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Background and Temperature Effects on Color Change in Eastern Gray Treefrogs

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Abstract.—Animal body coloration plays a crucial role in a wide range of ecological functions, including communication, predator avoidance, and thermoregulation. Being able to change color can further enhance these functions, as it allows organisms to fine-tune their appearance to deal with environmental heterogeneity or changes in their environment. Organisms frequently encounter conditions where requirements of camouflage and thermoregulation conflict, potentially forcing a trade-off in which function to emphasize. This may elucidate whether predator avoidance or metabolic demands represent a greater potential cost to survival and are thus under stronger selection. We examined the ecology of environment- and temperature-dependent color change in Eastern Gray Treefrogs (*Dryophytes versicolor*) under naturalistic conditions by allowing frogs to position themselves freely within a large outdoor enclosure filled with natural perches. We first corroborated that frogs were indeed capable of changing color and that any frog-background match was not due to environmental color preferences. We show that measures of frog coloration (luminosity, saturation, and hue) correlate strongly and consistently with the coloration of their environment, but that only frog hue significantly correlates with temperature. We also found no evidence that frogs simultaneously optimize camouflage and thermoregulation by choosing light backgrounds on warm days and dark backgrounds on cold days. Overall, our results suggest that under average temperature conditions, Eastern Gray Treefrogs predominantly adjust body coloration for camouflage.

Animal body coloration plays a crucial role in a range of ecological functions (Cuthill et al., 2017). Some animals use body coloration to communicate with conspecifics, including signaling species identity (Couldridge and Alexander, 2002), sex (Bell and Zamudio, 2012), fecundity (Lüdtke and Foerster, 2019), body condition (Brenes-Soto et al., 2017), or other aspects involved in mate choice (i.e., Houde, 1987). Color may also serve in defense against natural enemies. Defensive coloration may take the form of aposematism, where bright colors either across the entire body or certain body patches communicates that the bearer is chemically defended or an otherwise unproductive prey (Mappes et al., 2005; Stevens and Ruxton, 2012). Or it may take the form of camouflage, where animal colors and patterns are used to match the surroundings to prevent detection by visual predators (Endler, 1984; Ruxton et al., 2004). In ectotherms, which require external sources of heat to maintain an active body temperature necessary for metabolic and behavioral processes (e.g., foraging, digestion, escape from predators), coloration may also confer thermoregulatory advantages because darker colors warm up faster than brighter colors (Hoppe, 1979; Geen and Johnston, 2014; Laumeier et al., 2023).

Being able to change color may further enhance these functions, as it allows organisms to fine-tune their appearance to deal with environmental heterogeneity or changes in the physical environment. Animals from a broad range of taxa become lighter when placed on white backgrounds and darker on black backgrounds (King et al., 1994; Kronstadt et al., 2013; Stevens et al., 2014; Smith et al., 2016), consistent with background matching to improve camouflage. Likewise, several taxa change the brightness and thus the solar radiation absorption of their skin, darkening to become more solar-absorptive to increase body temperature when it is cold (Kronstadt et al., 2013; Smith et al., 2016), and brightening to become more solar-reflective to prevent overheating when it is hot (Tattersall et al., 2006; De Velasco and Tattersall, 2008).

When sitting on a dark perch on a cold day, color change may simultaneously improve camouflage and thermoregulation. But commonly in nature, organisms are confronted with conflicting stimuli, especially in highly heterogeneous environments. What do animals do when the requirements of camouflage and thermoregulation conflict? Do they allocate equally to both functions, or do they accommodate one requirement (e.g., camouflage) at the expense of the other (e.g., thermoregulation) (Smith et al., 2016)? The answer to this question may also elucidate whether predator avoidance or metabolic demands are under stronger selection because they represent a greater potential cost to survival.

To better understand the ecological significance of color change, it is necessary to examine the relative importance of background- and temperature-dependent color change, and their interaction, under more realistic natural conditions. In this framework, the *optimization hypothesis* predicts that organisms choose backgrounds that allow them to simultaneously maximize camouflage and thermoregulation. For example, on days with a cool ambient temperature, organisms may settle on dark backgrounds and subsequently adopt a dark color, and on days with a warm temperature, they may settle on bright backgrounds and adopt a bright color. The *camouflage hypothesis* predicts that individuals match their body coloration to the coloration of their background irrespective of body temperature, while the *thermoregulation hypothesis* predicts that individuals become darker at low temperatures and brighter at high temperatures irrespective of their background. Finally, the *trade-off functions hypothesis* predicts that body coloration is affected by both background color and temperature, but that one function dominates.

In this study, we examined the interactions between color change for camouflage and thermoregulation in Eastern Gray Treefrogs (*Dryophytes versicolor*) under naturalistic conditions in a large outdoor enclosure. Although the common name "Eastern Gray Treefrogs" suggests that these frogs are mostly gray, the etymology of their Latin name *versare* (to change + color) alludes to the fact that they may change color. While it is frequently assumed that these frogs change color

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for camouflage (i.e., Mueller, 2006), to date experimental data have only documented an effect of temperature and light levels on body coloration (Hargitt, 1912; Edgren, 1954). We therefore first corroborated that the diversity of body colorations found in Eastern Gray Treefrog populations is indeed due to individual color change and not to the existence of different color morphs. To do this, we compared body coloration of the same frogs photographed at two different time points. To rule out that any organism-background match arises from the organism choosing to settle on a background that matches its own coloration (background preference) instead of color change (i.e., Kang et al., 2012), we also compared background coloration at which the same frogs settled at two different time points. To test the predictions of our hypotheses about whether color change in Eastern Gray Treefrogs is involved in camouflage and thermoregulation, we compared (1) whether the frogs' body coloration matches to the coloration of their background (*camouflage hypothesis*), (2) whether frogs are brighter at higher temperatures (*thermoregulation hypothesis*), (3) whether there is a stronger relationship between body coloration and background coloration than between body coloration and temperature (or vice versa; *trade-off hypothesis),* and (4) whether frogs simultaneously maximize camouflage and thermoregulation by showing temperature-dependent perch color choice and selecting dark sites on cold days and bright sites on warm days (*optimization hypothesis*).

Materials and Methods

We allowed a sample of 67 frogs to position themselves freely within a large outdoor enclosure filled with natural perches. Frogs spent 5 days in the enclosure and could freely choose the color environment as well as the temperature and microclimate of their diurnal retreat sites. We took pictures of the frogs after they had been in the enclosure for 2 and 4 days.

Study Species and Study Site.—Eastern Gray Treefrogs (*D. versicolor;* previously classified as *Hyla versicolor*) are a common and widespread anuran in much of the eastern portion of North America (Conant and Collins, 1998; Dodd, 2023). They forage at night, but spend the day resting on branches and leaves, adopting a water-conserving position with tucked in legs and belly pressed to surface. Their dorsal coloration can range from beige, brown, gray, to green (Fig. 1). The dorsum may be uniform, or show a pattern of darker markings that are frequently bordered in black (Fig. 1). Their groin area is yellow, the inner portion of their thigh is yellow and black. These frogs are also chemically defended and distasteful, and a clay model study documented that the black/yellow thigh color functions as an aposematic signal (Cannizzaro and Höbel, 2023). Intraspecific communication, however, does not seem to be influenced by body color traits. There is sexual dimorphism in throat color, with males having black throats and females having white throats (Höbel et al., 2022), but there is mixed evidence on whether throat color functions as an intraspecific signal involved in mate choice—mated males have on average darker throats than unmated males (Höbel et al., 2022), but during laboratory mate choice trials females did not preferentially approach frog models with darker colored throats (Reichert et al., 2014; Augusto-Alves et al., 2025). Females also did not preferentially approach frog models varying in dorsal body coloration (Augusto-Alves et al., 2025). For the above reasons, we believe that color change for communication is not a confounding factor when asking about the putative functions of color change for background matching or thermoregulation in these frogs.

We conducted the experiment during late June/early July 2015, which corresponds to the end of that year's breeding season. The enclosure was located at the University of Wisconsin–Milwaukee (UWM) Field Station in Saukville, WI; it was constructed from lumber posts and hardware mesh walls (2.7×2.7 m). The floor of the enclosure was soil with local vegetation (grass/herbaceous vegetation), and we added fresh branch cuttings from the surrounding trees to provide frogs with a selection of natural perches. Branches were selected to maximize diversity in terms of color, texture, thickness of branches, and leaf area (see Fig. 2A). We also placed two shallow water dishes into the enclosure.

All frogs originated from our study ponds at the UWM Field Station. Most were captured as amplexed pairs and the females



Fig. 1. Representative examples of Eastern Gray Treefrogs photographed during our study in Wisconsin, USA, showing variation in dorsal coloration, variation in pattern of dorsal markings, and perch color choice.

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FIG. 2. Representative examples of the perches that were available to the frogs inside the test enclosure (A). Location of the regions of interests (ROI) selected for coloration analysis (B). W e extracted two ROIs from the frog body (base, pattern) and two ROIs from the environment (perch, background).

participated in mate choice trials before entering into the color change trials. Frogs were kept in small groups in ExoTerra Faunarium terraria in the lab at the UWM campus for about 1 week before being introduced into the outdoor enclosure. To increase sample size, we also captured some single males; those did not participate in behavioral trials prior to the color change experiment. Two days before frogs were placed into the enclosure, we marked them for individual recognition either via toe-clipping (Perry et al., 2011) or by implanting a fluorescent alpha-numeric tag beneath the skin of the ventral side of the thigh of the right hind limb (VI Alpha Tags, size 1.0×2.5 mm, 0.1 mm thick; Northwest Marine Technology Inc., Shaw Island, WA, USA).

We introduced the frogs into the enclosure in two groups of 33 and 34 frogs (separated by 1 week). Frogs were given 2 days between introduction into the enclosure and between sampling days (i.e., setup on day 0 and sampling on days 2 and 4). On sampling days, we searched the enclosure for frogs, measured their skin temperature using an Extech IR400 thermometer, followed by a picture of the frog and a picture of a Tiffen Q-13 color chart held at the frog's location, both taken with a Canon EOS Rebel T5i camera under natural light. Frogs were photographed before they were captured for individual identification. While searching for other frogs, we placed the already photographed/identified frogs in plastic terraria (ExoTerra Faunarium; set up in a shady spot in the enclosure) to ensure they were photographed only once that day. After all detectable frogs had been photographed, we released them back into the enclosure by placing the opened plastic terraria on the ground in the center of the enclosure (i.e., frogs were not returned to their original perches but had to move to a new one by themselves). Sampling always took place in the afternoon (1300–1600 h) and each sampling period lasted about 1.5 h. After the second sampling period (end of day 4 of a given group of frogs), all frogs were removed from the enclosure and released at their pond of origin. The field station's weather station, located 300 m from the enclosure, collects data every 30 min and provided information on ambient temperature during the observation period.

We obtained 109 pictures from 67 different frogs. Not all frogs were found during each sampling period, resulting in some frogs contributing one ($n=25$) and others contributing two ($n=42$) pictures to the final data set.

Image Analysis.—We assessed coloration over human visible wavelengths (i.e., excluding UV). Dorsal coloration of Eastern Gray Treefrogs shows negligible UV reflectance (Augusto-Alves et al., 2025; suppl. Fig. 1), hence excluding UV from the image analysis should not bias the results. Multispectral images were created for each picture using MICA toolbox v.2.2.2. (Troscianko and Stevens, 2015) with ImageJ v.1.54g (Schneider et al., 2012). We used the oval selection tool in ImageJ to denote four regions of interest (ROIs) for color analysis (Fig. 2B). All ROI were oval and contained 48–52 pixels. Because the dorsal coloration in Eastern Gray Treefrogs often shows a pattern of darker markings, we selected two "frog" ROIs to capture this variation: (1) color around the darker pattern (= "base"), (2) color inside the darker pattern ("pattern"). Environments are often heterogeneous, and frogs might consider their perch (the exact place they are sitting on) as the relevant substrate for color matching, or they might consider the most common background color as the relevant substrate to adjust to. Hence, we selected two "environment" ROIs: (3) perch the frog was sitting on (="perch"), and (4) the most common color in the background (="background").

MICA provides RGB (red-green-blue) measures that we converted to hue, saturation, and luminosity (HSL system). In this system, hue corresponds to the color value, which indicates if the color is yellow or green. It is a circular parameter reported as an angle between 0° and 360° on a color wheel. A hue of "0" corresponds to red, ~120° corresponds to green, and ~240° corresponds to blue. Saturation quantifies the amount of gray in the color (ranging from 0 to 1, where lower values correspond to a grayer or more faded color). Luminosity quantifies to the brightness of the color (ranging from 0 to 1, with lower values corresponding to darker colors).

Statistics.—All statistical analyses were performed in JMP 11 (SAS Institute Inc., Cary, NC). Before statistical analysis, we verified that the data met normality assumptions by visually inspecting the quantile-quantile plots of luminosity, saturation, and hue. We subsequently used Box-Cox transformation on the hue data to improve normality.

Statistics: Descriptive Statistics of Color and Pattern.—Most frogs show a pattern of darker marking on their back (Fig. 1). To test whether base coloration and pattern coloration of the same frog are correlated, we used linear mixed models (implementing REML). We used the entire data set of 109 pictures for this analysis. We entered frog base color as predictor variable and frog pattern color as response variables. We also entered "group" as a random term because measurements of the same group of frogs that was introduced together in the enclosure at the same time are not independent, and we entered frog ID as a random term to account for some frogs providing two data points. We ran three models, one focusing on luminosity, one on saturation, and one on hue. We calculated effect sizes to obtain

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an estimate of the strength of the association between base and pattern coloration. For this we first calculated partial eta square from the *F* statistics and degrees of freedom (Lakens, 2013), and then converted those partial eta square values into the better-known Pearson's *r*. Here, values around $r = 0.10$ are considered small effect size, values around $r = 0.30$ are medium effect size, and values above $r = 0.50$ indicate large effect size (Cohen, 1988). Significant correlation of high effect size would indicate that focusing on base color would accurately capture color variation in this species.

Statistics: Habitat Color Preference.—Because our experimental design allowed frogs to choose their perches, any observed background matching could arise from color change or from frogs settling on a background that matched their own coloration. We tested for the possibility of habitat color preferences with Pearson correlations, using the perch and background coloration data from the 42 frogs we photographed twice. If frogs have habitat color preferences, a frog's perch color on one day should predict its perch color on another day. Accordingly, if there are habitat color preferences, we would expect a significant positive correlation with a Pearson's correlation coefficient (*r*) close to 1, and 95% confidence interval (CI) of correlation coefficients overlapping 1. By contrast, if frogs do not have habitat color preferences, we would expect either nonsignificant positive correlations where 95% CI of Pearson's *r* do not overlap 1, or significant negative correlations. We ran three correlations (luminosity, saturation, hue) examining perch color preferences, and three correlations (luminosity, saturation, hue) examining background color preferences.

Statistics: Ability of Color Change.—The diversity of frog body colors observed in Eastern Gray Treefrog populations (Fig. 1) could be due to polymorphism or individual color change (Wente and Phillips, 2003). We tested for those possibilities with Pearson correlations, using the body coloration data from the 42 frogs we photographed twice. If color diversity is due to polymorphism, a frog's color on one day should predict its color on another day. Accordingly, if there is polymorphism, we would expect a significant positive correlation with a Pearson's correlation coefficient (*r*) close to 1, and 95% CI of correlation coefficients overlapping 1. By contrast, if frogs can change color, we would expect either nonsignificant positive correlations where 95% CI of Pearson's *r* do not overlap 1, or significant negative correlations. We ran three correlations, one focusing on luminosity, one on saturation, and one on hue of frog coloration. We focus on base coloration because base and pattern coloration are tightly correlated (see results).

Statistics: Environmental Factors Affecting Body Coloration.—To test whether frog coloration was affected by environmental coloration or temperature, we used linear mixed models (implementing REML). We entered frog color as the response variable, and perch color, temperature, and the perch color × temperature interaction as the predictor variables. We also entered "group" as a random term because measurements of the same group of frogs that was introduced together in the enclosure at the same time are not independent. We also entered frog ID as a random term to account for some frogs providing two data points. We ran three models, one focusing on luminosity, one on saturation, and one on hue. We repeated the above analysis by computing linear mixed models that used background color instead of perch color as the predictor variable. We again ran three models, one focusing on luminosity, one on saturation, and one on hue. For the above tests, note that hue data are circular (360° on a color wheel) but were analyzed on an ordinal scale, which is technically incorrect. To verify that the analysis nevertheless is sound, we repeated the hue models only including values between 30°–330°. This omitted comparison between values that may be numerically very different yet close on the color wheel (i.e., 5° and 355°) and hence represented the largest potential to skew our results. Test statistics were similar as with the complete data set (see Results). We calculated effect sizes to compare whether perch or background coloration had a stronger influence on frog coloration. For this we first calculated partial eta square from the *F* statistics and degrees of freedom (Lakens, 2013), and then converted those partial eta square values into the better-known Pearson's *r*. Here, values around $r = 0.10$ are considered small effect size, values around $r = 0.30$ are medium effect size, and values above $r = 0.50$ indicate large effect size (Cohen, 1988).

To test whether frogs simultaneously maximize camouflage and thermoregulation by showing temperature-dependent environment color choice and selecting dark sites on cold days and bright sites on warm days, we used linear mixed models (implementing REML). We entered perch color as the response variable, and mean daytime air temperature of the day on which the frogs were photographed as the predictor variable. We also entered frog ID as a random term to account for some frogs providing two data points because they were photographed twice over the course of the experiment. We ran three models, one focusing on luminosity, one on saturation, and one on hue.

Results

Descriptive Statistics for Color and Pattern.—Dorsal coloration of Eastern Gray Treefrogs in our population ranged from various shades of beige and gray to various shades of green and dark brown (Fig. 1). In our sample ($n = 109$), 48% were gray or beige, 47% were green, and 5% were brown and 67% of the frogs showed a pattern and 33% did not. Base coloration and pattern coloration were significantly positively associated, and the effect size of the relationships was always of large magnitude (luminosity: $F_{1,69.5} = 78.2$, $P < 0.0001$, $r = 0.73$; saturation: $F_{1,69.2} = 111.8$, $P < 0.0001$, $r = 0.79$; hue: $F_{1,70.3} = 58.7$, $P < 0.0001$, $r = 0.67$; in all cases 95% CI of Group(rand) and Frog ID(rand) overlapped 0). This suggests that focusing on base coloration in the following analyses accurately captures variation in frog body coloration.

Frogs Do Not Have Individual Habitat Color Preferences.—Frogs used a wide variety of perch types: brown branches, lichen-covered branches, wood frame of the enclosure, green leaves, dry grass, and soil. Environment coloration of frogs that were photographed twice were never significantly positively correlated between samples (perch coloration: luminosity: $r = 0.06$, 95% CI = −0.25 to 0.35, $P = 0.73$; saturation: $r = 0.15$, 95% CI = −0.16 to 0.44, $P = 0.33$; hue: $r = -0.38$, 95% CI = −0.61 to −0.08, $P = 0.01$; background coloration: luminosity: $r = -0.14$, 95% CI = −0.43 to 0.17, $P = 0.38$; saturation: $r = -0.12$, 95% CI = −0.42 to 0.19, $P = 0.44$; hue: $r = 0.09$, 95% CI = −0.22 to 0.39, $P = 0.56$).

Frogs Do Change Coloration.—Body coloration of frogs that were photographed twice were never significantly positively correlated between samples (luminosity: $r = 0.19$, 95% CI = −0.12 to 0.47, $P = 0.23$; saturation: $r = 0.19$, 95% CI = −0.12 to 0.47, $P = 0.23$; hue: $r = -0.38$, 95% CI = −0.07 to 0.51, $P = 0.13$). The presence of dorsal markings could also change over time: of the 42 frogs we had two pictures of, 63% showed markings in both cases, 17% never showed markings, and 20% changed between showing markings and not doing so.

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Determinants of Frog Color Change.—Frogs match the color of their environment. Frog coloration (luminosity, saturation, and hue) was consistently and significantly positively associated with perch coloration (Figs. 3A–C; Table 1 top) as well as background coloration (Figs. 3A–C; Table 1 bottom). Effect size comparison further suggest that perch coloration is a stronger predictor for frog luminosity and saturation, while background coloration is a better predictor for frog hue.

The range of frog body temperatures observed in this study was 10.7–36.2 °C (mean ± SD = 20.8 ± 5.5 °C). Frog coloration was also associated with body temperature, but not as consistently as with environmental coloration. Temperature only affected hue but not the achromatic components of coloration (luminosity, saturation) (Figs. 3D–F; Table 1).

Test statistics examining the relationship between environment hue and frog hue were similar between the complete and the truncated data set. The significant effect of temperature was lost in the truncated model, likely because removing < 30° frog hue values also removed most of the data points associated with very warm temperatures that seem to drive the negative temperature-hue relationship (see Table 1, Fig. 3F).

Frogs Do Not Show Temperature-Dependent Environment Color Choice.—Frogs did not choose lighter environments on warmer days and darker environments on colder days. Mean daytime temperature (range: 15.2–21.7 °C) was not significantly associated with luminosity ($F_{1,106.9} = 0.19$, $P = 0.66$), saturation ($F_{1,80.9} = 0.17$, $P = 0.68$), or hue ($F_{1,97.8} = 0.003$, $P = 0.96$) (in all cases 95% CI of Frog ID(rand) overlapped 0).

Discussion

We provide the first quantitative description of the ecology of color change of Eastern Gray Treefrogs. We analyzed digital images taken under natural conditions in a large outdoor enclosure and show that Eastern Gray Treefrogs are capable of physiological color change, and that their body coloration is mostly affected by background color and to a much lesser extent by temperature.

Gray Treefrogs showed background matching, which is a widespread defensive strategy found in both invertebrate and vertebrate animals (Heinen, 1994; Stevens et al., 2014; Kang et al., 2015; Smith et al., 2016; Nokelainen et al., 2022). Background matching can occur through behavioral choice of appropriate backgrounds that resembles the organism's own body coloration (habitat color preference) or by organisms changing their body coloration to resemble the background color (physiological color change). Both strategies are used in nature by anurans (i.e., Morey, 1990; Heinen, 1994; Wente and Phillips, 2005; Polo-Cavia et al., 2016), but our data show that background matching in Gray Treefrogs arises from physiological color change, not habitat color preference.

Factors Affecting Color Change in Frogs.—Previous work has uncovered a range of internal and external factors affecting anuran color change. Anurans change color in response to sex and stress hormones (Richards, 1982; Kindermann et al., 2013), to light levels (Edgren, 1954; Tattersall et al., 2006), to temperature (i.e., Kats and van Dragt, 1986; Tattersall et al., 2006; Park et al., 2023), and to background coloration (i.e., Nielsen and Dyck, 1978; Nielsen, 1980; Choi and Jang, 2014; Polo-Cavia et al., 2016).

Coloration is the outcome of several components: luminosity quantifies the brightness of the color, saturation quantifies the amount of grayness or fadedness in the color, and hue is the parameter that captures the color value (i.e., if it is yellow or green). Hence, color change can involve modifying one or a combination of these components, and be in response to one or a combination of these components of the background color. In our study, background coloration had the strongest influence on luminosity and saturation and least on hue. Ten studies of seven other species of anurans from three families showed a similar pattern: all studies documented brightness changes in response to background variation (10/10 studies), followed by fewer

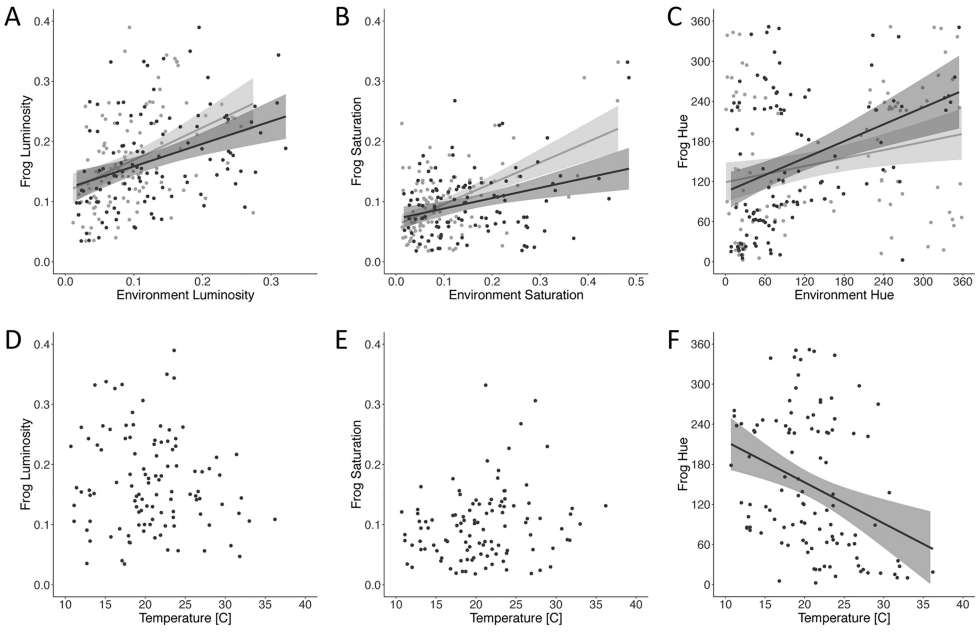

Fig. 3. Effect of environmental coloration (A–C) and temperature (D–F) on dorsal coloration of Eastern Gray Treefrogs. Frogs showed strong and consistent background matching in terms of luminosity, saturation, and hue. Perch coloration is indicated by light gray symbols/shading and background coloration is indicated by black symbols/dark gray shading. Temperature only had an effect on frog hue (F).

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TABLE 1. Results of six linear mixed models testing the effect of environmental coloration and temperature on dorsal color properties of Eastern Gray Treefrogs. Shown is data for adjustments to the substrate the frogs were sitting on (perch) as well as for the most common coloration in their environment (background). Significant terms are set in bold. *Truncated hue model including only 30°–330° data; CI = confidence interval.

	Perch			
Term	**df**	***F***	***P***	**Effect size**
Luminosity	**1,78.2**	**19.10**	**<0.0001**	0.44
Temperature	1,58.6	2.33	0.10	0.20
Luminosity × temperature	1,85.3	1.07	0.33	0.11
Group (rand)	95% CI = −0.0006 to 0.0009; 2.6%			
Frog ID (rand)	95% CI = −0.0001 to 0.0035; 31.9%			
Saturation	**1,104.9**	**29.6**	**<0.0001**	0.47
Temperature	1,20.5	1.23	0.28	0.24
Saturation × temperature	1,98.8	0.69	0.41	0.08
Group (rand)	95% CI = −0.0001 to 0.0001; 0%			
Frog ID (rand)	95% CI = −0.0003 to 0.0014; 22.4%			
Hue	**1,102.3**	**4.19**	**0.04**	0.20
Temperature	**1,82.0**	**15.09**	**0.0002**	0.39
Hue × temperature	1,100.4	1.73	0.19	0.13
Group (rand)	95% CI = −0.0001 to 0.0001; 0%			
Frog ID (rand)	95% CI = 903–10829; 22.9%			
***Hue**	**1,44.5**	**8.76**	**0.005**	0.41
*Temperature	1,51.7	3.35	0.066	0.25
*Hue × temperature	1,44.9	1.65	0.21	0.19
*Group (rand)	95% CI = −0.0001 to 0.0001; 1.9%			
*Frog ID (rand)	95% CI = 884–4879; 54.4%			
	Background			
Term	**df**	***F***	***P***	**Effect size**
Luminosity	**1,102.5**	**14.9**	**0.0002**	0.36
Temperature	1,84.6	1.86	0.18	0.15
Luminosity × temperature	1,103.8	2.67	0.11	0.16
Group (rand)	95% CI = −0.0011 to 0.0021; 8.2%			
Frog ID (rand)	95% CI = −0.0011 to 0.0022; 9.8%			
Saturation	**1,101.6**	**8.85**	**0.004**	0.28
Temperature	1,83.1	1.93	0.17	0.15
Saturation × temperature	1,97.1	0.63	0.43	0.08
Group (rand)	95% CI = −0.0001 to 0.0001; 0.0%			
Frog ID (rand)	95% CI = −0.0003 to 0.0085; 25.3%			
Hue	**1,103.1**	**9.89**	**0.022**	0.30
Temperature	**1,88.43**	**8.95**	**0.036**	0.30
Hue × temperature	1,96.6	2.18	0.14	0.15
Group (rand)	95% CI = −0.0001 to 0.0001; 0%			
Frog ID (rand)	95% CI = 270 to 63545; 15.6%			
***Hue**	**1,65.5**	**6.53**	**0.013**	0.30
*Temperature	1,23.8	0.48	0.50	0.14
*Hue × temperature	1,54.0	1.75	0.19	0.18
*Group (rand)	95% CI = −430–457; 0.4%			
*Frog ID (rand)	95% CI = −645–2696; 27.6%			

reports of saturation change (5/8 studies), and fewest reports in hue change (2/9 studies) (Nielsen and Dyck, 1978; Nielsen, 1980; Kats and van Dragt, 1986; Heinen, 1994; King et al., 1994; Stegen et al., 2004; Choi and Jang, 2014; Kang et al., 2016; Polo-Cavia et al., 2016; Park et al., 2023). In our study, the effect of temperature on frog coloration was limited to changes in hue. This is in contrast to data from eight studies involving seven other species of anurans: six report a significant effect of temperature on frog coloration, observing that colder frogs are darker (i.e., lower luminosity; other color parameters were rarely evaluated) (Hargitt, 1912; Edgren, 1954; Kats and van Dragt, 1986; Heinen, 1994; King et al., 1994; Stegen et al., 2004; Tattersall et al., 2006; Park et al., 2023). Finally, and in line with our observations, is that the five other studies that simultaneously tested for background color and temperature effects on anuran skin coloration universally find that background coloration has the stronger effect (Kats and van Dragt, 1986; Heinen, 1994; King et al., 1994; Stegen et al., 2004; Park et al., 2023).

Color Change for Background Matching vs. Thermoregulation.—In ectotherms, coloration may help organisms to remain hidden from predators (camouflage) or to maintain suitable body temperature (thermoregulation) (Smith et al., 2016). Both functions are important to survival, yet may not always be jointly realized. We found strong evidence for a role of color change in

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background matching, with frog hue, saturation, and brightness showing strong and consistent positive relationships with environment color. The relationship between frog color and temperature was less consistent; at higher temperatures frogs were not significantly brighter or less saturated, but hue decreased significantly with increasing temperature (hotter frogs were more yellow). Different hues absorb solar radiation at different rates, and while yellow is more absorptive than white, it absorbs solar radiation less than green (Paminto et al., 2021). A change in hue may thus provide some thermal benefits, although the difference in heat absorption is very small (<1°C). We also found no evidence that frogs accommodate conflicting requirements of thermoregulation and camouflage by selecting habitat colors that suit their thermal needs (i.e., choosing a dark perch during cold days when adopting a dark coloration simultaneously optimizes thermoregulation and camouflage).

Overall, our results are in line with other studies that have examined the relative importance of color change for thermoregulation and background matching in free-ranging animals. Data from treefrogs (this study), juvenile toads (Heinen, 1994), rattlesnakes (Da Cunha et al., 2024) and bearded dragon lizards (Smith et al., 2016) all report that temperature, if it affects body coloration at all, does so to a lesser degree than background color. One caveat might be that the above studies were carried out during the respective species' prime activity periods, where temperatures may be sufficient for regular biological activities and do not require much additional adjustment. Our study was conducted in early summer and pictures were always taken in the early afternoon. It is possible that under similarly benign thermal conditions color change does indeed not have thermoregulatory function, but that it may come into play in spring when temperatures are overall lower, or at the coldest (early morning) or hottest (late afternoon) hours of a given day. Experimental studies that subjected frogs to low temperatures (4 °C) do report extreme darkening of body coloration (Edgren, 1954; Kats and van Dragt, 1986), which would be in line with color change for thermoregulation at temperature extremes. In addition, Park et al. (2023) found that frogs are not as good at background matching under very low compared to average temperatures (5 vs. 25 °C), which would be in line with a trade-off that emphasizes thermoregulation at low and camouflage at average temperatures. Then again, extremely low temperatures (<5 °C) may induce changes in body coloration that reflect a loss of control over color change ability and are completely unrelated to thermoregulation.

It is also possible that organisms respond differently to the lower and upper extremes of the temperature range, or that the responses are very transient. At very low temperatures organisms may only remain dark long enough until they have reached active body temperature and then shift to favoring the background matching function of color change. And at very high temperatures organisms may use behavioral means of thermoregulation (i.e., move to other sites) instead of further changing their body coloration. For example, the treefrog *Bokermannohyla alvarengai* shows strong temperature effects on body brightness and can change from almost black to white as temperatures rise (Tattersall et al., 2006). Yet, most individuals in that study only remained in the sun for 30 min (until reaching body temperatures around 30°C) before switching to behavioral thermoregulation and retreating beneath stones away from the sun (Tattersall et al., 2006). During the 1.5 hr sampling periods of our study, we never observed behavioral thermoregulation (i.e., frogs did not move away from their perches). This may be because despite spanning a substantial range (10.7–36.2 °C), frog body temperatures in our study were still all within the critical thermal limits (i.e., lowest and highest temperatures that an organism can function, respectively) reported for Eastern Gray Treefrogs (CT_{min} = 8 °C and CT_{max} = 38.7 °C; John-Alder et al., 1988; Siddons and Searle, 2021). Eastern Gray Treefrogs have a broad distribution range that extends from approximately 25°N (central Texas, USA) to about 50°N (southern Manitoba, Canada) (AmphibiaWeb, 2026). Geographic variation in temperature-induced color change has been reported in fiddler crabs (Munguia et al., 2013), and it would be interesting to test whether color change for thermoregulation is more prominent in Gray Treefrog populations that occupy areas on the thermal extreme of their distribution ranges.

In this study, we examined the relative importance of color change for thermoregulation and camouflage of Eastern Gray Treefrogs. Strong and consistent background matching but only limited color adjustments with temperature suggests that for Gray Treefrogs predation risk may present a greater immediate survival cost than requirements of thermoregulation (or water balance, which in amphibians may be linked with thermoregulation). The effectiveness of camouflage depends on the viewing conditions as well as the visual system of the respective predator (Stevens and Merilaita, 2009). Treefrogs are preyed upon by a variety of predators including birds, snakes, and mammals (Toledo et al., 2007), and these predator types have very different visual systems (Osorio and Vorobyev, 2008). Better knowledge about principal predators and their visual systems are required to fully understand the role of color change in the effectiveness of predator avoidance in Eastern Gray Treefrogs.

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