

Covariation between Thermally Mediated Color and Performance Traits in a Lizard

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ABSTRACT

Physiological changes in response to environmental cues are not uncommon. Temperature has strong, predictable effects on many traits, such that many traits in ectotherms follow stereotyped thermal performance curves in response to increasing temperature. The prairie lizard—an abundant lizard throughout the central United States—has thermally sensitive, blue abdominal and throat patches. Currently, the role of these patches is not well understood. In this study, we set out to investigate whether individual plasticity in patch color paralleled individual plasticity in sprint speed (do they covary), and if the plasticity in these two patches signal redundant or independent information, testing competing hypotheses suggested for the evolution of multiple signals. We found that both abdominal and throat patch hue follow classical thermal performance curves, suggesting that at the species level hue is a good predictor of sprinting ability. At the individual level, we found that color and performance were statistically repeatable, so individuals with relatively high phenotypic values maintain relatively high phenotypic values across all temperatures. Additionally, we found that abdominal and patch hue covary with sprinting speed at the individual level. Together, these results suggest that the bluest individuals are the fastest individuals across temperatures. However, we found that abdominal and throat patch hue do not covary with each other at the individual level, suggesting that these signals may have independent functions. The importance of examining the function of individual variation cannot be overstated, and overall, more work is needed to better understand both the proximate and ultimate mechanisms underlying signal plasticity in this species and others.

Keywords: color, covariation, lizard, performance, signal, temperature.

Introduction

Dynamic traits are not uncommon. Within time frames spanning from seconds to years, individuals can experience different environmental factors (e.g., population density, precipitation, resource availability, temperature) that influence multiple traits and whole-animal function, such as colorful displays (Stuart-Fox and Moussalli 2009; Hutton et al. 2015), growth rates (Brett et al. 1969; Dunham 1978; Kingsolver and Woods 2016), fitness (Stephens et al. 1999; Welch and Harwood 2014), and performance (Bennett 1980; Huey and Kingsolver 1989; Angilletta et al. 2002*b*). These traits are said to be plastic, or phenotypically malleable in response to the environment (Pigliucci 2001; Piersma and van Gils 2011; Kelly et al. 2012). In ectotherms, many traits are plastic in response to temperature (Bennett 1980).

Thermal effects on performance have garnered much interest because of how performance can affect survival (Christian and Tracy 1981; Jayne and Bennett 1990; Calsbeek and Irschick 2007) and reproductive success (Husak et al. 2006). Thermally plastic traits follow stereotyped thermal performance curves (Huey and Stevenson 1979), where phenotypic values increase with temperature until an optimum is reached, after which phenotypic values rapidly decrease. Estimating these curves for both species and populations has yielded unique insight into how organisms adapt across environmental conditions (Huey and Kingsolver 1989; Wilson 2001; Phillips et al. 2016).

Interestingly, just as intraspecific populations can vary in thermal response, not all individuals within a population respond to temperature the same. Studies on metabolism (Careau et al. 2014*a*; Gifford et al. 2014) and locomotion (Preest and Pough 1989; Artacho et al. 2013; Careau et al. 2014*b*) have shown significant individual variation in thermal sensitivity. In addition, many of these traits are somewhat repeatable across temperatures (thermal repeatability [R_T]); that is, individuals with relatively high phenotypic values at one temperature generally maintain relatively high phenotypic values at all temperatures. Repeatability (R) is the ratio between among-individual variance and total phenotypic variance (Falconer and Mackay 1996) and serves as an indicator of the consistency of phenotypic traits over time. Additionally, some suggest that it can be used as an estimation of the upper limit heritability of a trait (Boake 1989; Falconer and Mackay 1996; Lynch and Walsh 1998; but see Dohm 2002).

Although the dynamic nature of physiology and performance has been studied for decades, interest in dynamic color signals has emerged only recently (reviewed in Hutton et al. 2015). Despite increasing interest, many exciting topics remain unexplored. So far, most color change studies have focused on thermoregulation (Walton and Bennett 1993; King et al. 1994;

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Silbiger and Munguia 2008; Smith et al. 2016), conspicuousness (King et al. 1994; Hanlon 2007; Stuart-Fox and Moussalli 2008, 2009; Vroonen et al. 2012), and results of dyadic encounters (Greenberg and Crews 1990; Ligon 2014; Smith et al. 2016). However, only three studies have investigated how temperature affects colorful signals (Morrison et al. 1996; Langkilde and Boronow 2012; Stephenson et al. 2016).

Some lizards in the family Phrynosomatidae have iridescent abdominal and throat patches that change color in response to changes in body temperature (*Urosaurus ornatus*: Morrison et al. 1996; *Sceloporus undulatus*: Langkilde and Boronow 2012; *Sceloporus consobrinus*: fig. 1), following a stereotypical thermal performance curve. At low temperatures, these patches reflect relatively long wavelengths. As temperature increases, patches reflect shorter wavelengths (i.e., become bluer). However, if temperature continues to increase beyond a threshold, the patches begin to reflect longer wavelengths again (i.e., become less blue; Morrison et al. 1996). Because the morphological plasticity of these signals mimics a thermal performance curve, one could predict that performance and color should covary. Previous work on anoles has revealed that genus- and population-level variation in temperature-dependent signaling (behavioral displays) closely resembles variation in performance across temperatures (Ord and Stamps 2017), but to our knowledge no studies have examined possible covariation between signal production and performance at the individual level.

In this study, we investigated acute thermal effects on performance and color as well as covariation between performance and color in individual prairie lizards (*S. consobrinus*), a species in the *S. undulatus* clade (Leaché and Reeder 2002). Like *S. un-*

dulatus and *U. ornatus*, male prairie lizards have colorful abdominal and throat patches that rapidly reflect shorter wavelengths (become bluer) with increasing body temperature (fig. 1). Here, we tested whether color correlates to individual performance abilities across temperatures (as suggested in Langkilde and Boronow 2012) at the individual level, drawing conclusions from trait repeatability, thermal sensitivity, and covariation between performance and color. Specifically, we tested whether individual prairie lizards maintain their rank in terms of performance and patch color across temperatures (i.e., are sprint speed and patch color repeatable), whether individuals vary in thermal sensitivity (i.e., the magnitude of performance or color change across temperatures), and whether there is significant individual covariation between performance and color. Finally, we examined covariation of color between abdominal and throat patches to test the hypotheses of Møller and Pomiankowski (1993), which attempt to explain the evolution of multiple ornamental signals in individuals. In brief, multiple signals can send multiple messages, be redundant, or be unreliable (not tested here). Significant covariation between abdominal and throat patch color would suggest that signals might be redundant, and a lack of covariation would be consistent with signals having independent functions.

Material and Methods

Animals

We used 24 captive male *Sceloporus consobrinus* hatched from eggs at the University of Central Arkansas. Each male was sexually mature and had well-developed abdominal and throat patches. None of these lizards had previously had their sprint

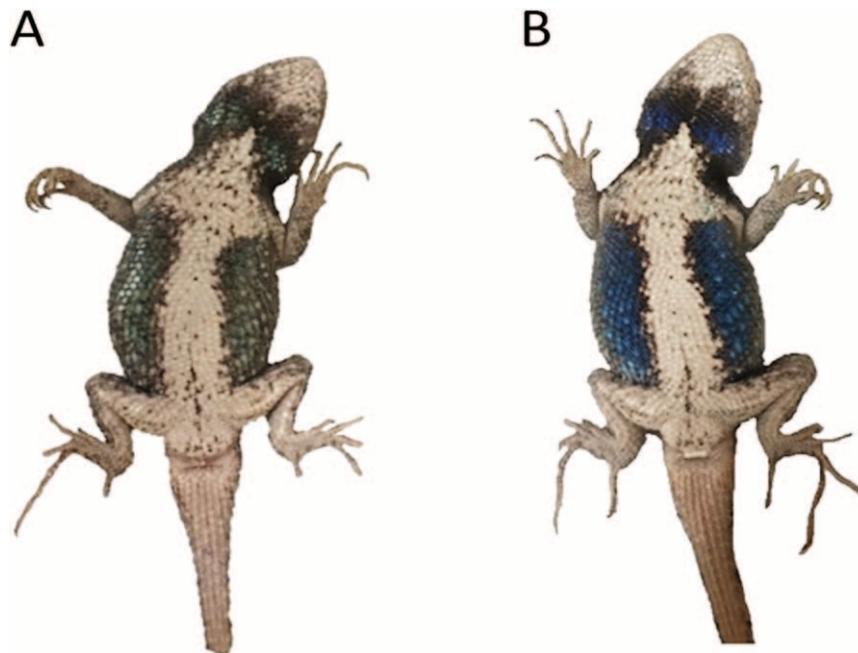


Figure 1. Individual male *Sceloporus consobrinus* ventral surface at 22°C (A) and 37°C (B).

speed quantified, so we do not suspect any training effects to influence our measurements. Lizards were housed individually in 45 × 20 × 25-cm cages with a sand substrate and egg carton, which served as a perch and a hide. Each cage had an individual 40-W incandescent bulb placed above the back of the cage to provide localized heat. This setup created a gradient of temperatures within the cage ranging from ~25°C at the front of the cage (room temperature) to ~32°C immediately below the light. Lights were set to a 13L:11D photoperiod. We fed lizards a combination of vitamin-dusted crickets (*Acheta domesticus*) and dubia roaches (*Blaptica dubia*) each day after the conclusion of sprint speed trials. We do not believe that feeding affected our sprint speed measurements; Huey et al. (1984) have previously shown that lizards that have recently eaten are not significantly slower than their unfed counterparts (but see Martin 1996 for evidence of an effect in juveniles). We supplied water by spraying cages twice each day.

Morphological Measurements

For each individual, we measured snout-vent length (SVL; ± 0.5 mm), hind limb span (the distance between the tips of the longest toes when legs are fully extended perpendicular to the body; ± 0.5 mm), and mass (± 0.1 g). We obtained reflectance spectra of abdominal and throat color patches at five temperatures (22°, 26°, 30°, 34°, and 37°C) using an Ocean Optics Flame miniature spectrometer with a PX-2 Pulse xenon light source (Ocean Optics, Dunedin, FL). Lizards were held in hand for measurements. We used a probe holder held perpendicular to the measured surface that maintained a distance of 5 mm. Lizards were incubated for 1 h before measurement (following Langkilde and Boronow 2012). Temperature order was randomized, but because of logistical constraints, each lizard received the same randomized temperature order. For each individual, we took two spectra from the left abdominal patch and one from the left throat patch. We then measured body temperature to ensure minimal deviation from the target temperature (maximum deviation <1°C). We did not quantify color at more than two temperatures within 1 d. Animals were given approximately 6 h between temperature regimes to minimize effects of temperature change directionality (temperature increase or decrease; Stephenson et al. 2016) and responses to corticosterone, which is more than enough time for corticosterone levels in lab-reared *Sceloporus* to return to baseline (Trompeter and Langkilde 2011). Although handling an animal does not induce a strong stress response (Langkilde and Shine 2006), work in another *Sceloporus* species has shown that color can be affected by plasma corticosterone levels (Calisi and Hews 2007).

Using the pavo package (Maia et al. 2013) in R (ver. 3.4.1; R Development Core Team 2017), we averaged reflectance over 5-nm bins (following Stuart-Fox et al. 2006), smoothed spectra using locally weighted smoothing, and extracted brightness, saturation, and hue (Montgomerie 2006; Maia et al. 2013) for each patch measurement per individual. Brightness represents the total reflectance over the spectral range (Delhey et al. 2003; Siefferman and Hill 2005; Andersson and Prager 2006), with

higher brightness appearing closer to white (total reflectance). Saturation is calculated as the difference between the wavelengths of maximum and minimum reflectance divided by the brightness (Smiseth et al. 2001; Andersson et al. 2002; Andersson and Prager 2006) and represents color intensity. Hue is the wavelength at maximum reflectance (Andersson 1999; Keyser and Hill 2000; Andersson and Prager 2006). For abdominal patches, we averaged the two measurements to obtain one measurement of each color variable.

Sprint Speed

To quantify sprint speed, we incubated lizards at the same five temperatures, with each lizard again receiving the same randomized temperature order (but a different temperature order than used for color measurements) for 1 h. Animals were recorded at 300 frames per second using a Casio Exilim EF-X1 camera as they ran down the middle 1-m segment of a 1.5-m track wrapped in screen to provide traction. Each animal was run three times per temperature, with a 1-h rest period between trials (following Huey and Dunham 1987). We assumed the fastest sprint speed for each temperature to be the maximum speed for an individual.

We digitized each video to obtain *x*- and *y*-coordinates of the tip of each lizard's snout every fifth frame as it ran down the track using the Simple Acceleration and Velocity Recording Application (Donihue and Kazez 2014). The scaled position data for each run were smoothed using the mean square error quantile spline in the assist package (Wang and Ke 2015) in R. The maximal instantaneous velocity attained during each trial (from the three runs down the raceway) was calculated from the fitted splines (as in Walker 1998).

Statistical Analyses

All statistical analyses were performed in R, except for just noticeable difference (JND) estimations, which were performed in Avicol version 6 software (Gomez 2011). We used linear regression to test for relationships between body size (SVL) and response variables (e.g., speed, hue) as well as between hind limb span and sprint speed. Likely because of our small body size range (SVL range: 50–57 mm), we found no significant relationships between body size and response variables or between hind limb span and sprint speed (all *P* > 0.05; similar to Huey et al. 1990; Angilletta et al. 2002a; Donihue 2016), so no analyses included morphological covariates.

To test for overall thermal effects on sprint speed and color morphology, we used linear mixed effects models with temperature as the fixed effect and individual identification (ID) as the random effect. These models were run using the lme function in the nlme package (Pinheiro et al. 2017), and conditional *R*²'s were extracted using the sem.model.fits function in the piecewiseSEM package (Lefcheck 2016). Additionally, we used the rcorr function in the Hmisc package (Harrell 2017) to test for correlations between color metrics and sprint speed within temperatures.

Because we were concerned with phenotypic variation and covariation among individuals, it was necessary to partition variance and covariance into within- versus between-individual components (Dingemanse and Dochtermann 2013). To test for thermal repeatability, sensitivity, and trait covariation, we used the MCMCglmm package (Hadfield 2010) in R. All response variables were standardized to a mean of 0 and a standard deviation of 1. Because we were interested in a holistic analysis across temperatures, we standardized the entire data set at once. Standardizing within a temperature would quantify correlations within a temperature instead of covariation across temperatures. Model testing included 1,000,000 iterations, a thinning interval of 1,000, and a burn-in period of 10,000 iterations. Because thermal performance curves are often not well characterized by linear models, we explored linear and second-order polynomial functions to maximize explanation of variance across temperatures in repeatability and sensitivity models.

We tested for thermal repeatability (R_T) three ways. For sprint speed only, we calculated Kendall's coefficient of concordance between the fastest and second-fastest sprint speed measurements within a temperature. Next, we performed a two-way ANOVA with temperature and individual ID as fixed factors and either sprint speed or a color metric as the dependent factor. We then used the package rptR (Stoffel et al. 2017) to calculate the intraclass correlation coefficient attributed to individual ID (following Lessells and Boag 1987). Finally, we used the package MCMCglmm as described above. In these models, we included temperature as a fixed effect, individual ID as a random effect, and noninformative priors in each model. Additionally, we ran all models again with temperature as a second-order polynomial and compared linear with polynomial models using deviance information criterion (DIC; analogous to Akaike information criterion for Bayesian models; Spiegelhalter et al. 2002). We concluded differences in the ability for the model to explain observed variance if $\Delta\text{DIC} > 2$, with the model reporting the lower DIC explaining more variance. The R_T was calculated as the ratio of between-individual variance (V_I), which is variance attributed to the random effect (ID), to total phenotypic variance (V_P), which is between-individual variance plus variance related to fixed effects ($V_P = V_I + V_R$). We considered R_T significant if the 95% credibility intervals did not overlap zero. Additionally, we pooled color metrics within temperature classes three ways (above and below 26°C, above and below 30°C, and above and below 34°C) to examine how repeatability changes across temperatures. Although color is a thermally sensitive trait in *S. consobrinus*, at some point colors may become fixed and function as a static signal.

To test for between-individual variation in the thermal sensitivity of color and sprint speed, we used univariate random regression models. These analyses quantify individual variation in thermal reaction norms (which estimate thermal sensitivity) by estimating variance in y -intercepts (V_I), variance in slopes (V_S), and covariance between intercepts and slopes ($\text{COV}_{I,S}$). To test for differences in individual slopes, we compared a model that includes V_I , V_S , and $\text{COV}_{I,S}$ with a model that included only V_I . We used DIC to compare models as described above.

Similar to how total phenotypic variance can be decomposed into within- and between-individual components, phenotypic correlations between traits can also be decomposed. Within- and between-individual correlations additively contribute to the total phenotypic correlation (Dingemanse and Dochtermann 2013). For labile phenotypic traits with moderate to low repeatabilities, the observed phenotypic correlation might not reflect the underlying between-individual correlations. Therefore, in such cases, it is important to partition phenotypic correlations into their within- and between-individual components. We used bivariate random regression models to test for correlated thermal reaction norms (individual correlations; r_{ind}) between sprint speed and color across temperatures as well as between color metrics among patch types (e.g., r_{ind} between abdominal and throat hue). This approach is simply called random regression. The bivariate random regression model quantifies correlations with no dependent or independent variable defined. One powerful component of generalized linear mixed effects models is that they do not necessarily have to have normally distributed residuals because you can specify the distribution in the model; however, our residuals approximated a normal distribution. Because individual maximum sprint speed was highly related to individual mean sprint speed within a temperature trial (linear mixed effects model with ID as a random effect; conditional $R^2 = 0.92$), we used maximum sprint speed in these models. We ran nine bivariate random regression models that each contained two response variables. For six of the models, which tested for covariation between performance and signaling morphology, the two response variables were (1) sprint speed and (2) one color metric (brightness, saturation, or hue) of either the abdominal or throat patches. For the remaining three models, which tested for covariation of color metrics between patch types, the two response variables were (1) hue, saturation, or brightness of the abdominal patch and (2) hue, saturation, or brightness of the throat patch (with the second response variable matching the color metric of the first response variable). In each model, we included a covariation term, ID as a random effect, and noninformative priors. We then compared each model with a model with individual covariation constrained to 0. If the unconstrained model had a DIC value a minimum of 2 points lower than the constrained model, we concluded significant covariation between the phenotypes.

Finally, we used Avicol version 6 software (Gomez 2011) to calculate JNDs (1) between temperatures and (2) between individuals with patches reflecting the longest and shortest wavelengths at 34°C (the average body temperature measured in field caught *Sceloporus*; $34.2^\circ \pm 2.3^\circ\text{C}$ [mean \pm 1 SD; 101 observations]; C. D. Robinson and M. E. Gifford, unpublished data) to estimate whether lizards can detect differences in colors observed. We used the Vorobyev and Osorio (1998) tetrachromatic color model, which calculates the quantum catch (the amount of light captured) of photoreceptors, taking into account photoreceptor sensitivity, and then projects the measured colors into tetrahedral space, with the relative distance between colors in this space proportional to conspicuousness (Vorobyev and Osorio 1998). A JND of 1 or greater indicates that colors are distinguishable from

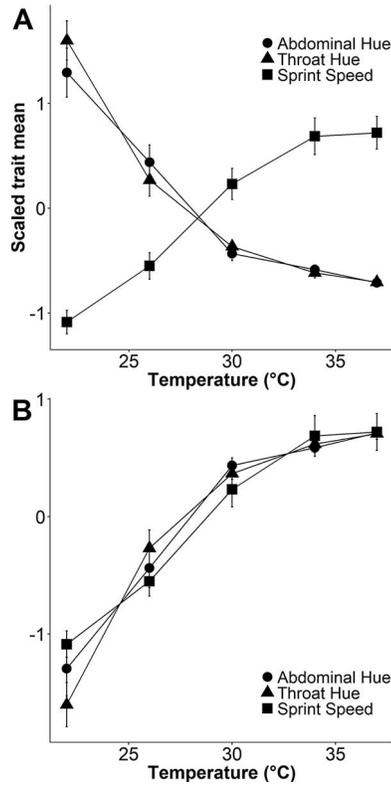


Figure 2. A, Standardized thermal performance curves for sprint speed, abdominal hue, and throat hue. Error bars represent ± 1 SE. B, Same data as A but with the sign reversed on abdominal and throat hue to illustrate species-level similarity in trait variation in response to temperature.

each other. Because the lizard visual system is generally thought to be conserved (Loew et al. 2002; Fleishman et al. 2011), we ran spectral measurements through the Vorobyev and Osorio (1998) color model using the visual model of the tetrachromatic lizard *Crotaphytus dickersonae* (Macedonia et al. 2009). Our model assumed equal cone densities (following Macedonia et al. 2009), a Weber fraction of 0.05 (used for amphibians; Siddiqi et al. 2004),

and a measure of standard daylight irradiance (D65 spectrum; Wyszecki and Stiles 1982).

Results

Temperature Effects

Overall, temperature had a significant effect on sprint speed (linear mixed effects model with ID as random effect; conditional $R^2 = 0.761$, $P < 0.001$; fig. 2), abdominal (conditional $R^2 = 0.652$, $P < 0.001$; fig. 2) and throat hue (conditional $R^2 = 0.693$, $P < 0.001$), and abdominal brightness (conditional $R^2 = 0.560$, $P < 0.001$). Temperature had a marginal effect on throat saturation (conditional $R^2 = 0.394$, $P < 0.054$) but no significant effect on abdominal saturation or throat brightness (both $P > 0.48$). Summary statistics are provided in table 1.

Within temperatures, few color metrics were correlated with sprint speed (table 2). At 22°C, abdominal hue ($r = 0.491$, $P = 0.020$) and brightness ($r = -0.470$, $P = 0.027$) were significantly correlated with sprint speed; at 30°C, throat hue correlated with sprint speed ($r = 0.425$, $P = 0.049$); and at 37°C, abdominal brightness correlated with sprint speed ($r = -0.525$, $P = 0.008$). No other color metric was correlated with sprint speed at any temperature. However, after Bonferroni correction ($P = 0.0017$; 0.05 of 30 comparisons; Rice 1989), no color metrics were associated with sprint speed. Similarly, when adjusted for the false discovery rate, no P values reached significance at $P < 0.05$.

Thermal Repeatability

Sprint speed was significantly repeatable within individuals (Kendall's coefficient of concordance = 0.965, $P < 0.001$). Repeatability was significant across temperatures for all variables using both intraclass correlation coefficient and Markov chain Monte Carlo (MCMC) approaches (table 3), with sprint speed ($\Delta\text{DIC} = 13.65$), abdominal patch hue ($\Delta\text{DIC} = 20.518$), and throat patch hue ($\Delta\text{DIC} = 51.458$) being better explained by second-order polynomials than linear models in MCMC analyses.

Table 1: Summary statistics (mean ± 1 SE) for performance and color variables measured across five temperatures ($N = 24$ for all measurements)

	22°C	26°C	30°C	34°C	37°C
Sprint speed (m s^{-1})	1.28 \pm .03	1.44 \pm .04	1.67 \pm .04	1.81 \pm .05	1.82 \pm .05
Abdominal:					
Hue (nm)	545.23 \pm 9.66	510.98 \pm 6.17	479.78 \pm 2.84	472.40 \pm 1.63	468.23 \pm 1.49
Brightness (%)	29.78 \pm 1.12	27.41 \pm 1.03	30.01 \pm 1.31	27.00 \pm .81	26.09 \pm .93
Saturation	.47 \pm .03	.53 \pm .03	.53 \pm .03	.56 \pm .04	.56 \pm .04
Throat:					
Hue (nm)	550.71 \pm 7.47	497.61 \pm 6.17	472.27 \pm 1.99	462.29 \pm 1.93	458.75 \pm 1.93
Brightness (%)	26.90 \pm 1.07	22.15 \pm 1.33	27.73 \pm 1.15	26.15 \pm 1.21	23.48 \pm 1.20
Saturation	.43 \pm .03	.67 \pm .05	.48 \pm .04	.50 \pm .04	.56 \pm .05

Table 2: Phenotypic correlations between color metrics and sprint speed within each temperature

	22°C		26°C		30°C		34°C		37°C	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Abdominal:										
Hue	.491	.020	-.008	.973	.256	.239	.151	.481	.210	.326
Bright	-.470	.027	-.238	.274	-.213	.330	-.326	.120	-.525	.008
Saturation	.051	.822	.324	.131	.252	.246	-.131	.542	.115	.592
Throat:										
Hue	.320	.157	-.061	.782	.425	.049	.221	.300	.324	.122
Bright	-.288	.205	-.227	.297	-.121	.593	-.215	.313	-.011	.960
Saturation	-.189	.411	.154	.483	-.027	.904	-.020	.925	-.259	.221

Note. Correlation coefficients in bold represent a significant ($P < 0.05$) relationship before Bonferroni correction.

Thermal Sensitivity

Individuals differed in thermal sensitivity for sprint speed, abdominal and throat hue, and throat saturation; adding random slopes improved model fit for these metrics (for all Δ DIC values, see table 4). Additionally, the inclusion of a second-order polynomial greatly improved model fit for sprint speed and both hue models. All other models were best fit to models with linear, homogenous slopes (table 4).

Correlated Thermal Reaction Norms

Using bivariate random regression models in MCMCglmm, we found that both abdominal and throat hue significantly covary with sprint speed across temperatures (fig. 3; table 5). No other metric of patch morphology covaried with sprint speed. Brightness (Δ DIC = 7.542) and saturation (Δ DIC = 6.175) covaried between abdominal and throat patches across temperatures, although hue did not (Δ DIC = 0.209).

JNDs

Our JND results between temperatures are presented in table 6. Generally, colors at 22° and 26°C are distinguishable from colors at every other temperature. For abdominal patches, colors above 30°C are indistinguishable from each other (all JNDs < 0.99), suggesting that colors are essentially static within individuals (table 6). For throat patches, colors at 30°C are slightly distinguishable from 37°C (JND = 1.08; table 6). Finally, at 34°C, colors between individuals reflecting the longest and shortest wavelengths are distinguishable for both patch types, with variation in throat patches being more easily distinguished (JND = 4.55) than abdominal patches (JND = 1.63).

Discussion

Colorful signals have many functions, including advertising individual quality. At the species level for *Sceloporus consobrinus*, both sprint speed and patch hue are represented by stereotypical thermal performance curves (fig. 2). Here we show significant covariation in thermal performance curves between patch hue and sprinting speed at the individual level (fig. 3). Individuals

who are more thermally sensitive in patch hue are also more thermally sensitive in sprinting performance. Additionally, because each trait is statistically repeatable (i.e., individuals with relatively high phenotypic values at a temperature maintain relatively high phenotypic values at all temperatures), our analyses suggest that individuals who are most blue also tend to be the fastest. Neither brightness nor saturation is indicative of sprinting performance.

Signaling current individual sprinting ability (i.e., advertising one's acute physiological state) could be important for social interactions. In some species, male dominance (Garland et al. 1990; Robson and Miles 2000; but see Perry et al. 2004) and reproductive success (Husak et al. 2006) are related to sprint speed. Although a definitive mechanism underlying this relationship is not clear, a plausible explanation could be the relationship between sprint speed and testosterone (Klukowski et al. 1998), an important hormone that influences aggressive (Moore 1988; Wingfield et al. 1990; Cavigelli and Pereira 2000) and courtship (Lindzey and Crews 1986; Wiley and Goldizen 2003; Wade 2005) behaviors. Additionally, in some species males who are faster are better at chasing off conspecific intruders (Braña

Table 3: Repeatability measurements for performance and color variables across temperatures

	ICC (95% CI)	MCMC (95% CI)	Model term
Sprint speed	.505 (.292–.671)	.419 (.267–.580)	SOP
Abdominal:			
Hue	.226 (.042–.404)	.297 (.119–.545)	SOP
Brightness	.559 (.358–.700)	.605 (.398–.750)	L
Saturation	.729 (.555–.837)	.719 (.569–.845)	L
Throat:			
Hue	.223 (.049–.400)	.331 (.152–.557)	SOP
Brightness	.487 (.270–.659)	.484 (.279–.679)	L
Saturation	.434 (.221–.604)	.477 (.260–.667)	L

Note. Models reported included either a linear (L) or a second-order polynomial (SOP) term from Markov chain Monte Carlo (MCMC) comparisons; see text for deviance information criterion (Δ DIC) values. CI, credibility interval; ICC, intraclass correlation coefficient.

Table 4: Deviance information criterion (Δ DIC) values for thermal sensitivity models relative to model with only linear, homogenous slopes

	Model terms				Best model
	LH	LR	SH	SR	
Sprint speed	...	23.403	13.715	39.928	SR
Abdominal:					
Hue	...	54.319	24.645	102.216	SR
Brightness	...	1.984	1.978	.016	LH
Saturation	...	2.703	1.020	3.958	LH
Throat:					
Hue	...	22.797	62.388	100.219	SR
Brightness	...	4.671	2.117	6.714	LH
Saturation	...	4.075	.091	3.924	LR

Note. Model terms include the following: linear, homogenous slopes (LH); linear, random slopes (LR); second order, homogenous slopes (SH); or second order, random slopes (SR). Best model was selected as the model with the lowest DIC value, with a significant difference observed when Δ DIC > 2. When two lowest DIC models did not differ by 2, the more parsimonious model was selected as best.

2003; Husak and Fox 2006), so sexual selection should favor males who are faster and, consequently, bluer (in *S. consobrinus*).

Although both abdominal and throat hue both appear to covary with sprint speed, hue is the only color metric that did not covary between abdominal and throat patches across temperatures. This surprising pattern could suggest that each patch can send multiple messages and that there is divergent selection acting between abdominal and throat patches (Grether et al. 2004). In other words, abdominal and throat patch hue could redundantly signal physiological response to temperature yet independently send additional messages (Møller and Pomiankowski 1993). Independent messages between abdominal and throat patches in phrynosomatids have been observed before (Meyers et al. 2006; Weiss 2006; Calisi and Hews 2007; Weiss et al. 2009). However, the signals in *S. consobrinus* appear to

potentially have both redundant and independent roles (i.e., sending multiple messages). Work in a chameleon species (Ligon and McGraw 2013) and across agamids (Chen et al. 2012) suggests that divergent roles for colorful signals evolve when sexual selection pressures are high; further work is needed in *S. consobrinus* to understand how selection acts on dynamism in abdominal and throat patch color.

Further support for independent signaling stems from differences in how repeatability changes across temperatures (fig. 4). We examined 26°, 30°, and 34°C as artificial cutoffs to assess repeatability changes across temperatures. Abdominal hue displays similar repeatabilities above and below each cutoff. However, repeatability of throat hue is substantially higher from 30°–37°C than it is from 22°–30°C (95% credibility intervals do not overlap) and from 34°–37°C than it is from 22°–34°C, suggesting that there are fewer rank order changes with respect to throat color than abdominal color as temperatures increase.

Interestingly, JND calculations suggest that conspecifics might be able to detect changes within an individual and between patch types. Estimated JND values for abdominal patch hue between 30° and 37°C were all less than 1 (table 6). Therefore, assuming conservation of the lizard visual system, these patches would be indistinguishable across this temperature range. This was not true for throat patches. JND between throat hue at 30° and 37°C were greater than 1. However, the JND estimation for this comparison suggests that the detectability of these differences is small (JND = 1.08); in quick interactions, these differences may be meaningless. Further, estimations of JNDs between 30° and 34°C as well as between 34° and 37°C suggest indistinguishable changes within each temperature pair, highlighting that the potential ability of lizards to detect the differences between 30° and 37°C should be taken with careful consideration. Regardless, for both patch types, hue potentially functions as a static rather than a dynamic signal within individuals around species-average field active body temperatures.

Although within-individual changes might not be noticeable within individuals above 30°C, the variation observed between individuals is considerably stronger. Specifically, the magnitude

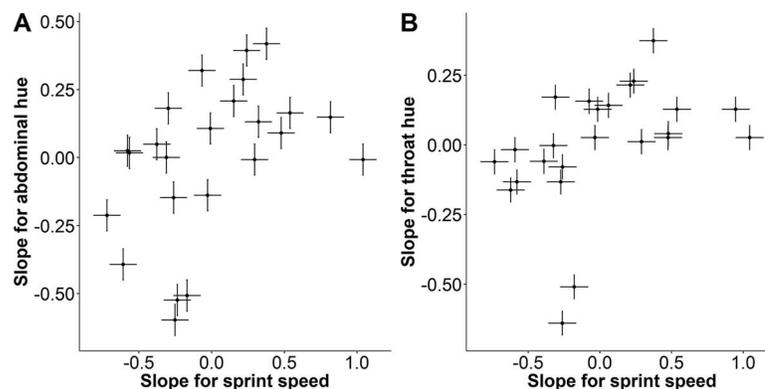


Figure 3. Thermal sensitivity in abdominal hue (A) and throat hue (B) in relation to thermal sensitivity of sprint speed in prairie lizards. Values extracted from univariate random regression models using best linear unbiased predictors for the random effect. Both color metrics show positive covariation with sprint speed across temperatures.

Table 5: Individual correlations (r_{ind}) between sprint speed and color metrics across temperatures

	r_{ind} (95% CI)	ΔDIC
Abdominal:		
Hue	.459 (−.035 to .764)	3.781
Brightness	−.428 (−.778 to .058)	1.130
Saturation	.073 (−.515 to .486)	.822
Throat:		
Hue	.368 (−.047 to .686)	3.129
Brightness	−.202 (−.652 to .332)	.705
Saturation	−.263 (−.636 to .356)	.589

Note. Deviance information criterion (ΔDIC) values represent covariation model versus a model with individual covariation constrained to zero. ΔDIC values in bold represent a significant difference ($\Delta\text{DIC} > 2$). CI, credibility interval.

of differences in JND values is much more noticeable in throat patches (JND = 4.55) as opposed to abdominal patches (JND = 1.63). Therefore, individual differences, particularly in throat hue, may be substantial enough that selection can favor bluer phenotypes.

In this study, we quantified sprint speed using instantaneous velocity; this method generally yields faster measurements than other techniques, such as photocell timed racetracks, because the distance between measurements is smaller (e.g., between five video frames vs. 10 cm). Indeed, the mean maximum sprint speed we measured (1.82 m s^{-1}) was slightly higher than others have reported (in *Sceloporus undulatus*: 1.72 m s^{-1} [Angilletta et al. 2002a]; 1.65 m s^{-1} [Crowley 1985a]; 1.73 m s^{-1} [Crowley 1985b]; 0.97 m s^{-1} [Pinch and Claussen 2003]) but slower than reported for *S. undulatus* by Bonine and Garland (1999; 2.51 m s^{-1}). Further, animals used in our study were smaller than the *S. undulatus* used in other studies (mean SVL in our study was 53.2 mm compared with 63 mm in Angilletta et al. 2002a; mean mass in our study was 5.05 g compared to 10.45 g in Bonine and Garland 1999). This is somewhat expected, as *S. consobrinus* is generally smaller than *S. undulatus*. However, given the size differences and expected linear relationship between body size and sprint speed, we would expect our sprint speeds to be slower than those measured from larger animals. Therefore, our measurement technique could explain the slightly

higher values than reported elsewhere despite the size differences. Regardless, because of the similarities in measured sprint speeds among studies, we feel confident that our measurements are representative of true maximum performance in our sample of lizards.

Our measures of repeatability reported in table 2 are lower than those calculated in other studies on lizard sprint speed (e.g., Huey and Dunham 1987; Sorci et al. 1994; Bonine and Garland 1999; Husak and Fox 2006; Peterson and Husak 2006). In this study, repeatability is measured as a ratio of between-individual to total phenotypic variation across all temperatures. Other studies have reported Kendall's coefficient of concordance (Huey and Dunham 1987) or Pearson's correlation coefficients between sprint trials run on different days (Bonine and Garland 1999; Peterson and Husak 2006) or between the fastest and second-fastest runs for an individual (Sorci et al. 1994; Husak and Fox 2006; Peterson and Husak 2006) under the same thermal conditions. When assessing repeatability between fastest runs at the same temperature using these statistics, our repeatability estimates range between 0.938 (Pearson's correlation) and 0.965 (Kendall's coefficient of concordance). These values are similar to values reported by Bonine and Garland (1999) for *S. undulatus* (0.918; Pearson's correlation). These results suggest that we have strong intraindividual reproducibility of sprint speed.

In sum, the colorful abdominal and throat patches of prairie lizards appear to serve as acute signals of individual ability, with the bluest individuals being the fastest. This is the first study to illustrate the relationship between a dynamic signal and performance despite the growing interest in dynamic signals (Hutton et al. 2015), albeit in laboratory animals. However, these signals appear to become static at ecologically important temperatures, defined here as temperatures over which social interactions become more likely. If color is a useful signal of quality to conspecifics at these temperatures, selection would be expected to decrease within-individual variation across temperatures such that color should always reflect quality. Indeed, phenotypic repeatability becomes much higher for throat patches at these ecologically important temperatures, suggesting that selection acts more strongly across these temperatures (Brodie 1993). Future research should attempt to measure selection directly on the dynamism of color and pose similar questions to a broader range of taxa to better understand the evolutionary history and significance of dynamic signals.

Table 6: Just noticeable difference (JND) estimations of patch hue between temperatures

	Abdominal hue					Throat hue				
	22°C	26°C	30°C	34°C	37°C	22°C	26°C	30°C	34°C	37°C
22°C	...	2.94	2.75	3.51	3.48	...	3.2	2.77	3.44	3.77
26°C	2.77	2.61	2.94	3.43	3.91	3.68
30°C99	.7869	1.08
34°C965
37°C

Note. Numbers in bold represent values suggesting indistinguishable color differences (JND > 1).

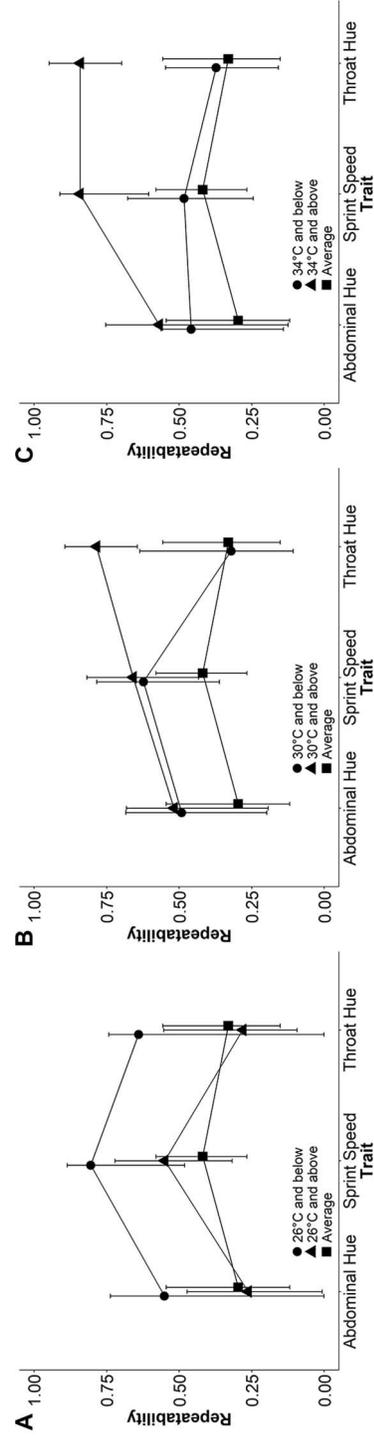


Figure 4. Repeatability values for sprint speed and abdominal and throat hue using 26°C (A), 30°C (B), and 34°C (C) as comparison points to examine repeatability changes across temperature. Error bars represent 95% credibility intervals. Points offset for clarity.

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