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The Effect of the Visual System and Habitat Light on the Colors of Anolis Lizard Visual Signals

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By

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ABSTRACT

FAILING, EMELIA The Effect of the Visual System and Habitat Light on the Colors of *Anolis* Lizard Visual Signals
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Lizards of the genus *Anolis* communicate almost exclusively with visual signals that include the extension of a colorful, extensible throat fan called a dewlap. Dewlap color exhibits impressive diversity across anoline species and is thought to have evolved due to two simultaneous sets of selection pressures: (1) selection for high detectability, and (2) selection for a color that is different from the dewlap color of other sympatric species of *Anolis* in order to facilitate species recognition.

In order for a dewlap display to be successful, it must be "detected" by the intended viewer. We hypothesize that a detectable dewlap should be distinct from its natural background in terms of brightness and color. We collected and analyzed spectral data for dewlap color and habitat light conditions for four species of anoles inhabiting the island of Puerto Rico. Background and dewlap colors were plotted in a three-dimensional tetrahedral perceptual color space based on the relative stimulation of each of the four types of cone photoreceptors of the anoline visual system. We found that for each species, dewlap colors were distinct from the range of background colors. We also found that for three out of the four species, dewlaps were typically brighter than the background patches of their habitats.

We carried out an additional behavioral experiment testing the likeliness of an anoline visual response being elicited as a function of the difference in brightness between a stimulus and a complex background. Our data suggest that the more a dewlap differs in brightness from the brightness patches in its background, the greater its visibility. Results from both experiments support the hypothesis that natural selection for high detectability in a complex environment has played a major role in the evolution of anoline lizard visual signal color.

Introduction

The diversity of visual signals across the animal kingdom is astounding and the success of these signals is absolutely crucial in the communication and survival of many species. The colors of visual signals in particular are highly diverse, even among closely related species, and can serve a variety of important functions such as indicating breeding or dominance status, indicating condition or establishing species identity. Determining the evolutionary forces that give rise to the vast diversity of visual signals is a widely pursued goal in the study of animal communication (Fleishman & Persons 2001).

In order for a visual signal to be successful, it must be seen by the intended viewer which involves distinguishing the signal from the complex visual background of the habitat in which it's observed (Fleishman & Persons 2001). The colors of the signal and its background are seen as a result of light arriving at various patches of color and reflecting from the patches to the viewer's eye (Endler & Mielke 2005). The effectiveness of a signal is therefore dependent on the sensory system of the receiver as well as the habitat light conditions in which it is observed (Fleishman 2000).

A concept known as "the sensory drive hypothesis" claims that in a given environment, visual signals that more effectively stimulate the sensory system of the viewer have an evolutionary advantage over those that result in less stimulation. For example, in the case where a population occupies a new habitat with a different visual environment than their original habitat, natural selection should favor any phenotypic change in the visual signal that maximizes its visibility to the viewer (Endler 1992). Populations of species occupy a vast diversity of light habitats and signal diversity evolves because different habitat conditions select for the most effective communicative signal in that habitat, which in turn promotes divergence in signal design (Leal & Fleishman 2004).

Anolis is a relatively common genus of lizard with a wide range stretching from the northern half of South America to as far north as North Carolina including almost every island of the Caribbean. Anoles have a poor sense of smell, and though some species have the ability to vocalize, their response to sound in the wild is unknown (Losos 2009). The anoline visual system, on the other hand, is well understood and is quite impressive. Anoles have color vision that extends into the ultraviolet, and are the only other group of vertebrates, along with predatory birds, that have two foveae in the retina that are thought to aid in depth perception (Fleishman 1992). Unlike human color vision which is trichromatic, anoline vision is tetrachromatic, meaning their eyes contain four different classes of cone photoreceptors that have peak sensitivities in longwave (l), mediumwave (m), shortwave (s) and ultraviolet (uv) light (Losos 2009).

With such advanced eyesight, it is no surprise that anoles communicate almost exclusively with visual signals (Fleishman 1992). The anoline visual display consists of a series of bobbing head movements as well as the opening and closing of an extensible colorful throat fan called a dewlap. Visual displays are used in a variety of contexts including communication in courtship, intrasexual, agonistic encounters and the most common use is by territorial males which display spontaneously to repel other males in the vicinity (Fleishman, 1992). Approximately 361 species of anoles have been recognized and there is great diversity in dewlap color, shape and size between species (Losos, 2009). An overarching question in the study of anoline visual signals, is what causes this diversity in dewlap design.

The overall goal of our research was to investigate the driving forces behind the evolution of dewlap color in four species of Puerto Rican anoles: *Anolis pulchellus*, *Anolis krugi*, *Anolis gundlachi* and *Anolis cristatellus*. These species are all descendents of a single

ancestor that colonized Puerto Rico and dewlap characteristics vary between them (Fleishman, Leal, Persons 2009). *A. krugi* and *A. cristatellus* have dewlaps that appear yellowish due to high transmission and reflection at wavelengths of 500nm and longer. *A. gundlachi* possess a low reflective and transmissive dewlap that is spectrally broad which make it appear brown. The dewlap of Anolis puchellus reflects strongly at long wavelengths and absorbs short wavelengths and therefore appears red (Fleishman, Leal, Persons 2009). We investigated the hypothesis that dewlap colors have evolved in response to two simultaneous sets of selection pressures: (1) selection for high detectability: making it easy for conspecifics to detect the signaler, and (2) selection for a color that is different from the dewlap of other sympatric species of *Anolis* in order to facilitate species recognition. We predicted that for a dewlap to be highly detectable, it should be distinct from the patches of color and brightness in its natural background. Additionally, for a dewlap to facilitate species recognition, similar appearing sympatric species should have distinctly different dewlap colors.

In order to identify the different components that could be playing a role in the evolution of dewlap color, we determined the spectral intensity and quality of the light in each species habitat as well as the spectral transmission and reflectance properties of the dewlap of each species(Fleishman 2000; Leal & Fleishman 2004). In order to visualize our data with respect to the anoline visual system, we used a color space model similar to Endler and Mielke (2004). Their study compared color patterns as birds them see them using a color tetrahedron in which each apex represented one of the four avian cone photoreceptors. We used a similar tetrahedron model in our study, where each apex represented each of the four anoline cone photoreceptors. The relative stimulation of each cone class by a given color was given a value between 0 and 1. Each apex of the

tetrahedron represents a value of 1 for that cone. For example, the UV apex signifies only US cone stimulation and the greatest output from the UV cone. A value of zero for a given cone class plots on the opposite side of the tetrahedron. For example, Endler and Mielke (2004) demonstrated that different avian plumage colors stimulate different cones. One specific color from the orange crown of a male regent bower bird had a reflectance peak between 600 and 700nm, therefore primarily stimulating the l cone. For this reason, the color plotted closest to the l cone apex within the avian color space. In these models, the greater the distance between two points, the easier they are to discriminate from one another. Using this model, we interpreted that the further the dewlap color plotted outside of the range of colors of its background, the more visible it was to the intended viewer.

A study by Olgas (2012) used similar methods to analyze spectral data for dewlap color and habitat light conditions for Jamaican anoline species. Dewlap detectability was determined by comparing dewlap color to an averaged background color. Natural backgrounds consist of a mosaic of patches that vary in color and brightness, so when the viewer sees a signal, the viewer does not simply compare two patches with only two colors, but instead an entire color pattern (Endler & Mielke 2005). Therefore, in determining how distinguishable a dewlap is against its natural background, one must consider the entire spread of background colors, not just one averaged point. To expand upon the methods of Olgas (2012), the first experiment described in this study assessed an entire range of background colors in order to explore the complexity of the components of a natural background.

Fleishman and Persons (2001) found that the detectability of a colored stimulus can be quantified based on the difference in spectral quality and brightness between the

stimulus and its background. This was determined through experiments in which a flag was waved in a periphery of anole and detection was assessed dependent on the anole's recognition of the flag against its background. Their study used monochromatic backgrounds of uniform brightness. We used a similar method in our second experiment to better understand the relationship between the intensity of a dewlap and its effectiveness in stimulating the anoline visual system when observed against a complex background, characteristic of its natural habitat. To do this, we constructed a background of randomized patches of varying brightnesses in order to replicate a more natural visual background.

Methods

Field sites

Spectroradiometeric data was collected over the course of ten days in late June/early July 2012 in Puerto Rico. We were based at the El Verde field station in the Luqillo National Forest and collected data at four distinct field sites. The first was the old growth forest region surrounding the research station. Within this location, a high number of *Anolis gundlachi* were observed on tree trunks throughout the densely vegetated and low lit habitat. A few individuals of *Anolis cristatellus* were also found on the edges of forested areas. The second field site was located approximately two miles from the station in a fully lit, open field where individuals of *Anolis puchellus* were observed. The third field site, where we collected data on *Anolis cristatellus* was in the Cambalache State Forest preserve, and consisted of both partial shade and partial sun habitats. The fourth site, was a partially shaded area along a stream in disturbed habitat near the edge of the El Yunque forest preserve, where we collected data on *Anolis krugi*. Our total sample size had varying

numbers of data for each species dependent on the number of present individuals and our ability to locate each. Individuals of *A. cristatellus* and *A. gundlachi* were most common and more easily observed and therefore had higher sample sizes of ten individuals each. *A. krugi* and *A. puchellus* were much less common and therefore had smaller sample sizes of five individuals each.

Habitat Light Collection

Data collection occurred between 08:00 and 17:00h each day. In the case of heavy rain, sampling was delayed due to the small amount of lizards remaining out of shelter and also to assure the safety of the equipment. A selected habitat was traversed until a male anole was sighted. We remained at a distance of approximately 3 m, making sure not to disturb or disrupt the anole. Each individual was observed for up to ten minutes, or until a display occurred. After ten minutes, if no display occurred, a female was captured and placed near the male to induce a dewlap broadcast. When a display occurred, it was photographed using a Nikon D5000 SLR camera and immediately afterwards, we moved in and set up two perpendicular 0.75 m transects in front of the exact display site. Evenly spaced markers along the transects were used as guides to record twenty one radiance measurements of the background behind the observed lizard display using an Ocean Optics JAZ spectroradiometer with a radiance probe (collimating lens). We directed the probe at a diffuse white standard in order to collect irradiance data from the front, and the back of the display site (i.e directions perpendicular to the expanded dewlap from behind the viewer and in front of the viewer to capture the irradiance illuminating the dewlap). This measured the spectral quality of all light striking the flat surface from a full hemisphere centered on the white standard. Radiance was

calibrated by recording the spectral radiance from a Li-Car Li-1800 irradiance calibration lamp with a radiance attachment.

Dewlap Spectral Characteristics

Individuals of each species from each field site were collected for further spectral assessment. Lizards were placed in holder, preventing any body or head movements. The dewlap of each individual was extended by manually pinching and pulling the hyoid bone forward. Reflectance and transmission characteristics of the dewlap were then measured using the Ocean Optics Jaz spectroradiometer with a reflectance measurement probe. We illuminated the dewlap using an Ocean Optics PX-2 pulsed xenon lamp and recorded the light reflecting from the surface. Transmission was measured by positioning the fiber optic 2 mm from the dewlap, directly opposite the light source. Reflectance was measured from a single fused silica fiber surrounded by 6 illuminating fibers. Reflectance characteristics of the bodies were also measured for some of the individuals.

Data Calibration and Modeling

Calibrated radiance spectra collected in the field and converted into 10nm steps by taking the median for 10nm surrounding each point. Irradiance spectra was produced by multiplying the radiance recorded off the diffuse white standard time pi. Anoles have cone photoreceptors including a cone for long wavelengths, middle wavelengths, short wavelengths and ultraviolet wavelengths. Each cone has its own type of colored oil droplet that functions to filter light received by the cones and thus adjust the spectral sensitivity to each cone (Fleishman et. al 1993). The visual system of *Anolis* goes through a process called chromatic adaptation, meaning for each lighting environment the output

from each cone class becomes roughly equal overtime as it adjusts to the background. For each light habitat measured, we equalized the output of the cones of each species by adjusting the cones to the "back irradiance" measurement from that light habitat sample, which represented the average light striking the eye of a theoretical lizard viewing the dewlap of the lizard we measured. Next, we multiplied dewlap, body and background radiance values by the relative stimulation of each photoreceptor for each species. The output of each cone constituted a number between 0 (no stimulation) and 1 (full stimulation). That number determined where the specific radiance value plotted within a four dimensional color space, represented by a tetrahedron. The four apices represented full stimulation of that specific cone and the wall opposite to the apices represented zero stimulation of that cone.

Methods (Behavioral Experiment)

Study subjects

Experiments were carried out between 21 January and 11 March 2013 on adult male *A. sagrei*. Ten individuals from a feral population in Florida were acquired from a commercial supplier. Lizards were maintained in small trapezoidal cages with front and side walls 19 cm in length, a back wall 10 cm in length and a total height of 24 cm. The room holding the lizards was set on a 12 h:12h light:dark cycle and kept at a constant 80 °C and 60 % relative humidity. Individuals were given water every other day and fed black solider fly larvae 3 times a week. The walls of each cage were painted an opaque white except for the front wall which was transparent glass. The tops of each cage were screened and near the front of each cage, a 17 cm wooden cylinder was suspended 7 cm from the bottom to serve as a perch for the lizards.

Overview

Stimulus cards of differing spectral quality were presented to the lizards through a small hole within a background of randomized brightness patches. At the start of each trial, a distractor arm was put into motion to direct the gaze of the lizard towards a fixed location. Immediately afterward, a movable flag covering the hole in the background was lifted to reveal a specific stimulus card to the lizard. We recorded a positive response whenever the lizard shifted its gaze toward the revealed stimulus card within the time it was exposed. One experimental set contained six trials, each testing one of six different stimulus cards of differing spectral quality or brightness. Five full sets were conducted on ten individuals over a seven week period. The success of the stimulus card at drawing the lizard's attention was quantified by tallying the number of positive responses of each lizard per stimulus.

Experimental arrangement

The experimental setup was arranged on a movable 45 cm by 60 cm table. At the beginning of each trial, the table was moved in front of the cage being tested. Lizards were observed with a video camera positioned 30cm from the front of the table at a 45° angle from the center of the perch. The apparatus angled 10° from the front of the table contained the stimulus background, movable flag and an open space for the stimulus card to be placed. In order to reduce the effects of shadowing, these objects were pressed between two 15 cm by 20 cm pieces of transparent glass, leaving enough room between them for the flag to be moved with ease. The background contained a small opening (1.25cmx1.25cm) through which the stimulus card was viewed (Figure 1). The stimulus

card was revealed by the upward movement of a flag, controlled by a pen motor and located between the background and card. Neutral gray cardstock extended from the top, bottom and sides of the background and served to block the pen motor and to reduce experimenter/lizard interaction between trials. Lizards were observed on a video monitor outside of the experiment room.

Stimulus design

The stimulus consisted of a stimulus card which was revealed by the upward motion of a flag and viewed through a small opening in the background. The stimulus flag was a rectangular piece of cardstock, mounted on a pen motor by a 7 cm wooden arm. Stimulus motion was created with a custom-built linear voltage ramp generator connect to and amplified oscillograph pen motor. At the start of each trial, the stimulus flag was positioned directly behind the background opening, blocking the stimulus card from the lizard's view. It was then moved upward at a constant velocity for 0.5 s until the stimulus card was in full view to the lizard through the opening in the background. The stimulus flag was held at this position, exposing the stimulus card for approximately 3 seconds, before moving back in place in front of the

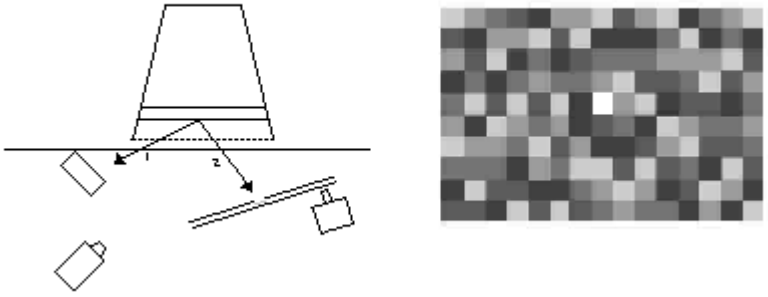


Figure 1: (left) Diagram of the experimental arrangment viewed from above. The gaze of the lizard located on the perch was initially directly in the direction 1, toward the distractor arm. The stimulus flag was then set into motion revealing the stimulus card. If the lizard noticed, it shifted its gaze to direction 2. (right) A "lizard's-eye-view" of the background and the opening where the stimulus card was viewed.

stimulus card. In order to be certain that the stimulus card was properly revealed, an additional camera was placed aside the cage, directed toward the experimental apparatus. This was observed on a monitor outside the experimental room, giving the experimenter a "lizard's eye view" of the stimulus.

The background was made up of a 10 x 15 matrix of 1.25cm x 1.25cm squares of five different brightness's (80%, 60%, 45%, 35%, 25%) printed onto cardstock (Figure 1). The pattern and order of these background patches was randomized and a square close to the middle of the matrix with a brightness of 45% was removed and "replaced" by a flag behind the background with the same brightness of 45%. Stimulus cards were designated as either 0, 1, 3, 4, 6, and C, representing brightness's of 100%, 80%, 45%, 35% and 0%. The card designated "C" had a brightness of 35% and an additional orange pigment. The experiment was designed so that three stimulus cards had brightness's that fell within the background brightness's and three that did not (the color card is considered outside the background spectra due to its additional pigment). A full experimental set was made up of 6 different stimulus trials, testing the effectiveness of the stimulus cards at eliciting a response. One trial was a control trial where the moving flag and stimulus card were the same brightness.

Experimental procedure

Trials were carried out between 09:00 and 17:00h. At the beginning of a set of trials, the table was positioned in front of the cage, lining up the hole in the background with the lizards head. Lizards were allowed to be positioned in either direction on the perch, so long as the video camera retained full view of the head. Once the table was set, the first stimulus card was inserted into place. Stimulus cards were presented in random

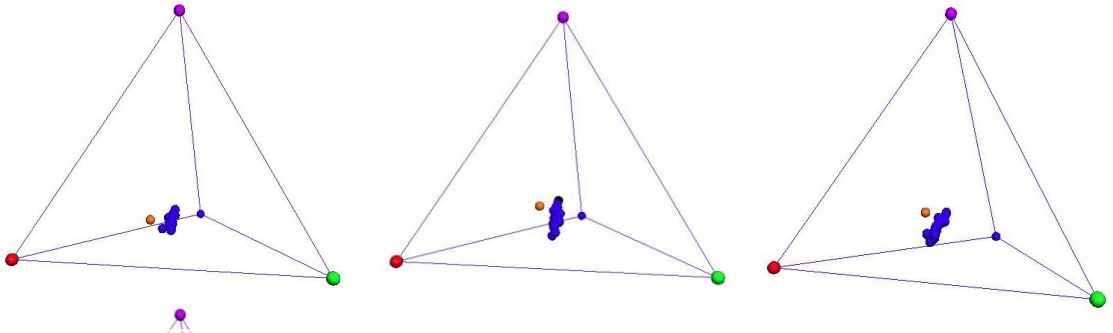
order for each set. Once the experimenter left the room, the lizard was given a three minute acclimation period before the presentation of the first trial. Immediately preceding each stimulus presentation, a distracter arm located in the front left side of the table near and consisting of a rectangle flag controlled by a pen motor, was moved back and forth until the lizard shifted its gaze toward the direction of the arm. After a 2 s delay, the flag was set into motion and the lizard's response to the revealed stimulus card was recorded. A positive response was defined as any eye shift or head movement toward the direction of the stimulus within 5 seconds of the stimulus presentation. After completion of the trial, the stimulus card was changed, and a 3 minute interval was allowed until the next stimulus presentation. After 3 trials, or a "half-set", the table was moved to the next perched lizard. One "half-set" was conducted for each lizard each experiment day. If a lizard refused to perch or was incorporative and a set was uncompleted, that set was continued the next experimental day. A least one day of rest was given between experiment days. Results were analyzed with a Freidman two-way analysis by ranks (Siegal 1956).

Results

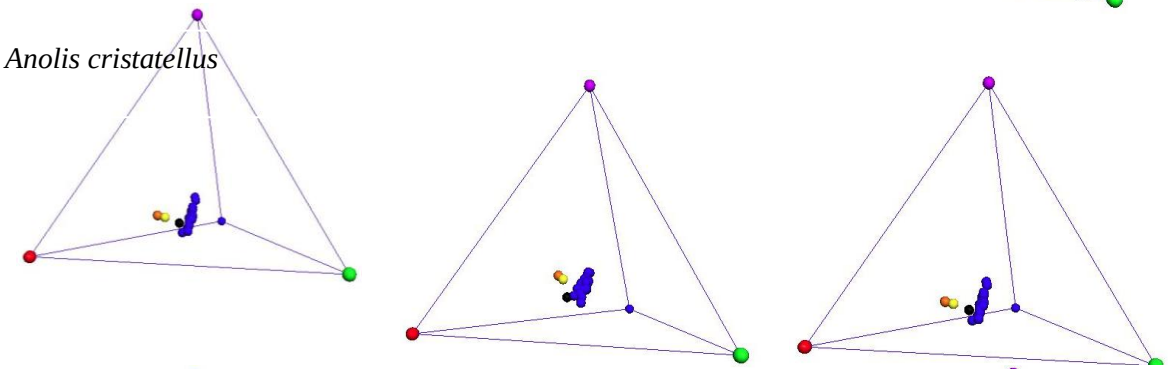
For experiment 1, we collected habitat light data for a total of 30 individuals across four different field sites. Due to differences in densities in each habitat, the sample distribution was not even (*A. puchellus* – 5, *A.krugi* – 5, *A. gundlachi* – 10, *A. cristatellus* – 10). Figures 2 shows the color tetrahedrons for 3 individuals of each species analyzed. Dewlap colors fell distinctly outside the range of background colors for each individual. Due to the multicolor characteristics of the dewlaps of *A. cristatellus* and *A. puchellus* , the dewlap was split into two separate colors. Body colors plotted either within the range

background colors, or plotted consistently closer to the range of background colors than any dewlap color for each individual.

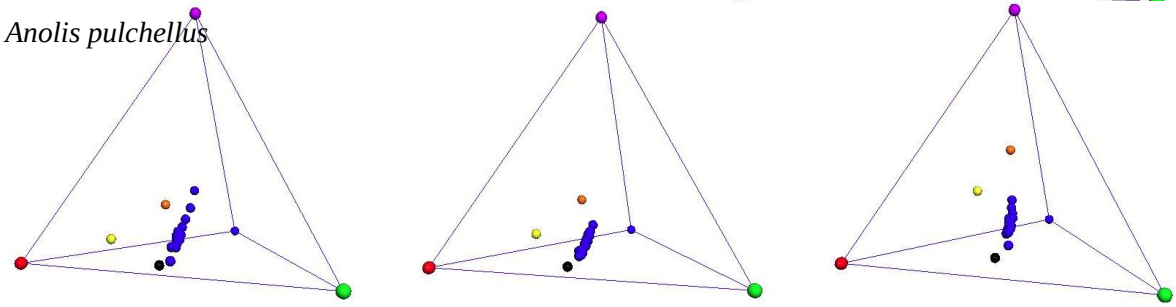
Anolis gundlachi



Anolis cristatellus



Anolis pulchellus



Anolis krugi

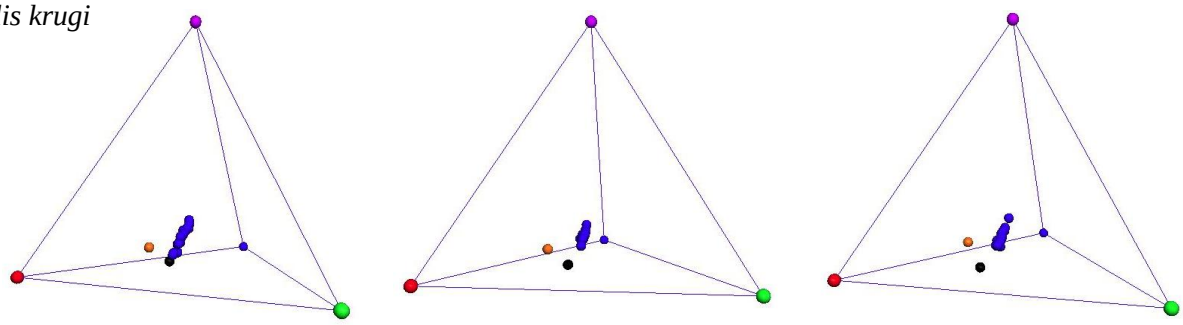


Figure 2: Four dimensional color space models for 3 individuals of each species of Puerto Rican anole. The red, green, blue and purple apices represent full stimulation of the short, medium, and UV cone. Blue dots represent background colors, orange and yellow dots represent dewlap colors and black dots (when visible) represent body colors.

Figure 3 shows all dewlap colors and background colors collected for each species. All background and dewlap colors took up a small portion of the color tetrahedron. Backgrounds and dewlaps of *A. puchellus* show the greatest diversity in color.

Figure 4 shows all the dewlap colors for each species plotted together in the same color space. Dewlap colors plotted in a relatively constrained mass, which, as a whole, fell closest to the l cone apex. Dewlap colors showed an overall greater stimulation of the long wavelength cone and expressed low output values from the middle wavelength cone and short wavelength cone. Despite considerable overlap, dewlap colors of all four species are clearly separated in some way. Dewlaps of *A. krugi* and *A. puchellus* plot the furthest away from one another. Figures 3-4 show the percentage of body and dewlap brightnesses that were mostly brighter,

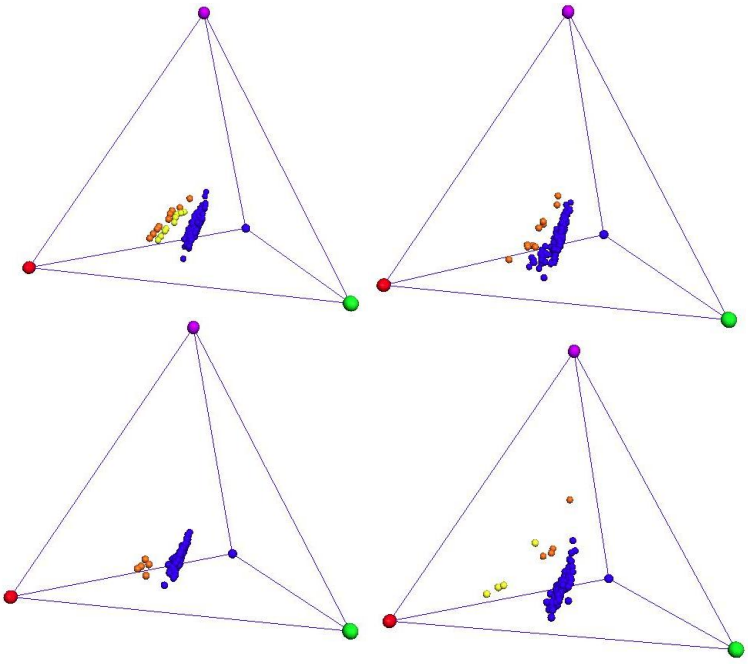


Figure 3: Four dimensional color space models with all dewlap and background colors plotted for each species. Note: sample sizes of *A. pulchellus* and *A. krugi* were smaller (n=5).

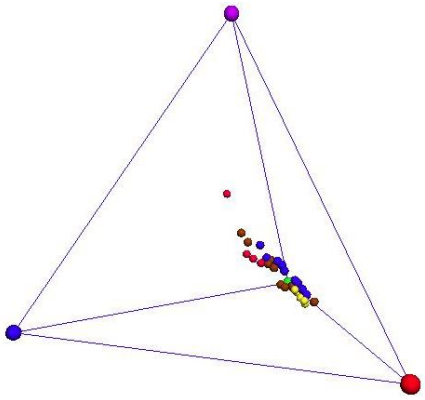


Figure 4: Four dimensional color space model with all dewlaps from each species plotted together. Red dots are *A. puchellus, blue dots are A. gundlachi* ,yellow dots are *A. krugi* and brown dots are *A. cristatellus.*

darker or within the range of background brightnesses for each species. If a dewlap or body measurement was brighter or darker than 70% of the background measurements, it was considered "brighter" or "darker" than the spread of background brightnesses. *A. cristatellus, A. gundlachi and A. krugi* had dewlaps that were generally brighter than their backgrounds and bodies that were generally darker than their backgrounds. The majority of *A. pulchellus* body measurements were either brighter, or within range of the background brightnesses and the majority of *A. pulchellus* dewlaps were either darker or within range of the background brightnesses.

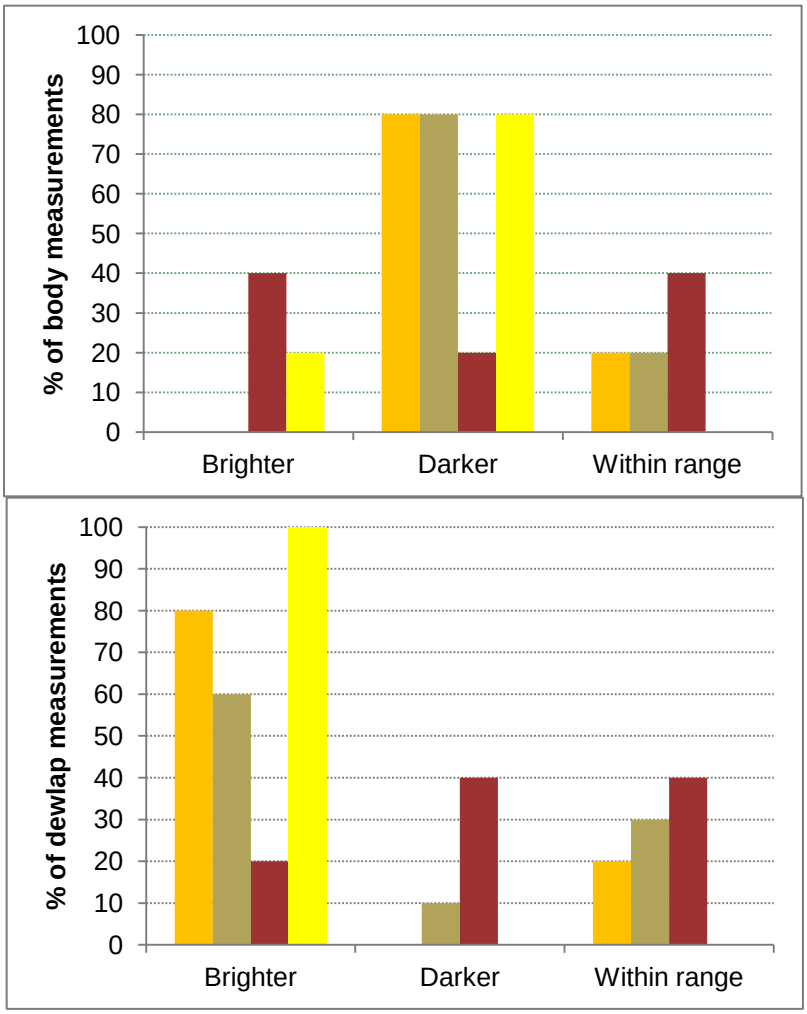
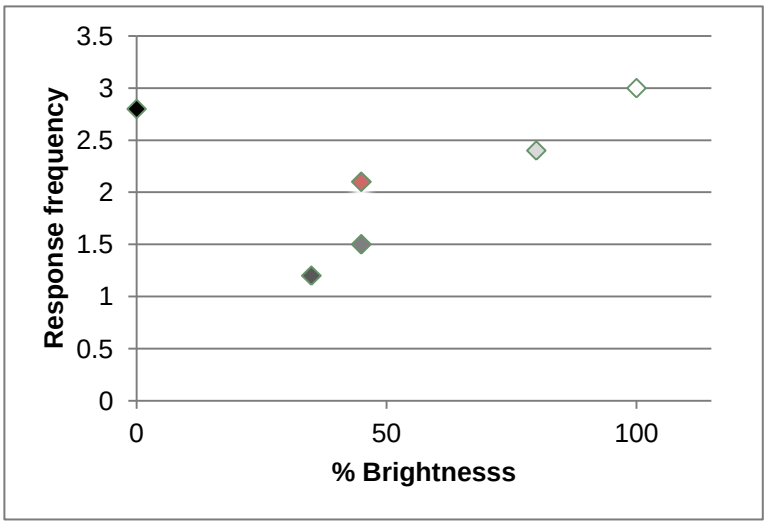


Figure 5: (top) the percentage of relative body brightnesses that were either brighter, darker or within range of their background brightnesses. (bottom) the percentage of relative dewlap brightnesses that were either brighter, darker, or within range of their background brightnesses.

Results (Behavioral experiment)

Our second experiment tested the likeliness of an anoline visual response being elicited as a function of the difference in brightness between a stimulus card and a complex background. The background was made up of square patches of differing

brightnesses (80%, 60%, 45%, 35%, 25%). Brightnesses of 100%, 80%, 45%, 35% and 0% were designated to individual stimulus cards. An orange pigment was added to an additional card with a brightness of 35%. The movable flag that revealed the stimulus had a brightness of 35%. In general, the more the stimulus card differed in brightness from the flag and from the range of background brightnesses, the stronger the response it elicited. The highest response frequency was elicited by the brightest stimulus card (100% brightness). The second highest response frequency was elicited by the darkest stimulus card (0%). The control stimulus card with the same brightness as the flag showed the lowest response frequency. All trials were significant except the color card trial (P>0.01). This was an unexpected result, as the addition of a color pigment would be expected to elicit a stronger response than brightness contrast alone.



Flag/stimulus card (%brightness)	P
4 (35%)/0 (100%)	0.009*
4 (35%)/1 (80%)	0.010*
4 (35%)/3 (45%)	0.317
4 (35%)/6 (0%)	0.008*
4 (35%)/ C (45%)	0.021

Figure 7: (top) The response frequency of each of the six stimulus cards of differing brightness. (bottom) The results of the statistical tests for significant differences between each trial and the control trial. Asterisks indicate significance.

Discussion

The results from our color space models show that for each species, body colors

plotted close to, or within the range of natural background colors, making the bodies cryptic. The dewlap color of each species plotted distinctly outside the range of the natural background colors. The dramatic difference between dewlap colors and background habitat expresses evolutionary convergence of dewlap colors toward high detectability in Puerto Rican anoles. Dewlap colors *A. pulchellus* and *A. krugi* were furthest apart in the color space. These two species are very similar with respect to size and can be found in the same fields in higher elevations (Fleishman 2000). *A. pulchellus* has a highly saturated red/orange dewlap with a UV patch, while that of *A.krugi* is a desaturated yellow. Evolutionary pressures from being similar in appearance and residing in similar habitats could explain why the dewlaps of *A. pulchellus* and *A. krugi* have evolved into distinctly different colors. Overall, the unclear distances between dewlaps of each species in color space expresses a lack of reliability on dewlap color evolving for species recognition. However, the distinct differences in dewlap color in anoles that have similar adult body size and habitat preference make the hypothesized function of species recognition plausible.

Overall, we found that dewlaps of each species are spread out and distinct, but seem to be clumped in a mass, constrained by limits within the color space. The mass of dewlap colors plotted nearest to the long photoreceptor apex, representing an overall greater stimulation of the long wavelength cone. Dewlaps did not express high outputs from the ultraviolet, short, or middle wavelength photoreceptors. This pattern could be explained by potential restrictions of the anoline visual system. Oil droplets located at each photoreceptor result in the sensitivity range of the middle wavelength cone to be completely overlapped by the sensitivity range of the long wavelength cone (Lowe et al 2002). This means that any stimulation of the middle photoreceptor would also result in

the stimulation of the long photoreceptor. This would explain why within the anoline color space, no colors plotted closer to the middle cone apex than to the long cone apex.

Restrictions in color space models could also be explained by the inability of certain animals to produce specific pigments. For example, fur colors are highly constrained because mammalian coloration is typically dominated by melanin pigments (Sumner and Mollon 2003). Dewlap and anoline body coloration are caused by combinations of pigments and structural colors. The orange, yellow and red colors of Puerto Rican anoles are caused by pteridine and carotennoid pigments (Macedonia et al., 2000; Ortiz and Maldonado 1966). It is possible that these pigments restrict the range of dewlap colors to a confined space in the color tetrahedron.

The results from our brightness data show that dewlaps are generally brighter than their backgrounds in *A. krugi, A. cristatellus and A. gundlachi* individuals. Bodies for these species are generally darker than their backgrounds. The results for *A. pulchellus* were rather ambiguous, and this could be due to the small sample size of only five individuals. Stronger trends might be observed if more individuals were tested. Our color and brightness results both support the hypothesis that natural selection for high detectability in a complex environment has played a major role in the evolution of dewlap color. The hypothesis for high detectability is also supported by the results from experiment 2. Stimulus cards that were brighter or darker than the brightnesses of the background elicited the highest response. These results suggest that the more a dewlap differs in brightness from the brightness patches in its background, the greater its visibility.

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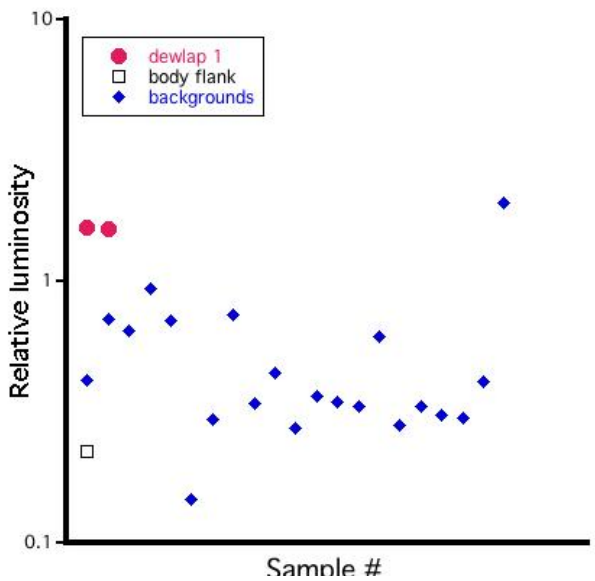
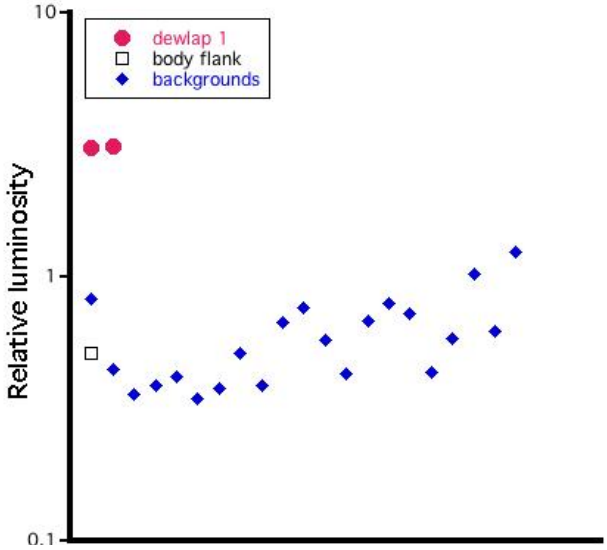
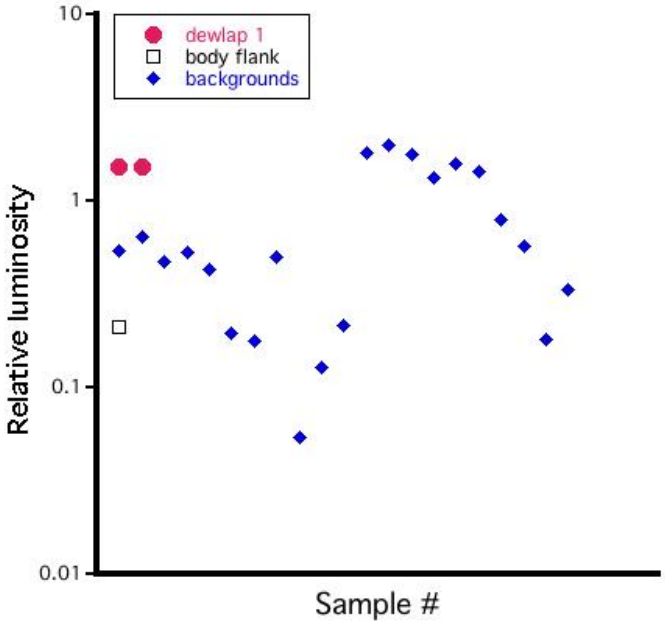
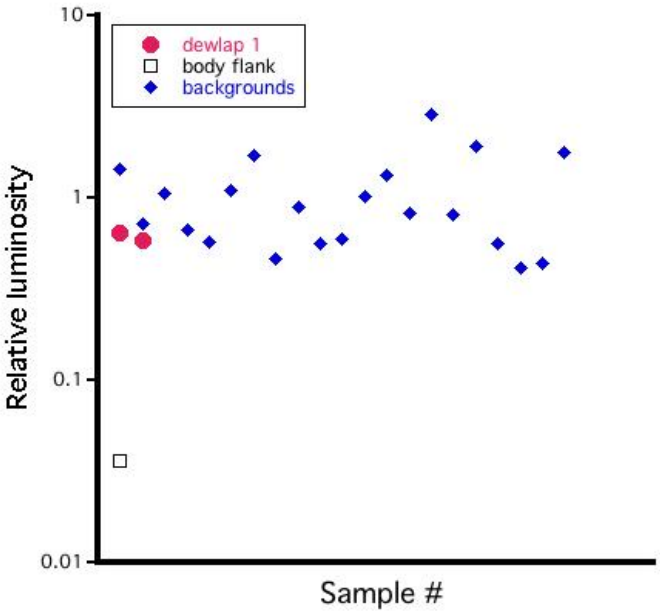
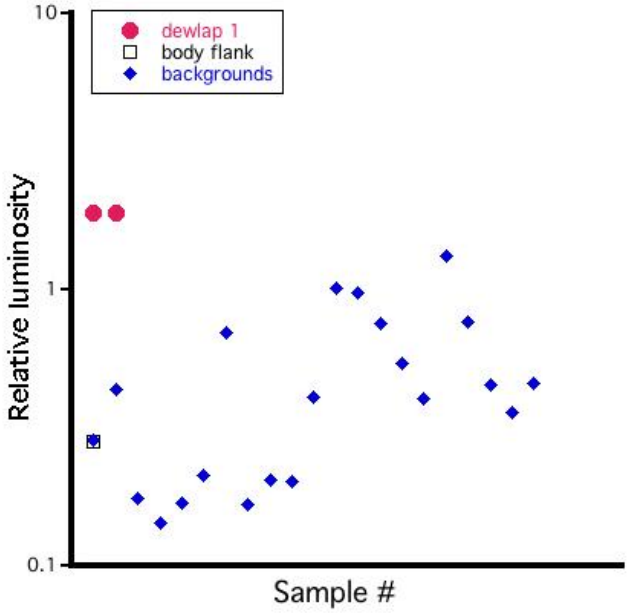
Appendix:
Anolis cristatellus







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Relative luminosity
Sample #
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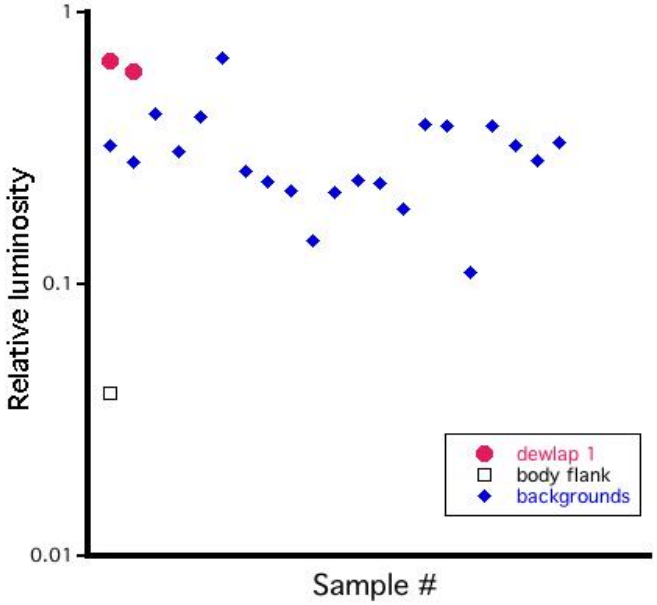
backgrounds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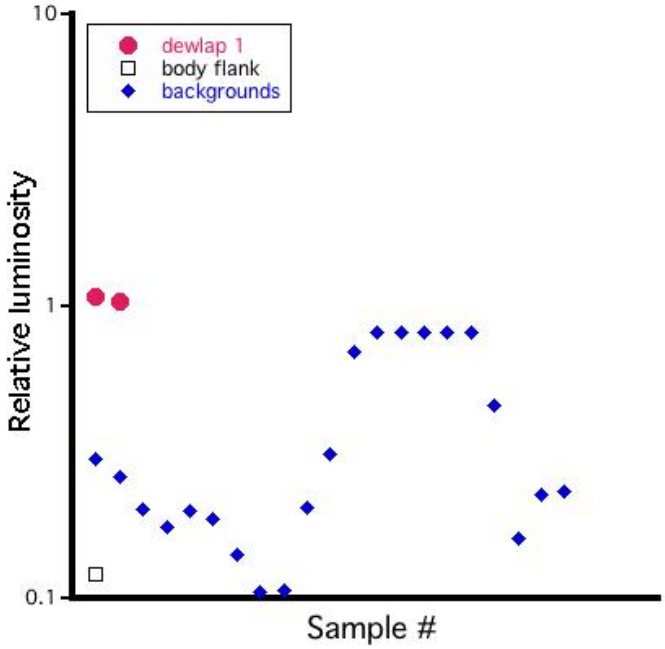
backgrounds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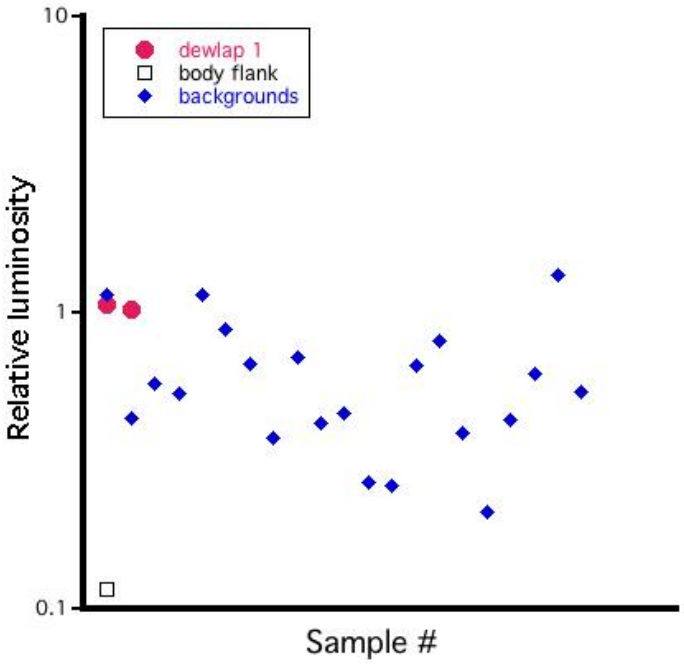
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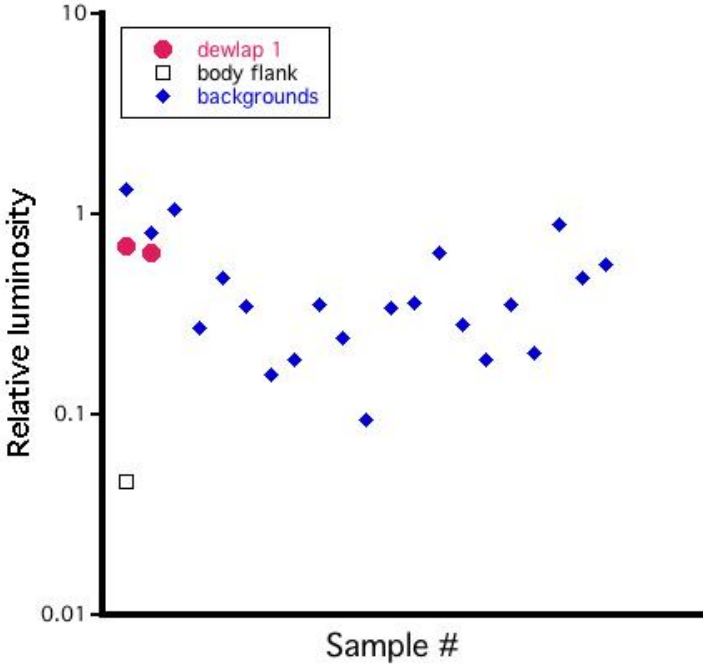
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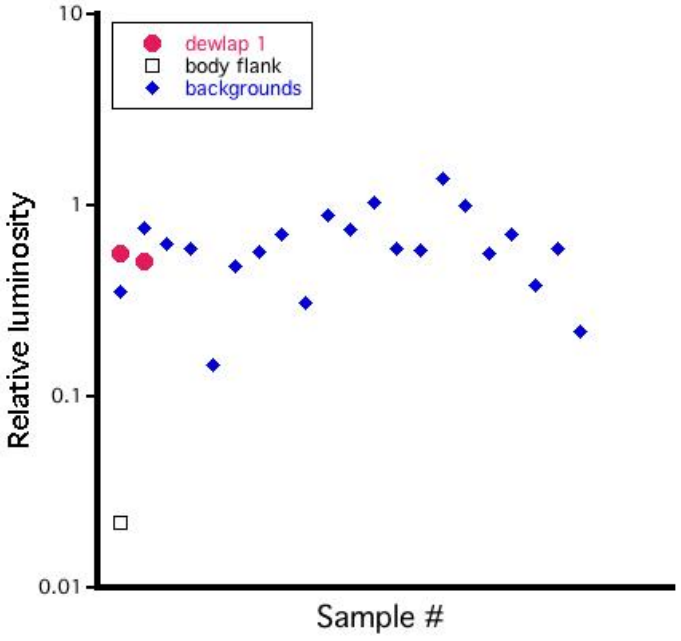
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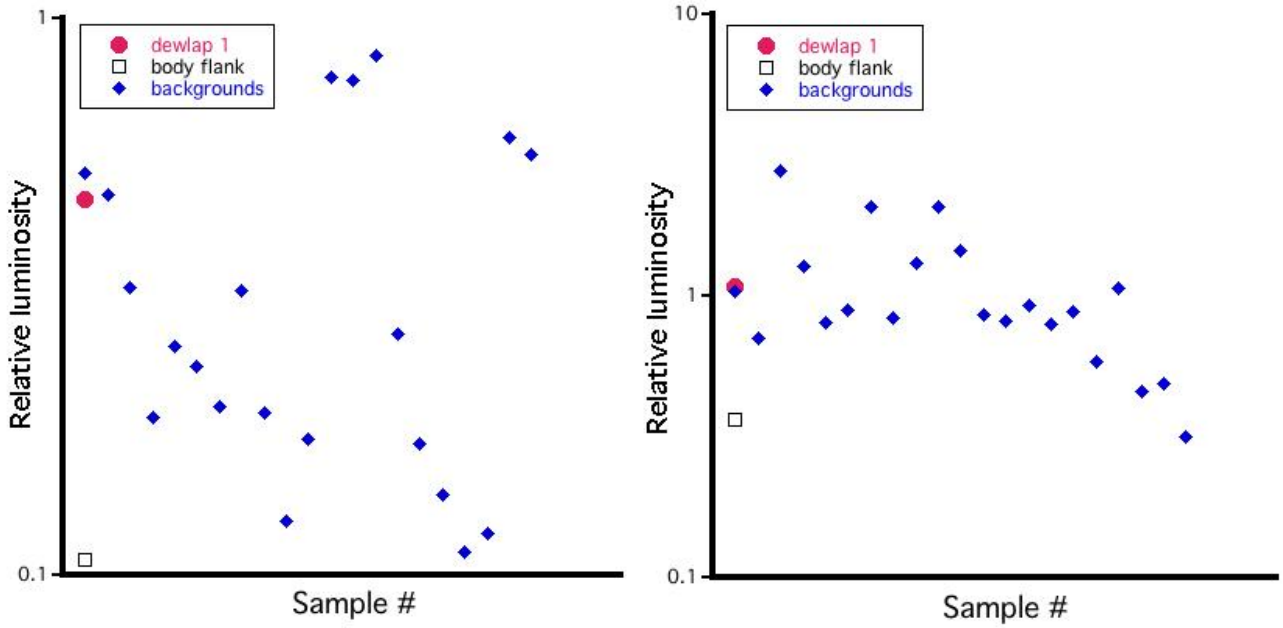
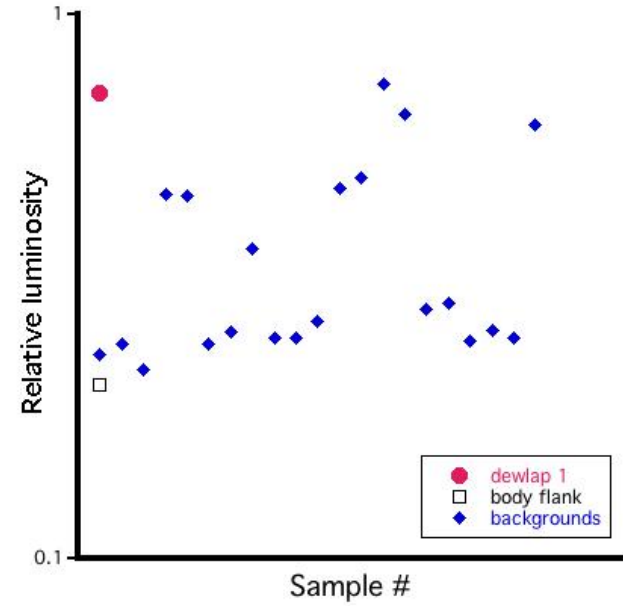
Sample #

Anolis gundlachi

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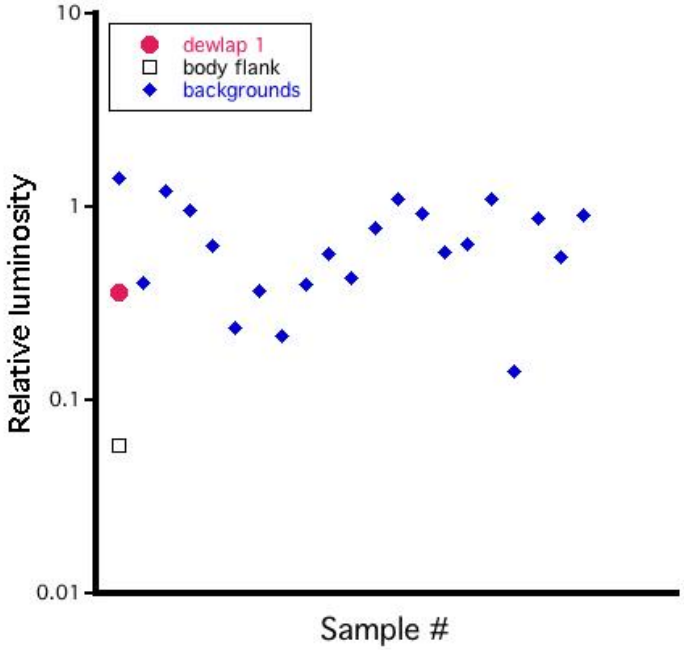
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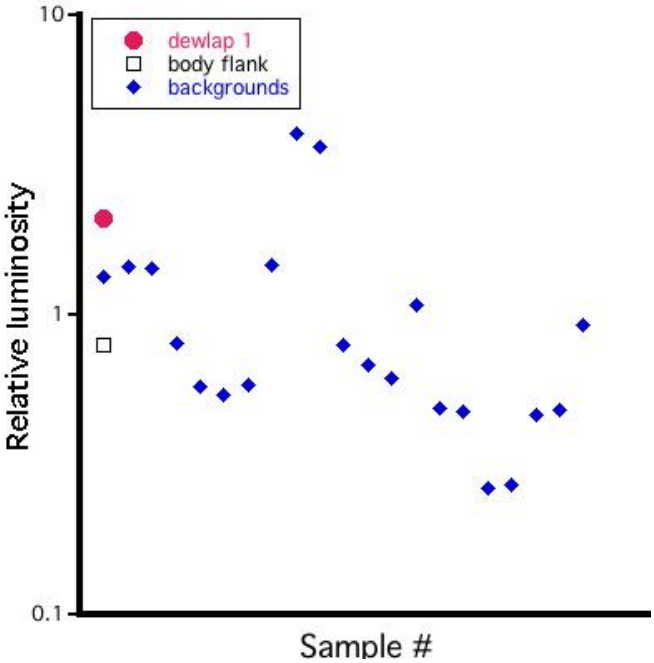
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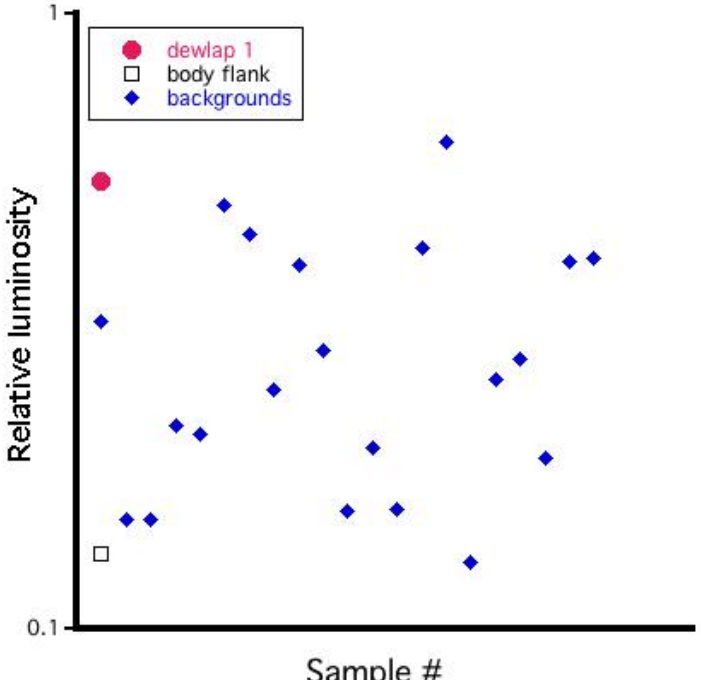
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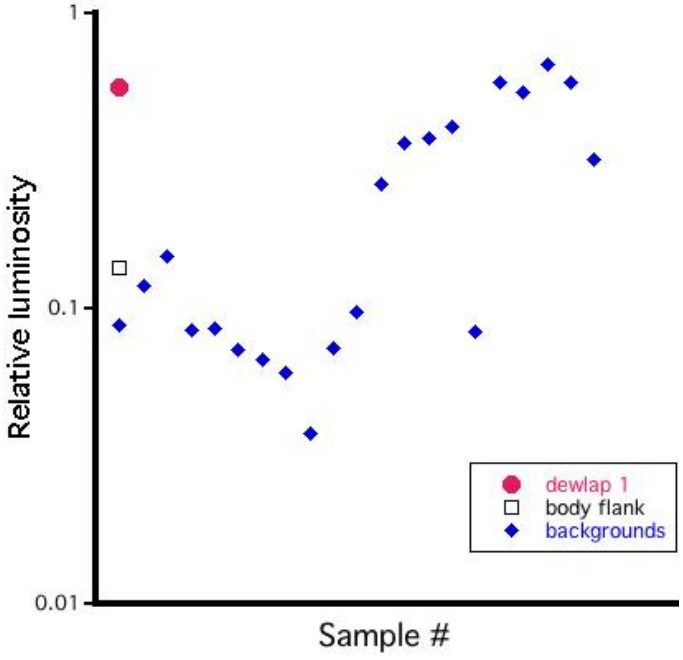
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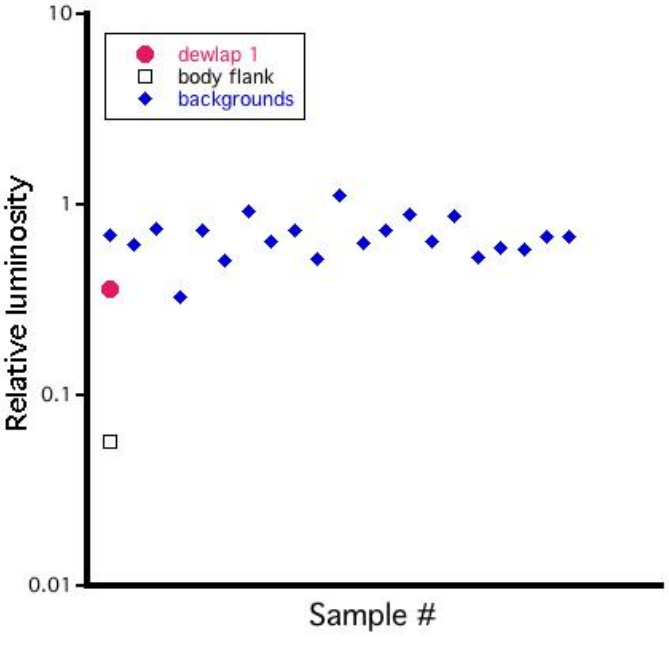
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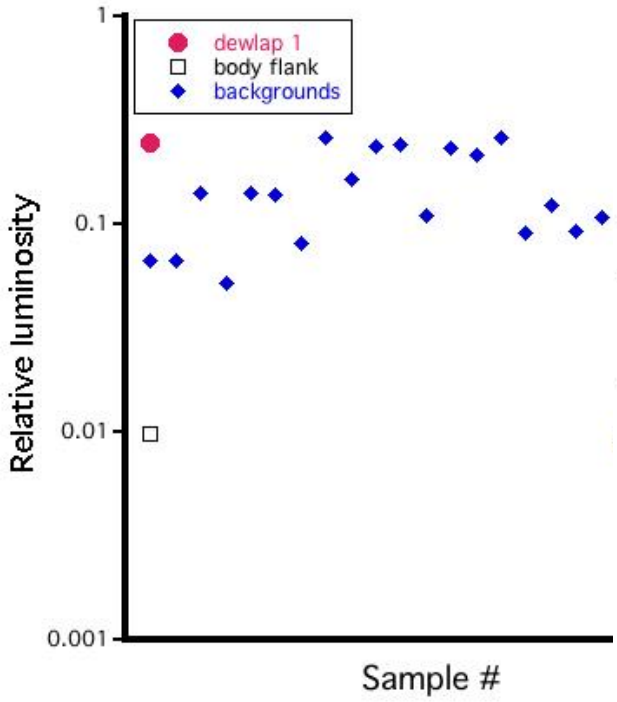

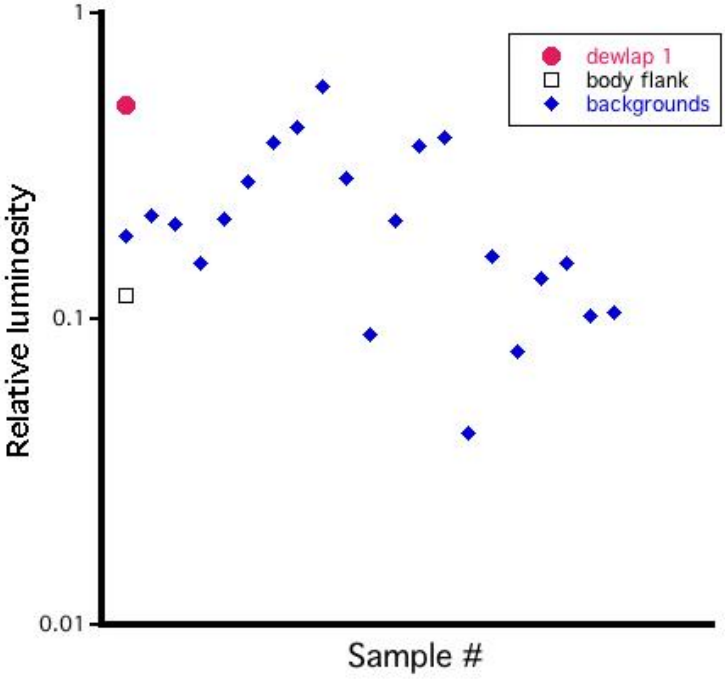

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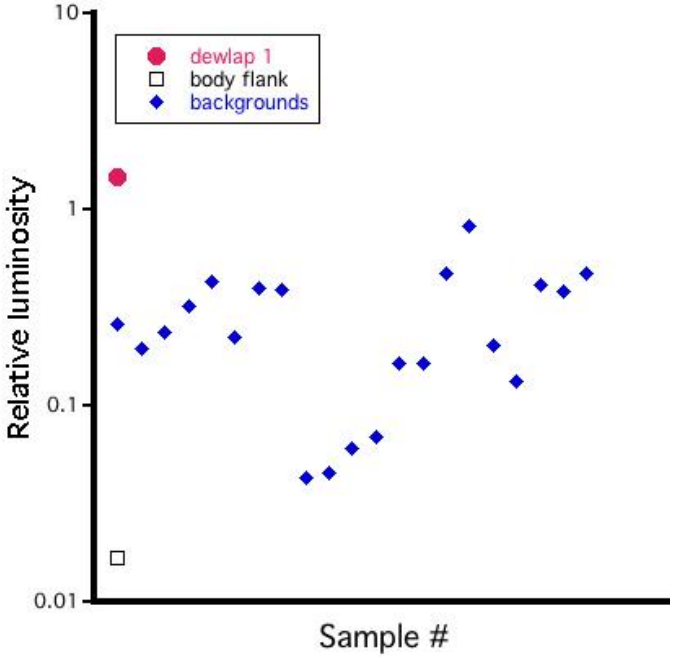

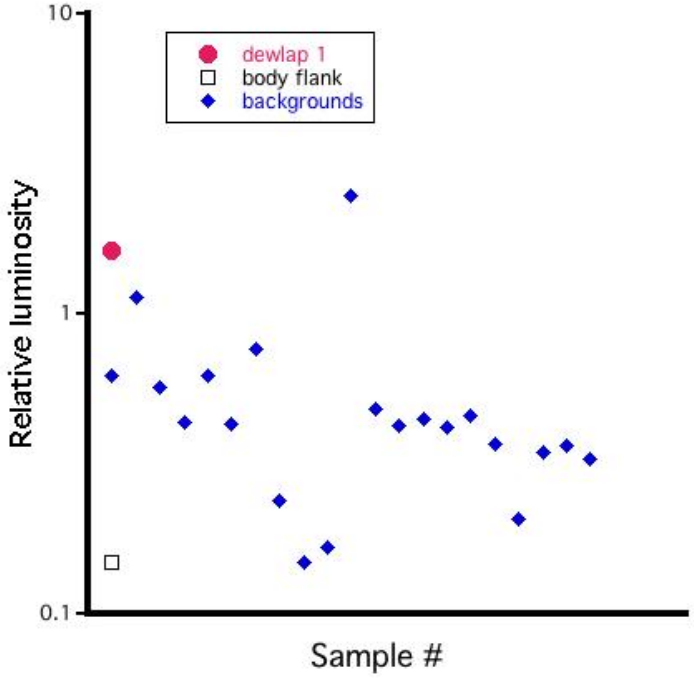

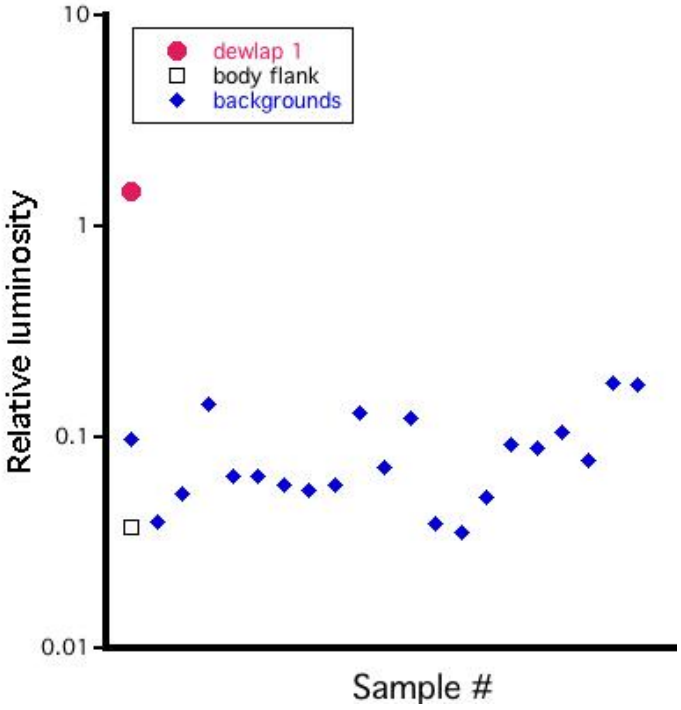
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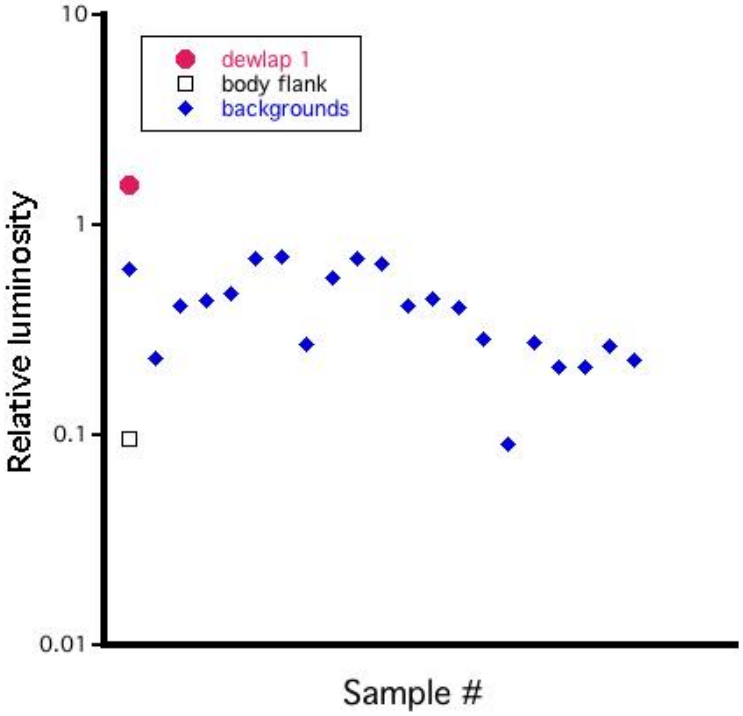
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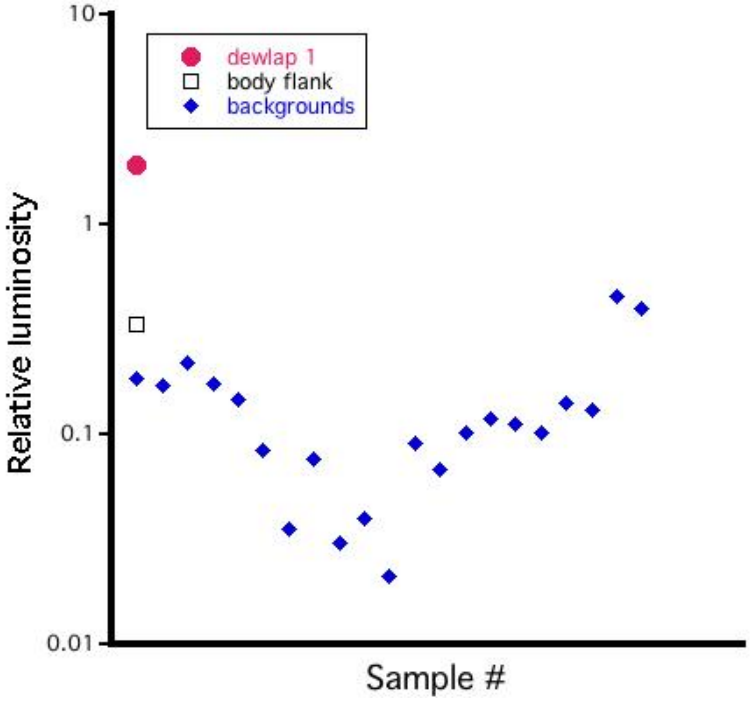
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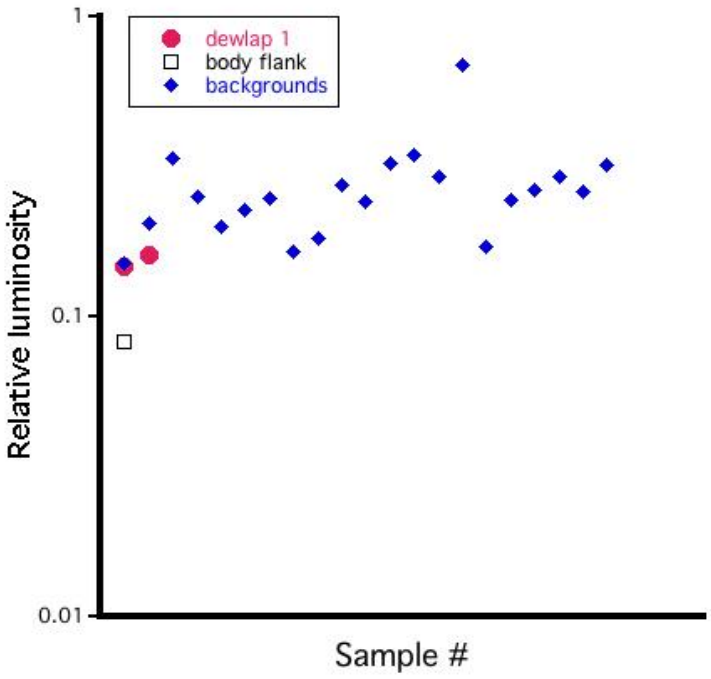
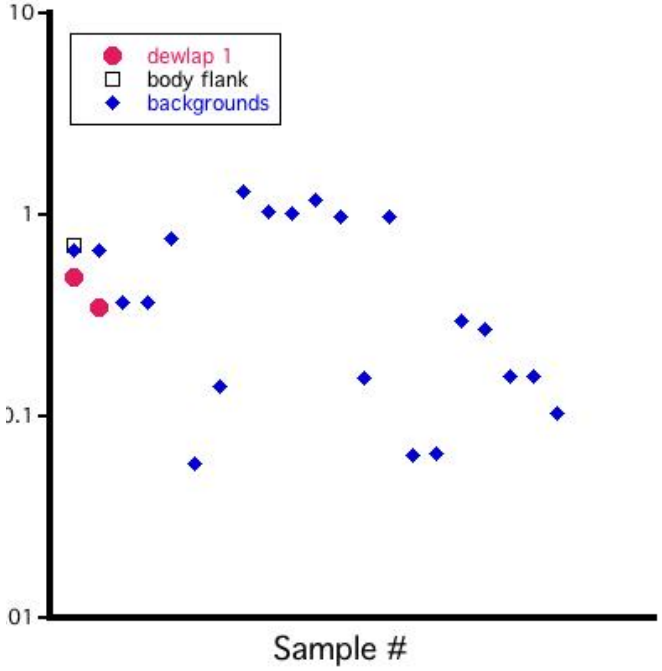
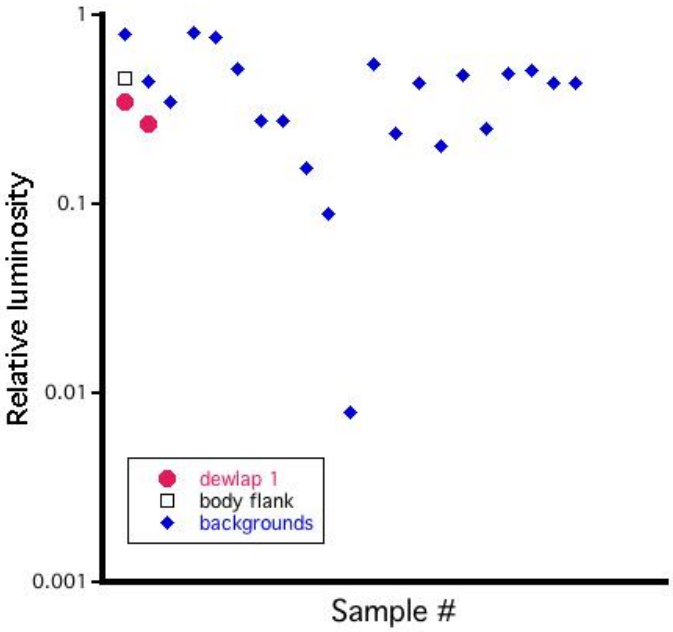
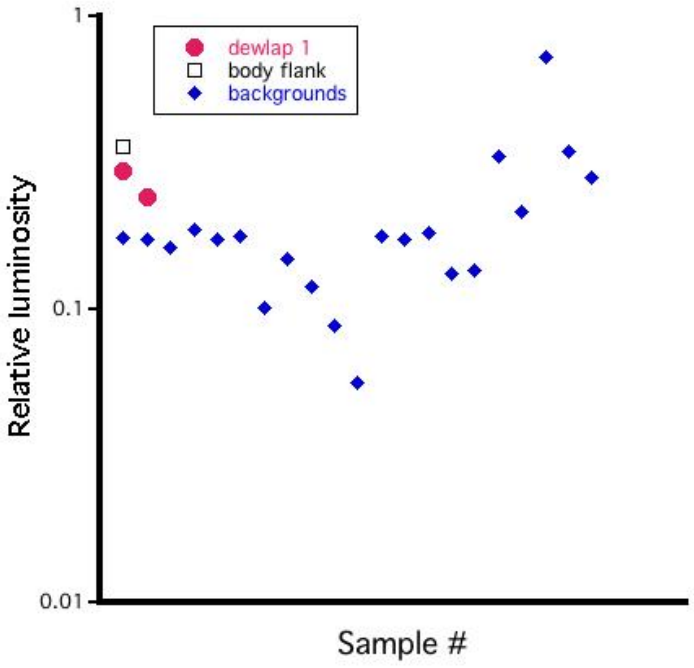
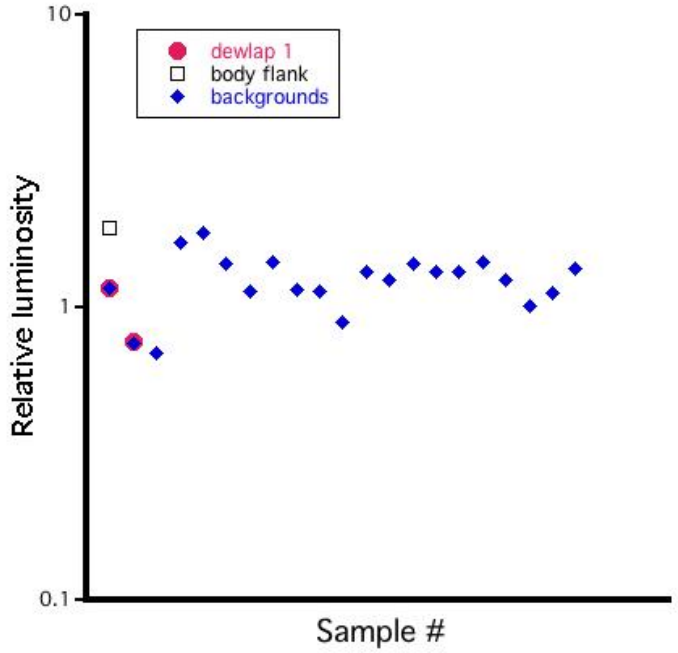
Anolis puchellus







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