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Hot Boys Are Blue: Temperature-Dependent Color Change in Male Eastern Fence Lizards

TRACY LANGKILDE[1,3] AND KATHERINE E. BORONOW[2]

[1]*Department of Biology, Pennsylvania State University, University Park, Pennsylvania 16802 USA*
[2]*Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138 USA*

ABSTRACT.—**Color is important for signaling, camouflage, and thermoregulation in many species. The costs and benefits of coloration can vary under different scenarios, increasing fitness under some conditions but decreasing it under others. Some animals are able to resolve these conflicts by changing color. Color change can increase fitness by maintaining crypsis across variable environments, by minimizing costs associated with signaling, and by aiding thermoregulation when environmental conditions change. We examined the effect of temperature on short-term color change in males of the sexually dichromatic Eastern Fence Lizard, *Sceloporus undulatus*. Color is associated with social dominance in this species and may be important in facilitating camouflage and thermoregulation. This study revealed that dorsal color and badge color are affected by temperature. This suggests that short-term color change in this species may aid thermoregulation and provide an honest signal of thermally dependent performance.**

Color plays an important role for many species, with members of almost every phylum using color to perform important functions such as signaling (to both conspecifics and predators), camouflage (to avoid detection by predators and prey), and to aid in thermoregulation (Dawson, 2006).

The costs and benefits of coloration vary across time and space and with environmental conditions. Conspicuous coloration can increase fitness by attracting mates but can impose severe costs by making the animal more visible to visual predators (Godin and McDonough, 2003; Stuart-Fox and Ord, 2004). Dark colors can aid heating rates, providing a thermal advantage and reducing the energetic costs of homeothermy by permitting more-rapid heating, but can increase the risk of overheating when solar heat load is high (Bittner et al., 2002; Hetem et al., 2009).

Some species are capable of short-term (physiological) color change. The cytological and physiological basis of color change is well understood, involving migration of pigments within chromatophores (Bagnara and Hadley, 1973; Hadley, 1996). Physiological color change has been documented in over a dozen reptile species and anecdotally reported in many others (e.g., Wilson, 1940; Cooper and Ferguson, 1973; Walton and Bennett, 1993; Castrucci et al., 1997). However, only a handful of studies have focused on environmental factors associated with color change in lizards (Gibbons and Lillywhite, 1981; Morrison et al., 1996; Rosenblum, 2005; Stuart-Fox et al., 2006). For these ectothermic animals, color change may play an important role in thermoregulation (Bittner et al., 2002). Darker colors aid heat absorption at cool temperatures, when it is beneficial for animals to heat rapidly, and lighter colors reduce heat absorption at high temperatures to prevent overheating, which is often a problem for reptiles (Kearney et al., 2009).

This study examines the importance of temperature in eliciting color change in the Eastern Fence Lizard, *Sceloporus undulatus*. Color is important for social signaling and crypsis and is purported to have a role in thermoregulation in this species (Cooper and Burns, 1987; Seitz and John-Alder, 1994; Smith and John-Alder, 1999). Eastern Fence Lizards exhibit striking sexual dimorphism, with males developing colored abdominal badges upon maturity (Cox et al., 2005) (Fig. 1). In addition to this morphological color change through ontogeny, short-term changes in badge coloration have been observed in the field (T.L. and K.E.B., pers. observ.). Ontogenetic and seasonal changes in coloration occur in a western subspecies, *Sceloporus undulatus erythrocheilus* (Rand, 1990). To our knowledge, the environmental triggers of this change are unknown. We tested the role of temperature in eliciting short-term changes in coloration within male Eastern Fence Lizards to gain insight into the functional significance of this phenomenon.

MATERIALS AND METHODS

Twenty adult male lizards were collected from each of two sites in early June: Lee County, Arkansas and Escambia County, Alabama, United States. Maturity was based upon size and the presence or absence of developed ventral badges, and sex was determined by the presence of enlarged post-anal scales (Parker, 1994; Cox et al., 2005). Coloration can be affected by levels of stress hormone (e.g., corticosterone; Calisi and Hews, 2007). Therefore, lizards were held in captivity for 17 ($\pm$ 5 SD) days prior to this experiment to allow them to adjust to captivity and for their corticosterone to return to background levels (Langkilde and Boronow, 2010). The windows in the room where lizards were held were covered with dark sheets to block external light, and overhead fluorescent tubes supplied constant light.

Males were held individually in experimental arenas (33 $\times$ 19 $\times$ 11 cm, L $\times$ W $\times$ D) under treatment conditions for 1 h prior to being photographed. The external walls of the experimental arenas were lined with white paper toweling to ensure that the lizards could not see one another during trials. Determining the timeline of any color change was beyond the scope of this study, but would provide important additional information on this phenomenon. We assessed the effect of temperature on color by comparing the color of the same lizard exposed to each of two temperature treatments: "warm" and "cool." "Cool" body temperatures were achieved by allowing the lizards to equilibrate to the ambient room temperature (lizard mean body temperature: 25.07 $\pm$ 0.3°C, mean $\pm$ SE). "Warm" body temperatures were achieved by suspending heat lamps 20 cm above the floor of the arenas (lizard average body temperature: 29.75 $\pm$ 0.4°C, mean $\pm$ SE). Body temperatures achieved during the warm and cool trials were within the daily range of this species (Ballinger et al., 1969; Crowley, 1987). Each lizard was tested on two consecutive days, with one-half of the individuals being tested at warm temperatures on the first day and the other

[3]Corresponding Author. E-mail: tll30@psu.edu
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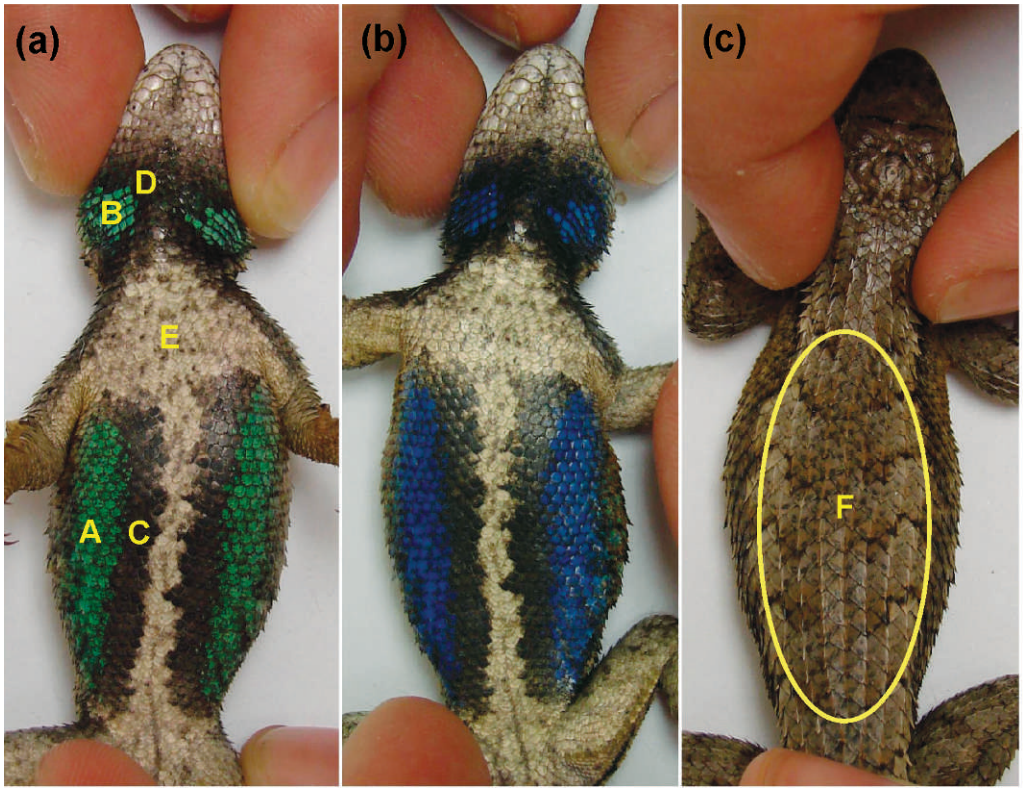

FIG. 1. Photographs of an individual male *Sceloporus undulatus* showing (a) the ventral surface at the "cool" temperature (24.6°C), (b) the ventral surface at the "warm" temperature (28.8°C), and (c) the dorsal surface at the "cool" temperature (24.6°C). The locations for which average color measures were taken are indicated by yellow letters: A = colored abdominal badge, B = colored throat badge, C = black abdominal badge, D = black throat badge, E = chest, and F = dorsal surface.

half being tested at cool temperatures on the first day. Lizards were housed in cloth bags overnight between trials.

Color measurements.—Color measurements were obtained from digital photographs. The lizards' dorsal and ventral surfaces were photographed against a piece of white paper within 30 sec of their being removed from the experimental arenas. All lizards were photographed in the same room under fluorescent room lighting. Photographs were taken with a tripod-mounted Cybershot DSC-H7B digital camera (Sony Corporation, Tokyo, Japan). The highest resolution settings (effective pixel count of 8.1 megapixels), optical zoom (1.5), and macro functions were used to provide adequate resolution for this purpose and to avoid Nyquist limit problems (Stevens et al., 2007). We manually set the exposure settings (shutter speed 30, F 3.2) and white balance to avoid inappropriate weighting of color values resulting from automatic color balance. No auxiliary source of light was used. This camera saves the images as a JPG rather than a TIFF or RAW file, which can cause problems of lost information; however, the lowest compression setting (fine) was used, minimizing this effect.

Digital photographs were analyzed using Adobe® Photoshop® software (Adobe Systems Incorporated, San Jose, CA, USA). The average color of six areas was determined: the colored abdominal badge (15 scales), the colored throat badge (4 scales), the black abdominal badge (4 scales), the black throat badge (4 scales), the chest (15 scales), and the dorsal surface (80% of the area) (Fig. 1a; see Langkilde and Boronow, 2010 for more details). An area at the center of each location was selected using the Elliptical Marquee Tool, its average color was obtained using the Average Filter function, and the Color Picker Tool was used to obtain values for the red (R), green (G), and blue (B) color channels (corresponding to the three color photoreceptors) (Endler, 1990). Color measurements obtained using this method are highly repeatable (Langkilde and Boronow, 2010).

Digital photographs provide a reliable method of quantifying color but only capture light in the human-visible spectrum (e.g. Villafuerte and Negro, 1998; Garcia et al., 2003). This can be problematic for species that signal in the ultraviolet spectrum (Stegen et al., 2004). Like humans, lizards have color photoreceptors that respond best to red (long wavelength), green (medium wavelength), and blue (short wavelength) light (Loew et al., 2002). However, lizards have an additional color photoreceptor that can detect light at ultraviolet (UV) wavelengths (Fleishman et al., 1993; Loew et al., 2002). The color badges of *Sceloporus undulatus* exhibit low reflectance within UV wavelengths compared to other wavelengths, suggesting that any UV signal in these badges is weak (Stoehr and McGraw, 2001). However, because UV-sensitive cones are often far more sensitive than other cone types, even low levels of UV reflectance can give a strong neural signal in lizards (Jacobs, 1992). The use of spectrophotometry, which measures reflectance within the UV range, rather than digital photography in future research may advance the understanding of potential UV signaling in this species.

Data analyses.—Digital photographs provide an excellent method of quantifying animal coloration (Villafuerte and Negro, 1998). However, we needed to address several issues before analyzing resulting data. Following the guidelines of Stevens et al. (2007), we took digital photographs of a set of reflectance standards (Q13 Color Separation Guide and Gray Scale, Eastman Kodak Company, Rochester, NY, USA), fit a calibration curve to these data, and derived a linearization equation to linearize the

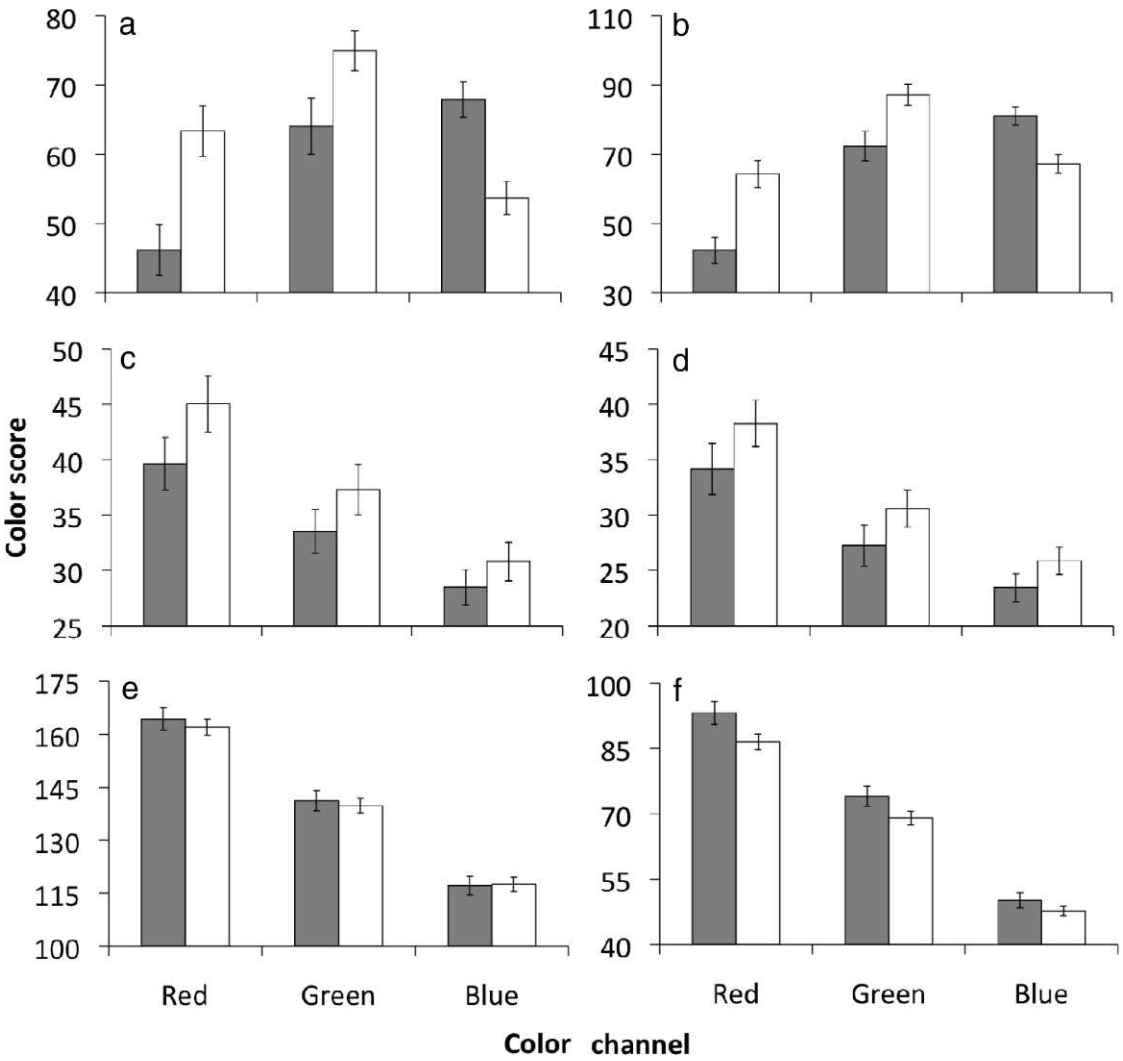

FIG. 2. Color of the colored abdominal (a) and throat (b) badges, black abdominal (c) and throat (d) badges, chest (e), and dorsal surface (f) of male *Sceloporus undulatus* under two temperature regimes: "warm" (grey bars; body temperature = 29.75 ± 0.4°C) and "cool" (white bars; body temperature = 25.07 ± 0.3°C). Bars represent mean ± 1 SE values for the red, green, and blue color channels for 40 lizards.

response of our camera to changes in light intensity. We then equalized the R, G, and B color channels to remove the effects of biases inherent in the camera's processing.

All data were natural-log transformed to meet the requirement of parametric tests. Because we were interested in quantifying specific changes in color, we tested the effect of temperature on R, G, and B color values separately rather than using principle components analysis to summarize overall change in coloration. This was done using repeated measures ANOVA with values attained at "warm" and "cool" body temperatures as the repeated dependent variable and with site as the factor. Statistical analyses were performed in JMP version 7 (SAS Institute Inc., Cary, NC, USA). All tests were two-tailed with alpha-levels set at 0.05.

RESULTS

Temperature affected the color of the colored abdominal and throat badges, the black abdominal badge, and the dorsal surface of male Eastern Fence Lizards (Table 1). The colored badges were green at cool temperatures and blue at warm temperatures (Figs. 1a,b; 2a,b). At cooler temperatures, black abdominal badges were significantly lighter (higher values) in the red channel, and dorsal color was significantly darker (lower values) in the red channel (Fig. 2c,f). At both of these body locations, the same patterns were approaching significance in the green channel. The color of the black throat badge and the color of the chest were not affected by temperature (Fig. 2d,e). Compared to lizards from Alabama, lizards from Arkansas had bluer colored abdominal and throat badges (vs. green), blacker colored throat badges (vs. grey), and a more orange-colored chest (vs. brown) (Table 1). The effect of temperature on color was consistent between these populations (all temperature × site interactions were nonsignificant).

DISCUSSION

This study revealed that temperature triggers short-term color change in Eastern Fence Lizards. Temperature-dependent color change can increase the efficiency of thermoregulation by altering the rate at which heat is gained or lost (Norris, 1965; Hoppe, 1979; Margalida et al., 2008; Hetem et al., 2009). We observed a darkening of the Eastern Fence Lizards' dorsal surface at cooler temperatures. This is likely caused by a change in melanosome distribution, reflecting a simple physiological response to temperature of the hormones responsible for

TABLE 1. Results for the effect of temperature, treatment, and site on coloration of male Eastern Fence Lizards, *Sceloporus undulatus*. All interactions were nonsignificant.

		Temperature			Site		
Location	Color	*F*	df	*P*	*F*	df	*P*
Color abdominal badge	Red	17.63	1, 32	<0.0001	4.20	1, 32	0.04
	Green	8.87	1, 32	<0.01	6.19	1, 32	0.02
	Blue	16.98	1, 32	<0.0001	3.67	1, 32	0.06
Color throat badge	Red	25.27	1, 32	<0.0001	5.04	1, 32	0.03
	Green	13.65	1, 32	<0.001	18.64	1, 32	<0.0001
	Blue	15.09	1, 32	<0.0001	11.19	1, 32	0.001
Black abdominal badge	Red	4.65	1, 32	0.03	0.57	1, 32	0.45
	Green	3.65	1, 32	0.06	0.38	1, 32	0.54
	Blue	2.51	1, 32	0.12	0.11	1, 32	0.74
Black throat badge	Red	2.15	1, 32	0.15	5.47	1, 32	0.02
	Green	2.42	1, 32	0.12	5.75	1, 32	0.02
	Blue	2.11	1, 32	0.15	3.91	1, 32	0.05
Chest	Red	0.17	1, 32	0.68	15.53	1, 32	<0.0001
	Green	0.07	1, 32	0.80	15.00	1, 32	<0.0001
	Blue	0.05	1, 32	0.82	5.01	1, 32	0.03
Dorsal	Red	4.65	1, 32	0.03	1.88	1, 32	0.17
	Green	3.47	1, 32	0.07	1.64	1, 32	0.21
	Blue	1.25	1, 32	0.27	0.32	1, 32	0.57

controlling melanosome distribution (Duellman and Trueb, 1986; Filadelfi et al., 2005). However, the nature of this association means that it would also aid thermoregulation. Darker dorsal coloration at cooler temperatures will aid heat absorption, permitting an individual to attain a higher body temperature more rapidly, while lighter dorsal coloration at warmer temperatures will help to reduce heat loads. Similar temperature-dependent color change has been observed in *Anolis carolinensis* and Kenyan chameleons, a response which has been attributed to aiding thermoregulation, as lizards become darker when it is cold (Wilson, 1940; Walton and Bennett, 1993). Temperature-dependent color change was similar for lizards from both populations used in this study, although there was an overall difference in coloration between these populations. This conforms to previous findings in this species and may relate to differences in size, age, or habitat use of lizards from these sites (Leal and Fleishman, 2004; Langkilde and Boronow, 2010).

The most striking color change documented was in the colored abdominal badges: the color of these badges shifted from green to blue with an increase of only 4°C (Fig. 1). The blue badge color in *Sceloporus* is a structural color generated by iridophores through selective reflectance (Morrison et al., 1995). The color change reported here is likely caused by changes in iridophore platelet spacing with temperature (Morrison et al., 1996). Eastern Fence Lizards display their ventral badges to conspecific males by laterally compressing the body and orienting the abdomen towards the rival (Cooper and Burns, 1987). The color of these badges correlates with dominance in these lizards (Cooper and Burns, 1987). In ectotherms, body temperature affects a range of performance variables such as locomotor speed, endurance, and bite force (Huey, 1982; Crowley, 1985; Rome et al., 1992). Therefore, we speculate that this dramatic change in color with temperature could provide an honest indicator of performance ability. Both conspecifics and predators could use the colored badges as a signal to assess a male's ability to fight, their mating performance, and the likelihood of escaping attack (Greene, 1988; Andersson, 1994). Our results suggest that the role of temperature-sensitive badges as signals of performance may be a fruitful avenue of future investigation. Future research on the relative importance of color and temperature for mate choice and social dominance in this and other color-changing species would shed light on the adaptive signaling function of color change.

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