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Clothing color mediates lizard responses to humans in a tropical forest

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Abstract

Identifying how ecotourism affects wildlife can lower its environmental impact. Human presence is an inherent component of ecotourism, which can impact animal behavior because animals often perceive humans as predators and, consequently, spend more time on human-directed antipredator behaviors and less on other fitness-relevant activities. We tested whether human clothing color affects water anole (*Anolis aquaticus*) behavior at a popular ecotourism destination in Costa Rica, testing the hypothesis that animals are more tolerant of humans wearing their sexually selected signaling color. We examined whether clothing resembling the primary signaling color (orange) of water anoles increases number of anole sightings and ease of capture. Research teams mimicked an ecotourism group by searching for anoles wearing one of three shirt treatments: orange, green, or blue. We conducted surveys at three different sites: a primary forest, secondary forest, and abandoned pasture. Wearing orange clothing resulted in more sightings and greater capture rates compared with blue or green. A higher proportion of males were captured when wearing orange whereas sex ratios of captured anoles were more equally proportional in the surveys when observers wore green or blue. We also found that capture success was greater when more people were present during a capture attempt. We demonstrate that colors "displayed" by perceived predators (i.e., humans) alter antipredator behaviors in water anoles. Clothing choice could have unintended impacts on wildlife, and wearing colors resembling the sexually selected signaling color might enhance tolerance toward humans.

Abstract in Spanish is available with online material.

KEYWORDS
Anolis aquaticus, communication, Costa Rica, dewlap, escape behavior, forest fragmentation, risk-taking, sexual selection

1 | INTRODUCTION

Ecotourism has gained popularity because it provides tourists with a way to observe and interact with wildlife while having a relatively low environmental impact (Pavelka, 2012; Zeiger & McDonald, 1997). Although some countries have been successful in implementing ecotourism programs that improve wildlife preservation efforts (Brunnschweiler, 2010; Diedrich, 2007), studies continue to find certain aspects of ecotourism to be unintentionally harmful by negatively impacting animal behavior, physiology, and survival (Meissener et al., 2015; Müllner, Linsenmair, & Wikelski, 2004). Though much research has been conducted to determine how humans impact wildlife broadly, our understanding of how groups of ecotourists or researchers affect the organisms they seek, on the smaller scale, is still developing (Barnett, Payne, Semmens, & Fitzpatrick, 2016; French, Denardo, Greives, Strand, & Demas, 2010; Klein, Humphrey, & Percival, 1995). In particular, animals often perceive humans as predators, which can alter their behavior and activity (Frid & Dill, 2002). When organisms expend a large amount of energy and time on predator avoidance (e.g., avoiding humans), they allocate less toward reproduction, acquiring resources, and other essential fitness-relevant activities. This could lead to long-term changes in a population's morphology and behavior (Ball & Baker, 1995, 1996; Khater, Murariu, & Gras, 2016), fewer possible reproductive events (Fraser & Gilliam, 1992), and decreased population sizes (Nakaoka, 2000; Remeš, Matysioková, & Cockburn, 2012; Schoener, Spiller, & Losos, 2001). Previous studies have determined that certain human behaviors such as choice of clothing and use of cameras (i.e., shutter noises and flash) affect animal behavior. For instance, when exposed to camera shutter noises, female crested anoles (*Anolis cristatellus)* decreased their display behavior, as the sound of shutters resembled a predator call (Huang, Lubarsky, Teng, & Blumstein, 2011). Other studies have found that foraging (Carrera, Favaro, & Souto, 2008; Nevin & Gilbert, 2005; Trulio & Sokale, 2008), activity rates (Bunkley, Mcclure, Kleist, Francis, & Barber, 2015; Corcoran et al., 2013), and antipredator behaviors (Bruintjes & Radford, 2013; Wale, Simpson, & Radford, 2013) are likewise impacted by human presence.

Animals use body movements and colorful signals for inter- and intraspecific communications (Stoehr, Hayes, & Wojan, 2016; Watkins, 1997). Coloration can convey information about health and abilities (McGraw, Mackillop, Dale, & Hauber, 2002; Polo-Cavia, López, & Martín, 2013; Taylor, Clark, & McGraw, 2011) and can be used for courtship (Reynolds & Fitzpatrick, 2007; Rowe & Weatherhead, 2011), species recognition (Alatalo, Gustafsson, & Lundberg, 1994; Detto, Backwell, Hemmi, & Zeil, 2006; Grether, Drury, Berlin, & Anderson, 2015), camouflage (Espanha, Vasconcelos, & Eterovick, 2016; Krupa & Geluso, 2000; Zylinski, How, Osorio, Hanlon, & Marshall, 2011), and male–male competition (Rémy, Grégoire, Perret, & Doutrelant, 2010; Zhou & Fuller, 2016). Because of its strong ties to signaling and communication, determining how organisms respond to and alter their behavior in relation to anthropogenic coloration, specifically human clothing color, is of interest, especially in ecotourism areas. Notably, Gould, Green, Altenau, and Blumstein (2004) found that when spiny-cheeked honeyeaters (*Acanthagenys rufogularis)* were approached by researchers wearing clothing colors that were the same as the birds' plumage, there was a reduction in flight initiation distance (FID). FID is the distance between an animal and an approaching threat (i.e., predator, human) when the animal begins to flee and is a robust measure of animal risk assessment and indicates an animal's tolerance of humans (Blumstein, Samia, & Cooper, 2016; Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015; Tätte, Møller, & Mänd, 2018). In contrast, when researchers wore clothing with colors not present in the birds' plumage, FID increased. The authors suggested that these results may be attributed to the "species confidence hypothesis," which states that species are more tolerant of colors that are found on their bodies than colors that are not (Burley, 1986; Burley, Krantzberg, & Radman, 1982).

A recent study conducted by Putman, Drury, Blumstein, and Pauly (2017) expanded on the species confidence hypothesis by showing through the use of animal visual models that responses toward clothing color might be explained not only by the colors found on animal bodies, but by existing sensory biases toward colors used in intraspecific sexual displays. They found that when researchers wore blue clothing that resembled the sexually selected signaling color of western fence lizards (*Sceloporus occidentalis*), the FID of lizards decreased and capture rate increased as opposed to when researchers wore colors that were not associated with male sexual displays (Putman et al., 2017). These results were independent of clothing conspicuousness (measured by quantifying just noticeable difference values, luminance, and chromatic contrasts, between shirts and the background environment), indicating that color was more important than contrast against the background environment. The expanded version of the species confidence hypothesis from the Putman et al. (2017) study will be referred to as the adapted version of the species confidence hypothesis in this paper. Additional research has shown that brown anoles (*Anolis sagrei*), which have red-orange dewlaps (a male sexual display), exhibit greater responses toward red stimuli compared with blue or green (Fleishman et al., 2016), further supporting the idea that animals might have sensory biases for colors used in sexual displays.

The sexes might also differ in responses to clothing color due to differences in the sensory systems of males and females (Cummings, Bernal, Reynaga, Rand, & Ryan, 2008; Fernández-Juricic et al., 2013). Several studies have shown sex differences in behavioral responses to intraspecific signals. In lizards, female fence lizards (*Sceloporus undulatus*) respond more quickly to fast motion displays whereas males respond more quickly to slow motions (Nava, Moreno, & Wang, 2012). Males of the superb fan-throated lizard (*Sarada superba*) respond preferentially to the blue and black colors of males' tri-colored dewlap (blue, black, and orange) whereas females are more responsive to the orange (Zambre & Thaker, 2017). Based on this previous body of literature, it is likely that male competitors and female mates might differ in their detection abilities and preferences for male sexually selected signaling colors within their species, and hence, the sexes might also differ in their responses to colored clothes.

The goal of our study was to test whether the adapted version of the species confidence hypothesis (i.e., sensory bias toward colors used in species-specific sexual displays) can be applied more broadly and explain animals' tolerance or lack thereof to certain colors. We focused our study on water anoles (*Anolis aquaticus*), which are an ideal study organism as males have a distinct sexual display (the dewlap), and populations are restricted to streamside habitats that are not often in contact with humans. Our study was conducted in southern Costa Rica at Las Cruces Biological Station, which is characterized by premontane wet tropical forest with areas of different land-use histories. Las Cruces Biological Station is a relatively popular station for researchers and tourists, but most visitors do not venture to the streams where the anoles reside—we have been working at these sites for multiple years and have rarely encountered tourists in the streams (Putman and

Swierk, pers. comm.). Thus, these anoles very rarely interact with humans, but as the popularity of ecotourism grows, their contact with humans could increase. Male water anoles differ from females in the presence of a dewlap, which is a flap of skin under the chin that is extended during sexual displays. They also have distinctive sexual coloration: the sexually selected signaling color of the dewlap is orange to the human eye (Figure 1). Anoline dewlaps can be used as an honest indicator of health (Cook, Murphy, & Johnson, 2013; Driessens, Huyghe, Vanhooydonck, & Damme, 2015), can convey bite force (Baeckens, Driessens, Huyghe, Vanhooydonck, & Damme, 2018; Henningsen & Irschick, 2012), and are used for intra- and inter-sexual interactions (Steffen & Guyer, 2014). In water anoles, specifically, dewlap size scales with traits implicated in intrasexual combat and is likely used as an honest signal of fighting ability (Petelo & Swierk, 2017; Putman, Azure, & Swierk, 2018). Because the dewlap is an integral form of communication, we predicted that anoles would be less apprehensive and allow researchers to approach them at closer distances, increasing capture, and encounter rates, when researchers wore orange. We predicted that anoles would be less fearful of orange than other colors (here, we also test blue and green) because of a sensory bias toward their sexually selected signaling color.

2 | METHODS

2.1 | Study organism and study sites

We studied water anoles, *Anolis aquaticus*, a small (55 to 71 mm snout-vent length; SVL) semi-aquatic tropical lizard (Savage, 2002). These lizards commonly perch around slow-moving streams on rocks or trees surrounding the stream to escape into the water away from predators. We collected data from 11 June to 16 July 2018 at Las Cruces Biological Station (8° 47' 7'' N, 82° 57' 32'' W) in Coto Brus County near San Vito, Costa Rica. There were two groups of three researchers that sampled anoles from one of three river sites each day: primary forest, secondary forest, and abandoned pasture between 0800 hr and 1300 hr. Each site was representative of a different forest fragment type affected by human disturbance (e.g., cattle grazing and logging). All study sites were well away from established hiking trails and so anoles at each site rarely, if ever, encounter humans. Although anoles could have habituated to our presence over the course of the study, because shirt treatments and visits to sites were counter-balanced, this should not systematically bias our results.

2.2 | Shirt treatments

Two research teams (of three people maximum) wore one of three shirt treatments (Figure 1): blue, green, or orange. The shirt treatments were systematically assigned to each team in a balanced design in which the colors were pre-assigned to each group before data collection began. Shirts were long-sleeved Sport-Tek® brand (model LST353LS in colors True Royal, Forest Green, and Deep Orange), and researchers wore khaki, brown, or black field pants during anole surveys.

We selected shirt colors based on how they are viewed by the human visual system as would most researchers and ecotourists. The orange shirt treatment was selected because it resembled the sexually selected signaling color of the water anoles' dewlap. The green shirt treatment was selected because it most closely matched the tropical forest environment of our field sites (Figure 1). The blue shirt treatment was used as an alternative to the sexually selected signaling color hypothesis to test the responses of lizards lacking the color blue and to compare to the responses of fence lizards from Putman et al. (2017), which were most tolerant of blue (their sexually selected signaling color). Blue does not appear on the anole bodies, is less prominent in the environment compared with green, and is a distinct color from orange (based on peak reflectance within the visible spectrum). In contrast, both orange and green may be present on the anole as orange is found on the male dewlaps and the anoles respond to stress by transitioning from a brown to green color along their lateral stripes (Boyer & Swierk, 2017), but this is not associated with sexual displays.

We measured reflectance spectra of the shirts using a spectrophotometer (AvaSpec-Mini2048CL, Avantes Inc.) with an Avalight-XE xenon light source emitting in the range 190–1000 nm. Shirt spectra were taken relative to a white reflectance standard and were then computed with AvaSoft-Full software (Avantes). We calculated hue, brightness, and intensity of color (Montgomerie, 2006) using the pavo package in R (Maia, Eliason, Bitton, Doucet, & Shawkey, 2013). Orange was the brightest and had the highest intensity compared with blue or green (Table 1). Previous

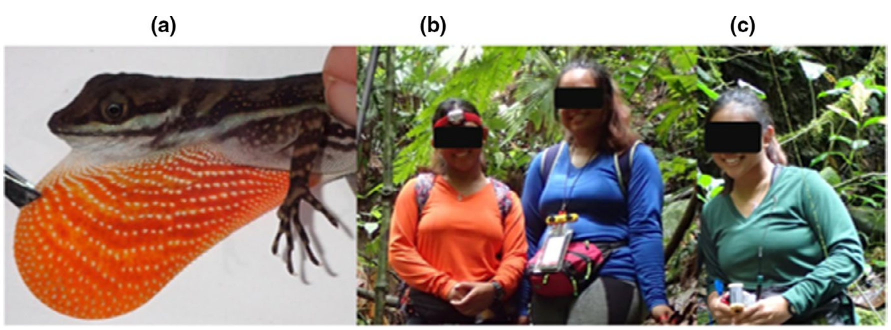

FIGURE 1 Photographic mosaic showing the orange coloration of the male water anole dewlap (a) along with our three shirt colors (orange: b, blue: b, and green: c). Photographs of researchers wearing the shirts were taken in the field, but during a time when they were collecting data for a separate study. Faces have been obscured for privacy

TABLE 1 Colorimetric variables calculated from reflectance spectra for each shirt treatment

Shirt treatment	Total reflectance	Mean brightness	Intensity	Hue
Blue	863	2.87	23.69	419
Green	1,017	3.38	47.56	506
Orange	7,452	24.76	80.22	700

Note: Total reflectance equals the sum of reflectance values over all wavelengths. Mean brightness equals the average reflectance over all wavelengths. Intensity indicates the peak reflectance of the spectrum. Hue is the wavelength (nm) of peak reflectance.

research examining lizard responses to different colored stimuli found that the initial selection of color treatments via human perception resulted in a good approximation of lizard responses after subsequent validation using visual models (Fleishman et al., 2016; Putman et al., 2017).

2.3 | Data collection

All methods were approved by the UCLA Animal Research Committee (ARC; 2016–051-03C). Data for this study were collected by two main teams of researchers that varied in size between one and three persons (typically 2–3 people; mean ± *SD* number of people per color treatment was blue: 2.33 ± 0.59, green: 2.50 ± 0.89, orange: 2.60 ± 0.51). Research teams collected data for this study while comprehensively searching for anoles for another study. All anole surveys were conducted during relatively clear and sunny portions of the day and mean ± *SD* ambient air temperature did not differ among shirt color treatments (blue: 24.2 ± 1.3°C, green: 24.5 ± 1.2, orange: 24.2 ± 0.6). Shirt treatments were pre-assigned to ensure relatively equal distribution among study sites, research team, and timing within the field season. The start and end times during each survey were recorded and used to calculate the total search time; any breaks were noted and were subtracted from the total search time. All water anoles sighted were recorded, including adult males, adult females, and juveniles. When an anole was spotted, the individual person or team attempted to capture it if it had not been previously captured and marked (see below). It is possible that during capture a single person, two people, or the entire team might be involved in an attempt to catch an individual anole. Thus, capture attempts involved between 1 and 3 people. Once an anole was captured, it received a unique ID consisting of two colored dots using non-toxic nail polish and was released at the location where it was captured. To avoid resampling uncaptured individuals, areas were only searched once per survey (following the methods of Putman et al., 2017). The researcher(s) responsible to capture (or failure to capture) a given anole were recorded, including person ID and shirt color worn.

The total number of anoles observed, in addition to number of successful captures and unsuccessful captures, were recorded for each sampling period. A capture was considered unsuccessful if an individual or team failed in their attempt to catch an anole. An unsuccessful capture suggests that the anole in question may have perceived the researcher/team as more of a threat and consequently was more motivated to commence antipredator behaviors. This measure of capture success was used in a previous study on lizard responses to clothing color (Putman et al., 2017). The number of anoles sighted during each habitat survey was divided by the total search time to create a sighting rate (number of anoles per hour).

2.4 | Statistical analyses

We used R (R v3.5.1, R Core Team, 2018) to complete all statistical analyses. To determine the factors affecting number of anoles per hour, we ran a linear mixed-effects model (LMM) using the lme4 package (Bates, Mächler, Bolker, & Walker, 2015) with sighting rate as the dependent variable and shirt treatment (blue, green, and orange), site (primary forest, secondary forest, abandoned pasture), and number of people present as fixed factors. We square-root transformed anoles per hour to meet the model assumption of normality. Team composition, specifically the combinations of researchers in the team for each survey, was included as a random effect. Six researchers contributed to the data collection of this study and there were two main teams of three researchers, but throughout the course of the experiment team composition varied. Thus, by including team composition as a random factor, we could control for variance attributable to differences in number of observers and their abilities. In regard to team composition, we had 16 unique combinations of researchers among both teams. We used likelihood ratio tests to determine the overall effects of fixed factors on anole sightings, and we ran pairwise comparisons (multiple comparisons of means) using the multcomp package (Hothorn, Bretz, & Westfall, 2008), adjusting p-values via the false discovery rate (a post hoc test to account for multiple comparisons). We looked for significant interactions between shirt color and site and number of people, but found none. We could not examine the effect of anole sex on anole sighting rate because the sexes of our unsuccessful captures were unknown.

We used a binomial generalized linear mixed model (GLMM) to determine the effect of shirt treatment on anole capture (y/n). We included site and number of people present during a capture attempt as fixed factors and team composition as a random factor. We had 23 unique combinations of observers across all capture attempts of anoles. In this analysis of capture success, team composition refers to the number of individual researchers directly involved in capturing a given anole. We used likelihood ratio tests to determine the fixed factor effects and the multcomp package to conduct pairwise comparisons as described above. We also looked for significant interactions between shirt color and site and number of people, but found none.

We tested whether shirt color differentially affected the proportion of males captured compared with the proportion of females captured out of the total number of captures (uncaptured individuals not included in analysis). Males might be more responsive to orange (which resembles the sexually selected signaling color of their dewlaps) than females due to sex differences in sensory systems. We ran a generalized linear model with a binomial distribution with sex (male/female) as the dependent variable and shirt color as the independent variable. We set the orange shirt treatment as the reference so that blue and green were compared with orange.

3 | RESULTS

3.1 | Anole sighting rates

We conducted 49 anole surveys over the course of the study and had an approximately even distribution of sampling events across the three shirt treatments and three study sites (Table 2). Shirt color affected the number of anole sightings per hour (X^2 = 6.533, *df* = 2, *p* = .038; Figure 2). Research teams wearing all orange had a significantly higher number of anole sightings per hour compared with teams wearing all green (Estimate = 0.333, *SE* = 0.134, *Z* = 2.490, *p* = .038) and teams wearing all blue (Estimate = 0.285, *SE* = 0.134, *Z* = 2.124, *p* = .051). Number of people present during a survey did not affect anole sightings (X^2 = 2.187, *df* = 1, *p* = .139), whereas site did (X^2 = 7.895, *df* = 2, *p* = .019). Surveys at the abandoned pasture site resulted in significantly fewer anole sightings than in the secondary forest (Estimate = −0.315, *SE* = 0.126, *Z* = −2.502, *p* = .019) and significantly fewer sightings than in the primary forest (Estimate = −0.337, *SE* = 0.134, *Z* = −2.506, *p* = .019). All other comparisons were non-significant (all $p > .20$).

3.2 | Anole capture success

We attempted 218 captures of anoles during this study (Table 3). The capture rate of anoles was greater when wearing orange (80% success) compared to green (66%) or blue (63%), and shirt color affected capture rate (X^2 = 6.048, *df* = 2, *p* = .049; Figure 3). Pairwise comparisons of the difference in proportion of anoles captured when wearing orange versus green (Estimate = 0.984, *SE* = 0.447, *Z* = 2.201, *p* = .058) or orange versus blue (Estimate = 0.911, *SE* = 0.440, *Z* = 2.069, *p* = .058) approached significance. Site did not have a significant effect on anole capture success (X^2 = 3.943, *df* = 2, *p* = .139), such that we experienced a similar capture success across all three sites: 75% success in primary forest, 68% in secondary forest, and 63% in abandoned pasture. Number of people contributing to a capture attempt, however, positively affected capture success (X^2 = 4.726, *df* = 1, *p* = .030). Finally, a higher percentage of males than females were captured under the orange treatment (70% of captures were male) compared with green (44% male; Estimate = −1.067, *SE* = 0.488, *Z* = −2.187, *p* = .029). The percent of males caught when wearing blue (56% male) was no different than when wearing orange (Estimate = −0.588, *SE* = 0.493, *Z* = −1.194, *p* = .233).

4 | DISCUSSION

Our study corroborates previous research that animals are more tolerant of colors that resemble their sexually selected signaling color compared with other colors, supporting the adapted version of the species confidence hypothesis. Notably, we add to the evidence suggesting that squamate reptiles, a taxon in which many species have excellent color vision, partly base antipredator behaviors on the color(s) of the perceived threat. Clothing color that resembled the sexually selected signaling color of water anoles (orange) significantly increased anole sightings and had a positive effect upon the anole capture success of researchers. Our results are in agreement with those of Putman et al. (2017), in which western fence lizards were less fearful of an observer wearing colors that were similar to their sexually selected signaling color. Our study provides support that clothing color impacts the behavior of lizards and should be acknowledged by those designing research studies as well as ecotourism experiences.

We found that water anoles in a tropical forest ecosystem responded differently to teams of researchers wearing different colored shirts. We initially selected shirts based on how they are viewed through the human visual system. To the human eye, green appears as a relatively inconspicuous color within the forest environment in comparison with orange and blue (Figure 1). However, wearing green did not result in more anole sightings per hour, nor more successful captures. Blue, on the other hand, appears to be a rare and a potentially novel color within the forest environment, suggesting that the fear response of anoles might have increased and capture rates decreased when researchers

Shirt treatment	Primary forest	Secondary forest	Abandoned pasture	Total
Blue	4	9	5	18
Green	4	7	5	16
Orange	5	3	7	15
Total	13	19	17	

TABLE 2 Number of anole surveys within the three sites (primary forest, secondary forest, and abandoned pasture) and the three shirt treatments

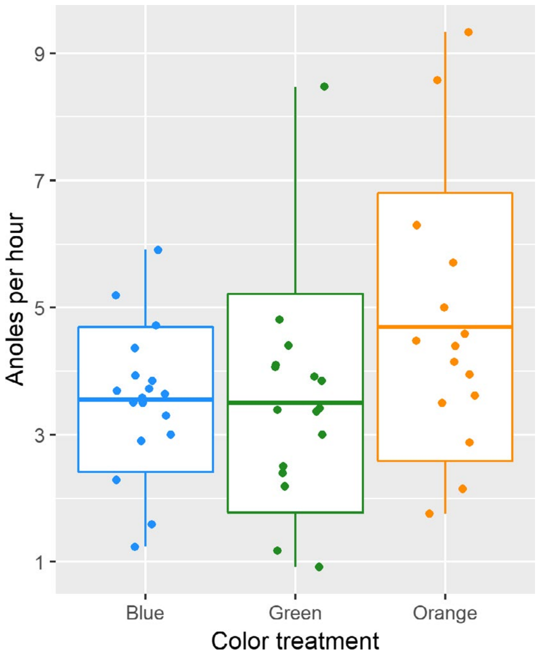

FIGURE 2 Boxplots showing the mean, *SD*, minimum, and maximum number of anole sightings per hour within the three shirt treatments (blue, green, and orange). Dots represent the spread of raw datapoints (jittered to reduce overlap)

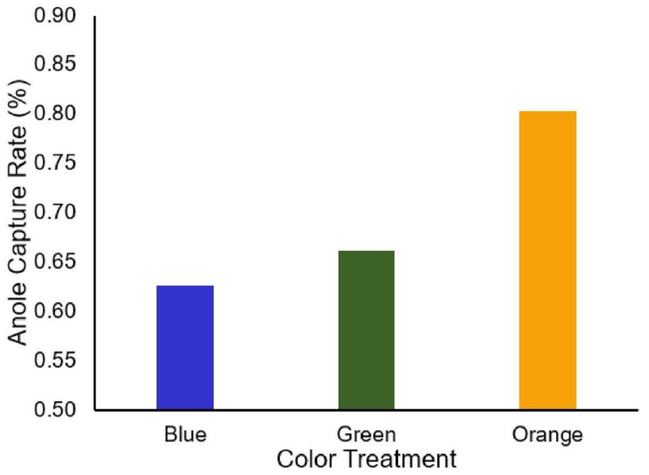

FIGURE 3 Proportion of successful anole captures under each shirt treatment: blue, green, and orange

TABLE 3 Number of successful and unsuccessful captures of individual water anoles under each of the three shirt treatments

Shirt treatment	Successful captures	Unsuccessful captures
Blue	52	31
Green	49	25
Orange	49	12
Total	150	68

Note: Unsuccessful captures were any non-captures that involved a capture attempt but failed. Successful captures were any captures that involved a capture attempt and were successful.

wore this color (Gutzwiller & Marcum, 1997). Yet, anole sightings and capture rates were similar under both the blue and green shirt treatments. The orange treatment, which appeared most similar to the color of the male water anole dewlaps, resulted in greater sighting and capture rates, suggesting that anoles were more tolerant of this color. Spectral analyses revealed that our blue and green treatments were less intense compared with orange (Table 1), and so, our results might be driven by increased achromatic contrast of orange instead of chromatic (i.e., color) differences. Yet, instead of fleeing as soon as they detected an oncoming threat to reduce costs associated with monitoring (the flush early and avoid the rush hypothesis, sensu Blumstein, 2010), orange shirts did not lead to fewer water anole sightings based on this established escape theory. Thus, our study demonstrates that more intense colors do not always have negative effects on animal sightings.

Additionally, we found that more males than females were captured when we wore the orange shirt treatment in comparison with the green shirt treatment. It is possible that males have a greater visual sensitivity to this color compared with females due to underlying differences in their sensory systems (Fernández-Juricic et al., 2013). It should also be noted that we observed males displaying their dewlaps on three separate occasions, but only when we wore orange shirts. Again, these results could also be due to the greater brightness and intensity of the orange shirt treatment, but the behaviors we recorded go against established escape theory, which states that animals should flee as soon as detecting an oncoming threat (Cooper, Samia, & Blumstein, 2015).

The idea that animals better tolerate anthropogenic colors that are used in their species-specific sexual displays might be explained through an existing sensory bias. Sensory biases for colors have been demonstrated in a variety of taxa from insects to birds and fish (Gaskett, Endler, & Phillips, 2017; Ninnes, Adrion, Edelaar, Tella, & Andersson, 2015; Spence & Smith, 2008), and many studies have examined color preferences in regard to foraging and mating (see Kemp & Grether, 2015). Yet, animals also show preferences for sexual colors outside of foraging and mating. For instance, birds with lilac and red sexual displays show a preference for these colors when selecting grit (small stones used to break down food by the gizzard) (Møller & Erritzøe, 2010). In addition, a study on brown anoles (*Anolis sagrei*) found that anoles were more responsive to red stimuli cards compared with green or to blue, and red was most similar to the male dewlap color in this species (Fleishman et al., 2016). The authors hypothesized that because the study population exhibited a bright red dewlap, this could have resulted in red being a more interesting color than blue (the color that elicited the least response in their study).

Studies on the escape behavior of multiple anole species have determined that behavior is influenced by a number of factors, such as perch height, distance from refuge, and microhabitat (Cooper, 2010; Les, Gifford, Parmerlee, & Powell, 2014; Losos & Irschick, 1996).

Throughout this study, the initial antipredator response of some anoles to human approach was to remain immobile, which agrees with the observations of others in which anoles paused when fleeing or relied on crypsis before escaping (Jones & Jayne, 2012; Parmerlee, Larimer, & Powell, 2006). It is also possible that water anoles might be less fearful of humans wearing their sexually selected signaling color because humans do not have characteristics of typical anole predators, and hence, humans represent a potentially novel organism. Thus, anoles might attune to humans wearing their sexually selected signaling color out of an existing bias for the color and remain stationary to monitor the unknown threat. It is likely that repeated attempts by humans to capture individual anoles might reduce their responses toward this color (Ten Cate & Rowe, 2007). These ideas are speculative and warrant further research.

Ecotourism operates on the idea of leaving only footprints when visiting natural areas. The ecotourism industry aids in economic development (Gurung & Seeland, 2011), increases appreciation of local communities and natural areas (Ormsby & Mannle, 2006), and provides aid for local conservation efforts (Stem, Lassoie, Lee, Deshler, & Schelhas, 2003). Activities usually include those that allow the public to interact with and observe nature, while minimizing their impact upon the environment. We determined that human clothing, specifically shirt color, can affect the sighting rates of water anoles and, potentially, the stress associated with human interactions (Bertin et al., 2008; Geffroy, Samia, Bessa, & Blumstein, 2015). Though we cannot apply this finding to all anole species or animals in general, we contribute a foundation to further research concerning the impacts of anthropogenic coloration. Thus, we call for researchers to conduct similar studies to determine the impacts of clothing as well as other apparently innocuous human activities on animal behavior. Furthermore, scientists conducting research with organisms that have distinctive sexually selected signaling color may consider wearing clothing that resembles the signaling color to reduce their impact upon their study organism's behavior or increase efficiency of research (e.g., improve capture rates of study organisms). By making informed clothing choices, it may be possible to reduce the animal's stress response and the possible expenditure of energy and time toward predator avoidance (Preisser, Bolnick, & Benard, 2005; Wang, Ings, Proulx, & Chittka, 2013). Overall, our study illustrates the importance of clothing color in the context of both biological research and ecotourism.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the questions of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTION

A. F., B. J. P., and L. S. designed and carried out the study; A. F., and B. J. P. prepared and wrote the original draft; L.S. reviewed and edited subsequent drafts.

ANIMALS IN RESEARCH

Research permits for this study were acquired from the Ministry of Environment and Energy, Republic of Costa Rica (Permit: R-SINAC-PNI-ACLAP-043–2018). All methods were approved by the UCLA Animal Research Committee (ARC-2016–051-03C).

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.18931zcs3 (Fondren, Swierk, and Putman 2019a,2019b).

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