are more detectable against dark backgrounds and dark dewlaps are more detectable against bright backgrounds. After examination of our data, we found that lizard bodies had a higher probability of detection than their dewlap counterparts (data not shown).

garmani	
gra	0.188484776
lin y	0.050356243
lin w	0.162254737
opa	0.184188292
val	0.281673158
sag	0.154485456
valencienni	
gra	0.3699714
lin y	0.264529784
lin w	0.302120731
opa	0.340867292
gar	0.288558119
sag	0.239725018
sagrei	
gra	0.133790395
lin y	0.133061657
lin w	0.249543164
opa	0.106613588
gar	0.154199888
val	0.238644227

Table 4. Chromatic contrast values of each species between the dewlap of the primary species and the dewlaps of congeners within the habitat. Values represent the distances in color space between the corresponding species and the primary species (bolded). All values are with respect to the primary species' habitat light conditions.

When assessed in color space, we found that bodies had far smaller chromatic contrast values than dewlaps (Fig. 3). The proximity to the background suggests that bodies are more camouflaged and similar to the habitat and thus less detectable than dewlaps. Out chromatic contrast data appears more reliable because it is unlikely that anoles would possess conspicuous bodies as opposed to cryptic ones that would draw attention to the individuals even when they are not displaying. If it were the case that bodies were intended to be more detectable, one could suggest that this leaves the dewlap with little function.

Lizard	**Minimum Distance Rank from Other Species out of 81**	**Average Distance Rank from Other Species out of 81**
A. garmani	4	4
A. grahami	2	10
A. lineatopus yel	3	3
A. lineatopus white	15	15
A. opalinus	3	5
A. sagrei	17	4
A. valencienni	55	46

Table 5. Rankings of the chromatic contrasts (Cc) between the dewlap of each primary species and the secondary species within the habitat. Chromatic contrast values from Table 4 were ranked against the chromatic contrast values between secondary species and random colors. Minimum distance represents the smallest chromatic contrast value between the primary species and one of the secondary species. Average distance represents the average of all chromatic contrast values between primary species and secondary species. Both minimum and average distances (Cc values) were ranked to express how close the nearest secondary dewlap was to the primary dewlap in color space and whether this was closer than randomly generated colors.

Furthermore, if bodies were more detectable than dewlaps, we could postulate that predation would be high and population numbers low, which does not appear to be the case. For this reason, we determined that our data was not entirely reliable. Due to our more conclusive chromatic contrast data, we believe that our brightness contrast measurements have caused the apparent error in our p(d) values. We believe that in averaging the measurements for habitat lighting, we ignored particular elements of each individual habitat. Habitat backgrounds resemble mosaics of different elements such as bark, leaves, and spots of light, so in averaging them together we produce a background spectrum distinct from any of the individual elements. The body spectra are likely to have evolved to match one specific habitat elements. Bodies were generally much darker than the overall average background (giving them a high calculated probability of detection), but they were probably, in fact, cryptic because they match individual habitat elements in brightness.

We found little support for our species recognition hypothesis. We hypothesized that reliability of species recognition depends on the chromatic contrast between the dewlaps of different species. In this case we predicted that if dewlap color is evolving for the function for species recognition, individual dewlaps should have a greater chromatic contrast with the existing dewlaps of other species within the individual's habitat. A number of previous studies have illustrated sympatric anoline species with dramatically different dewlap colors, so it is not implausible for the function of recognition to exist (Fleishman 2000; Leal and Fleishman 2002; Fleishman et al. 2009). Importantly to note however, is that

most of the time these very distinct dewlaps belong to Puerto Rican populations of anoles. In our assessment of Jamaican anoles, we found that dewlaps do not differ greatly from one another. Instead, the dewlaps of all six species in the areas we sampled tended to occupy a small portion of perceptual color space (Fig. 3). The chromatic contrast values between the dewlaps ranked extremely low, illustrating a lack of distance between each (Table 5). Indeed, greater distances were established between dewlaps and randomly generated colors than between dewlaps themselves; all chromatic contrast values between dewlaps remained below 0.37 (Table 4).

At this point we must consider the nature of the pigments produced by anoles. Though we generated a wide range of "potential dewlap" colors, we cannot necessarily consider them all realistic. Dewlap and body coloration are products of combinations of pigments and structural colors (Macedonia et al., 2000). In fact, anoline skin consists of three chromatophore layers, each consisting of different components. The most superficial layer of xanthophones contains pteridines and carotenoids to selectively absorb wavelengths of light, the second layer contains iridophores that act to reflect and scatter incoming light (i.e. act as structural coloration), and the innermost layer consists of melanin (Macedonia et al., 2000). In anoles carotenoids are most commonly observed as red, yellow, and orange and pteridines occur in the UV range of the spectra. A study performed by Ortiz and Maldonado found that the orange, yellow and red colors found in Puerto Rican anoles were caused by pteridines and carotenoids. Macedonia et al. 2000 found many dermal similarities between the Puerto Rican anoles and Jamaican anoles,

including the presence of the pteridines responsible for red/orange coloration of the dewlap (drosopterin, isoxanthopterin, pterin, and biopterin) as well as yellow-based carotenoids. The greatest physiological difference found between the Puerto Rican and Jamaican anoles was the presence of xanthopterin in Puerto Rican anoles but an absence of this pteridine in Jamaican species (Macedonia et al. 2000). Though it has not been discussed whether or not this characteristic can be solely responsible for the lack of color divergence in Jamaican species, it does suggest that this population may be more limited than those of Puerto Rico. Fleishman et al. (2009) suggest that available space within the color tetrahedron may be restricted by total habitat light intensity, thereby limiting the range of possible dewlap colors. We can also question whether there are further limitations based on physiological characteristics. It may be possible for selection that causes some species to diverge from each other, but it may not be possible for other species simply because the necessary pigments have never evolved in this group of lizards. In terms of Jamaica, we can only postulate that this is the case based on the convergent behavior of the dewlap colors seen within color space.

The existence of these color-specific characteristics suggests that color production in anoles can be variable but also limited. For this reason, it would have been ideal to restrict the color space occupied by randomly generated colors in this study. If we had limited our random colors, it is possible we would have acquired different chromatic contrast values between dewlaps and random colors, thus potentially skewing our results for both hypotheses. Regardless, we have reason to believe that though the values and rankings may be shifted, the results

would still illustrate dewlap divergence from the background for reasons of detectability and convergence of species dewlaps in similar color space.

Though our data is less consistent than we had hoped, we feel that we have put together a somewhat substantial argument for the dewlap diversity seen in Jamaican anoles. Chromatic contrast and anoline tetrahedral color space expressed large differences between dewlaps and habitat backgrounds. Though each species did not have the highest detectability or the greatest chromatic contrast to the background in its own habitat, contrast values ranked above random suggesting a divergence from the habitat spectra. The extent of this deviation in turn suggests that Jamaican anoles are evolving to have more visible dewlaps. Furthermore, our data has shown that as the dewlaps appear to be diverging from the background, they do not appear to be diverging from one another. We postulated that one driving force of dewlap evolution could be the need to instant and infallible species recognition, but we found no support of this. Unlike Puerto Rican species, Jamaican anoles do not appear to have extensively distinct dewlaps. Chromatic contrast values between the dewlaps of coexisting species were all extremely low and for the most part dewlaps occupied the same general color space. The culmination of this data has led us to conclude that the dewlap diversity found in Jamaican anoles has evolved largely as a function of enhanced detectability with little regard for species recognition.

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