

Color Vision and Color Discrimination in *Anolis sagrei*

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ABSTRACT

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Anolis is a genus of fairly common lizards; over 300 species of *Anolis* inhabit areas close to the equator. One of their most unique features is the dewlap, a colorful throat fan that the lizards can extend and contract to denote certain behaviors. Dewlap color and pattern varies between species, and therefore aids in species identification. For this reason, color vision and color discrimination is especially important in *Anolis* lizards.

Over a 10-week period a series of training experiments using color markers were done with four lizards of the *Anolis sagrei* species. The lizards were trained to move a color marker of a trained color and uncover a worm (2 were trained to orange, 2 to blue). In the second set of experiments, a second color marker was introduced which was a series of 4 color markers in a color span ranging from a similar color to the trained marker to a very different color. It was predicted that the lizards would make more errors when the two markers were close in color, and fewer errors when the color marker was more different.

Two potential patterns were predicted: as the colors got more different the number of errors made would gradually decrease, or, once the color markers could be discriminated the number of errors would significantly decrease and that value would stay constant as the two colors became increasingly different. The findings of this experiment give physical results to support or contradict predictions made by anoline eye computer models, and contribute to a deeper understanding of the driving force of dewlap color evolution. Future experiments can be done with a larger sample size, and with color markers that eliminate brightness as a factor.

Color Vision and Color Discrimination in *Anolis Sagrei*

Introduction

Anolis is a genus of fairly common lizards inhabiting areas close to the equator. Anoles evolved millions of years ago, yet only four *Anolis* fossils have been scientifically described: one 20 million years old with skeletal anatomy indistinguishable from present day *Anolis* species. *Anolis* lizards range in size from 33-191 mm (body length) with a tail that is 1-4 times the body length (Losos 2009). There are over 300 species of *Anolis* lizards inhabiting North America from Florida west to the eastern part of Texas, as well as Central America, the northern half of South America, and islands in the Caribbean and Pacific Ocean (Losos 2009). These various species are specific to certain areas; some have communities of 10 or more *Anolis* species, while other areas are inhabited by only one species. Despite overlapping territories, sympatric species are reproductively isolated and hybridization rarely occurs (Losos 2009). This means species identification by Anoles is acute and accurate. Though body size and coloration play a role, another distinguishing characteristic between species is the dewlap, a colorful throat fan that the lizards can extend and contract to denote certain behaviors. Dewlaps vary in color, size and pattern based on species, but closely related species do not necessarily have dewlaps with similar characteristics. Accompanying their dewlap displays, anoles also exhibit a series of head bobbing motions (Fleishman 1992). The length and frequency of these bobs is species specific and also aids in species identification.

Anoles have excellent eyesight and color vision, which extends into the ultraviolet area of the light spectrum (Fleishman et al. 1993; Fleishman and Persons 2001). The

lizards rely heavily on their vision and as a result they are extremely sensitive to movement. Responding to motion is a main factor in finding food, and recognizing predators, but also in communication between individuals. Signals must stimulate the sensory system to capture the attention of the receiving individual (Fleishman, 1992). Dewlapping is the most conspicuous form of *Anolis* communication. Typically, dewlaps are larger and more conspicuous in males than females, and males may dewlap several times a minute at times of high activity. There are various communicative purposes of the colorful pattern shown during extension of the dewlap. Dewlaps are used for courtship and attracting females, to alert other males in the area to the presence of a territory holder, and may signal to predators as a warning to cease pursuit (Losos 2009).

Divergent evolution caused a trend toward different colored dewlaps (Fleishman 2000), aiding in species identification. However, there is only speculation about why the colors evolved the way they did. One hypothesis suggested that dewlaps evolved to be conspicuous based on the light environment where the specific species lived. This would mean that anoles in darker, forested habitats would have brightly colored dewlaps in order to be easily seen, and anoles inhabiting open fields with high levels of sunlight would have darker dewlaps to contrast with the bright background. Within these general environments are separate microenvironments to which anoles are classified based on where they reside spatially. Trunk-ground anoles are medium sized and stay within 1 meter of the ground on a tree trunk surface or another kind of broad, flat area. Trunk-crown anoles stay near the top of the canopy, are usually green but can change color to a darker brown. Trunk anoles reside between trunk-ground and trunk-crown species with some overlap, they are small and grayish in color to blend into the tree trunks. Crown

giants are the largest anole species and live high in the canopy; most are green with a spiny crest on their back. Grass-bush anoles live in low lying vegetation and are small with very long tails. The last category is the twig anoles: very small and thin with short limbs; they forage for food instead of sit-and-wait predation (Losos 2009). The visibility in the microhabitat where each classification of anole spends its time could also play into dewlap color. Microenvironments in close proximity could potentially have very different light conditions, thereby affecting visibility in favor of certain dewlap colors (Leal and Fleishman 2002). However, Fleishman (2000) concluded that the ‘need to be detected’ is a driving force for dewlap color, but the evolution of dewlap colors of each species is more complex than simply being determined by the amount or spectral quality of light present in a given habitat. Other factors include the need to have colors not easily detected by predators, and biochemical limitations on the physical production of colors and patterns. In addition, colors of species that occupy overlapping habitats may need to be distinctly different in order to prevent mistaking one species for the other.

The various capabilities of a species’ eye affect the use of vision for social communication within that species. True vision requires a light sensitive pigment to trap the light energy in a photon and convert it to nerve impulses that are interpreted by the brain (Bradbury and Vehrencamp 1998). Photoreceptor cells, also called cones, house photopigments, which are packed side by side in the retina of the eye. A greater number of photoreceptor cells increase the ability of the retina to resolve fine detail. Anoles, like most lizards, are sit-and-wait predators, so their eyes are located on the sides of the head to maximize the monocular field. The anoline eye contains a retina, a central fovea and temporal fovea, which are depressions in the retina with increased visual sensitivity due

to a high concentration of photoreceptors. When viewing its environment, the lizard will adjust so the object of interest is seen with the fovea for optimal acuity (Losos 2009).

Color is perceived by different wavelengths of light being absorbed by certain photoreceptors in the retina. These varying wavelengths are perceived as different colors. For example humans possess trichromatic vision, in which three types of photoreceptors have peak absorption in the blue, green, and red wavelengths respectively. The resulting nerve impulses and chemical signals sent to the brain are understood as a certain color depending on which classes of cone cells absorbed wavelengths of light, and the relative intensity of stimulation of each class. Anole eyes are tetrachromatic, meaning the retina contains 4 types of cone cells to perceive color, and since the animals are adapted for a diurnal lifestyle, there are no rods, which are only used in low light. This means that in exchange for superior color vision, anoles have poorer visual sensitivity in dim light. The 4 types of cone cells are ultraviolet sensitive, short wavelength sensitive, middle wavelength sensitive, and long wavelength sensitive. Each cone has an optimal range of wavelengths it absorbs, and therefore the lizards have the ability to detect fine differences in color. An oil droplet is present in each photoreceptor filters out short wavelength light. In the non-UV photoreceptors this eliminates UV rays from being absorbed so they do not interfere with other light waves entering the eye. UV light has a tendency to scatter so the droplets improve clarity of the image seen. There is an oil droplet on the UV photoreceptor, however it is colorless and allows all wavelengths through.

Color vision also has lower spatial and temporal resolution compared to black and white vision. Nevertheless it has evolved in many species because it strengthens an

animal's ability to detect and recognize objects as well as identifying objects' spatial relationships to each other. This aids in orientation of the animal and is a key advantage in visual navigation. Color vision plays an important role in communication between individuals and between species. Brightly colored integument signifies a warning to predators, in the poison dart frog, for example. Bright colors are also used in courtship and mating, as seen in the peacock. Color can aid in species identification. In the case of the blue-footed booby, individuals will show each other their feet to ensure they are of the same species. Signals of color can also be aggressive or territorial, as seen, for example in the colored fins of the Siamese fighting fish.

Color discrimination is probably important to *Anolis* lizards for species identification based on dewlap color. Photoreceptors in the eye absorb wavelengths of a certain range, however these ranges overlap. If a wavelength of light falls in a range where two types of photoreceptors overlap, for example the short and middle cone cells, then the signals subtract and result in the appropriate color sensation. Each type of photoreceptor has range of wavelengths they absorb in the shape of a bell curve with a peak at the top of the curve (Fig 1. Fleishman 2001). Brightness is determined as a value on the dark to light scale and does not require seeing the actual colors, while hue is the chromatic definition of vision (Kelber 2003). The anoline eye has mostly double long wavelength sensitive cones, which are responsible for detection of movement and brightness, both colorless (Fleishman 2002). The single long, middle, short wavelength and UV -sensitive cones are responsible for color vision and discrimination. These cones are less abundant in the anoline eye suggesting detection of movement is more important to Anoles than color vision, demonstrated by their sit-and-wait predation style.

A big evolutionary question regarding *Anolis* is why dewlap color diverged into so many colors and patterns, and what drove the evolutionary change toward one color over another. Though this reason may not be clear yet, what is clear is the necessity of a signal to be seen. Therefore, signals with high detection rate and visibility by conspecifics and heterospecifics would be favored by evolution (Fleishman 2001). The anoline eye can discriminate between shades of colors--they have to for conspecific identifications--but how different do two colors have to be in order to tell them apart? In their own habitat, background color contributes to vision, and often in a forested habitat the green vegetation reduces quality of the image. Fleishman and Persons (2001) found that contrast between a stimulus color and background color was needed for optimal detection of the signal. Stimuli were also more likely to be detected when brightness contrast with the background was increased, however only with brightness input that would stimulate the middle and long wavelength sensitive cones.

The possibility that the difference between two different colors will not be detected depends on the visual noise present. At all times, photoreceptors in the retina are firing randomly with no correspondance to visual stimuli. These “noise” signals from each photoreceptor add together, as would a normal stimulus signal, and get sent to the brain. This phenomenon creates a certain amount of noise that is constantly present in each signal sent to the brain. At low light levels this noise is roughly constant. As intensity of a light stimulus increases the noise level increases, and is typically proportional to the strength of the visual stimulus itself (Kelber 2003). Though usually small enough not to interfere with vision, there is a point when the noise stimuli are great enough that differences between colors are undetectable. Where differences in color are

small, the photoreceptor noise will make them impossible to distinguish reliably. At higher light levels a stronger signal is sent to the brain based on visual stimuli, and this causes noise levels to also increase. The Weber Fraction gives the percent a signal has to change to be detectable. Computer models have been developed to predict how similar two colors must be for noise to be too great to allow for two spectra to be discriminated. The Kelber model is based on Hemholtz's (1896) quantitative modeling of thresholds which states that "discriminability of any two colors is given by their separation in color space (ΔS), and that the behavioral response depends on ΔS alone". When $\Delta S=1$ then a difference in stimuli is detectable above noise, so two colors can be distinguished, and as ΔS becomes greater than 1, colors become easier to tell apart. The computer model relates color differences to distances in geometric space; so the closer two points (representing two colors) are in geometric space the more similar the colors are on the color spectrum. The plotting of colors in geometric color space is carried out by treating the relative stimulation of each class of photoreceptor as one axis. Thus any color can be plotted based on its relative stimulation of each of the photoreceptor classes found in the retina. Behavioral experiments can be done to practically determine when $\Delta S=1$ for two colors based on animals' responses to a stimuli. Since every species sees color slightly differently, and each has a unique eye, behavioral experiments must be done for each species that can then be incorporated into the computer model.

Going further, once a threshold is determined for how close two colors can be to still be discriminated, the pattern of discrimination with increasing ΔS values can be tested. One hypothesis states that when a threshold is reached, every other color further in color space than that value will be easily detected. A different hypothesis states that even

when the threshold is reached, increasing ΔS would cause a gradual, steady increase in discrimination ability. One other factor is the involvement of brightness in color discrimination. Whether animals are more sensitive to differences in signal hue or brightness is undetermined, as is the extent to which either is relied on for discrimination (Kelber 2003).

The experiments described in this paper tested color vision and color discrimination in *Anolis sagrei* through a series of training experiments. Lizards were trained to a specific color. This was followed by choice experiments where the animals had to discriminate between the trained color and a series of other color choices. The aim was to determine an effective training method for *Anolis sagrei*, to test for a threshold in color discrimination from the trained color, and to understand the pattern of error rate as colors become farther away on the color spectrum from the trained color. Since *Anolis sagrei* rely heavily on movement and brightness, these had to be eliminated or controlled in the experiment so that color was the only factor being tested.

Methods and Materials

The *Anolis sagrei*, collected from wild populations in Florida, were purchased from a commercial supplier (Carolina Biological). Five lizards were used for the series of experiments. Each lizard was placed in its own cage. Each cage had a clear removable plexi-glass wall on one side of the cage, and a screen top to provide sufficient air. An incandescent light bulb was positioned directly over each cage, and a small wooden pole was placed in the cage so the lizards could sit directly under the light. Each lizard was watered daily, and through experimentation was fed 4 times a week.

The series of training experiments required the association of food with a specific color. Mealworms were used for the first 4 trials, and then phoenix worms were used throughout the rest of the experiments. A small gray plastic “serving dish” consisted of two open compartments (left and right) where a worm was placed. Small Styrofoam balls were cut in half and a circular color swatch was attached to the flat end of the ball. Using sticky tack, these color markers were attached to the same side of the serving dish where the worm was located. By coin toss the color marker and worm were randomly alternated between the left and right sides. Three of the lizards were trained to a bright orange color, and the other two were trained to a pale blue color. A remote viewing security camera was set up directly outside the lizard’s cage, and the experiment was viewed through a monitor in a different area of the room. This way I was able to watch the lizards without being visible to them.

To start the experiment, the color marker was attached to the serving dish. Live worms were used which could actively move inside the dish. A time limit of 10 minutes was used. If the lizard did not eat the worm within the time limit the trial was counted as a fail. Stage 1 was the only exception where a successful trial meant the lizard jumped down from the perch and ate the live worm within 5 minutes. Each day, 3 trials were carried out per lizard. After 6 successful and successive trials, the experiment progressed to the next stage. If there was a failed trial at any point, the lizard would regress and 6 more successful trials in a row would be needed to proceed to the next stage.

In the second stage of the experiment, the worms were killed before being put into the serving dish to eliminate motion as a factor. The worms were killed overnight in a cold refrigerator. In the third stage, the sticky tack was removed from the color marker,

and it was placed on the serving dish so that 50% of the hole was covered. This progressed to 75% of the hole being covered if the lizard had 3 successful trials with 50% partial coverage. Many times the lizards had to knock off the marker in order to access the worm. Dead worms were used. In the fourth stage, the hole was completely covered by the marker so that the lizard was required to knock it off to eat the dead worm.

Each of the 5 lizards progressed through stages at various levels. When moving from one stage to the next, 2 trials of the earlier stage were done followed by 1 trial of the next stage. During this stage transition time, the color marker and worm were kept on the same side through trial 2 and 3 (especially when transitioning from stage 1 to stage 2).

After the initial training experiment, a second experiment involved choices between color markers. Once the lizard had been trained through all of the stages of experiment 1, two different color markers were placed over both holes (complete coverage) in the serving dish. In trials with the lizards trained to orange, the worm was always under the orange color marker, in trials with lizards trained to blue the worm was always under the blue marker. Worms were always dead, and were killed by removing the head with tweezers (modified from refrigerating the worms). A successful trial occurred when the lizard removed the appropriate color marker to which it was trained and ate the worm. If the lizard first uncovered the opposing color marker before uncovering the correct marker, it was given time to uncover the correct color marker. However, this trial was counted as a fail. The experiment was done over a time span of 7-8 weeks, averaging at 21 trials per lizard in a 2 week period.

The second part of the choice experiment replaced the opposing color marker with a series of 4 color markers in a color span ranging from a similar color to the trained

marker to a very different color. For lizards trained to orange, the opposing color span ranged from a lighter orange, to yellow, to green and to blue. For lizards trained to blue, the opposing color span ranged from a different shade of blue, to teal, to green and finally to yellow. Brightness (perceived intensity) of both all of the orange spectra and blue spectra color markers were measured, and showed no significant brightness differences between the color markers (See Figures 1 and 2). The dead worm was always placed under the trained color. The opposing colored marker was randomly chosen by a generated chart with equal numbers of each of the 4 colors. 48 trials for each of the 4 lizards were completed.

The last experiment was a replica of the previously described choice experiment using 4 opposing color markers, however it was done under limited light conditions. Only one lizard was used for this experiment. A 2.0 optical density filter was placed over the cage directly under the light source. The irradiance with the filter was .12 micromoles per m^2 compared to 12 micromoles per m^2 of light in the original experiment. The lizard was trained to orange, so the orange scale color markers were used in the dark experiment. 48 trials were done, 12 of each of the opposing color markers (A, B, C, D).

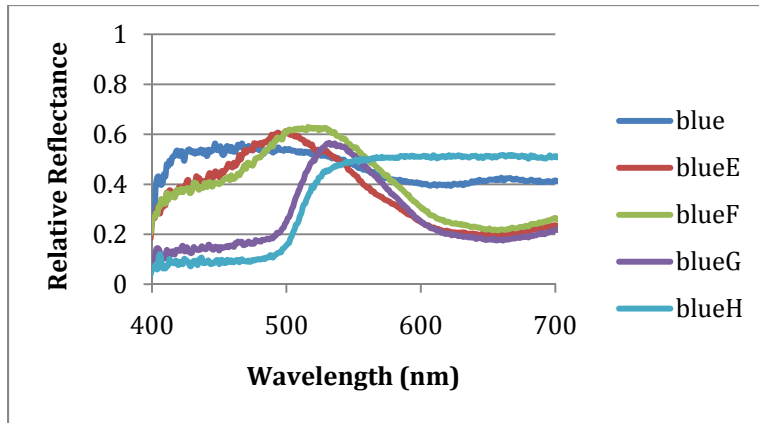


Figure 1. Relative reflectance versus wavelength for the blue range of training chip and testing colors. The values were multiplied by the spectral sensitivity and summed from 400 nm to 700 nm (roughly the range of light that influences brightness perception in lizards) to get a brightness value for each stimulus when viewed under the test conditions.

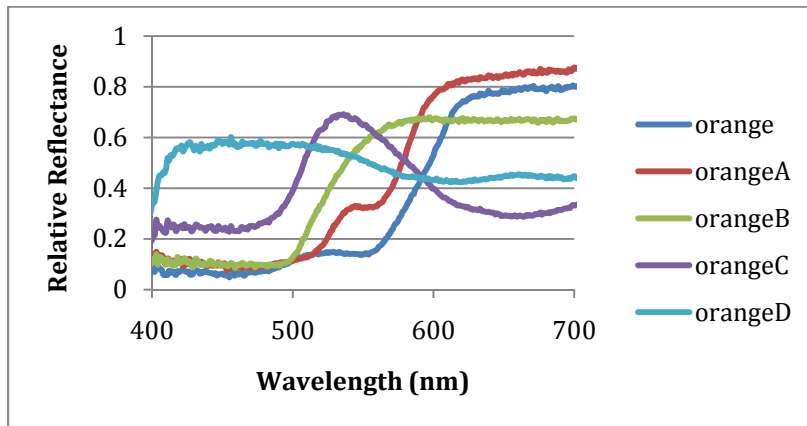


Figure 2. Spectral reflectance for the orange range of training chip colors. Perceived intensity (= brightness) was found by multiplying the spectral reflectance by the spectral sensitivity curve for the lizard to get the perceived intensity at each wavelength. The values for each wavelength were summed from 400 nm to 700 nm (roughly the range of light that influences brightness perception in lizards) to get a brightness value for each stimulus when viewed under the test conditions.

Results

Figures 3-6 show the results of the color choice experiment. Lizards 4 and 5 were trained to blue, and the corresponding range of opposing colors can be seen in Figure 3.

Lizards 2 and 3 were trained to orange, and the corresponding range of opposing colors

can be seen in Figure 4. A 65% correct threshold was used to determine if the lizards were actually distinguishing between the trained color and the opposing color.

Lizard 4 did not demonstrate, based on the percent threshold, an ability to successfully distinguish between the trained color (blue) and any of the opposing colors. Color choices E and F were more similar to the trained color and G and H were more different. More different colors from the trained color were not necessarily more easily discriminated; there is no pattern.

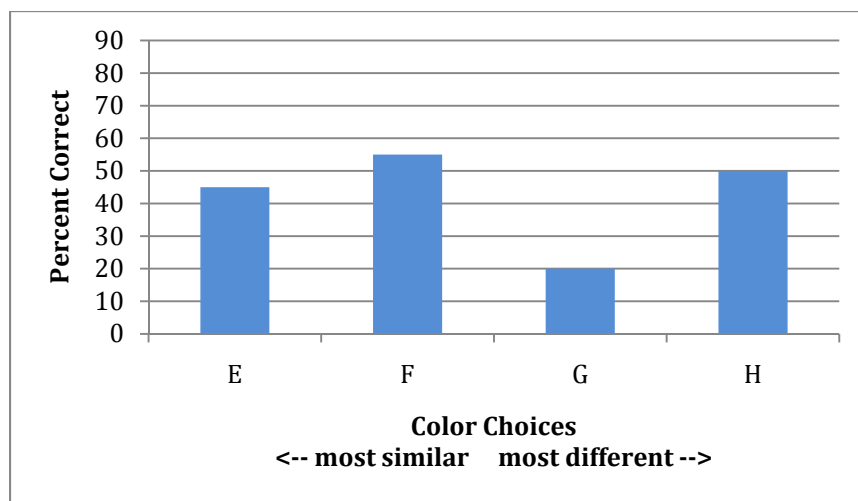


Figure 3. The results of choice experiments done with lizard 4 (trained to blue). Normal light conditions.

Lizard 5 (trained to blue) also did not choose the trained color successfully based on the threshold. There was no pattern showing an increase in percent correct as colors became farther away in color space from the trained color.

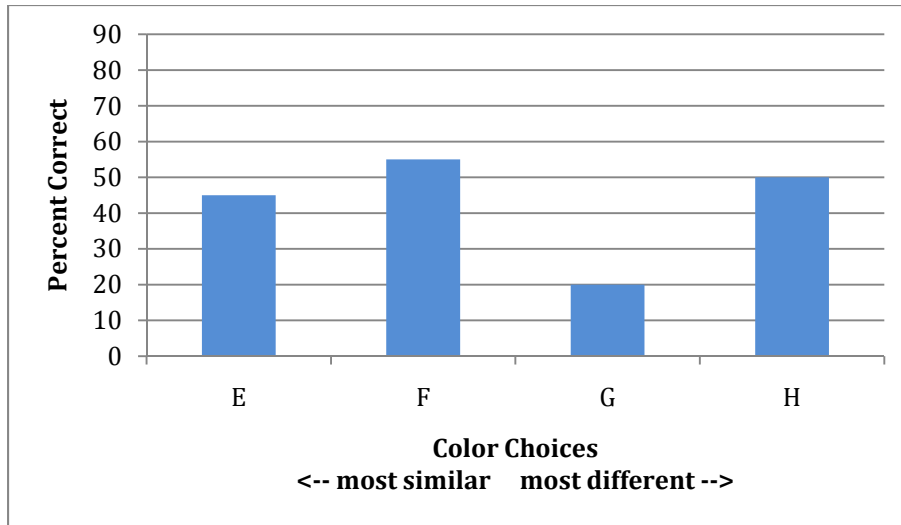


Figure 4. The results of choice experiments done with lizard 5 (trained to blue). Normal light conditions.

For the most similar choice (A) Lizard 2 achieved 40% correct and for choice B achieved only 25% correct. Neither of these were above threshold, meaning the lizard did not successfully discriminate between the trained color and choice A or B. Lizard 2 chose correctly 85% of the time against color C, and 70% of the time against color D. Both were above the threshold showing the individual discriminated successfully.

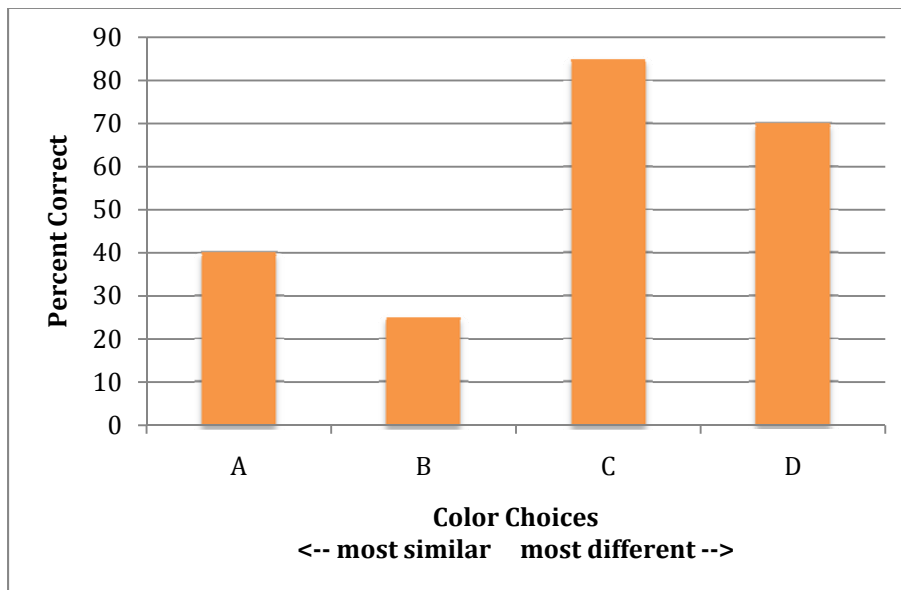


Fig 5. The results of choice experiments done with lizard 2 (trained to orange). Normal light conditions.

Lizard 3 discriminated successfully between the trained color and all of the opposing choice colors, except choice C with a 55% correct score. The individual chose color A correctly in 70% of the trials, and color B and D in 65% of the trials.

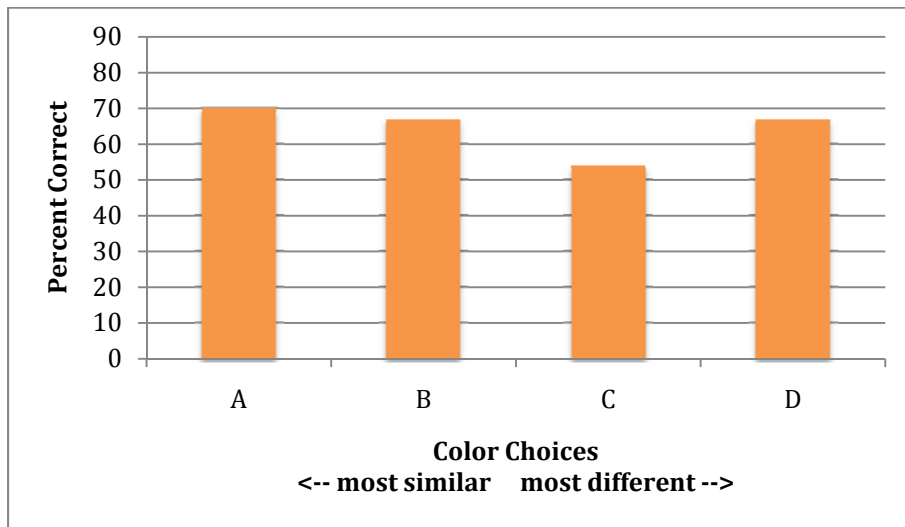


Fig 6. The results of choice experiments done with lizard 3 (trained to orange). Normal light conditions.

The last experiment was done in dim light; a 2.0 optical density filter was placed over the light source. This trial was done with Lizard 3 only. Colors A, B, and C were not successfully discriminated from the trained color; the percent correct did not reach the threshold. However, color D was correctly discriminated from the trained color in over 65% of the trials.

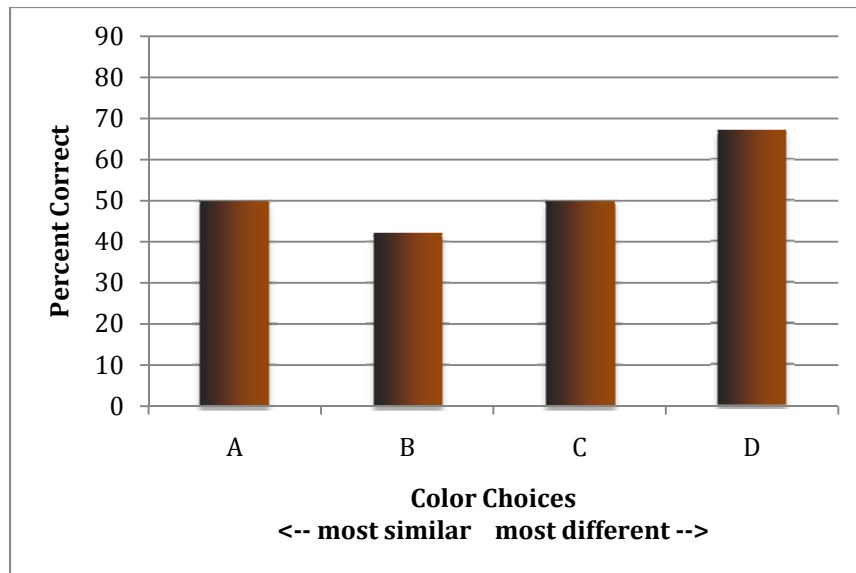


Fig 7. The results of the choice experiment done in dim light. Lizard 3 was used in this experiment.

Discussion

There are two theories regarding the importance of color discrimination in natural animal behavior. The first argues that the most important factor in making two color easy to discriminate is their distance in perceptual color space, which can be represented by a geometric distance between two points plotted in a geometrical space based on relative cone stimulation. It states: as two colors get farther away from each other in color space, there will be a gradual ability to more easily discriminate between the two colors. In this choice experiment, it would mean a gradual increase in percent correct as choices became more different. Fleishman and Persons (2001) found that detection probability for color stimuli presented in the anoline visual periphery were directly related to distance in perceptual color space.

A contrasting theory is based on a noise-limited threshold. Neurons in the eye fire randomly without stimulation, and the brain registers this as a signal. These signals create

a low level of “noise” present at all times in the eye. Each type of cone has a range of color that triggers it to fire. However, these ranges overlap with the ranges of other cones. Colors are differentiated based on where they fall within the overlap. For example, the color red would fall near the middle of a red cone’s range, whereas the color purple would fall between the ranges of a blue cone and a red cone. Two colors that are very similar would fall close together in color space. Noise levels vary based on species; the amount of noise an anoline eye produces has not been measured. When two colors are so alike that noise signals interfere with identification, the colors will be indistinguishable to the eye. This theory suggests that there is a threshold where noise no longer interferes with color discrimination. Colors more similar than this threshold cannot be discriminated, but colors more different than the threshold can be easily discriminated. Instead of a gradual increase in percent correct, a graph demonstrating this theory would have low percent correct before the threshold was reached and would then jump to a high percent correct. There would be little variation in percent correct after the threshold.

In my experiment, the graphs demonstrating this theory are in figures 5 (lizard 2) and 6 (lizard 3). In figure 5, only the two most different colors could be discriminated. This shows that the threshold is somewhere between colors B and C. In figure 6, all of the colors could be discriminated, with the exception of C, showing that the threshold is more similar to the trained color than choice A. The lizard successfully discriminated colors A and B which are more similar to the trained color than color C, therefore it was concluded that the threshold is still in fact closer to the trained color than color A. In Figures 3, 4 and 6 choice C seems to be an outlier. In both ranges of color, the orange and the blue range, C was green. Since green makes up much of the lizards’ natural habitat,

this may have been a cause for confusion for some of the individual lizards leading to a skewed result.

From the results it seems that the noise thresholds between individuals are different. However, a different theory suggests that each individual lizard had a different learning style to differentiate between the learned color and the opposing choice (A, B, C, or D). A lizard trained to orange in the original experiment, the brighter color, may have always looked for the brighter color when making choices in the later experiment.

Various behavioral responses to the colors may have also accounted for the wide range of patterns of correct choices.

This species of lizard, *Anolis sagrei*, tend to live in solitude without much interaction with other species. Most of their vision relies solely on motion sensing; the lizards usually rely on motion to catch prey and detect predators. Therefore, the majority of the cones in their eye are strictly for acutely detecting motion. This being so, one of the only functions of color vision for anoles is to differentiate species based on different colored dewlaps. Perhaps, since *Anolis sagrei* lives in an environment where there is little use for their color vision, it is simply not as honed as in other species. If color vision does not serve a daily purpose, it could mean that the animals are less likely to successfully discern colors. Eventually, if this were true, evolution may favor a modified color vision that is less acute. However, *Anolis sagrei* still has a developed tetra-chromat system, so this result is unclear.

In reality, the method of color discrimination may be a combination of the perceptual distance theory and the noise-limited threshold theory. Once colors can be discriminated past the noise threshold, instead of a jump in correct choices there may be a

gradual increase as colors become farther away in color space from each other. Further experiments could use a broader range of colors, or the color choices could differ more gradually.

An overarching question about dewlap colors is why colors have evolved to be so different between species. *Anolis sagrei* have an acute color vision system where they can discern colors fairly close together in color space. However, species in overlapping territories have dewlap colors far apart in color space. This may be due to anoles being most active at dawn and dusk when light in their environment is dim. As seen in the dark experiment, the ability to discriminate colors greatly decreases in low light. If anoles are interacting with other species in low light, dewlap display visibility and differentiation from conspecifics is important. This may drive the difference in colors between species in similar habitats.

Animals use signaling mainly for communicative purposes, so any signal presented to the animal's environment must be visible. Acuity of vision differs between species, as does the ability to see color. Even within the spectrum of color vision, animals perceive color differently based on types of cones in the eye. This experiment attempted to measure the acuity of *Anolis sagrei* color vision in hopes of finding clues to its evolutionary purpose. In a species that relies so heavily on motion detecting, anoles have highly developed color vision systems. Dewlaps in every species of anole have evolved to be purposefully conspicuous and are used for communication, including territorial signals and attracting mates. However the difference in dewlap color between species shows that dewlaps are essential in species identification. In gaining more knowledge

about the color vision of anoles, we can learn more about the driving factor of the evolution of so many dewlap colors within the *Anolis* genus.

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