



# Sexual dimorphism in dynamic body color in the green anole lizard

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## Abstract

Animals capable of rapid (i.e., physiological) body color change may use color to respond quickly to changing social or physical environments. Because males and females often differ in their environments, the sexes may use changes in body color differently, reflecting sexual dimorphism in ecological, behavioral, or morphological traits. Green anole lizards, *Anolis carolinensis*, frequently switch their dorsal body color between bright green and dark brown, a change that requires only seconds, but little is known regarding sexual dimorphism in their color change. We tested three hypotheses for the function of body color (thermoregulation, camouflage via background-matching, and social communication) to determine the ecological role(s) of physiological color change in anoles. First, we examined instantaneous body color to determine relationships between body color and body temperature, substrate color and type, and whether these varied between the sexes. Next, we examined the association between color change and behavioral displays. Altogether, we found that males were more likely to be green than females, and larger lizards were more often green than smaller ones, but there was no evidence that anole body color was associated with body temperature or background color during the summer breeding season. Instead, our results show that although the sexes change their color at approximately the same rates, males changed color more frequently during social displays, while females remained green when displaying. In sum, social communication appears to be the primary function of anole color change, although the functions of body color may differ in the nonbreeding season.

## Significance statement

Many animals can change their body color in response to their environments, and in many species, males and females experience different environments. In this study, we examined whether the sexes of green anole lizards use the ability to rapidly change their body color between green and brown for different functions. We found that, when a lizard was first sighted, its body color did not appear to match its background color in either sex (suggesting that color change does not contribute to avoidance of detection by potential predators), and body color was not associated with temperature for either sex (i.e., color was unlikely to influence body temperature). Yet, males changed color more often when performing social displays to other lizards, while females remained green during social displays. Thus, rapid color change plays an important role in social communication in both sexes, highlighting how males and females may use the same behavior to convey different messages.

**Keywords** Background matching · Camouflage · Physiological color change · Sexual dimorphism · Social signaling · Thermoregulation

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## Introduction

The color of an organism plays a critical role in its ecology. An individual with a body color similar to its environment can use camouflage to remain hidden from predators or prey (Kaufman 1975; Théry and Casas 2002), while elaborate colors and patterns may advertise toxicity (e.g., Maan and Cummings 2012) or signal information to potential mates or competitors (e.g., Griggio et al. 2010). Although the body color of most animals is relatively static, individuals of many

species may modify their body color across a variety of timescales (Duarte et al. 2017). Morphological color change is relatively slow, occurring over days or weeks (Leclercq et al. 2010), and generally depends on ontogenetic, dietary, or seasonal factors (Nery and Castrucci 1997). In contrast, physiological color change involves the rapid movement of pigments within skin cells, allowing color change to occur within milliseconds to hours (Stuart-Fox and Moussalli 2009; Figon and Casas 2018). A wide diversity of animals are capable of this dynamic process (insects: Raabe 1982; cephalopods: Hanlon 2007; fish: Sköld et al. 2008; amphibians: Novalés and Davis 1969; reptiles: Hadley and Goldman 1969; birds: Tarvin et al. 2016), which allows organisms to adjust their appearance quickly to shifts in the physical or social environment (Sköld et al. 2013). Because these environments can differ dramatically between sexes (e.g., Jenssen and Nunez 1998; Nunez et al. 1997), the use of physiological color change may also vary between males and females.

There are three major hypotheses for the function of animal body color change: physiological regulation, camouflage, and social communication (Caro 2005), each of which may produce different selective pressures on the sexes (e.g., Kodric-Brown 1998; Badyaev and Hill 2003; Bell and Zamudio 2012). In the context of physiological regulation, ectotherms, which must actively regulate their body temperature, may particularly benefit from the ability to rapidly shift between solar-reflective and solar-absorptive colors. Rapid color change may be less costly than behavioral mechanisms of thermoregulation (e.g., shuttling; Huey and Slatkin 1976), and may facilitate a more finely tuned response to shifts in temperature via the range of solar absorptivity of the skin (De Velasco and Tattersall 2008). Because adult males and females differ in traits associated with the maintenance of body temperature, such as body size and incubation of eggs (e.g., Sanger et al. 2018), they may differ in the use of body color to thermoregulate.

Second, organisms may rely on color change to maintain crypsis in a changing environment, as animals that are able to effectively match their substrate may prevent detection by visual predators. For example, azure sand grasshoppers, *Sphingonotus azureus*, increase their background matching when the risk of predation increases (Edelaar et al. 2017), and aquatic anole lizards, *Anolis aquaticus*, can change their body color to minimize predator detection of the outline (or, edge) of their bodies against a heterogeneous background (Wuthrich et al. 2022). Across a diversity of species, males are often more elaborately colored than females, and perform riskier behaviors that make them more vulnerable to predation (e.g., Stuart-Fox and Ord 2004; Møller and Nielsen 2006), so cryptic coloration may be generally more common in females (Gluckman and Cardoso 2010; Barreira et al. 2016).

Third, many animals use body color to communicate social information, including species identity (Endler 1983), sexual receptivity (Chan et al. 2009), health status (Rosenthal et al. 2012), aggression (Keenleyside and Yamamoto 1962), and dominance status (Korzan et al. 2008). Rapid color change, which may allow gradations in body color, can convey multifunctional signals, or provide information on an animal's immediate short-term motivational state (Hutton et al. 2015; Ligon and McGraw 2018). Additionally, whole body color change may be paired with behavioral displays to either increase the conspicuousness of the signaler to the receiver, or to allow individuals to communicate specific information using a particular combination of behavioral motions and visual signals (Endler 1992). As males and females engage in social interactions for different purposes, the sexes may also use color to communicate differently.

In this study, we analyzed the ecological role of physiological color change in the green anole lizard, *Anolis carolinensis*. Green anoles are highly visual, diurnal lizards that frequently, within seconds, change their dorsal body color between bright green and dark brown, potentially for a combination of social display, camouflage, and thermoregulation. Green anoles of both sexes communicate with conspecifics using visual displays that include push-ups, headbobs, and extensions of the dewlap (Jenssen 1977). These displays are often accompanied by changes in body color, with green body color often associated with social dominance, while brown generally signals subordination (Greenberg 1977; Jenssen et al. 1995; Andrews and Summers 1996; Wilczynski et al. 2015; Boyer and Swierk 2017). Brown body color in this species is also associated with physical or social stress (Greenberg and Crews 1990). Green anoles are often called “American chameleons” because of the classic assumption that they use body color to match their substrates (Gordon and Fox 1960; Hadley and Goldman 1969; Taylor and Hadley 1970; Medvin 1990), but more recent studies have shown no correlation between background color and body color in this species (Jenssen et al. 1995; Yabuta and Suzuki-Watanabe 2011). Finally, laboratory studies have shown that anole skin color changes, in part, in association with temperature, such that temperature influences the dermal photic response and the hormonal mechanisms that influence dorsal darkening (reviewed in Cooper and Greenberg 1992). Yet, there is no clear evidence that color is used in thermoregulation (Yabuta and Suzuki-Watanabe 2011). While the functions of body color have been previously tested in green anoles, studies of color in this species have rarely included females (but see Medvin 1990; Andrews and Summers 1996), and the hypothesis that the sexes differ in their use of color as a function of the physical and social environment has not yet been tested.

Here, we analyzed dynamic body color in wild populations of the green anole during the summer breeding season, including an explicit consideration of female body color. In Study 1 (Ecological Context of Body Color), we examined instantaneous body color to determine the factors associated with whether a given male or female lizard will be green or brown at first sighting in the field. We predicted that body color is associated with body temperature, such that lizards with the highest temperatures and/or at the hottest times of day would be green, thus reflecting more solar radiation, and vice versa (Cooper and Greenberg 1992). If anoles are actively using background matching to camouflage, and if lizard and vegetation colors appear similar to potential predator visual systems (an untested assumption here), green-colored anoles should be found more often on green substrates and brown-colored anoles on brown substrates. (See Macedonia et al. 2003 for a discussion of green anole dorsal color reflectance and chromatic contrast.) If body color is used to communicate social intent to conspecifics, lizards should be green more frequently during social displays than during other types of behavior. Further, because male anoles perform highly visible social displays far more frequently than females (Nunez et al. 1997; Johnson et al. 2011), we predicted that males are green more frequently, and that background matching is more important for females. Finally, because thermal stress during early anole development can cause embryonic malformations and/or mortality (Sanger et al. 2018), the relationship between color and temperature may be more critical for females during the breeding season.

In Study 2 (Behavior and Body Color Change), we used field behavioral data to examine color change in the context of social behaviors in more detail. Males perform social displays at higher rates than females, and so we predicted that males display body color change more frequently than females and spend a larger proportion of time with a green body color. We also predicted that lizards of either sex that perform more social displays should exhibit more frequent color change and present a green body color more than those that display rarely.

## Methods

### Study 1: Ecological context of green or brown body color

#### Field data collection

To study the relationship between body color and three potential functions (thermoregulation, background-matching, and social communication), we collected field data on 201 free-living adult green anole lizards, including 90 males and 95 females, in summer 2017. (Adult status was

determined by visual assessment of body size (snout-vent length (SVL) > ~45 mm). Sixteen lizards were excluded from analysis because their sex could not be confirmed without capture.) Field sites for this study included forested areas in Palmetto State Park, Gonzales County, Texas, and natural areas around Trinity University in San Antonio, Bexar County, Texas.

When an undisturbed lizard was located, we performed a 1–3-min focal observation, noting the time of day and when visual assessment was certain, the lizard's sex (using a combination of body size and shape, dewlap size, and tail shape). We recorded the type of the substrate on which the lizard perched (leaves, trunk, branch, plastic, metal, or rock) and the general color (green, brown, or other) of that substrate (e.g., leafy vegetation was green, tree trunks and branches were brown). We noted whether the lizard's initial body color was green or brown, as no lizards in this study were blotchy or actively changing colors upon our initial sighting of the animal. We also recorded each lizard's general behavior, categorized as basking (perching in full sun), stationary in shade (perching in full or partial shade), locomotor movement (crawling, running, or jumping among perches, with no clear social interactions), or social interaction (performing push-ups, headbobs, and/or dewlap displays). We then captured a subset of these lizards (41 males and 42 females) using a snare made of a dental floss loop attached to a fishing pole, generally within 1 min after observation. Immediately after capture, we measured each lizard's internal body temperature to the nearest 0.1 °C using a Type T, Copper-Constantan thermocouple inserted approximately 1 cm into the cloacal vent and connected to an automated temperature logger (HH603A, OMEGA; Muñoz et al. 2014). We confirmed the lizard's sex by checking for the presence of a large dewlap, hemipenes, and enlarged post-anal scales, all of which distinguish males from females. (In all cases, our initial visual assessment of sex was correct.) We measured the lizard's SVL to the nearest mm using a clear plastic ruler and measured its mass to the nearest 0.1 g using a Pesola spring scale. We also measured the temperature of the substrate the lizard was initially perching on by placing the thermocouple on the substrate surface. Additionally, we recorded the distance of this perch to the next closest available perch (hereafter, distance to next perch) as a general proxy for habitat exposure (e.g., Losos 1990). Nearest perches were determined to be the closest object, in three-dimensional space, on which an adult lizard could reasonably perch. Closer nearest perches indicate a more cluttered habitat, in which a lizard is less likely to be observed by conspecifics; farther nearest perches indicate a more open habitat, in which a lizard is more visually exposed. It was not possible to record data blind because our study involved focal animals in the field.

## Statistical analyses

We generated multivariate logistic regression models in R (R Core Team 2018) to estimate which environmental, behavioral, and body size variables best predicted the frequency that a lizard's body color would be green upon initial sighting. We included the following environmental predictors in the series of models: lizard body temperature, substrate temperature, distance to the nearest perch, substrate category, and substrate color. We also included sex, and whether the lizard was engaged in social interactions. We used SVL and mass in these models as measures of body size. All models included lizard body color as the dependent variable. We constructed a full covariates model, which included all possible predictor variables as covariates; models where each predictor variable was analyzed independently; and 35 additional models with combinations of variables that were morphologically or environmentally related. We also constructed a null model in which body color was assumed to be random. (See Appendix 1 for the full list of models tested.) We used the Akaike Information Criterion (AIC) to select the models that best fit the data. Following statistical convention, models with  $\Delta\text{AIC} < 2$  were selected as the best-fit models, and all of these models were considered to have equal weight (Akaike 1973; Burnham and Anderson 2002).

Following this modeling analysis, we performed a series of analyses aimed to individually evaluate each hypothesis (thermoregulation, background-matching, social communication). Although these analyses do not account for interrelationships among the variables, they allow us to compare our results to previous studies of the individual hypotheses. To consider the relationship of temperature and body color, we first performed a linear regression to determine if lizard body temperatures were associated with substrate temperature. Because these two measures were correlated ( $F_{1,83} = 128.5$ ,  $R^2 = 0.61$ ,  $p < 0.001$ , Supplementary Fig. 1), we performed subsequent analyses in two ways: (1) analyzing only the direct measures of body temperature, and (2) using substrate temperatures as a proxy for lizard body temperatures, as this generated a larger sample size. These two approaches generally gave qualitatively similar results, and where they differed, we present results from both analyses.

We performed a two-way analysis of variance (ANOVA) to determine whether substrate (or body) temperature differed as a function of the lizard's sex, its initial body color (green or brown), or an interaction of sex and body color. We also performed a one-way ANOVA to compare the average distance to the next perch between male and female anoles. Because hourly data were non-normally distributed across the day, we used Wilcoxon signed ranks tests to determine whether the total number of lizards observed, or the proportion of lizards that were green, differed between the sexes

throughout the day. All of these analyses were conducted in IBM SPSS statistical software (IBM Corp 2017; version 25).

To assess whether anoles selectively used brown or green perches with respect to their own body color, we used a chi-squared goodness of fit test with body color data from the subset of lizards that perched on a brown or green substrate (i.e., brown tree trunks and branches, or green foliage; lizards perching on substrates that were not green or brown were excluded from this analysis). We also used a chi-squared test to determine whether lizards exhibiting different behaviors (basking, locomotion, social interaction, or stationary in shade) were more likely to be green or brown. These analyses were also conducted in IBM SPSS.

## Study 2: Behavioral analysis of body color change

### Field data collection

To determine whether green anole body color change was related to social display behaviors, we examined 128 h of focal behavioral data on adult green anole lizards, collected in the 2010 summer (May–July) breeding season at Palmetto State Park in Gonzales County, Texas (one of the study sites used in Study 1, Ecological Context of Body Color). These data were initially collected to examine differences in anole behavior among three 1000-m<sup>2</sup> study plots that differed in vegetation structure and were all within 1 km of one another and connected via continuous forest canopy (see Battles et al. 2013; Dill et al. 2013; Stehle et al. 2017). During the 2–3-week study period in each plot, all adult lizards sighted (totaling 70 males and 100 females) were captured using a dental floss loop. Upon capture, the SVL of each lizard was measured with a clear plastic ruler to the nearest 1 mm, and the lizard was permanently marked with a unique combination of colored beads sewn into the dorsal tail musculature (Fisher and Muth 1989). Each lizard was then released at its site of capture.

Of the 170 marked adults, behavioral data were collected on 91 individuals. Sex was not recorded for some of these lizards, so 85 marked lizards (43 males, 42 females) were included in data analysis. Lizards were observed a minimum of 24 h after capture by walking slowly through a plot until an undisturbed lizard was identified. It was again not possible to record these data blind because we examined focal animals in the field. Behavioral data were recorded from a minimum distance of 10 m using binoculars. Each lizard was observed for 5–60 min in a single observation period (average observation period = 34 min, SE = 1.2 min), and no more than 3 h of observation was conducted per lizard. This yielded an average of 2.6 periods and 86 min observation per lizard (Stehle et al. 2017). Observers recorded each behavioral event during the observation, with a focus on social display behaviors and locomotor movements; the



initial color of the lizard prior to start of observation; and each time the lizard changed body color between brown and green (a change that generally happens within several seconds). Using these data, we calculated the frequency of color change (i.e., the number of times a lizard changed body color during an observation), the combined rate of push-ups and headbobs per observation (here called “push-bobs”), and the proportion of time the lizard was green in each observation. For lizards observed in multiple periods, we calculated the average rates of these behaviors per lizard for use in statistical analysis.

### Statistical analyses

To determine whether there was a sex difference in overall body color expression, we used an ANOVA to compare males and females in rate of color change and the proportion of time individuals were green. We used a series of Pearson correlation analyses, performed separately for each sex, to assess the relationships between the two measures of body color (rate of color change and proportion of time green) and rates of display behaviors (push-bobs per min) and body size (SVL). Lastly, to examine whether color change was associated specifically with social behaviors, and not merely with general activity, we used correlation analyses, separately for each sex, to determine the relationship between movement rate and body color measures (rate of color change and proportion of time green). We performed all data analysis using IBM SPSS.

## Results

### Study 1: Ecological context of green or brown body color

We used multivariate logistic regression models and AIC model selection to determine which environmental, behavioral, and body size factors most strongly influenced the probability that a given individual lizard’s body color would be green. Thirty-two of the 37 total models analyzed fit the data better than the null model (null:  $\Delta\text{AICc} = 173.6$ ). However, none of the environmental factors (lizard body temperature, distance to the nearest perch, and substrate type or color) or social display behavior were predictive of green body color. Body size measurements were included as covariates in all 4 of the top models (those with  $\Delta\text{AICc} < 2$ ; Table 1). Sex alone did not increase the probability of being green ( $\Delta\text{AICc} = 129.6$ ), but both sex and SVL ( $\Delta\text{AICc} = 1.1$ ) and a combination of sex, SVL, and mass ( $\Delta\text{AICc} = 1.8$ ) did predict green coloration, such that lizards that were male and larger-bodied were more likely to be green than female and smaller-bodied lizards (Fig. 1).

Our follow-up analyses of individual hypotheses of body color were consistent with these modeling results. In our analysis of body color and temperature, we found no difference in substrate temperature between green and brown lizards ( $F_{1,180} = 0.45$ ,  $p = 0.50$ ). However, there was a marginally significant main effect for sex where males used slightly warmer substrates than females ( $F_{1,180} = 3.52$ ,  $p = 0.062$ ), but there was no interaction between sex and color ( $F_{1,180} = 1.62$ ,  $p = 0.20$ , Fig. 2). Of the subset of lizards for which we obtained body temperature measurements, only sex had a significant effect on temperature, with males warmer than females (color:  $F_{1,78} = 0.50$ ,  $p = 0.48$ ; sex:  $F_{1,78} = 9.50$ ,  $p = 0.003$ ; color  $\times$  sex:  $F_{1,78} = 0.20$ ,  $p = 0.66$ ). Males used more exposed substrates (those with larger distances from their current perch to the next) than females ( $F_{1,169} = 18.41$ ,  $p < 0.001$ ), but habitat exposure did not differ by body color for either sex (females:  $F_{1,84} = 0.009$ ,  $p = 0.92$ ; males:  $F_{1,83} = 0.07$ ,  $p = 0.80$ ).

The total number of individual anoles encountered across the day did not vary between sexes ( $Z = -1.06$ ,  $p = 0.29$ ), demonstrating that we were equally likely to find males and females throughout our observation period. However, the proportion of anoles that were green upon first sighting differed between males and females throughout the day ( $Z = -2.58$ ,  $p = 0.01$ ), with males most likely to be brown in the mid-afternoon (Fig. 3a), and females most likely to be brown early in the day (Fig. 3b). Across the behaviors observed (locomotion, basking, stationary in shade, and social), none were associated with green or brown body color for either sex (males:  $\chi^2(3, N = 90) = 0.689$ ,  $p = 0.88$ ; females:  $\chi^2(3, N = 95) = 1.998$ ,  $p = 0.57$ , Table 2).

We located a total of 58 males and 74 females on clearly green or brown substrates, with the remaining 57 lizards perched on substrates of other colors, including gray, red, black, and white. Of those using green or brown perches, neither green nor brown body color was more associated with green or brown substrates, respectively, than would be expected by random chance (males:  $\chi^2(1, N = 58) = 0.157$ ,  $p = 0.69$ ; females:  $\chi^2(1, N = 74) = 0.003$ ,  $p = 0.96$ , Table 3).

### Study 2: Behavioral analysis of body color change

In our study of body color change and social behavior, males exhibited green body color more frequently than females ( $F_{1,83} = 14.1$ ,  $p < 0.001$ ). On average, males were green 73% of the time, while females were green only 43% of the time. However, the sexes did not differ significantly in their rates of body color change (i.e., the frequency of color change during behavioral observation;  $F_{1,83} = 1.3$ ,  $p = 0.27$ ). Overall, rapid body color change was quite common, as 24/43 males changed their body color during our behavioral observations, and 25/42 females changed color. Changes in body color were observed in 36% of total observation periods,

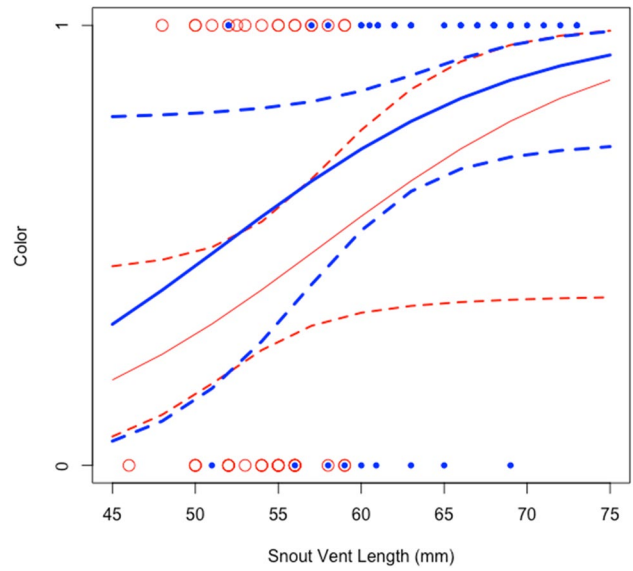
**Table 1** All multivariate logistic regression models considered to determine the factors that influence the probability that the dorsal body color of a green anole lizard is green upon its initial observation

Model	Sex	SVL	Mass	Lizard Temp	Substrate Temp	Closest Perch	Substrate Type	Substrate Color	Social Display	R <sup>2</sup>	AICc	Δ AICc
1		x								0.64	101.0	0.0
2		x	x							0.65	101.6	0.6
3	x	x								0.65	102.0	1.1
4	x	x	x							0.65	102.7	1.8
5		x	x							0.65	103.1	2.2
6	x		x							0.64	103.2	2.2
7		x		x	x					0.65	103.5	2.5
8		x	x	x	x					0.66	103.9	2.9
9	x	x	x			x				0.65	104.4	3.4
10	x	x		x						0.64	105.4	4.4
11	x	x	x	x	x					0.66	105.6	4.7
12	x			x	x					0.64	107.0	6.1
13		x	x			x		x		0.66	108.6	7.7
14		x	x		x	x				0.65	108.8	7.8
15	x	x	x		x	x				0.66	110.0	9.1
16	x	x	x		x	x		x		0.67	110.1	9.1
17	x	x	x	x	x	x		x		0.68	115.0	14.0
18			x	x	x					0.61	115.9	14.9
19				x						0.59	116.1	15.1
20				x	x					0.60	116.4	15.4
21			x							0.59	117.0	16.1
22				x	x			x		0.60	118.4	17.5
23				x	x		x	x		0.61	122.7	21.8
24				x	x		x			0.60	123.8	22.9
25	x					x				0.24	212.4	111.4
26	x									0.17	230.5	129.6
27	x				x					0.17	231.2	130.3
28	x							x		0.17	232.0	131.0
29	x								x	0.17	232.6	131.6
30	x					x		x		0.19	235.7	134.7
31										0.10	250.5	149.6
32					x					0.01	274.5	173.6
33										0.00	274.6	173.6

**Table 1** (continued)

Model	Sex	SVL	Mass	Lizard Temp	Substrate Temp	Closest Perch	Substrate Type	Substrate Color	Social Display	R <sup>2</sup>	AICc	Δ AICc
34									x	0.01	274.6	173.7
35								x		0.01	275.1	174.1
36						x		x		0.04	275.3	174.3
37							x			0.03	277.6	176.7

Color (green or brown) is the dependent variable in each model. Models are listed in order of increasing ΔAICc values. All models with ΔAICc < 2 (models 1–4) were selected as the best-fit models, and all of these models were considered to have equal weight



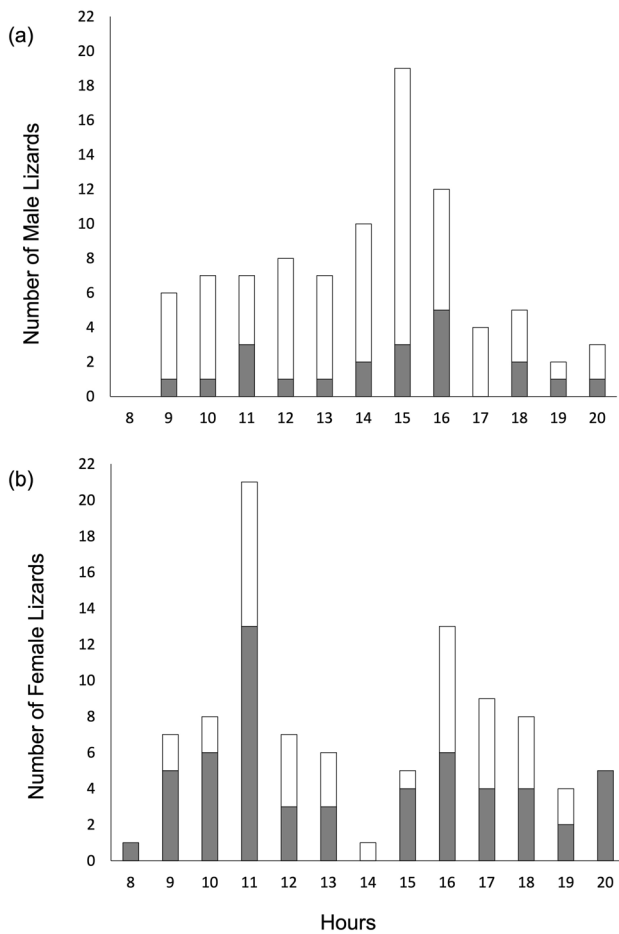
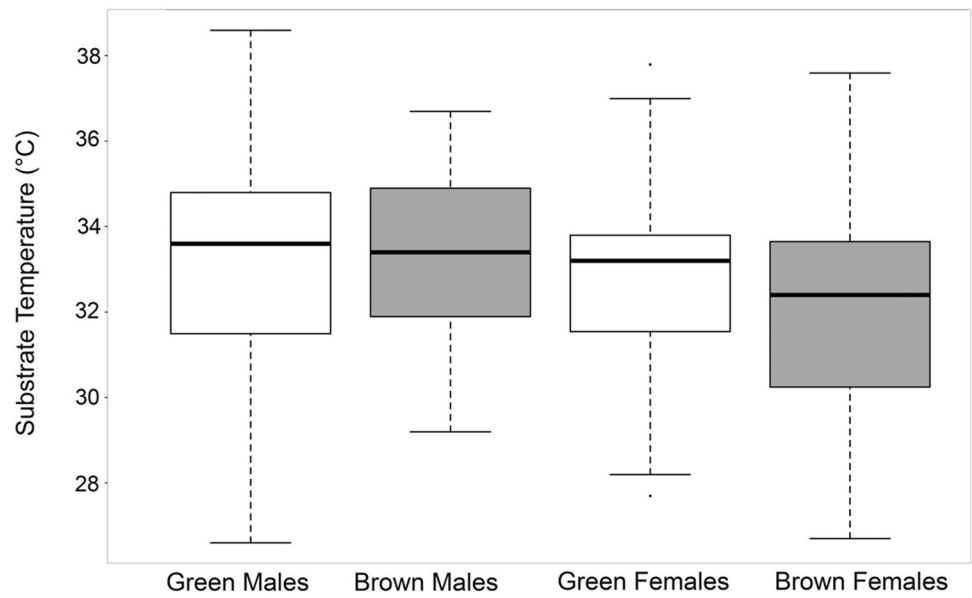
**Fig. 1** Snout-vent length (SVL) as a predictor of color (0=brown, 1=green) for male (thick blue lines) and female anoles (thin red lines), with 95% confidence intervals indicated by dashed lines for each sex. Male data are represented by closed blue circles; female data by open red circles. Size was a stronger predictor of body color for males than for females

and multiple color changes were observed in 54% of those observations.

Among males, push-bob rates were positively correlated with color change rates ( $r=0.30, p=0.045$ , Fig. 4a), such that lizards that performed more displays changed between green and brown body color more frequently. Yet, female anoles did not exhibit a relationship between color change and rate of push-bob displays ( $r=0.04, p=0.82$ , Fig. 4b). In contrast, in females, push-bob rates were positively correlated with overall proportion of time spent green ( $r=0.38, p=0.013$ , Fig. 4d), but there was no relationship between the proportion of time that males were green and the rate of push-bob displays ( $r=0.23, p=0.14$ , Fig. 4c). Female body size was not associated with proportion of time green ( $r=-0.09, p=0.58$ ) or rate of color change ( $r=-0.22, p=0.16$ ), and in males, body size was not associated with proportion of time green ( $r=0.11, p=0.50$ ), but smaller males changed their body color more frequently than larger males ( $r=-0.35, p=0.022$ ).

Male green anoles displayed and moved more frequently than females (push-bob:  $F_{1,83}=100.6, p<0.001$ ; total locomotor movement:  $F_{1,83}=28.2, p<0.001$ ), but male color change was not related to movement ( $r=0.08, p=0.61$ ). For females, color change was positively correlated with total locomotor movement rates ( $r=0.54, p<0.001$ ). However, the proportion of time spent green was not correlated with movement behaviors for either sex (males:  $r=0.16, p=0.31$ ; females:  $r=0.16, p=0.30$ ).

**Fig. 2** Median, second and third quartiles, and standard error of substrate temperature for green and brown males and females. Differences in body color were not related to differences in temperature for either sex



**Fig. 3** Number of lizards observed, 0800–2000 h, for males (a) and females (b). White bars indicate lizards found green, and gray bars indicate brown lizards

**Table 2** Number (and percent) of green- and brown-colored anoles observed as a function of behavior

		Locomotion	Basking	Stationary in Shade	Social
Males	Green	6 (7%)	6 (7%)	38 (42%)	19 (21%)
	Brown	3 (3%)	2 (2%)	10 (11%)	6 (7%)
Females	Green	10 (11%)	3 (3%)	25 (26%)	1 (1%)
	Brown	14 (15%)	6 (6%)	31 (33%)	5 (5%)

Behavioral categories include active locomotion, basking (i.e., perching in full sun without movement), stationary in shade (i.e., perching in partial sun or shade without movement), and social display behaviors (push-ups, headbobs, and dewlap extensions)

**Table 3** Number (and percent) of green- and brown-colored green anoles found on green and brown substrates

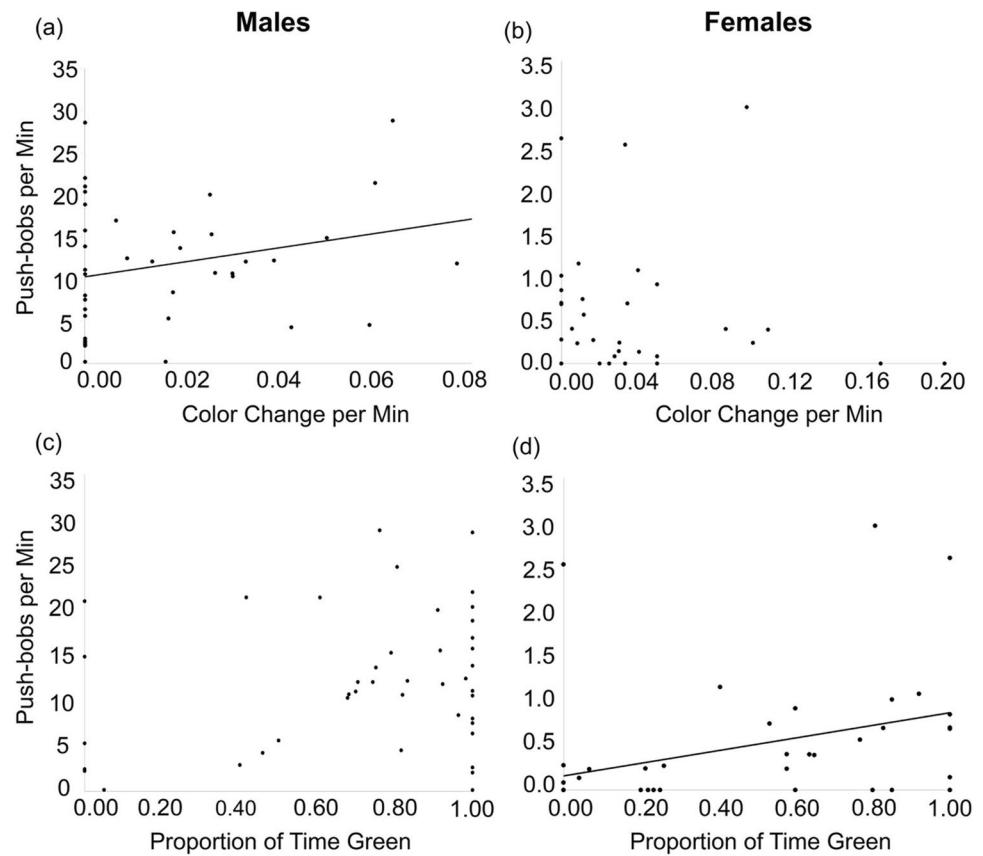
		Green body	Brown body
Males (n = 58)	Green Substrate	18 (31%)	6 (10%)
	Brown Substrate	27 (47%)	7 (12%)
Females (n = 74)	Green Substrate	20 (27%)	28 (38%)
	Brown Substrate	11 (15%)	15 (20%)

### Discussion

In two complementary field studies, we examined the ecological roles of physiological color change in wild populations of the green anole lizard. These studies tested whether males and females use color change differently in the contexts of body temperature, background matching, and social communication. Overall, we found no



**Fig. 4** Push-bob display behavior as a function of color change and green body color for males and females



evidence supporting the association of color change and body temperature or background color in either sex. However, our results showed that both males and females alter colors during social communication. Yet, the relationships among body color, display behavior, and body size differed between the sexes, illuminating the sexually dimorphic roles of dynamic body color.

Overall, both of our studies demonstrated that male green anoles exhibited green body color far more frequently than females (Fig. 3). Our behavioral observations in Study 2 (Behavior and Body Color Change) suggest that these sex differences are associated with social display behaviors, consistent with the hypothesis that the expression of body color in green anoles is influenced by sexual selection. Green body color in this species signals dominance (e.g., Greenberg 1977; Wilczynski et al. 2015), and during the breeding season, males in particular may be green more frequently as they compete for potential mates and defend perch sites (e.g., Jenssen et al. 1995). As for females who generally display darker brown colors, Andrews and Summers (1996) proposed that darker body color in females may function as a submissive social status to regulate interactions with males and may even signal receptivity to male courtship. It has also been suggested that female lizard coloration is correlated with female-female interactions or mate choice (Olsson et al. 2013), or

with reproductive status (Robertson and Rosenblum 2009). Together, the findings of these studies, and the results presented here, suggest that green and brown body colors are used in different social contexts between the sexes, and as such, may communicate different information when used by males and females.

Although our results from Study 1 (Ecological Context of Body Color) showed that simply engaging in social behavior did not predict whether an anole would be green or brown, our findings from Study 2 (Behavior and Body Color Change) demonstrate that both males and females use body color in conjunction with behavioral displays. Overall, males and females did not differ in their rates of color change, but they use body color change in different contexts. As males perform more frequent social displays, they increase their rate of body color change (Fig. 4a), a relationship not observed in females (Fig. 4b). Females in contrast, spent more time with green body color as they increased their display behavior (Fig. 4d), and exhibited more frequent color change in association with more frequent locomotor movements. In other words, females seem to change color as a function of their general level of activity and indicate engagement in social interactions by remaining green. On the other hand, males may use color change primarily to enhance the signals communicated by behavioral push-bob displays.

In both sexes, body color and other display behaviors may be context-dependent, and individuals modify their color and behavior according to with whom they are interacting (e.g., Jenssen et al. 2000; Keren-Rotem et al. 2016; Ligon and McGraw 2018). In line with this, in Study 1 (Ecological Context of Body Color) we found that while we were equally likely to observe males and females across the hours of the day, the number of individuals observed to be green at a given time of day differed between the sexes (Fig. 3). Males were more often found green earlier and later in the day, while females were more likely to be green in the mid-afternoon. This may be associated with the “dawn and dusk chorus” phenomenon in which territorial animals (often males) reinforce their territory defense before and after the nocturnal period of refuge (Staicer et al. 1996; Ord 2008). Our observational data in Study 2 (Behavior and Body Color Change) are unable to address this hypothesis, as they were collected in a wild population in which we were generally unable to definitively determine the target of most displays. Thus, we cannot assign given color change events to specific social contexts (i.e., territorial defense, courtship, or predator deterrence), but this may be a fruitful avenue for future study.

We did not find evidence in our observational study (Study 1; Ecological Context of Body Color) that green anoles use color to thermoregulate during the breeding season. In populations for which changing color provides a thermoregulatory mechanism, lighter body colors that reflect solar radiation should facilitate cooler body temperatures than darker colors. Previous experimental studies have shown support for color change in *Anolis* as a function of temperature, where cold temperatures physiologically inhibit lightening of the skin (reviewed in Cooper and Greenberg 1992). Further, a study of introduced green anoles in Japan found that early in the breeding season (March), lizards were more likely to be green in warmer air temperatures and brown in cooler temperatures (Yabuta and Suzuki-Watanabe 2011). Yet in our observations of active anoles during daylight hours, lizards with brown and green body color did not differ in temperature for either sex (Fig. 2). The present study was conducted during the summer (May–July), when temperatures are consistently warm (typical daily temperature range = 23–35 °C in Bexar County, Texas), suggesting that if color change does allow anoles to regulate body temperature, it may be less important to use color to reduce body temperature during warmer periods than to increase it during cooler periods, particularly if lower temperatures inhibit locomotor performance (e.g., *Pieris* butterflies; Kingsolver 1987). At least during the summer breeding season, our data suggest that thermoregulation is not the primary function of anole color change.

Further, body size can interact with body temperature and color, and these relationships may differ by sex. In general,

across terrestrial ectotherms, larger-bodied individuals have more stable body temperatures due to lower convective heat exchange and higher thermal inertia (Stevenson 1985). Because maximal body size of adult male green anoles is larger than that of females, our finding that males had higher body temperatures than females (Fig. 2) may be due to sexual size dimorphism in this species. In addition, the results of our multivariate logistic regression analysis showed that larger lizards are more likely to be green, and this relationship was stronger for males than for females (Fig. 1). This finding is consistent with the results of Lovern’s (2000) study of juvenile green anoles, in which larger juvenile males were more likely to be green than smaller males, but there was no relationship between size and color for juvenile females. Yet, in our behavioral study of color change (Study 2), we did not find a relationship between body size and the proportion of time spent green, for either sex. This difference may be due to the methodological differences between the two studies (noting color of each lizard at first sighting in Study 1, Ecological Context of Body Color, vs. longer-term focal observations in Study 2, Behavior and Body Color Change) and/or differences in statistical power ( $n$  for males = 94 in Study 1,  $n$  for males = 41 in Study 2), such that we were more likely to detect a relationship between color and size in Study 1. We propose that a study focused on testing the relationship between body size and color in anoles would help to tease apart these alternatives.

No other environmental variables were predictive of body color, in either sex (Table 1). Males used more exposed perch locations than females, potentially to advertise their presence to competitors or potential mates or to bask more effectively, but body color did not differ across perch site exposure (Supplementary Fig. 2). Further, we found no evidence of background matching in either sex (Table 3), suggesting that camouflage is unlikely to be the primary function of body color change in green anoles. Yet, females were far more likely to be brown than males (Fig. 3). It is possible that brown body color on any background may be less conspicuous to the lizards’ visual predators, but this remains to be tested with an explicit consideration of the predators’ visual systems (see Wuthrich et al. 2022). If so, this may be consistent with the general observation that female coloration is often more cryptic than that of males (e.g., Kodric-Brown 1998; Badyaev and Hill 2003; Stuart-Fox et al. 2007; Bell and Zamudio 2012).

In sum, we demonstrate that during the summer breeding season, physiological color change in green anoles is primarily associated with social communication. Although we find no support for the use of color change in thermoregulation or background matching, these functions of body color may be more critical in the nonbreeding season, when social communication is less important but cooler temperatures may necessitate the use of body color to maintain warmer

temperatures or enhance the need for crypsis. Further, the multiple functions of body color may conflict, especially when they rely on different aspects of color, or color on different areas of the body (Castrucci et al. 1997; Smith et al. 2016). For example, during the breeding season, effective social communication may provide a greater benefit than reducing predation risk via camouflage (e.g., Marshall and Stevens 2014; Keren-Rotem et al. 2016). The study of anole body color change in the nonbreeding season could thus help to identify whether seasonal tradeoffs exist among these functions, and whether the tradeoffs differ between the sexes. The study of physiological color change in both males and females provides a broader understanding of the mechanisms underlying rapid responses to a changing environment.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00265-023-03308-8>.

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**Data availability** All data and R scripts for analyses presented here are available on figshare at: <https://doi.org/10.6084/m9.figshare.c.6225672.v1>

## Declarations

**Ethics approval** All applicable international, national, and/or institutional guidelines for the use of animals were followed. Animal work was conducted with the approval of Trinity University's Animal Research Committee (protocols 81809-MJ1, 050317-MJ, and 011415-MJ1), and Texas Parks & Wildlife Department (scientific research permit #SRP-0310–045).

**Conflicts of interest** The authors declare no competing interests.

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