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The Effects of Limited Visual Acuity and Context on the Appearance of *Anolis* Lizard Dewlaps

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Abstract.—Male *Anolis* lizards display their colorful dewlaps in a variety of contexts, ranging from long-distance territorial displays to close-range agonistic and courtship displays. Anoles have eyes of high optical quality and a retina that contains tightly spaced, small-diameter photoreceptors. Highest visual acuity is associated with the center of the retina (=12.5 cycles $^{\circ-1}$), whereas acuity is much lower in the periphery. Anoles possess a small eye that creates a small retinal image, which limits their maximum visual spatial acuity to approximately 1/10 that of humans. In animal visual systems spatial resolution falls rapidly with distance from the stimulus. In some species, dewlap color patterns are fairly complex and may transmit various kinds of information. To gain insight into the visual information that conspecifics can potentially extract from dewlap color patterns, we modified high-resolution digital photographs reflecting the limits imposed by the acuity of the *Anolis* eye. For central retinal vision, from a distance of 0.5 m or less, the finest levels of dewlap pattern spatial detail were visible. At greater distances, and/or for peripheral vision, much less detail could be resolved. When viewed from 1 m away with peripheral vision, only the average color of the large patches could be detected, and all pattern detail was lost. The potential information content of the dewlap patterns changes dramatically with the context in which it is viewed. We show that a clear knowledge of an animal's sensory limitations can lead to greatly improved hypotheses about signal function.

Anolis is a genus of small lizards that is comprised of approximately 400 species (Losos, 2009). They are famous for their visual signaling system that utilizes a colorful expandable skin flap known as the dewlap. There is tremendous diversity, both within and among *Anolis* species, in the color and pattern of the dewlap (Nicholson et al., 2007). The role, or roles, of dewlap color patterns are reviewed in Losos (2009).

These studies usually assume that *Anolis* lizards can see as much spatial detail as a human viewer, although this is unlikely to be the case given the morphology of the anoline eye (Fleishman et al., 2017). Static spatial visual acuity is defined as the minimum extent of small spatial detail that can be discerned in a stationary image. Static spatial visual acuity can be quantified in cycles $^{\circ-1}$, or its reciprocal, the minimum resolvable angle (MRA). Acuity is limited by the optical quality of the eye, the acceptance angle and density of photoreceptors in the retina, the convergence ratio of retinal photoreceptors to optic nerve ganglion cells, and the size and shape of the eye (Cronin et al., 2014). In the visual system of anoles, most morphological characteristics favor very high acuity with the exception of the size of the eye. Relatively small eyes form relatively small-sized retinal images that limit the ability to resolve fine spatial detail. Using anatomical data (Makaretz and Levine, 1980) and behavioral experiments, Fleishman et al. (2017) established that the MRA for vision in the retinal periphery of *Anolis carolinensis* and *A. sagrei* is approximately 0.8° (= 1.25 cycles $^{\circ-1}$), and the visual acuity for the central fovea is about 10 times higher. Maximum behaviorally measured human visual acuity is, by comparison, approximately 10 times greater than that of *Anolis* lizards (Davson, 1972). Comparative studies have shown that retinal anatomy is similar across anoline species (Underwood, 1970; Fite and Lister, 1983; Loew et al., 2002). It is therefore reasonable to assume that any acuity estimates are similar across anoline species.

Two situational factors influence spatial resolution. First, retinal image size, and therefore spatial resolution, declines with distance to the viewer. Second, resolving power varies with position of the image on the retina. The low-acuity peripheral retina receives input from a broad visual field. When an image of potential importance is detected in the visual periphery, a reflex shift of eye position moves the image onto the high-acuity central foveal region, where it receives central attention (Fleishman, 1992). Therefore, an inattentive animal viewing a dewlap will perceive much less spatial detail than an attentive animal.

Anoline dewlaps possess a large variety of colors and patterns. In some species the small scales distributed over the dewlap skin are distinctly different in color from the skin. As a result, a very fine pattern of small dots, that we refer to as "dotted," extends over the surface of the dewlap. The dotted pattern of the dewlap is sometimes evenly distributed or can be arranged in patterns such as stripes (Fitch and Hillis, 1984; Brown et al., 2018). Several species' dewlaps are dominated by one color that has a relatively small area of the skin that exhibits a different color. Such "small area" patterns may take the form of stripes, circular regions (much larger in area than the dots referred to above), or as a marginal ring around the edge of the dewlap (Nicholson et al., 2007). Finally, there are several species that possess two large patches, or "large area" patterns, of differing color that cover a roughly equal area on the dewlap.

Multiple hypotheses, with varying degrees of experimental support, have been proposed for the precise nature and function of the information transmitted by dewlap color patterns. Dewlap color patterns probably play an important role in eliciting the attention of conspecifics by signaling territorial ownership, repelling rival males, attracting females to the territory, or maintaining reproductive activity in females (Crews, 1975; Fleishman, 1992; Fleishman and Persons, 2001; Leal and Fleishman, 2004; Fleishman et al., 2015, Gunderson et al., 2018). The different functions of conspecific signaling require that information about species identity be signaled in a manner that can be rapidly and reliably detected (Fleishman, 1992), particularly where multiple species exist in sympatry (Rand and Williams, 1970; Williams and Rand, 1977; Losos, 1985, 2009). Dewlap color patterns have also been shown to provide

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information about the signaler's health, quality, or both (Cook et al., 2013; Steffen and Guyer, 2014; Driessens et al., 2015), fighting ability (Vanhooydonck et al., 2005), individual identity (Forster et al., 2005), and mood and motivational state through short-term color changes (Brown et al., 2018). In addition, anoles adjust their behavior toward conspecifics based on distance (Steinberg and Leal, 2013), and it has been hypothesized that dewlap color patterns help conspecifics judge the distance to the signaler.

Dewlap displays occur in distinctly different social contexts that can affect the visual appearance of the dewlap as well as the types of information that must be transmitted. In the most common use of the dewlap display, adult males move throughout their territories and give spontaneous "assertion" displays (Carpenter, 1967) that serve to keep other males away from the territory and to attract females. The viewers of assertion displays are usually some distance (e.g., 1 m or more) away and inattentive (Fleishman, 1992). The effectiveness of the assertion display depends heavily on the dewlap's ability to unambiguously signal the presence of a lizard of a given species to inattentive conspecific viewers rapidly (Fleishman and Font, 2018).

When an intruding male enters a territory, the resident male will typically produce an agonistic threat display and then approach the intruder, occasionally stopping to display from a range of distances as it approaches. The resident male will next typically align itself alongside, and immediately next to, the intruder and produce threat displays (Carpenter, 1967). In addition, territorial males often move very close to females and perform "courtship" displays where the viewers are at very close range and attentive because they have just been approached directly. During intersexual interactions between conspecifics, dewlap displays may hypothetically transmit information about motivational state, individual identity, signaler quality, and cues about the distance to the signaler.

A particular dewlap pattern can transmit information only if the viewing animal can resolve its details. Different display contexts typically involve visual stimulation at different distances and stimulation of different regions of the retina. Therefore, spatial color patterns may contain different levels of informational detail in different display contexts.

In our study, we focus on static spatial visual acuity of the anoline visual system. Because our primary interest here is understanding how the spatial extent of patterns influences their visibility, we have focused on comparing examples of dotted, small-area, and large-area patterns. Across the genus, the most common pattern is solid color over the entire dewlap (Nicholson et al., 2007). Because such patterns do not change appearance with visual acuity, we do not consider them further here. As part of our ongoing research on color patterns of anoline dewlaps, we have photographed many dewlaps under controlled conditions. Here we have used our knowledge of anoline lizard visual acuity to modify the high-resolution digital images to reveal the extent of pattern detail that an animal viewer is likely to be able to perceive under different viewing scenarios (Fleishman et al., 2017; Caves and Johnsen, 2018). We have selected several species that illustrate different classes of dewlap color patterns. We present each dewlap under eight different viewing conditions: including foveal and peripheral vision at distances of 0.1, 0.2, 0.5, and 1.0 m. Using this analysis, we identified possible roles for different components of dewlap color pattern, based on how reliably they could be perceived in different display contexts.

Materials and Methods

Caves and Johnsen (2018) published software that allows the approximation of the effects of limited visual acuity on the extent of spatial detail that can be detected by an animal's visual system. The program carries out a two-dimensional Fourier transform on a scene of known size and distance, multiplies it by a modulation transfer function that reflects the MRA of the species of interest, and then uses reverse Fourier transform to recreate the original picture with spatial detail limited by the viewer's visual acuity.

The program accepts input of (1) a square digital color image of known true size, (2) a user-selected distance from viewer to image, and (3) the animal's visual acuity (specified as MRA). As output, the program creates images of the same size and dimensions that show what the image would look like to a human viewer with the specified static spatial visual acuity. It thereby illustrates the spatial information detail that can be perceived by a visual system with the chosen level of visual acuity.

The photographs utilized in our study were taken during fieldwork conducted between 2012 and 2014 in Puerto Rico, Jamaica, and in the Dominican Republic. Lizards were captured by noosing and held for less than 24 h and then released at the site of capture. A number of noninvasive measures of dewlap coloration were made. Lizards were photographed under natural sunlight and for this study, four species were photographed while the lizards were held by hand. The hyoid bone was grasped gently with a pair of forceps and the dewlap was held in a fully extended position with the animal oriented perpendicular to the camera. Lizards were photographed with a high-resolution digital SLR camera (Nikon ER or Nikon D5000). A color standard was positioned next to each lizard in the picture frame. We used the size of the individual squares on the color standard to determine the scale (m pixel^{-1}) for each photograph and used this to estimate the true width of each photograph. For two of the *Anolis* species, images taken of animals displaying in the wild were also analyzed. The length of the jawline of the displaying lizards was used as a size standard, and the lizards were assumed to be the same size as the individual of that species in the hand-held photograph.

All methods were consistent with the recommendations of the Guidelines for Use of Live Amphibians and Reptiles in Field Research (https://asih.org/sites/default/files/2018-05/guidelines_herps_research_2004.pdf). Procedures involving live animals were in accordance with the ethical standards of Union College and were approved in advance by the Institutional Animal Care and Use Committee.

Analysis of images was carried out with the R program "AcuityView" (Caves and Johnsen, 2018). Initially each image was cropped to a size of 1,024 × 1,024 pixels. We analyzed each image based on a distance to the viewer of 0.1, 0.2, 0.5, and 1 m. We analyzed each image at two levels of visual acuity: 0.8° (MRA) to represent the visual periphery and 0.08° for central fovea vision.

The visual acuity estimates are based on two sources. Fleishman et al. (2017) used a behavioral attention assay to estimate the visual acuity for the peripheral retina of *Anolis sagrei*, which yielded an estimate of 0.8° (MRA). Makaretz and Levine (1980) carried out a detailed anatomical analysis of the retina of *Anolis carolinensis* and determined that average cone densities in the fovea were 290,000 mm^{-2} and in the midperipheral retina were 3200 mm^{-2}. The ratio of ganglion cell densities: cone densities was close to 1.0 over most of the

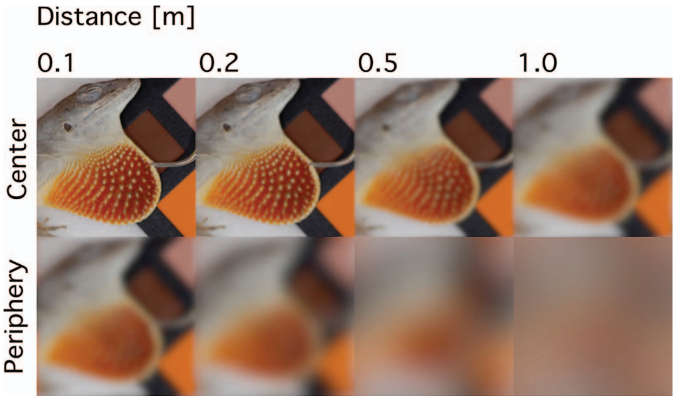

FIG. 1. The estimated appearance of the dewlap of *Anolis sagrei* from Jamaica. Images represent views from 0.1 to 1.0 m based on the static spatial acuity of the central fovea (center) and the visual periphery. This dewlap illustrates a "dotted" pattern and a "marginal" pattern.

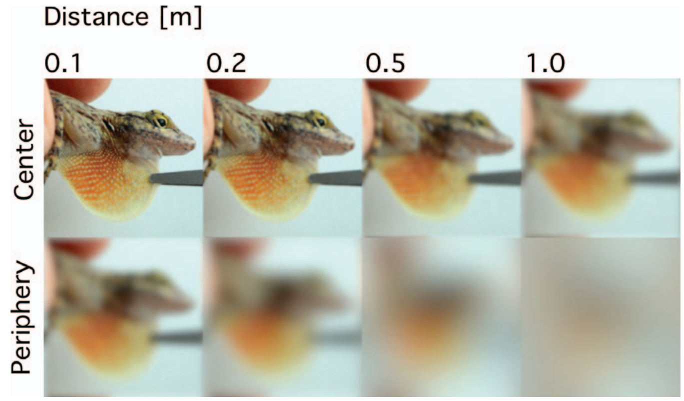

FIG. 3. As in Fig. 1 for *Anolis brevirostrus* from the Dominican Republic. This illustrates a "large-area" color pattern.

retina and slightly greater than 1.0 in the fovea, indicating that there is little convergence of photoreceptors cells onto ganglion cells and that cone densities limit acuity. Using these values, we calculated a MRA value of 0.8° for the periphery and 0.08° for the central fovea (see Pettigrew et al., 1988 and Fleishman et al., 2017 for details of these calculations).

There are a number of important caveats regarding the interpretation of the images produced for this paper. Our images do not represent visual scenes precisely as a lizard would see them but rather represent the appearance of the scenes to a human with the static spatial visual acuity of an *Anolis* lizard. There are several ways that the modified images probably differ from what a lizard would perceive. First, there are central perceptual mechanisms, such as edge enhancement, that can substantially alter the perception of a scene and for which we have not taken into account. Second, the color vision systems of humans and lizards are different (Fleishman et al., 1993; Loew et al., 2002) in that they have different numbers and types of cone photoreceptors (four for lizards, three for humans) with different spectral absorption characteristics, and there are differences in the relative densities of the different cone classes. Third, animals perceive images through two distinct perceptual pathways: a chromatic channel, which underlies perception of color, and an achromatic channel, which responds to variations in luminance (i.e., brightness), and is responsible for perception of fine pattern details and motion. In general, acuity for the achromatic channels is higher than acuity for the chromatic channel (Potier et al., 2018). The acuity values used to filter the images in this paper are based on the higher-acuity, achromatic channel. For lizard viewers, the spatial details of colors seen in these photographs are, thus, likely to be overestimated. On the other hand, different patches of color will nearly always differ in luminance, so that the shape and extent of different color patches, as perceived by a lizard viewer, should be accurately represented.

RESULTS

The modified images are shown in Figs. 1–6. Figures 1–3 and Fig. 5 illustrate dewlap appearance under control conditions (handheld), and Figs. 4 and 6 show displays under natural habitat conditions. We chose examples of species with dewlaps that illustrate spatial color at three different scales: dotted patterns (finest scale), small area (intermediate scale), and large area (larges scale).

Dotted patterns represent the finest spatial scale. Examples can be clearly seen in the finest resolution (0.1 m, central) images of Figs. 1 and 5. The dotted patterns are clearly visible when viewed by a lizard with its central fovea at distances of 0.5 m or less. However, scale dots blend into the skin color and disappear with foveal vision at 1 m, or for peripheral vision at all distances.

The next level of spatial detail is represented by small-area patterns. The single example here is the light-colored marginal ring shown in Fig. 1. The ring is clearly visible with foveal vision

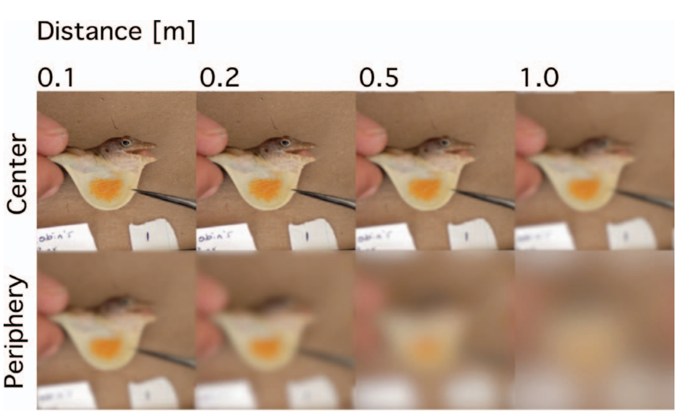

FIG. 2. As in Fig. 1 for *Anolis lineatopus* from Jamaica. This illustrates a "large-area" color pattern.

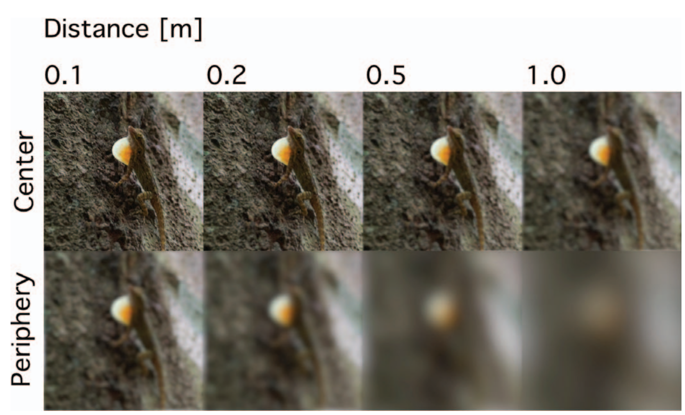

FIG. 4. Analysis of an image of *Anolis brevirostrus* displaying under natural conditions. The images have been analyzed as with the other dewlap images.

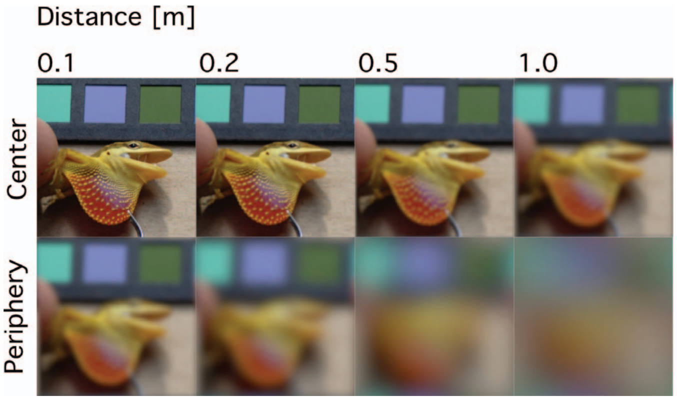

FIG. 5. As in Fig. 1 for *Anolis pulchellus* from Puerto Rico. This dewlap illustrates "dotted" and "large-area" color patterns.

at all distances tested. With peripheral vision, it disappears at 0.5 m or greater.

In large-area patterns, each color covers roughly half of the dewlap. Examples are shown in Figs. 2–6. For foveal vision at all distances and peripheral vision at 0.1 or 0.2 m, the distinct patches can clearly be seen. For peripheral vision at 0.5 m, in all cases, the two patches of color are at least partially blurred together. For peripheral vision from 1 m, the individual color patches are almost completely blurred together and almost no pattern detail is visible.

DISCUSSION

In a number of earlier studies of dewlap color and function it was assumed that lizards and humans would perceive dewlap spectral quality in the same way (e.g., Rand and Williams, 1970; Williams and Rand, 1977; Fleishman, 1992; Nicholson et al., 2007). We know now that colors may appear quite different to anoles and humans (Fleishman et al., 1993). Here we add a further caveat that the ability of *Anolis* to perceive spatial detail is far less than that of humans and so some dewlap patterns may convey information under some display contexts but not under other contexts.

The smallest pattern elements are the small scales that form the dotted patterns. These have the potential to provide very detailed information, but only during close-range encounters when the viewer's attention is directed at the displaying animal (see Figs. 1, 5, and 6). The dotted pattern would then likely be used for communication during close-range threat or courtship displays. Fine-scale dotted patterns could provide information about individual identity, or signal some aspect of strength or quality during close-range agonistic or courtship interactions. The dotted patterns may also help conspecifics gauge their distance from one another. Anoles typically view one another monocularly, which may make precise distance judgment difficult. Nonetheless, anoles have been shown behaviorally to assess interindividual distances fairly precisely (Steinberg and Leal, 2013). In a number of animal species that rely primarily on monocular vision, distance estimation with monocular viewing is based on the extent to which the lens must be curved to achieve focus (Harkness, 1977). Dotted patterns may provide distance information in two ways. First, because individual dots are only visible to the lizards at close range, the ability to see the individual colored scales might by itself be an indication of proximity (e.g., see Figs. 1, 5, and 6). Second, the array of finely spaced individual colored scales might serve as a useful focus target. By going rapidly into and out of focus, the dot patterns can improve the precision of focus-based distance estimation. Motivational state might also be communicated by dewlap scales that are capable of rapid color change in some species (Brown et al., 2018). Such change would be visible only to another individual at close range using foveal vision.

We present the marginal ring around the dewlap of *A. sagrei* as an example of a small-area pattern (Fig. 1). Two studies have shown that the color of the marginal ring of *A. sagrei* provides information about the quality of a displaying male (Steffen and Guyer, 2014; Driessens et al., 2015). The annular ring is visible to the foveal view at all measured distances, and for the peripheral view at distances of 0.1 and 0.2 m away. Therefore, information about individual quality could be signaled during displays from close or intermediate distance, but not during assertion displays where viewers are typically situated relatively far from the viewer. It is probably true, in general, of small-area patterns that they provide information to attentive viewers over a wider range of distances than the dot patterns but will not be visible to inattentive viewers outside of the territory. Therefore, small-area patterns may not be very important for species identification, because this information is a crucial component of long-distance assertion displays.

Large-area patterns (Figs. 2–6) are clearly visible for all measured distances for foveal vision. For peripheral vision, the individual patterns partially, or completely, blur into a single region at distances of 0.5 and 1.0 m away. Because acuity for color perception is lower than for luminance, we can expect lizards to see a single color that is an area-corrected average of the two colors in the pattern (see Fig. 6 for an illustration). There are two possible outcomes of the color averaging effect. The combined color might be less conspicuous against the background than either color alone. Marshall (2000) showed that for coral reef fish, the spatial averaging of perceived body-color patterns that occurs at distance causes the color patterns to shift from highly conspicuous at close range to effective camouflage for long-distance viewers. Alternatively, it is possible that the combined, averaged color is still highly visible (against the background) and may be recognizable to conspecifics as a species-identification signal (see color blending as viewed against natural backgrounds in Figs. 4 and 6). We have used visual perception modeling to measure the chromatic contrast and visibility of distinct and averaged large-area patterns in all species shown here and found that the average color created from combining the two patches is just as visible as each individual color alone (Fleishman, unpubl. data). Thus,

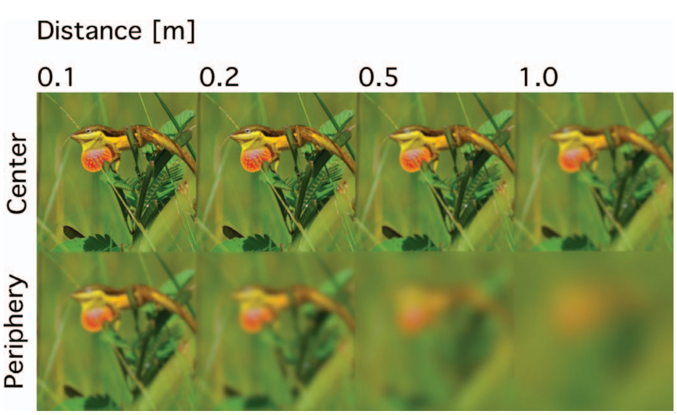

FIG. 6. *Anolis pulchellus* photographed during a natural display analyzed as in the other figures.

although it is apparent that the spatial arrangement of the large color patches is lost for peripheral vision from >0.5 m (in the species measured here), it is still possible that there is a conspicuous patch of visible color that may serve a communication function.

In summary, the images presented in this work illustrate how different spatial scales of color pattern have the potential to provide different classes of information depending on the conditions in which they are viewed. For close-range agonistic and courtship displays that are viewed by attentive viewers, very fine details of color pattern can be detected, allowing for the possibility that information such as individual identity, health status, mate quality, or motivational state can be conveyed. Fine patterns of individual colored scales may also offer a useful distance cue, because they become visible only at very close range. For assertion displays, the only useful signal in the dewlap color pattern is the spectral quality of the largest color patches, and in some viewing contexts, these large color patches are likely to blend, partially or completely. If, however, these averaged colors differ from natural environmental color patches, they can still potentially provide a signal of species identity and location.

Given that the static spatial patterns on dewlaps appear to be ineffective as signals for peripheral vision at distances that exceed 1.0 m, it is of interest to consider whether other sensory stimuli might be more effective in some situations. A few species of *Anolis* make simple sounds, but there is no evidence that they play any role in intraspecific signaling (Fleishman and Font, 2018). Chemical signaling is not thought to be widely used in *Anolis*, although Baeckens et al. (2016) showed that male *Anolis sagrei* exhibit a small, but significant, increase in tongue-flicking rates in response to female odor suggesting a potential role for chemoreception in locating conspecifics.

Visual motion is heavily used by anoles for signaling (Fleishman and Font, 2018). Motion may interact with static patterns in complex ways. In some displays by some species, the dewlap is held fully extended while the body is moved up and down, often very rapidly (Fleishman, 1992; Fleishman and Pallus, 2010), potentially blurring the spatial details of the dewlap. In other displays, the dewlap is slowly and alternatingly extended and retracted. Visual spatial acuity for slow, or moderate, moving stimuli is typically twice as high as stationary acuity (Davson, 1972; Nakayama, 1985), and such movements may actually enhance the visibility of fine pattern elements. Independent of dewlap motion, lizards rely on head and body movements in many signaling contexts. Because of the high acuity of visual motion, particularly in the visual periphery (Fleishman, 1992), such movements likely provide an alternative mechanism for signaling information such as species identity, individual identity, or motivation, that will be effective at much greater distances than the same information can be transmitted by dewlap spatial patterns (Fleishman, 1992; Fleishman and Font, 2018).

It is now widely recognized that we must take animal sensory systems into account when studying their signaling (and other) behavior. A large body of literature now exists, for example, using models of animal color vision in the analysis of the evolution of animal color patterns (Kemp et al., 2015). There is a rapidly increasing appreciation that differences in animal visual acuity can also impact a wide array of visually based behaviors, and a knowledge of acuity limits can add great insight into our understanding of signaling behavior and visual ecology more broadly (Veilleux and Kirk, 2014 Caves et al., 2018).

Our study demonstrates the importance of taking the perceptual capabilities and limits of an animal species into account when trying to untangle the details of its communication system. It is not difficult to misjudge the importance of a signal element because of large differences in the perceptual capabilities of human and nonhuman animals. An understanding of the animal's perceptual constraints also helps to provide important clues to the possible function of different display elements. For example, in the study of the role *Anolis* dewlaps in signaling species identity, it was important to learn that a number of these patterns are simply not visible under viewing conditions where the signaling of this information occurs. On the other hand, our analysis points to the possibility of a role for the fine-scale scale dotted patterns as a signal of fighting ability, quality, or individual identity at close proximity to the viewer. Thus, a detailed knowledge of sensory capabilities offers important clues and can suggest future directions of study that would not have been apparent prior to the analysis.

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