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Examining Correlates Of Color Signaling And Aggression In Female *Sceloporus Jarrovii*

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EXAMINING CORRELATES OF COLOR SIGNALING AND AGGRESSION IN FEMALE *SCELOPORUS JARROVII*

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ABSTRACT

Many animals have color signals used during aggression. While most often males are colorful and aggressive while females are cryptically-colored and less aggressive, in some species both males and females are colorful and aggressive. However, such species have received relatively less study. In the mountain spiny lizard, *Sceloporus jarrovii,* both males and females have bright blue abdominal patches displayed during aggressive interactions. In this exploratory study, I used this species to examine possible signaling functions of adult female color and its relationship to aggression in agonistic encounters.

Chapter 1 presents a study that aimed to identify phenotypic correlates of the color signal. I quantified color attributes of natural coloration and examined associations with phenotypic measures of body size (body length, body mass), bite force, health status including white blood cell (WBC) measures, *Plasmodium* parasite loads, mite loads, and plasma corticosterone level. Not surprisingly, patch size was positively associated with body size. The only variable significantly correlated with blue coloration was WBC counts (negative correlation). Furthermore, WBC counts were significantly positively correlated with corticosterone level. Hence coloration may signal health.

Chapter 2 presents an experimental study examining abdominal coloration and female-female interactions. I manipulated coloration by painting abdominal patches either off-white or blue, then conducted staged trials in which I presented a paint-manipulated "stimulus" female to a free-ranging "focal" female, and then measured responses of the free-ranging "focal" female (rates of behaviors, latency to respond). I did not detect an effect of paint treatment on focal

female behavior, , although I could not experimentally control size differences of females in trial pairs due to limited sample sizes. Using a Akaike Information Criterion approach, the best predictors of focal aggression were body size, bite force, and corticosterone levels, suggesting that female aggression in my data set was most influenced by body size, strength, and glucocorticoids. Future work should examine whether ultraviolet properties of the abdominal patches function in signaling and conduct a paint manipulation study in which size differences are experimentally controlled.

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CHAPTER 1

CORRELATES OF ABDOMINAL PATCH COLORATION IN FEMALE *SCELOPORUS JARROVII*

INTRODUCTION

Many animals use color signals directed toward a variety of receivers. Most often, color is used in sexual selection, which can include contexts involving agonistic encounters and mate choice (reviews in Houde, 1997; Grether, Kolluru, & Nersissian, 2004). Animals that use color in sexual selection are usually sexually dichromatic. Male are usually the colorful or conspicuous sex while females are often more cryptically colored (reviewed in Beddard, 1982), and often male-typical coloration is mediated by plasma testosterone (e.g. Cox, Zilberman, & John-Alder, 2008; Setchell *et al*., 2008). However, in some species both males and females have bright coloration used in sexual selection (e.g. Jawor *et al*., 2003; Emlen & Wrege, 2004), and the physiological control and function of such traits are less well understood.

The existence of ornamented females can be explained by two hypotheses. Females may be ornamented because of genetic correlations for traits favored in males (Lande and Arnold 1985), but there is little support for this idea (see reviews by Amundson, 2000 and Kraaijeveld *et al*., 2007). A second, more widely supported hypothesis suggests that females have gained ornamentation as the result of sexual selection by male choice or by intrasexual competition (Darwin, 1871; Stamps, 1973; Cain & Ketterson, 2012). Hence, the roles of coloration in males

and females are likely similar, although this has mostly been explored and supported in studies on avian species (Linville *et al*., 1998; Heinsohn, 2008). Sexual selection drives the ornaments of both male and female cardinals (*Cardinalis cardinalis*), which use their black masks as signals of resource holding potential (RHP) (Jawor *et al*., 2003). Male and female wattled jacanas (*Jacana jacana*) have ornamental shields and wattles that are associated with body size and dominance (Emlen & Wrege, 2004). Some female fish have ornamental color used as status symbols, such as the polyandrous pipefish (*Syngnathus typhle*, Bernet, Rosenqvist, & Berglund, 1998) and Lake Victoria cichlids (*Neochromis omnicaeruleus*, Dijkstra *et al*., 2009). During agonistic encounters, this color may be used as a badge of status to prevent encounters from becoming dangerous (Smith & Price, 1973; Smith & Harper, 1988). This is true of many birds (see review by Senar, 2006) and lizards (Zucker, 1994; Cooper, Wilson, & Smith, 2009) and has largely been studied in the males of many species, but evidence supports similar functions for ornamentation in females of several species (see review by Admundson, 2000).

Female coloration may also play a role in male mate choice in several taxa. Male rhesus macaques (*Macaca mulatta*) assess females' reproductive state by the red coloration of the females' hindquarters (Waitt *et al*., 2006). Assortative mating by plumage and bill coloration of northern cardinals (*Cardinalis cardinalis*) may be the result of male and female mate choice (Jawor *et al*., 2003). Reproductive coloration in female *Sceloporus virgatus* lizards stimulates male courtship (Weiss, 2006).

Multiple hormones can be associated with coloration across many taxa, and the roles of hormones in female coloration deserve further work. Experimentally administered testosterone affects male coloration of many animals (Fernald, 1976; Cardwell & Liley, 1991; Salvador *et al*., 1997; Cox et al., 2005; McGlothlin *et al*., 2008). Correlations of coloration with plasma levels of

corticosterone (CORT), testosterone, and estradiol occur in some species, and, for example each could be signaled by the different regions and patterns of coloration in both male and female *Sceloporus pyrocephalus* lizards (Calisi & Hews, 2007). "Nuptial" coloration of female lizards (associated with breeding and ovarian state) can be a function of the relative ratios of steroid hormones (Cooper & Crews, 1988; Cooper & Greenberg, 1992; Sköld *et al*., 2008). Hence, receivers potentially could obtain information about the signalers reproductive state and/or stress physiology. Ornamental coloration also can signal health status. Coloration correlates with parasite loads in male American goldfinches (*Carduelis tristis,* McGraw & Hill, 2000), female *Sceloporus pyrocephalis* lizards (Calisi, Malone, & Hews, 2008), male and female *Sceloporus occidentalis bocourtii* lizards (Megia-Palma *et al*., 2016), and male Lake Victoria cichlid fish (*Pundamilia nyererei*; Maan, Spoel, & Jimenez, 2006). Similarly, coloration signals body size in male blue-black grassquits (*Volatinia jacarina;* Doucet, 2002), female *Sceloporus virgatus* lizards (Weiss, 2006), and poison dart frogs (Hagman & Forsman, 2003).

In this exploratory observational study, I use adult female mountain spiny lizards (*Sceloporus jarrovii*) to examine possible correlates to the size and quality of their blue abdominal patches. This species is somewhat unusual because both males and females have ornamental coloration on their ventral surfaces. Both sexes display the abdomen during aggressive, intrasexual interactions (Ruby, 1978) and this coloration may signal resource holding potential (RPH), a term that encapsulates a variety of traits that may allow individuals to dominate conspecifics and thereby control resources. If brighter and larger patches are a signal of RHP, then females with these traits will be larger, stronger, and have lower rates of infection.

METHODS

Study Site

I captured thirty-nine adult female *Sceloporus jarrovii* from the area surrounding East Turkey Creek, in the Chiricahua Mountains of Southeast Arizona (31.56.00.0"N, 109.12.26.2"W). East Turkey Creek is a shallow, winding creek that runs through pine-oak forest with large boulders and rocky cliff faces interspersed along the length of the creek. Lizards were most often found within 20 meters of the creek on boulders or fallen trees. I captured lizards between the hours of 1000 and 1400. The field laboratory portions of this work were done at the facilities of the Southwestern Research Station (American Museum of Natural History), in Portal AZ.

Experimental Design

I measured a number of potential phenotypic correlates of coloration that included body size measures (body length, body mass, and tail length), measures of health and of endocrine status (white blood cell, WBC, counts; heterophil to lymphocyte ratio, H:L; percentage of RBCs infected with *Plasmodium*; mite loads; plasma levels of corticosterone). I attempted to measure testosterone from the collected plasma samples but values were all non-detectable for the dilutions we used with the commercial assay kit and no plasma remained for reassay.

All females were used in a separate behavioral study (see Chapter 2), hence their use in the behavior study affected when some variables for the current study were measured. In the behavior study, 19 females were used as stimulus females and their phenotypic traits were measured before the behavior trials when they were captured, which was the day prior to use in behavior trials lasting approximately 5 min. Another 20 females were used as the focal females,

and hence they were captured immediately after the behavior trials and then measured and bled. To assess whether this difference in timing of sampling affected the phenotypic measures, I compared mean trait values between females in these two groups, and the two groups of females did not differ significantly for any trait measured (Table 1).

I captured lizards by noosing, and within 2 min of capture I completed blood sampling and then made a blood smear. I placed females individually into numbered cloth bags for transport back to the field lab. I took GPS points (to ± 3m precision) at the site of capture to ensure that all individuals could be returned to site of capture. Once in the field lab, I counted mites while holding each lizard over a pan of water to catch any detached mites. I then measured snout-to-vent length (SVL, in mm), tail length (TL, in mm), and body mass (g) using a Pesola™ scale. After taking these measurements, I took digital images of the ventral patches for subsequent digital analysis of patch area and patch color attributes (described below). I also took measures of a potential correlate of perinatal androgenization, the 2D:4D digit ratio. In a number of tetrapod vertebrates this ratio reflects the degree of androgenization during development (e.g., Wong & Hines, 2016). Hence female *S. jarrovii* with more male-like digit ratios might be more masculinized and express more male-typical, saturated abdominal blue patches.

Blood Sampling and Smears

I took blood samples using heparinized microcapillary tubes to rupture the retro-orbital sinus, as outlined by Thaker, *et al.* (2009). All sampling was completed within 2 min of being noosed (capture method). A single drop of blood was used to make smears on pre-labeled microscope slides in the field (Presnell & Schreibman, 1997) and air dried, and the slides were fixed in 100% methanol at the SWRS lab, air dried and stored at room temperature. Upon return

to Indiana State University (ISU), the slides were stained with Geimsa (Protocol™ CAT#264-984). Total leukocytes per 10,000 RBCs were counted as described by Seddon and Klukowski (2012). I scanned slides under a light microscope at 1000x oil immersion to classify 100 leukocytes per individual as described by Campbell and Ellis (2007). The ratio of heterophils to lymphocytes was quantified as a measure of innate immunity (Vleck *et al*., 2000). Finally, I searched erythrocytes for 15 to quantify the percent infected by *Plasmodium spp*. (Pickering *et al*., 2000), which were identified following Garnham (1966).

The remaining blood sample was evacuated into a microcentrifuge vial and these whole blood samples were kept on wet ice for up to 4 hr while in the field. I centrifuged the samples and pipetted the plasma into clean microcentrifuge vials to be stored in known volumes of 100% ethanol (Goymann et al., 2007). I stored the plasma-ethanol samples at -20°C until corticosterone and testosterone assays were performed at ISU, using corresponding enzyme-linked immunosorbent assay kits (Enzo Life Sciences, Testosterone kit 900-065 and Corticosterone kit 900-097) previously validated and optimized on *Sceloporus jarrovii* by the Hews lab (following protocols by Wada, Hahn, & Breuner, 2007).

Ornamentation Attribute Measurements

Coloration is temperature-dependent in this genus (Sherbrook *et al*., 1994), hence I warmed all females at their mean preferred body temperature (33°C; Schuler e*t al*., 2011) for 20 min before pictures were taken (Langkilde & Boronow, 2012). After incubation, I held all lizards individually against a black foam pad under the same lighting in the same room between 1500 and 1700 hr, and their pictures were taken using a Canon™ Rebel XT digital camera with the auto-adjust and flash settings turned off to prevent differences in color due to lighting or camera

settings. I placed a ruler and Tiffen™ True Color chart in view of the camera to check for lighting differences in all pictures.

I analyzed patch area using ImageJ software (v1.3) to obtain a precise measurement of the area of blue coloration on each lizard (Girish & Vijayalakshmi, 2004). Patch attributes, including hue, saturation, and brightness were measured using Adobe™ Photoshop. Hue is defined as the discernible attribute of color, such as blue versus white. Saturation is the spectrum of a given hue between pure color and gray, such as royal blue versus sky blue. Brightness is a relative measure of the luminance of an object against a given background, wherein white is the brightest color and black is the least bright.

Statistical Analyses

For statistical analyses, all variables were first tested to determine whether they exhibited a normal distribution, and none required transformation. I summarized patch coloration using values for hue, brightness, and saturation in a principle components analysis ("color PC").

To assess simple trait relationships, all variables were first included in a Pearson's moment correlation matrix. I then used an Akaike information criterion (AIC) approach to detect the best model for predicting associations between color PCA scores and the morphological and physiological measures. Two subsequent sets of AICs were conducted to detect the best models for predicting associations between the previously mentioned variables and belly patch hue and saturation. For body size I included SVL and also a measure of body condition, calculated as the residuals from a regression of cubed root of body mass onto SVL**,** using a reduced major axis regression (recommended over OLS regression model when the two

variable had similar levels of measurement error)**.** All analyses were completed using IBM SPSS (v19, IBM Corp.).

RESULTS

I captured thirty-nine adult female *Sceloporus jarrovii* from May 16 – June 6, 2016. Most of these 39 females were heavily gravid in May and had undergone parturition by June when we captured them. Reproductive condition was not confirmed via palpation, but post-parturient females appear very emaciated and with a flaccid body wall. As a measure of body condition, I calculated body mass residuals from a reduced major axis regression of the cubed root of body mass onto SVL (Figure 1).

Phenotypic Variation.

Females in this population at this time of year varied in coloration (Figure 2) and in the other phenotypic traits that I measured (Figure 4)**.** Females used in the two groups for the behavioral study (not described herein) did not differ significantly in mean values of any trait measured (Table 1), despite the experimental design of that study, which caused some differences in the timing of when I measured some traits.

Summarizing Color Variation

Principle components analysis (PCA) summarized the three measured patch color attributes (hue, saturation, and brightness in a single principle component with an Eigenvalue >1. This component explained 46.5% of the variance (Tables 2, 3). Hence, subsequent analyses

included this PC as the independent variable (color PC). Most of the variance in color was in hue and saturation, with very little variation in brightness (Figure 2).

Correlates of Color Variation

Simple Pearson's correlation analyses of these relationships revealed that variation in WBC count was significantly associated with variation in coloration, as summarized by principle components analysis (Figure 4). None of the other variables measured were significantly associated with the color PC.

Correlations Among Non-Color Traits

Overall body size, as measured by with SVL correlated positively with the white blood cell ratio H:L ($r^2 = 0.347$; $p = 0.035$; Figure 5), and with mite load ($r^2 = 0.465$; $p = 0.003$; Figure 5). BMRes was negatively correlated with capture date ($r^2 = 0.145$; $p = 0.043$; Figure 5). Patch area had a positive relationship with SVL ($r^2 = 0.589$; $p = 0.001$), with BMRes ($r^2 = 0.417$; $p < 0.001$), and a negative relationship with capture date ($r^2 = -0.409$; $p = 0.031$).

Models for Predicting Color Variation

I tested twenty linear models using the Akiake's Information Criterion (AIC) method, in which I assessed combinations of thirteen variables (Table 4). These models were tested using three separate targets. The first set of models tested associations between the aforementioned variables and color, as summarized by the PCA of hue, saturation, and brightness. The best models in this first AIC analysis included CORT alone. This model was followed closely by CORT + capture date and the percent of estimated tail length + CORT as dependent variables

and had Δ_i scores of 3.927 and 3.929, respectively (Table 5A; Figure 3). The second AIC analysis tested for associations between just patch hue and the aforementioned variables. Each of the best models included CORT (Table 5B). The final AIC analysis I ran tested for associations between just patch saturation and the other phenotypic variables. Once again, each of the top models contained CORT (Table 5C).

DISCUSSION

This exploratory study was conducted to determine whether any morphological and physiological measures of fighting ability and immune function are associated with the abdominal patch color attributes of adult female *Sceloporus jarrovii*. If so, they would potentially be information that could be signaled by attributes of patch coloration.

First, I found that females at this time of year varied in coloration and the other traits. This is interesting because expression of ventral coloration in female *Sceloporus* likely is mediated by steroid hormones (e.g., Calisi & Hews, 2007). While seasonal variation in plasma hormone levels has been documented for *S. jarrovii* females (e.g., Woodley & Moore, 1999a-b), variation in abdominal coloration in female has not been well-evaluated, especially regarding association with circulating steroid hormone levels. If coloration is a reproductive signal, then such associations might be expected. Unfortunately, the levels of testosterone were too low for my assay kits to measure, and could not be included in the analyses.

I then ran a series of exploratory analyses examining individual trait associations. With one exception, none of the measured variables were significantly correlated with patch color (color PC score). Hence, variation in patch coloration (hue saturation, brightness, as summarized in the PCA) was not associated with variation in SVL, patch area, residual body mass, parasite

loads (mite counts or *Plasmodium* count), H:L ratio, or the potential measure of perinatal androgenization, the 2D:4D digit ratio (Wong & Hines, 2016).

The one exception was WBC count, which was significantly and positively correlated with patch color attributes. Hence patch coloration may signal health, although WBC count was not included in the best models for predicting patch coloration. Ornamental coloration can signal immune function in some male lizards (e.g., Martin & Lopez, 2009), in male and female cardinals (Maney *et al*., 2008) and lizards, and in male fish (Clotfelter, Ardia & McGraw, 2007). However, most of these examples are directly tied to coloration resulting from carotenoids, a class of pigments which is not known to be present in the Phrynosomatid lizards (Morrison, Rand, & Frost-Mason, 1995) including the orange gravid coloration of *Sceloporus viratus* (Weiss et al., 2011).

In the analysis of individual trait correlations, I also found that SVL, BMRes, and capture date were correlated with patch area. This suggests that patch area is a signal of body size, which varies with reproductive condition during the season in which these data were collected. This conclusion is supported by several studies involving other male and female *Sceloporus* lizards (Weiss, 2006; Langkilde & Boronow, 2010). The correlation between patch area and capture date is likely due to the reproductive status of the females, as their skin, and thus, their ornamentation, is stretched with pregnancy. No studies have followed females of this species to determine whether patch color or size changes with seasonality; however, the appearance and size increase of throat coloration synchronously with reproductive condition in females of the closely related species, *Sceloporus virgatus*, is a well-known phenomenon (Weiss, 2002).

The plasma levels of CORT did not differ between stimulus females, bled immediately on capture, and focal females, bled immediately after experiencing an STI (Figure 6). Although

not a focus of this research project, this result is of general interest as it suggests that females do not elevate CORT after a 5-min encounter with a conspecific female. Given that capture and bleeding times were under 3 min, the total time post-encounter averaged 8 min. This is a fairly short time for CORT elevation to be detected (c.f., Hews & Abel Baniki, 2013)

Plasma CORT levels were not associated with any aspect of the abdominal patches in the simple Pearson's correlation analyses. However, CORT was in the most explanatory models in the AIC analysis to explain patch coloration as described by the PC analysis, and for hue and saturation alone. Furthermore, in species for which CORT is associated with coloration, the coloration is carotenoid-based (Brawner *et al*., 2000; Loiseau *et al*., 2008; Cote *et al*., 2010). Carotenoid based colorations might be more likely to be associated with CORT, for example, because of potential associations with diet (Brush, 1981; Endler, 1983). As stated above, carotenoids appear to not occur in phrynosomatid lizards (Morrison, Rand, & Frost-Mason, 1995; Morrison, Sherbrook, & Frost-Mason, 1996), including orange gravid coloration of *Sceloporus virgatus* females (Weiss et al., 2011; Weiss, Foerster, & Huddon, 2012).

The AIC analyses involved a series of linear models, to see which best predicted patch coloration as summarized by the color PC score and also for hue and saturation alone. The best models for the color PC scores included capture date, plasma CORT levels, and the percent of the total estimated tail length (%estTL); the next best models had Δ_i values of more than 5. The fact that only capture date, plasma CORT levels and a measure of tail length could predict variation in patch coloration (as summarized by the color PC) suggests that patch coloration may serve in signaling the reproductive status of adult females and energy state, as the tail is a site of fat storage. During pregnancy, viviparous and ovoviviparous lizards can experience changing plasma levels of CORT (Woodley & Moore, 2002; Cartledge & Jones, 2007), but there is also

evidence to the contrary (Girling & Cree, 1995). Reproductive state is changing dramatically from pregnant to post-parturient during the 21-day period when I collected these data, thus the abdomen and patches were stretched early during the collection period but were nearer to typical size late in my collection period. The best models for the two subsequent set of AIC models for hue alone or for saturation alone were the same models as for the color PC, with some minor differences in order.

Blue abdominal patch coloration in adult female *S. jarrovii* lizards may serve in signaling health status (specifically WBC counts), and the size of the abdominal patch may serve as a signal of body size. Capture date was also in the best models predicting variation in patch color (as summarized by PCA), suggesting there was some seasonal variation in coloration. Capture date also was significantly associated with body size, which was changing during the time this study was conducted as heavily pregnant females gave birth. Future studies should test the association between the variables included in this study, other steroid hormones, and the attributes of females' patches, but with better delineation of reproductive condition, by focusing intensive sampling across the breeding season to help tease apart possible signaling roles and physiological mechanisms.

TABLES

Table 1. Mean values of potential phenotypic correlates of color attributes of abdominal patches in adult female *Sceloporus jarrovii* lizards. The abbreviations are used in statistical models and figures elsewhere in this chapter. Stimulus and Focal females were used in a behavioral study (Chapter 2) involving staged intrusion trials. Because the difference in timing of when blood samples and bite force values were measure these data are presented separately. The degrees of freedom (d.f.) and results of unpaired Student T tests, and P value from comparing each mean are also given.

Table on following page.

Abbreviation	Variable description	Mean (±1 SE) Stimulus Female	Focal Females	d.f.	T_{calc}	P value
SVL	Snout-to-vent length, a measure of body length	65.89	63.125	20,19	-0.99	0.33
BMRes	Residual from regression of body mass onto SVL	0.49	-1.14	20,19	-1.78	0.08
PatchArea	Area (in mm) of the blue abdominal patch, left side	0.51	0.60	20,19	-0.54	0.59
% EstTL	Tail length as a % of predicted total tail length	0.91	0.91	20,19	0.63	0.53
2D4D	Ratio of 2nd digit length to 4th digit length, left hand	0.96	0.98	20,19	0.86	0.40
CapDate	Date of capture			20,19		
WBCc	Number of WBCs per 10,000 RBCs	1376.32	1660.00	20,19	1.09	0.28
H:L	Ratio of heterophil numbers to lymphocyte numbers	0.34	0.30	20,19	-0.73	0.47
Plasmod	% RBCs (of 500) infected with *Plasmodium* protozoa	0.12	0.13	20,19	0.52	0.60
MiteC	Number of mites	36.32	34.75	20,19	-0.12	0.90
CORT	Plasma corticosterone concentration (ng/ml)	7.99	5.51	17, 17	-1.30	0.20

Table 2. The total variance explained by each component in a principle components analysis of color attributes of the abdominal patch. The measured color attributes included hue, saturation, and brightness using Adobe Photoshop software.

Total Variance Explained

	Initial Eigenvalues			Extracted Sums of Squared Loadings		
Component	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	1.396	46.52	46.52	1.40	46.52	46.52
2	0.932	31.06	77.58			
3	0.672	22.42	100.0			

Table 3. Factor loading scores for the one component with an Eigenvalue greater than 1.0, in the principal components analysis summarizing abdominal patch color attributes.

Component Matrix[a]	
	Component
	1
Hue	.794
Saturation	-.663
Brightness	.570

Table 4. Models to explain color variation used in subsequent linear modeling using an Akaike's Information Criterion (AIC) approach and their explanations. Variable abbreviations are found in Table 1.

Model #	**Model**	**Explanation**
1	SVL	This model contains a measure of body size.
2	CORT	These models contain measures of immune function and parasitic infection.
3	WBCc **+** *Plasmod* **+** MiteC **+** HL	
4	WBCc ***** *Plasmod* + MiteC + HL	
5	WBCc ***** *Plasmod*	
6	WBCc **+** *Plasmod*	
7	WBCc + *Plasmod* + CORT	
8	MiteC **+** HL	
9	MiteC + HL + CORT	
10	PatchArea	This model contains patch area.
11	%EstTL	These models contain a measure of the percent of the estimated tail length present.
12	%EstTL + CORT	
13	%EstTL + PatchArea	
14	%EstTL + PatchArea + BMres+ SVL	
15	%EstTL + PatchArea + BMres	
16	CapDate	These models contain the capture date.
17	CapDate + CORT	
18	CapDate + CORT + Patch Size	
19	CapDate + PatchSize	
20	2D4D	This model contains the digit ratio.

Table 5. The top models to explain color variation, calculated using linear models for each Akaike Information Criterion (AIC), determined by those models for which the ΔAIC_i is less than 10 with subsequent calculations of AIC scores. K describes the number of variables included in each model. RSS is the residual sum of squares. AICc is the AIC score adjusted for small sample size. ΔAIC_i is the difference between the scores of each model from the score of the best model. w_i is the weight of evidence for each model as the best model. Variable abbreviations are found in Table 1. The target for 5A is the color score from the principal components analysis of hue, saturation, and brightness. The target for 5B is hue. The target for 5C is saturation.

Table 5A.

Model #	**Model**	**K**	**RSS**	**AICc**	**ΔAIC_i**	**w_i**
2	CORT	1	34.144	38.644	0	0.760
17	CapDate + CORT	2	39.142	42.571	3.927	0.107
12	%EstTL + CORT	2	39.534	42.573	3.929	0.107
7	WBCc + *Plasmod* + CORT	3	32.539	47.206	8.562	0.011
18	CapDate + CORT + Patch Size	3	44.712	47.809	9.165	$7.78*10^{-03}$
9	MiteC + HL + CORT	3	44.791	47.811	9.167	$7.77*10^{-03}$

Table 5B.

Model #	**Model**	**K**	**RSS**	**AICc**	**ΔAIC_i**	**w_i**
18	CapDate + CORT + PatchArea	3	347.334	356.873	0	0.468
2	CORT	1	355.162	358.17	1.297	0.245
17	CapDate + CORT	2	351.923	358.812	1.939	0.178
12	%EstTL + CORT	2	357.742	360.631	3.758	0.715
7	WBCc + *Plasmod* + CORT	3	353.726	363.265	6.392	0.019
9	MiteC + HL + CORT	3	360.262	363.280	6.407	0.019

Table 5C.

Model #	**Model**	**K**	**RSS**	**AICc**	**ΔAIC_i**	**w_i**
2	CORT	1	250.481	254.870	0	0.459
12	EstTL + CORT	2	249.018	255.907	1.037	0.273
17	CapDate + CORT	2	254.057	257.046	2.176	0.155
18	CapDate + CORT + PatchArea	3	256.157	259.696	4.826	0.041
7	WBCc + *Plasmod* + CORT	3	255.481	259.98	5.110	0.036
9	MiteC + HL + CORT	3	255.481	259.98	5.110	0.036

FIGURES

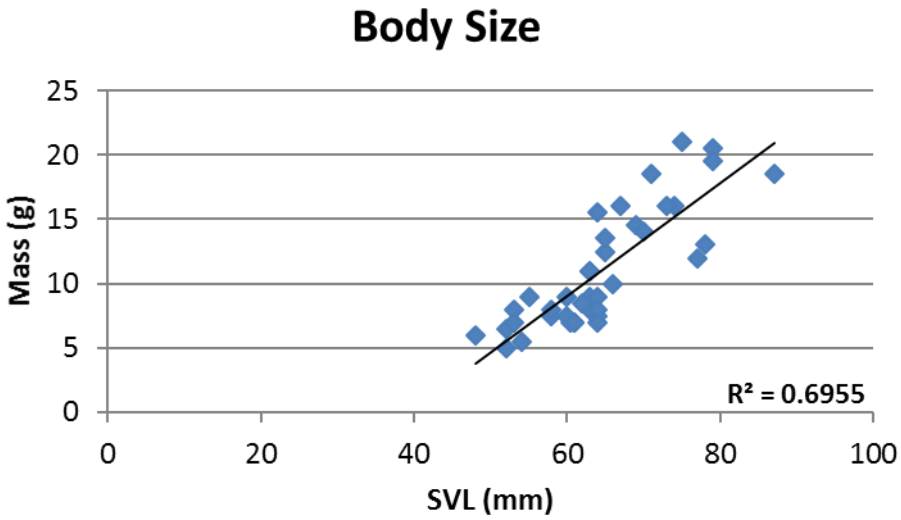
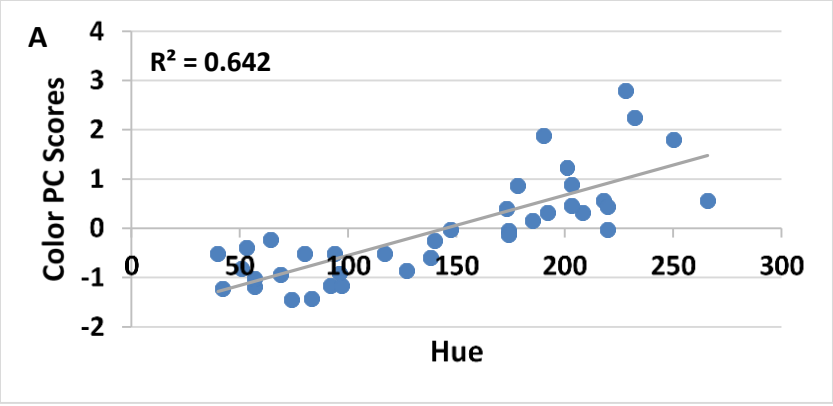
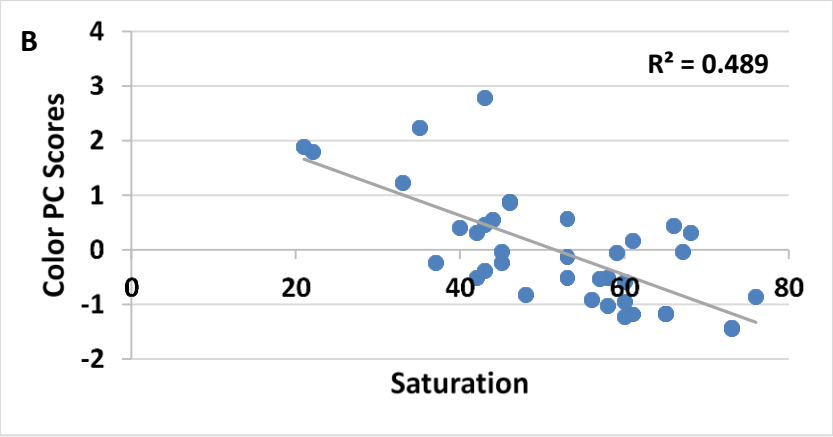


Figure 1. The relationship between body mass, with residuals calculated from a reduced major axis regression, and snout-to-vent length (SVL) in adult female *Sceloporus jarrovii*. R^2 value is from a simple linear regression on Microsoft™ Excel.





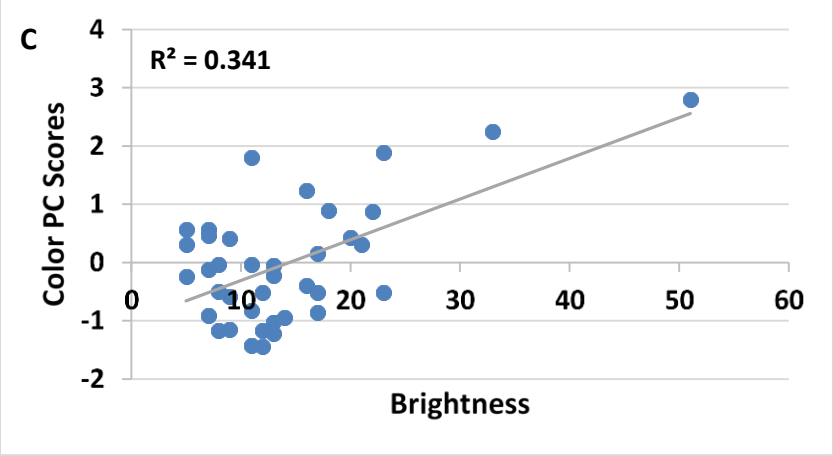


Figure 2. The relationship between the factor loading scores of a principal components analysis of patch color attributes and the individual color attributes, including hue (A), saturation (B), and brightness (C). R^2 values are from simple linear regressions on Microsoft™ Excel.

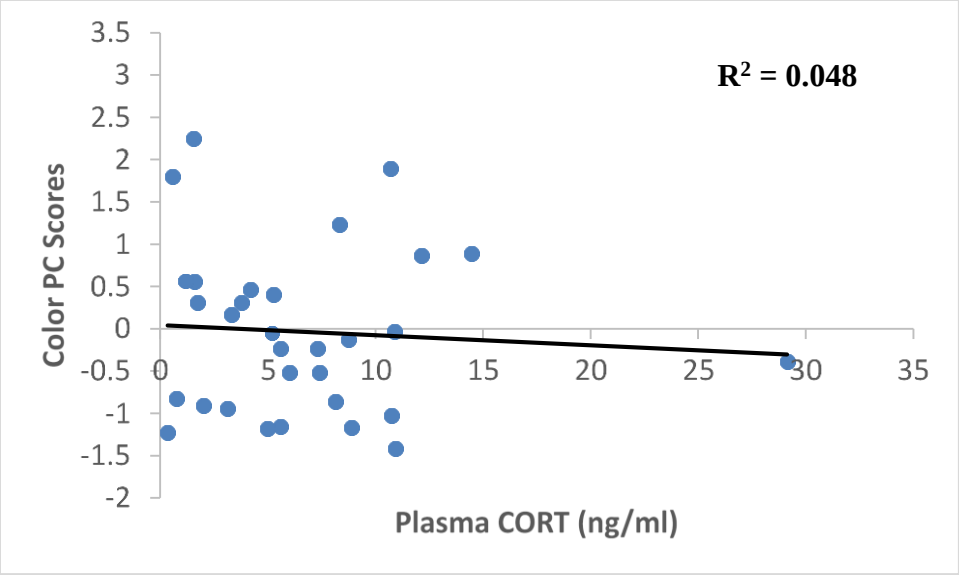


Figure 3. The relationship between abdominal color in adult female *Sceloporus jarrovii*, as summarized by a principal components analysis (PCA) and plasma levels of corticosterone (CORT, ng/ml). R^2 value is from simple linear regression on Microsoft™ Excel.

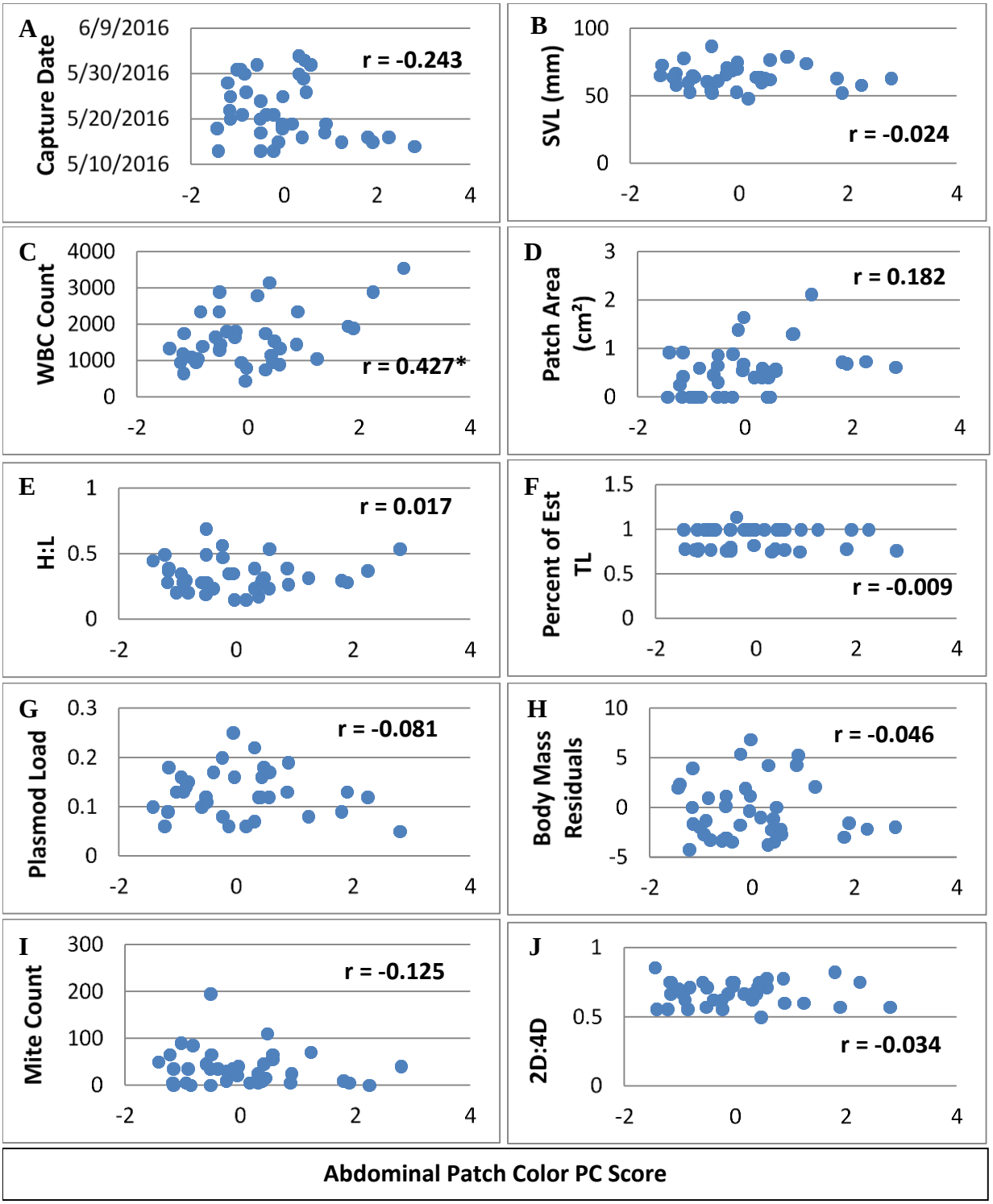


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Figure 4. The relationship between abdominal color in adult female *Sceloporus jarrovii*, as summarized by a principal components analysis (PCA) and each variable included in the AIC models, including capture date (A), snout-to-vent length (SVL, B), white blood cell (WBC) count (C), patch area (D), heterophil to lymphocyte (H:L) ratio (E), the percent of the total tail length (TL) present (F), *Plasmodium* (Plasmod) load (G), body mass residuals (H), mite count (I), and the ratio between the 2^{nd} and 4^{th} digits (2D:4D) of the front left claw (J). Only one PC was extracted from the PCA and high positive PC loading indicate high values hue and brightness (whiter), while high negative loadings indicate high values of saturation (bluer). The number on each plot is the simple Pearson Product Moment correlation coefficient (*, $p < 0.05$).

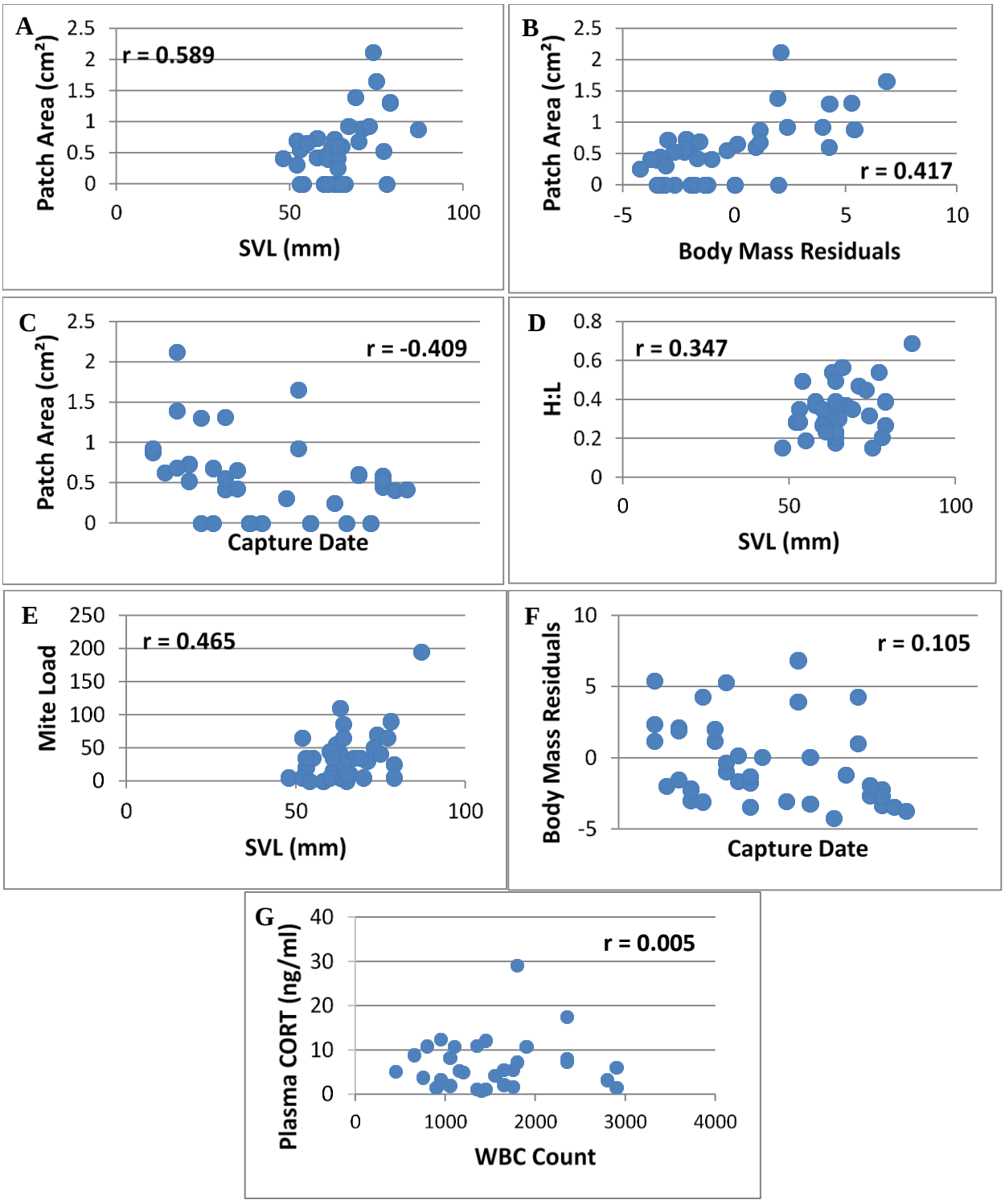

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Figure 5. The significant relationships among the potential phenotypic correlate variables (see Figure 2). These include the relationships between (SVL) and parch area (A), body mass residuals and patch area (B), capture date and patch area (C), SVL and the heterophil to lymphocyte ratio (H:L, D), SVL and mite load (E), capture date and body mass residuals (F), white blood cell (WBC) count and plasma levels of corticosterone (CORT, G). The number on each plot is the simple Pearson Product Moment correlation coefficient. Non-significant correlations are not shown. Abbreviations defined in Table 1.

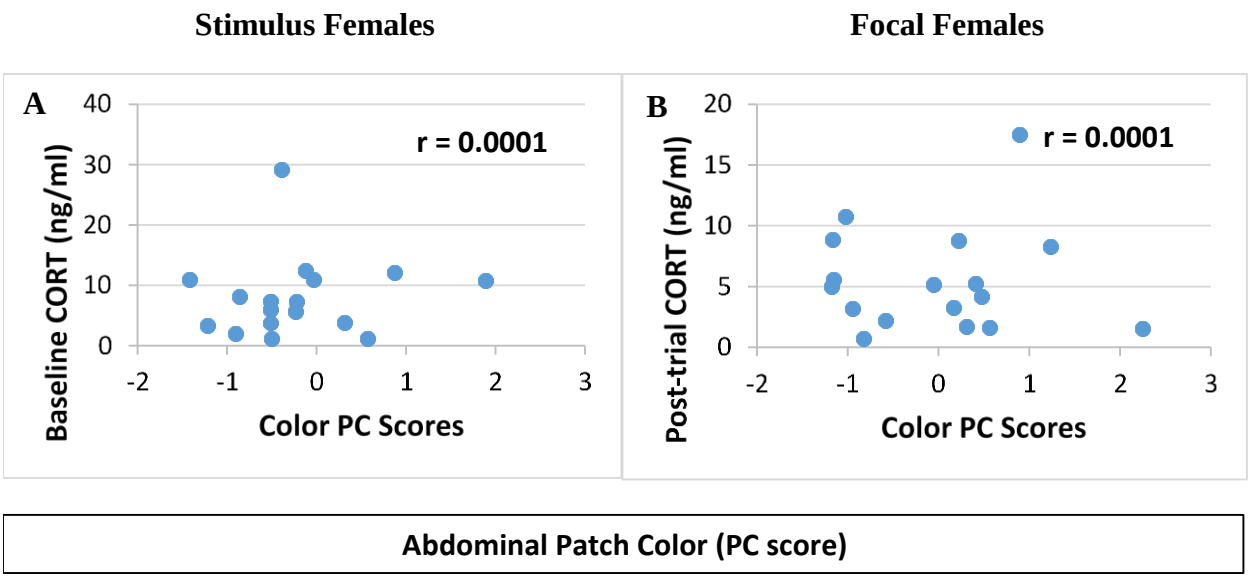

Figure 6. Relationship between plasma corticosterone (CORT) values, for Stimulus (A) and Focal (B) females from staged intrusion behavior trials (Chapter 2), and variation in their ventral patch coloration (PC1 score). Because the difference in timing of when blood samples were taken these data are presented separately. For a stimulus female, blood samples were taken immediately after we encountered and captured her; for a focal female, the sample was taken immediately after ending observations for her behavioral trial. The number on each plot is the simple Pearson Product moment correlation coefficient.

CHAPTER 2

FEMALE AGGRESSION IN *SCELOPORUS JARROVII:* ROLES OF ABDOMINAL BLUE PATCHES

INTRODUCTION

Coloration has a variety of roles in animals (Beddard, 1892). Color can lead to increased fitness in some conditions while decreasing it in others, such as in the case of the bright coloration of male guppies which makes them more successful in mating, but also more conspicuous to predators (Godin & McDonough, 2003). Color can also play a role in crypsis, thermoregulation, or the ability to maintain optimum body temperatures (Kettlewell, 1973), and aposematic, or warning, signaling (Siddiqi *et al*., 2004); however, these factors are unlikely to play a role in the ornaments of female *Sceloporus jarovii* (Phrynosomatidae), the focus of my research, because their patches are only visible during social displays (Ruby, 1978).

Most often, males are ornately colored and females are drabber; however, both male and female *S. jarrovii* express blue ventrolateral color patches on the throat and abdominal regions (Weins, 1999). There are two leading hypotheses for the occurrence of male-typical ornamentation in females. One hypothesis states that female ornaments are the consequence of genetic covariance to males and serve no purpose in females (Lande & Arnold, 1985; Price, 1996). This hypothesis has little support (see reviews by Amundson, 2000 and Kraaijeveld *et al*.,

2007). Another hypothesis which is supported in several species states that female ornaments are the result of direct sexual selection by male choice or female-female competition (Darwin, 1871; Cain & Ketterson, 2012; Stamps, 1973). Thus, the function of female coloration may be similar to the function of coloration in males. These hypotheses are mostly being explored in avian species (Linville *et al*., 1998; Heinsohn, 2008).

Male coloration in phrynosomatid lizards is important for species and sex determination and in aggressive encounters (see review by Cooper & Greenberg, 1992), but much less is known for females. Coloration in male lizards frequently serves as a badge of status (Zucker, 1994; Cooper *et al*., 2009), and is displayed during aggressive encounters which change in seasonal intensity (Klukowski & Nelson, 1998), allowing both individuals to assess one another and avoid physical conflict (Smith & Price, 1973) that could lead to potentially fatal injury (Enquist & Leimar, 1990; Lopez & Martin, 2001). Male-male aggression has been well studied in many animals due, in part, to the prevalence of this behavior in many species as a method of obtaining and retaining access to mates (see reviews by Cooper & Greenberg, 1992 and Baird, 2013). Ornamentation, which frequently functions in male aggressive encounters and could also in females, has been found in males to serve as an indicator of fighting ability and physical measures of prowess, known as resource holding potential (RHP) (Parker 1974; Korzan *et al*., 2000; Korzan *et al*., 2002; Plasman *et al*., 2015).

One species in which female ornamentation and female-female aggression frequently occurs is *Sceloporus jarrovii* (Figure 7). Females of this viviparous species show increased aggression toward consexuals just after giving birth (reviewed in Ruby, 1981; Woodley & Moore, 1999a-b). While the hormonal components underlying female aggression in *S. jarrovii* have been documented (Woodley & Moore, 1999a-b; Woodley & Moore, 2000a-b), there are

still many gaps in our understanding of the phenomenon. These gaps include the role of color patches in aggressive encounters and their correlates to other variables that may predict health and or fighting ability, such as bite force (Anderson, McBrayer, & Herrel, 2008) and immunity. There is another species within the infraorder Iguania that is one of the most heavily studied lizard species for female-female aggression. Female Galapagos marine iguanas (*Amblyrhynchus cristatus*) have a similar pattern of seasonal levels of female-female aggression as is found in *S. jarrovii*, with peak aggression occurring just after oviposition (Rauch, 1988). Similar correlations were found in the hormonal control of aggression in *A. cristatus* (Rubenstein & Wikelski, 2005). Aggression in female *A. cristatus* occurs to protect nest sites (Rauch,1988). Though female *S. jarrovii* are viviparous rather than oviparous, they may elevate aggression to protect the young from cannibalism, which has been documented for this species (Robbins *et al*., 2013), and/or to defend resources for their young during the weeks following birth.

Other factors affect aggressive behavior and fighting ability in male lizards, and may also in females. Larger individuals may be first to display aggression and display more frequently than smaller individuals (Tokarz *et al*., 1985). Larger individuals typically have stronger bite forces than smaller individuals and are therefore able to inflict greater damage on opponents in physical combat (Herrel *et al*., 2005; Lappin & Husak, 2005; Herrel *et al*., 2006; Husak *et al*., 2006). Finally, individuals with better health maintain better stamina (Schall, Bennett, & Putnam, 1982) and higher plasma testosterone concentrations (Dunlap & Schall, 1995), and are thus more likely to succeed in aggressive encounters (Moore & Marler, 1987; Marler & Moore, 1988; Robson & Miles, 2000; Lappin & Husak, 2005).

I studied female-female aggression in *Sceloporus jarrovii,* the Mountain Spiny Lizard. This species makes an excellent model due to its relative abundance, small size, and relative ease

of capture and study, as well as prior published studies. Previous studies on *S. jarrovii* found correlations between plasma testosterone, estrogen, and corticosterone levels and level of aggression between females (Moore, 1986; Woodley and Moore, 1999a-b; Woodley et al., 2000a-b). Here I experimentally examine the role of the abdominal color patches in female-female aggression. Specifically, I conducted staged encounters to determine whether free-ranging ("focal") females differ in their behavioral responses to the introduction of a paint-manipulated ("stimulus") female. The hypothesis that blue is used as a signal used in female-female encounters predicts that the behavior of the focal females will differ in trials involving blue-painted (experimental) versus white-painted (control) stimulus females. If blue-painted females are perceived as having higher RHP than the focal female, the focal may act more submissively to and retreat from blue-painted females or show less aggressive behaviors. If focal females behave more aggressively towards blue-painted females, then blue does not signal RHP and there are several possible hypotheses for why aggression may have increased.

METHODS

Capture and Housing Methods

Experiments took place in Arizona from mid-May to early June, when female-female aggression in this species is at its peak (Woodley and Moore, 1999b). I captured 48 adult female *Sceloporus jarrovii* in the Chiricahua National Forest, in oak-dominant forest with low-flowing streams surrounded by large boulders. I captured females by noosing, a standard procedure involving a slip-knot tied to the end of a long pole. I took GPS coordinates of the site of capture. Lizards were brought back to captivity where I measured mass, snout-to-vent length (SVL), and bite force, and took pictures of their ventral surface for color analyses. Animals were housed

overnight in terraria on shelving units in the Live Animal Housing Facility (LAHF), a locked, screened porch designed for reptiles at the Southwestern Research Station (SWRS). I released females within 1-3m of the site of capture after all necessary data were obtained.

Experimental Design & Aggression Trials

For the female-female encounters, I paint-manipulated females and recorded the responses of free-ranging "focal" females to manipulated "stimulus" females in staged territorial intrusions (STIs). On the day when a stimulus female was captured, I painted the abdominal patches using mixtures of white and blue Apple Barrel brand non-toxic acrylic paint. The stimulus female was painted either as control (N=14) or experimental (N=16); experimental females were "blue-painted" and controls were "white-painted". The blue paint was matched to the top 25% of brightness of female patches seen within the population by examining images from previous studies (Hews *et al*., *unpublished data*) and mixing a 4:1 ratio of blue and white paint. The off-white paint was used as a proxy for maximum patch brightness possible within the population, also matched using images from previous studies to the natural off-white coloration of *Sceloporus jarrovii* abdomens and mixing a 1:6 ratio of blue and white paint. I used stimulus females up to two times in STIs with novel resident (focal) females. On the day after capture, a stimulus female was used up to two STI trials.

For an STI trial, I located a free-ranging female to serve as the focal female. I then exposed this focal female to either a control or a stimulus female, and recorded behavior of the focal. I followed standard protocol to measure aggression by conducting STIs in the field (Marler & Moore, 1988; Hews & Martins, 2013), in which a stimulus female tethered to a telescoping cane fishing pole was placed approximately 0.5m from free-ranging focal female at a slight

decline and within the focal female's line of sight. The base of the pole was anchored using a rock to ensure that the stimulus female was unable to drag the pole. In the field, behavior was monitored for 5 minutes and all movements and actions of resident female was noted on a voice recorder to be scored later. I recorded focal females' behaviors including latency to first behavior, and numbers of behaviors including "retreat", "head turn", "head-bob" and "push-up" displays with 2- or 4-leg modifiers (c.f. Martins 1994), "full-show display", and "charge". Retreats are defined as an individual sprinting 0.5 - 2 m away for a period of time lasting 30 sec to 2 min. Head turns are when an individual simply turns its head to face a new direction and could signal that the individual is looking for possible threats, an escape route, or is simply uninterested in the intruder (Morrison, 2011). Head-bobs involve an individual moving its head in up-and-down motions which could be relatively slow or rapid; if the head-bobs include a 2- or 4-leg body-raising modifier, then the behavior is called a "push-up". These two behaviors are grouped together because of their similarity in aggressive signaling function (Martins, 1994). A full-show display involves an individual elevating its body with all four limbs, flattening its torso ventrolaterally to display its abdominal patches and appear larger, and pacing or hopping around the intruder (Martins, 1993). A charge is when an individual sprints toward the intruder and usually precedes physical contact or biting. If aggression was intense to the point of possible serious harm occurring to either female, I ended the trial early. After ending the STI, I captured the focal female by noosing and immediately took a blood sample (see below). Focal females were then taken back to the lab at SWRS for body size measurements, mite counts, bite force measurements, and digital images. If the focal female was not captured the behavior data from the trial were discarded.

Some focal females appeared to be postparturient (N = 10). This was deduced from several factors, including how flaccid the body walls and skin of the female's torso appeared, the lack of the obvious distended abdominal region of pregnant females, and the seasonal change in appearance of females in the population at large. I did not abdominally palpate any females, but there was an obvious increase in the numbers of these "postparturient"-type females observed over the course of 1 week (dates 28 May – 6 June). This followed an initial period were the large majority of adult females appeared pregnant and then a 1-week period in which overall female activity was greatly reduced and sighting females became difficult.

I assessed several potential covariates that could contribute to explaining difference in behavior of the focal female. Hence, in addition to natural coloration of the focal female, I also assessed: 1) immune function (white blood cell counts, white blood cell to red blood cell ratios, heterophil to lymphocyte (H:L) ratio, 2) loads of the hematoparasite, *Plasmodium spp*, from thin smears; 3) corticosterone level 4) mite loads, and 5) potential correlates of fighting ability (body size, body mass and bite force). Specific details on these measures are provided below.

I took blood samples from all females and then made blood smears immediately following their initial capture. Details on these methods are outlined below. Hence a stimulus female had a blood sample taken the day before use in a STI trial, while a focal female had a blood sample taken immediately after her STI trial. In the lab I first obtained mite counts visually while holding a lizard over a pan of water to catch any mites that detached. This was done twice to ensure that an accurate estimate was obtained. I then weighed lizards with a Pesola scale to the nearest 0.1g and measured their snout-to-vent length (SVL). Next, I tested females for bite force using a force transducer (Kistler 9203) wrapped in a thin rubber pad to induce more vigorous

biting (Lappin *et al*., 2014). I then took a picture of each female's abdomen to measure the natural variation in the size and quality of patch color (see below).

Blood Samples

I took blood samples in the field within 2 min of capture from the retro-orbital sinus by rupturing the vessels with a heparinized microcapillary tube, as outlined by Thaker *et al*. (2009). Following Presnell, Schreibman, & Humason (1997), I made blood smears immediately in the field by placing a drop of blood on a pre-labeled microscope slide and air dried, and then fixed slides in methanol at the field lab at SWRS. Fixed slides were air-dried and stored at room temperature for up to 4 weeks. Once at Indiana State University (ISU), I stained slides with Geimsa (Protocol™ CAT#264-984). I visually scanned slides at 1000x oil immersion to count and classify 100 leukocytes per individual as described by Campbell and Ellis (2013). Total leukocytes per 10,000 RBCs were counted as described by Seddon and Klukowski (2012). The ratio of heterophils to lymphocytes (H:L ratio) was considered a measure of innate immunity and health status (Vleck *et al.*, 2000). I also scanned RBCs for 15 minutes (approximately 500 RBCs examined) and classified them for *Plasmodium* load (Pickering *et al*., 2000). *Plasmodium* were identified visually, following Garnham (1966).

At SWRS I kept whole blood samples on wet ice while in the field, for several hours. In the lab at SWRS, the cell fraction was centrifuged, and for each sample I pipetted the plasma into a clean microcentrifuge vial and stored it in known volumes of 100% ethanol (Goymann *et al*., 2007). Plasma-ethanol samples were stored at -20˚C until assays were performed. I processed hormone assays of corticosterone and testosterone using corresponding enzyme-linked immunosorbent assay (EIA) kits (Enzo Life Sciences Testosterone kit 900-065 and

Corticosterone kit 900-097) previously validated and optimized on *Sceloporus jarrovii* by the Hews lab (following protocols by Wada, Hahn, & Breuner, 2007).

Measurements of Color

To assess patch size and patch color attributes, I then took digital images of the patches. Because coloration in this species is temperature-dependent (Sherbrook *et al*., 1994), females were first warmed to their mean preferred body temperature (33˚C; Schuler e*t al.*, 2011), for 20 minutes (Langkilde & Boronow, 2012). Once removed from the incubator, I took digital images of ventral patches using a digital Canon™ camera. To prevent variation caused by lighting differences, I took all pictures at approximately the same time of day (1500-1700 h) in the same spot, marked with tape, in the same room. The camera flash and auto-adjust settings were turned off to prevent variations caused by camera settings. A Tiffen™ True Color chart and ruler were placed within the pictures and analyzed in each one to verify that no variation in color resulted from either lighting differences or the camera.

I measured size from the images using ImageJ (v1.3, Girish & Vijayalakshmi, 2004). I measured hue, saturation, and brightness of the blue patches using Adobe Photoshop (see Figure 7). Hue is defined as a discernable attribute of color, such as blue versus off-white. Saturation is the range between pure color and gray, such as sky blue or royal blue. Brightness is an attribute related to the luminance of an object in comparison with its surroundings. In the case of brightness, white would be the brightest color, while black would be the least bright.

Statistical Analysis

All analyses were run using IBM-SPSS (v19, IBM Corp.). In the analyses, I converted numbers of behavior acts to per minute rates (pmr) for each behavior. For analyses of aggression, I first calculated aggression values for each focal female using the factor loading scores from a principal components analysis with Varimax rotation ("Behavior PCA"), which yielded two significant components with Eigenvalues >1 ("Behavior PC1" and "Behavior PC2"). A second PCA included patch color attributes, such as hue, saturation, and brightness, and yielded only one significant component ("Color PC"). I calculated body mass residuals ("BMRes") from a reduced major axis regression of SVL and mass. I verified that all variables used had normal distribution, and thus needed no further transformations.

To determine whether paint treatment influenced the behavior of focal females, I used a MANCOVA in which latency, Behavior PC1, Behavior PC2, and each individual behavior were included as the dependent variables. Treatment (white- or blue-painted) was the independent variable and the size difference between each pair of females was a covariate. If more blue coloration signals RHP, then focal females who are naturally more blue should behave more aggressively toward white-painted stimulus females.

Two sets of Aikiake Information Criterion (AIC) analyses, each with thirty-seven linear mixed models, were used to detect the best model for assessing associations between focal females' Behavior PC scores and measures of their immune function, resource holding potential, and natural coloration. Hence, included in each model was size difference between each pair of females in a trial as the random factor, and as the dependent variable I used the Behavior PC scores from the first significant principal component (for the first set of AIC models) and the significant principal component from the behavior analysis (for the second set of AIC models).

All other variables that might affect behavior are included as independent variables, including focal female (natural) color, hormone measurements, body size, bite force, *Plasmodium* load, ectoparasite load, WBC count, and H:L ratio. If stronger females are more aggressive, then focal females' positive physiological measures, such as body mass residuals, should explain the greatest proportion of variance with their aggressive Behavior PC scores.

RESULTS

I conducted 29 trials in which I introduced the paint-manipulated stimulus females (blue or white paint) to focal females, but only captured 19 focal females. Trials were conducted from May 16 – June 6, 2016, between 1000 hr and 1400 hr. Average trial duration was 265 sec (range 120-429 sec). Female reproductive condition was not confirmed, though most females captured were heavily gravid during May and had just undergone parturition in June (readily apparent through visual inspection). Females varied in coloration and body size, even across this short period of the reproductive season (see Table 7). Coloration may vary with reproductive state and hormones, and hence affect behavioral responsiveness to intruders (Woodley & Moore, 1999a-b). Similarly, body size difference can affect behavioral responsiveness. Therefore, I used size differences and natural coloration of the focal female as covariates in my analyses of behavior.

Behavioral Responses

Principal components analysis (PCA) of the per minute rate of behaviors of focal females during the STI yielded two significant components, as indicated by Eigenvalues >1.00 (Table 8). The first component, "aggressive behavior", included head bobs and push-ups, full show displays, and charges and explains 58% of the observed variance. The second component,

"submissive behavior", included retreats and head turns and explains 24% of the observed variance. Hence subsequent analyses described below included the factor loading scores from these two significant components.

Paint-Treatment Effects

To assess paint treatment effects and whether variation in behavior (individual behaviors, PC1 & PC2, latency to respond) could be explained either by size difference of the female pairs or by natural coloration of the focal female, these variables were included as covariates in an initial multivariate analysis of covariance (MANCOVA) testing the effect of treatment (white-painted or blue-painted) on the focal females' Behavior PC scores. Neither body size difference of female pairs nor natural color of the focal explained variation in latency to behave (size difference: $F_{10,8} = 1.186$, $P = 0.295$; natural color: $F_{10,8} = 0.053$, $P = 0.822$) or variation in behavior explained by PC1 (size difference: $F_{10,8} = 0.198$, $P = 0.663$; natural color: $F_{10,8} = 0.616$, $P = 0.446$) or PC2 (size difference: $F_{10,8} = 1.840$, $P = 0.196$; natural color: $F_{10,8} = 0.540$, $P = 0.474$, Figure 9). Because the covariates were non-significant they were dropped from the model. When size difference and focal female color were dropped, Treatment (blue- versus white-paint) did not significantly explain behavior in MANCOVAs testing either individual behavior rates, latency to first behavior, or when using the factor loading scores (PC1, PC2) from the PCA of behavior rates (Table 9, Figure 8).

AIC analyses

To determine the best models for predicting behavior, as summarized by Behavior PC1, a total of thirty-seven models containing combinations of sixteen different variables (defined in

Table 6) were run (Table 10). The top five models and the model containing SVL alone are presented separately with descriptive statistics (Table 11A). The top model contains SVL, BMRes, and bite force. Associations between the individual variables included in Table 11A and Behavior PC1 are shown in Figures 10 and 11.

The same process was used to determine the best models for predicting the behavior summarized by Behavior PC2 (see Table 10 for models). The descriptive statistics for top five models and the model containing SVL alone are shown (Table 11B). The top model contains SVL, BMRes, bite force, and CORT. Associations between the individual variables included in Table 11B and Behavior PC2 are shown in Figures 10 and 11.

DISCUSSION

I found no clear effect of abdominal patch manipulation of opponents on resident female behavior in STIs. When examining other possible predictors of behavior, I found that direct measures of fighting ability, such as body size and strength (measured in bite force) have the strongest predictive ability. Low sample size may have prevented detection of other effects, including coloration, on behavior. Further, in spite of focal and stimulus females being assigned as they were encountered, there was an apparently non-random assignment (based on size differences) for blue-painted versus white-painted STI trials (see Figure 9).

Unfortunately, this species was less abundant at our study site at East Turkey Creek in Portal, AZ in 2016 which prevented me from size-matching females in each trial. Surprisingly, the size difference between the focal and stimulus females in each trial had no significant effect on the focal's behavior. In other species across taxa, this is often an important factor in agonistic behavior (Stamps, 1977; Tokarz, 1985). It is possible that low sample sizes prevented detection

of the effect of body size differences on behavior. Pairs of females used in STIs had an even range of size differences, with an average size difference of 1.02 mm and a range of -11 to 16 mm (calculated as SVL of focal female minus SVL of stimulus female; Table 7). In addition, lack of a size effect may have been contributed to by having a fairly balanced number of preparturient (N = 9) versus postparturient (N = 10) focal females. Some researchers have proposed that aggression may vary with reproductive state (Woodley & Moore, 1999b). Interestingly, many researchers suggest female-female aggression in reptiles centers on defense of food (Simon, 1975; Stamps, 1977). About half of our trials (10/19) included postparturient focal females, and these females were observed to be foraging in 3 of the 10 trials (as opposed to 0 of the 9 trials using preparturient focals). Hence, access to food is likely an important factor in *S. jarrovii* female aggression.

The paint manipulation of the abdominal patches of the stimulus females also had no significant effect on the behavior of the focal females. This is contrary to the results found in several avian species with ornamented and aggressive females (Whiting *et al*., 2006). However, in animals for which aggression was not correlated to color on the visible spectrum, several species have UV-absorbing or -reflecting ornaments that may contribute to their behavior during agonistic encounters, as has been found in stickleback fish (Rick & Bakker, 2008), blue tit birds (Alonso-Alvarez *et al*., 2004), and Augrabies flat lizards (Whiting *et al*., 2006). Female *S. jarrovii* also have UV reflecting patches, which vary between individuals (Figure 13; and see Ossip-Klein *et al*., 2015), but the paint used on their abdominal patches did not differ in UV reflectance or absorbance. It is possible that females assess one another based on their UV reflectance rather than visible color because they likely have an opsin which detects UV light, as

confirmed for many other species within their family (Alberts, 1989; Fleishman, Loew, & Leal, 1993). Future studies should test this prediction.

The exploratory set of AIC models predicted that the best covariates of the focal female's behavior were her body size, as described by body mass residuals (calculated using RMA regressions), SVL, bite force, and plasma CORT levels. One interpretation is that female *S. jarrovii* have some concept of their own size and strength and this affects their agonistic behavior (Tokarz, 1985). In addition or alternatively, stimulus females may detect some aspect of the focal females resource holding potential (such as body size) that correlates with the predictive variables identified in the AIC analysis, and behaves differently to the focal female (such as less aggressively), who in turn response with increased aggression (Thompson & Moore, 1991). Plasma levels of CORT were negatively, but not significantly, associated with aggressive behaviors, as summarized by Behavior PC1. Experimental studies have demonstrated that CORT reduces levels of aggression in lizards (Tokarz, 1987; Denardo & Licht, 1993; Yang & Wilczynski, 2003), although not always (Greenberg & Crews, 1990).

Using the variables contained in the top models of the first AIC, subsequent ANOVA revealed that variation in Behavior PC2 (interpreted as submissive behaviors) was significantly associated with variation in bite force, CORT, BMRes, SVL, and the pair size difference. We failed to find variables that explained differences in PC1 (aggression by the focal female) in our STI trials, including paint treatment (blue, white), body size, size differences, and relative body mass. Low sample size and our large range of size differences between Focal and Stimulus females likely contributed to large variance in behavioral responses to intruder females.

TABLES

Table 6. The following variable abbreviations are used in statistical models and figures elsewhere in this chapter.

Abbreviation	Variable description
SVL	Snout-to-vent length, a measure of body length
BMRes	Residual from regression of body mass onto SVL
BiteForce	The force of an individual's bite on metal plates
PatchArea	Area (in mm) of the blue abdominal patch, left side
Hue	The base color of the abdominal patch, left side
Saturation	The purity of the color of the abdominal patch, left side
Brightness	The luminance of the color of the abdominal patch, left side
% EstTL	Tail length as a % of predicted total tail length
CapDate	Date of capture
WBCc	Number of WBCs per 10,000 RBCs
H:L	Ratio of heterophil numbers to lymphocyte numbers
Plasmod	% RBCs (of 500) infected with *Plasmodium* protozoa
Mite Load	Number of mites
CORT	Plasma corticosterone concentration (ng/ml)

Table 7. A comparison of attributes of females used in the behavior trials. Variables: SVL, snout-to-vent length; Color, factor loading scores from a Principal Component Analysis of measures of hue, saturation and chroma taken from standardized digital images of each female. Patch area is the size of the blue abdominal patch, in mm squared, measured using image analysis tools.

	Focal Females (N=19)			Stimulus Females (N=15)			Size Difference (Focal - Stim) in mm
	Mean	SD	Range	Mean	SD	Range	
SVL (mm)	63	6.496	58 to 78	66.846	7.581	52 to 77	Mean: 1.02 Range: -11 to 16 SD: 17.620
Patch Color score	0.205	1.179	-1.16 to 2.80	-0.345	0.784	-1.448 to 1.233	
Patch Area (cm^2)	0.681	0.459	0.4 to 2.118	0.925	0.612	0.247 to 2.118	

Table 8. Eigenvalues and component loadings of the two significant principal components that summarized the per minute rate (PMR) of behavior of focal females recorded during staged territorial intrusions with white-painted (White) or blue-painted (Blue) stimulus females. Component loading values in bold were significant at $P < 0.05$. *Abbreviations*: RetreatPMR (per minute rate of retreats), HdTrnPMR (per minute rate of head turns), HBPuPPMR (rate of head bobs and push-ups), FllShwPMR (rate of full show displays), ChgPMR (rate of charges).

	Component	
	1	2
Eigenvalue	2.912	1.197
RetreatPMR	-.299	**-.731**
HdTrnPMR	-.067	**.872**
HBPuPMR	**.941**	.138
FllShwPMR	**.940**	.107
ChgPMR	**.957**	.073

Table 9. Results from a MANCOVA testing for an effect of paint treatment on each behavior of the focal female recorded during staged territorial intrusions. Focal females were exposed to either a blue-painted or white-painted stimulus female, and the resulting per-minute rates of behavior and latency to first response of each focal female were recorded. Individual behaviors recorded include retreats (RetreatPMR), head turns (HdTrnPMR), head bobs and push-ups (HBPuPPMR), full show displays (FllShwPMR), and charging (ChrgPMR). Also included are the two principle components from the behavior PCA, in which "BehavPC1" includes the aggressive behaviors from the first significant component and "BehavPC2" includes the submissive behaviors from the second significant component. The covariate, which was the signed size difference between the focal and stimulus female, was not significant.

Dependent Variable	**F value (d.f. = 1,17)**	**P value**
Latency	1.841	0.191
BehavPC1	0.590	0.566
BehavPC2	0.765	0.482
RetreatPMR	0.651	0.535
HdTrnPMR	0.768	0.472
HBPUPMR	0.231	0.797
FllShwPMR	0.384	0.687
ChrgPMR	1.115	0.352

Table 10. The linear mixed models used in the two sets of Akaike's Information Criterion (AIC) and their explanations, for predicting behavioral responses of focal females in the staged territorial intrusion trials. The first AIC was used to test the best model for predicting behavior, as summarized by behavior PC1, which contains head bobs, push-ups, full show displays, and charges. The second AIC was used to test the best model for predicting behavior, as summarized by behavior PC2, which contains head turns and retreats. Variable descriptions can be found in Table 1. The categorical variable "FocSizCat" (for SVL, either FOC > Stim or FOC < Stim) was included as fixed factor in all models.

Table on following page

Model#	Model	Explanation
1	SVL	These models include measures of size and strength.
2	BMRes + BiteForce	
3	SVL + BMRes + BiteForce	
4	SVL + BMRes + BiteForce + CORT	
5	WBCc + *Plasmod* + MiteC + HL	These models include measures of immune function and rates of infection from parasites.
6	WBCc * *Plasmod* + MiteC + HL	
7	WBCc * *Plasmod*	
8	WBCc + *Plasmod*	
9	WBCc + *Plasmod* + CORT	
10	MiteC + HL	
11	MiteC + HL + CORT	
12	CORT	
13	ColorPC	These models include ornamental patch descriptors.
14	Hue	
15	Brightness	
16	Saturation	
17	PatchSize	
18	PatchSize + Saturation	
19	%EstTL	These models include the percent of the estimated total tail length present.
20	%EstTL + CORT	
21	%EstTL + PatchSize	
22	%EstTL + PatchSize + BMR + SVL	
23	%EstTL + PatchSize + BMR	
24	CapDate	These models include time the date of capture and treatment group of the focal females.
25	CapDate + CORT	
26	CapDate + ColorPC	
27	CapDate + ColorPC + PatchSize	
28	CapDate + PatchSize	
29	TreatStim + ColorPC	These models include the treatment group (blue- or white-painted stimulus female) that each focal female was presented.
30	TreatStim + Sat	
31	TreatStim + Bright	
32	TreatStim + Hue	
33	TreatStim + *Plasmod* + WBCc	
34	TreatStim + MiteC + HL + *Plasmod* + WBCc	
35	TreatStim + MiteC + HL	
36	TreatStim + BiteForce	
37	TreatStim + %EstTL + PatchSize	

FocSizCat (for SVL, either FOC > Stim or FOC < Stim) included as fixed factor in all models

Table 11A. The top six models for predicting Behavior PC1 (aggressive behaviors of focal female in the STI trials). Top models were determined by those with ΔAIC_i values less than ten, and the model containing SVL alone are presented here along with additional descriptive statistics. K describes the number of variables in each model. RSS is the residual sum of squares. AICc is the AIC score adjusted for small sample size. ΔAIC_i is the difference between the scores of each model from the score of the best model. W_i is the weight of evidence for each model as the best model. ER is the evidence ratio with respect to the best model. The categorical variable "FocSizCat" (for SVL, either FOC > Stim or FOC < Stim) was included as fixed factor in all models. The complete set of model data can be found in Appendix 2.1. Variable abbreviations are defined in Table 1.

Model #	**Model**	**k**	**RSS**	**AICc**	**ΔAIC_i**	**w_i**
3	SVL + BMRes + BiteForce	3	23.273	27.273	0	0.537
4	SVL + BMRes + BiteForce + CORT	4	22.825	28.865	1.592	0.242
2	BMRes + BiteForce	2	26.548	29.881	2.608	0.146
37	TreatStim + BiteForce	2	17.625	31.625	4.352	0.061
12	CORT	1	30.533	35.733	8.460	0.008
25	CapDate + CORT	2	28.169	36.836	9.563	0.005
1	SVL	1	57.478	59.764	32.491	$4.73*10^{-8}$

Table 11B. The top six models for predicting Behavior PC2 as determined by those with ΔAIC_i values less than ten and the model containing SVL alone are presented here along with additional descriptive statistics. K describes the number of variables in each model. RSS is the residual sum of squares. AICc is the AIC score adjusted for small sample size. ΔAIC_i is the difference between the scores of each model from the score of the best model. W_i is the weight of evidence for each model as the best model. ER is the evidence ratio with respect to the best model. The categorical variable "FocSizCat" (for SVL, either FOC > Stim or FOC < Stim) was included as fixed factor in all models. The complete set of model data can be found in Appendix 2.2. Variable abbreviations are defined in Table 1.

Model #	**Model**	**k**	**RSS**	**AICc**	**ΔAIC_i**	**w_i**
4	SVL + BMRes + BiteForce + CORT	4	26.978	32.978	0	0.759
2	BMRes + BiteForce	2	33.837	37.171	4.193	0.093
3	SVL + BMRes + BiteForce	3	33.818	37.814	4.836	0.068
12	CORT	1	33.897	39.097	6.119	0.036
37	TreatStim + BiteFrc	2	25.903	39.903	6.925	0.025
20	%EstTL + CORT	2	31.161	39.827	6.849	0.024
25	CapDate + CORT	2	31.853	40.519	7.451	0.017
1	SVL	1	57.546	59.832	26.845	$1.12*10^{-6}$

FIGURES

Figure 7. Variation in coloration of the abdominal patches of adult female *Sceloporus jarrovii*.

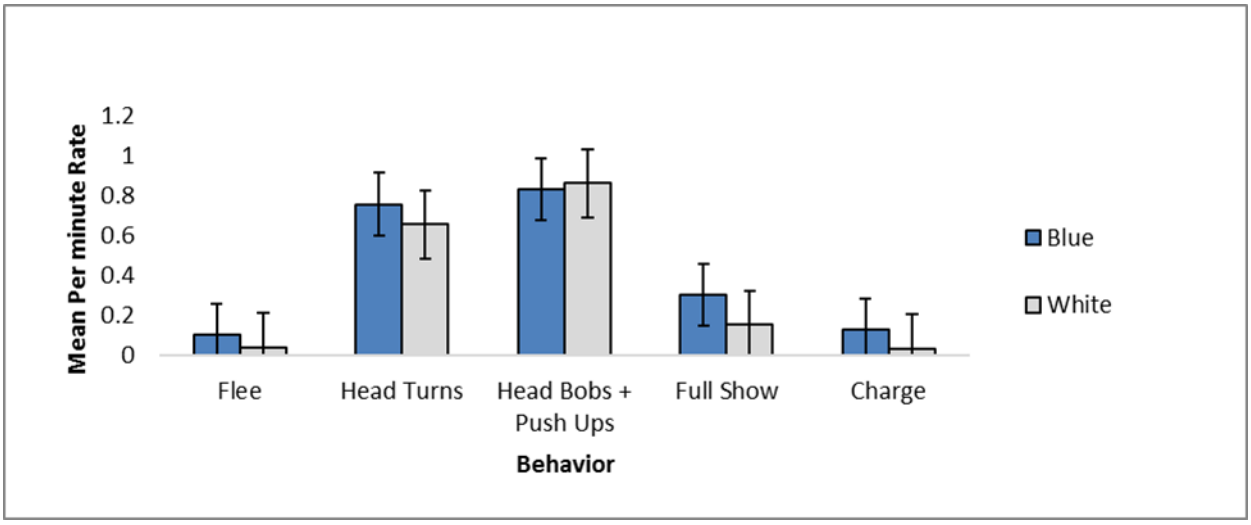

Figure 8. Per minute rates of behavior of focal females recorded during staged territorial intrusions with either a blue-painted (Blue, N = 10 trials) or white-painted (White, N = 9 trials) stimulus females. Trials averaged 265.33 seconds in duration (range 120-429 sec). Means ± 1 SE.

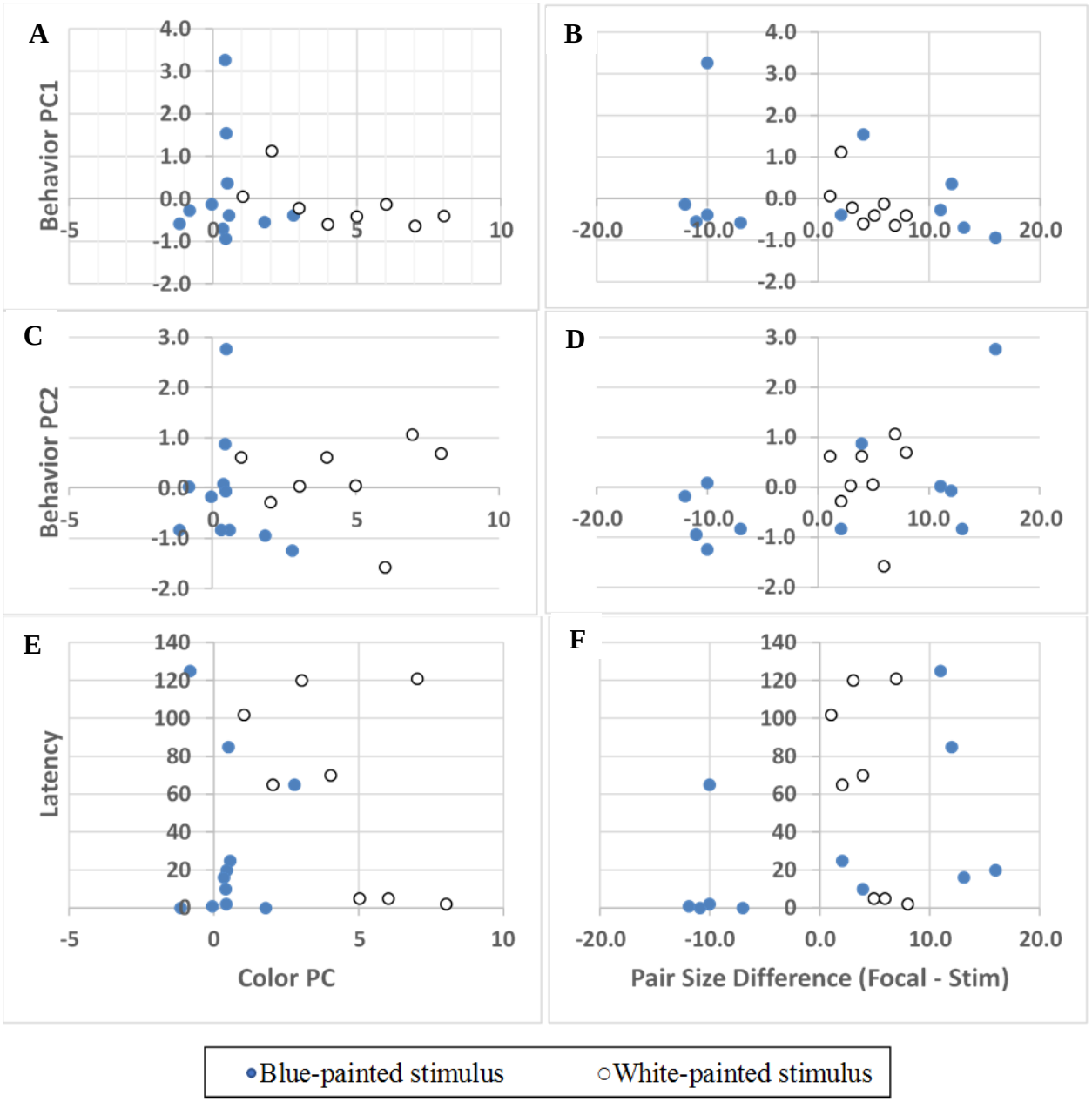

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Figure 9. Distributions of behavior, natural color, and the difference in sizes between pairs of females (Focal – Stimulus) for focal females in trials with blue-painted stimulus females or with white-painted stimulus females. These include the distribution of factor loading scores from the PCA of natural color ("Color PC") and the first component of the PCA of behavior ("Behavior PC1"), which includes retreats and head turns (A), the distribution of the size difference between pairs and their scores from Behavior PC1 (B), the distribution of focal females' Color PC scores and their Behavior PC2 scores, which includes head bobs and push-ups, full show displays, and charges (C), the distribution of the size difference between each pair of females and their Behavior PC2 scores (D), the distribution of focal females' Color PC scores and their latency to their first behavior (D), the distribution of the size difference between each pair of females and their latency to their first behavior (E).

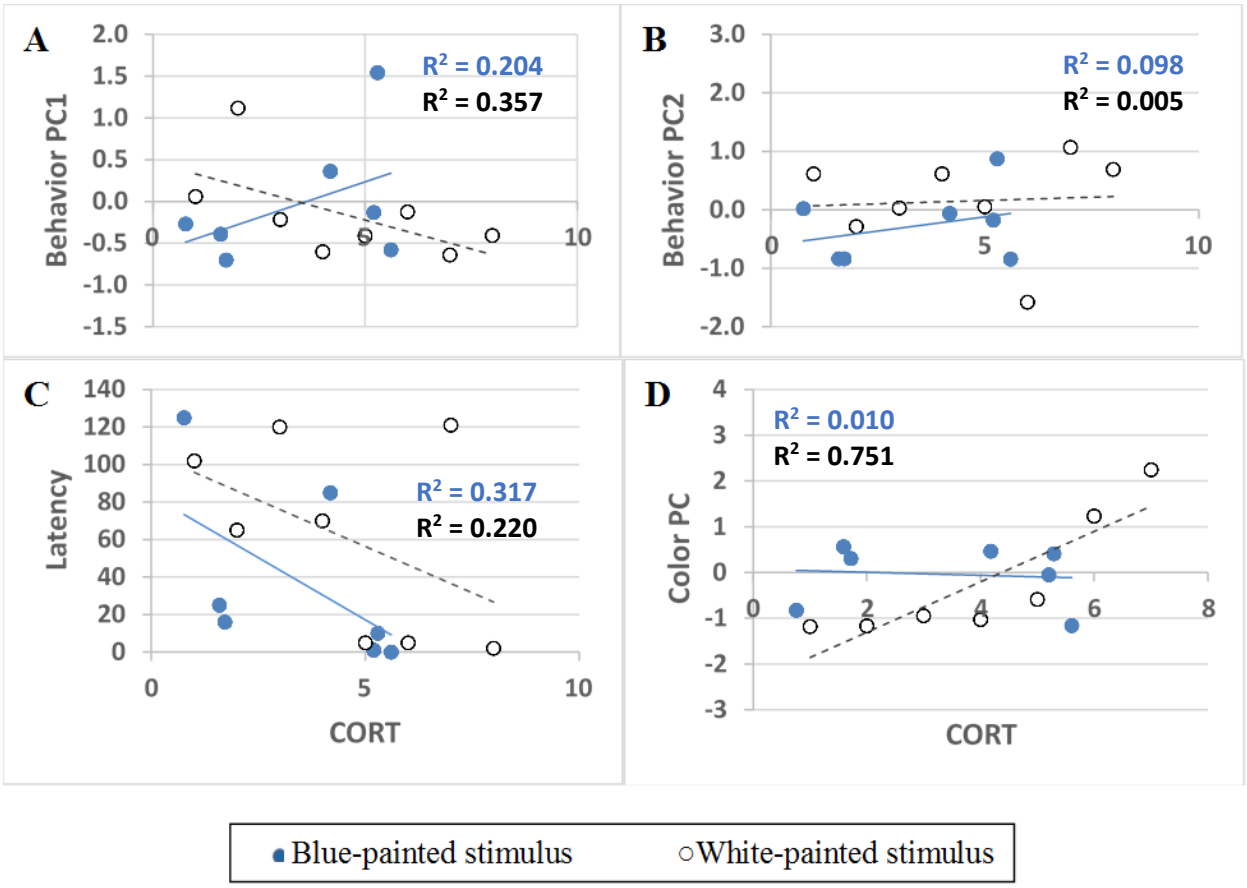

Figure 10. The relationships between corticosterone (CORT) and responses of focal females in the staged trials, including aggressive behavior (A), submissive behavior (B), latency (C), and the focal female's natural coloration ("Color PC", D). PC1 is defined by head bobs, push-ups, full show displays, and charges. PC2 is defined by retreats and head turns. The R^2 values are from simple linear regressions on Microsoft™ Excel.

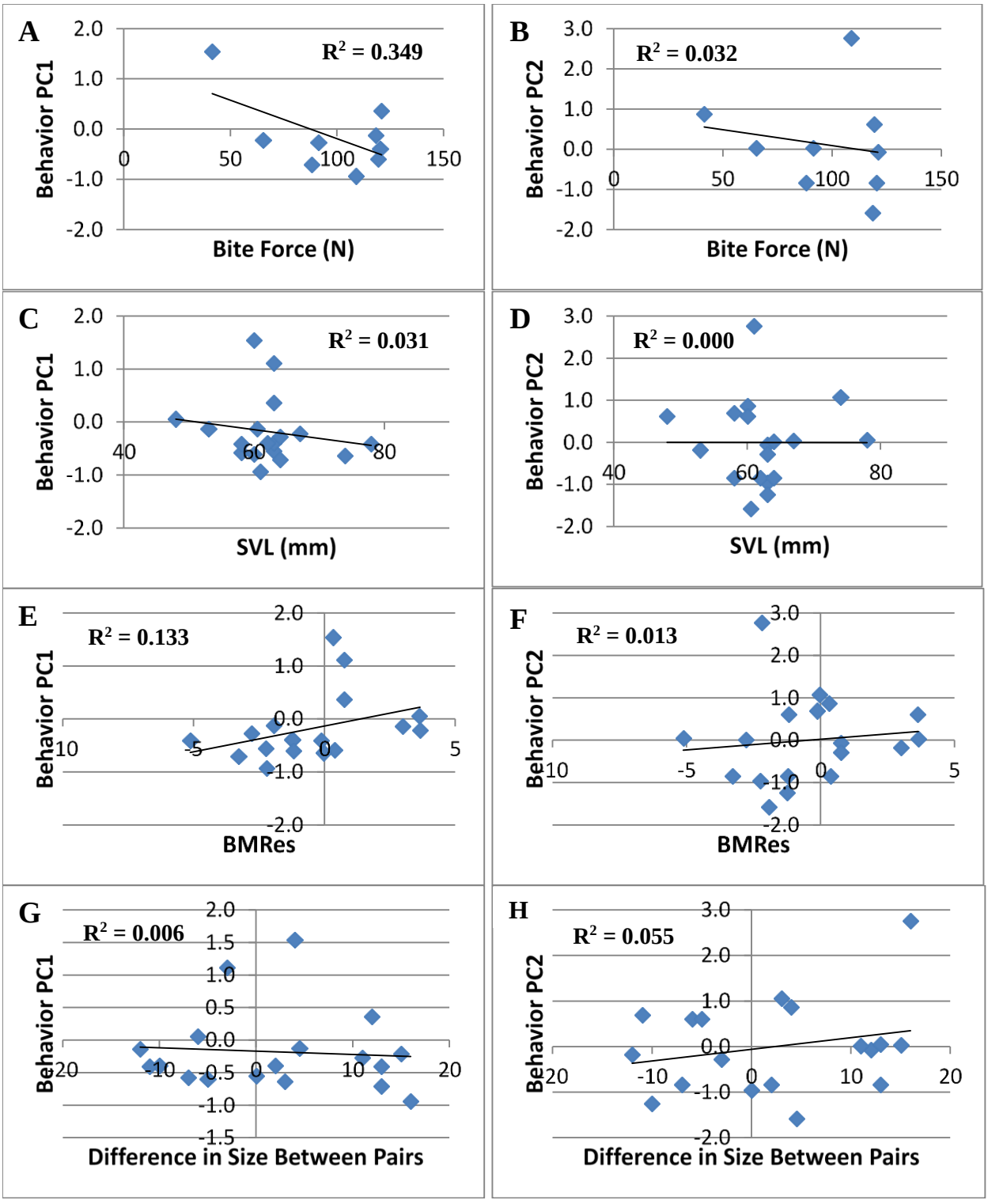

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Figure 11. The relationship between the variables identified in the top Akaike's Information Criterion models [including bite force (A-B), snout-to-vent length (SVL, C-D), body mass residuals (BMRes, E-F), and the size difference between pairs (G-H)] and behavior, as summarized by two principal components (PC1 and PC2). Behavior PC1 contains head bobs, push-ups, full show displays, and charges. Behavior PC2 contains retreats and head turns. The R^2 values are from simple linear regressions on Microsoft™ Excel.

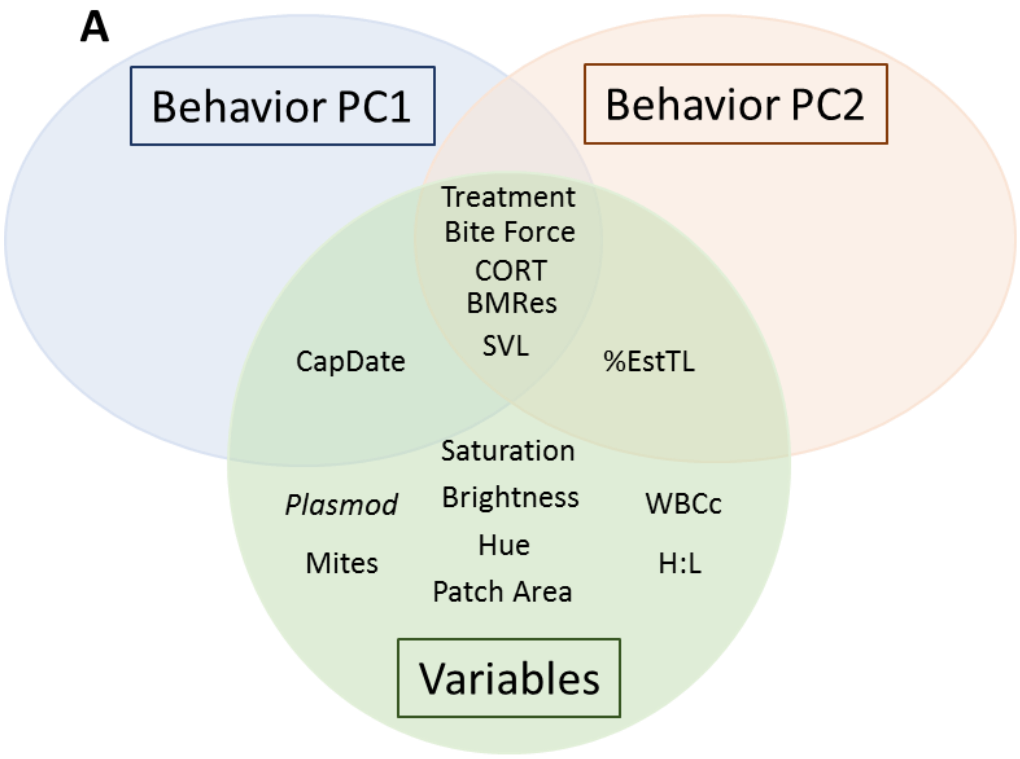

Figure 12. Summary of the variables from the most predictive models for behavior, as summarized by a principal components analysis. Behavior PC1 contains head bobs, push-ups, full show displays, and charges. Behavior PC2 contains retreats and head turns. Variables in the center of the diagram predicted both Behavior PC1 and Behavior PC2. Variables overlapping with only one Behavior PC predicted only that set of behaviors. Variables at the bottom had no predictive power. Variable abbreviations and descriptions can be found in Table 1.

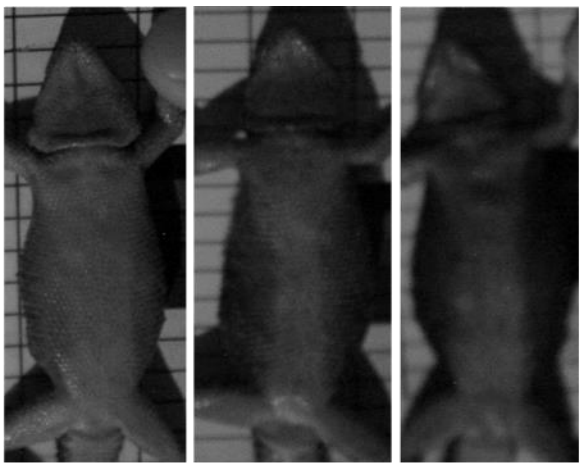

Figure 13. Female *Sceloporus jarrovii* ventral patches vary in their degree of UV reflectance, shown here as lowest to highest degree of UV reflectance.

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APPENDIX

Appendix 1.1. The complete model data for the Akaike's Information Criterion (AIC) of color, as summarized by a principal components analysis of hue, saturation, and brightness. Models are ordered by lowest to highest ΔAIC_i. K describes the number of variables included in each model. RSS is the residual sum of squares. AICc is the AIC score adjusted for small sample size. ΔAIC_i is the difference between the scores of each model from the score of the best model. w_i is the weight of evidence for each model as the best model. The six best-supported models are in bold. Variable abbreviations are found in Table 1.

Models on following page.

Model #	Model	K	RSS	AICc	ΔAIC_i	Wi
2	CORT	1	34.144	38.644	0	$7.60*10^{-1}$
17	CapDate + CORT	2	39.142	42.571	3.927	$1.07*10^{-1}$
12	%EstTL + CORT	2	33.144	42.573	3.929	$1.07*10^{-1}$
7	WBCc + *Plasmod* + CORT	3	32.539	47.206	8.562	$1.05*10^{-2}$
18	CapDate + CORT + Patch Size	3	44.712	47.809	9.165	$7.78*10^{-3}$
9	MiteC + HL + CORT	3	44.791	47.811	9.167	$7.77*10^{-3}$
19	CapDate+ PatchSize	2	51.448	53.698	15.054	$4.09*10^{-4}$
16	CapDate	1	54.509	56.744	18.1	$8.92*10^{-5}$
15	%EstTL+ PatchArea + BMres	3	104.954	107.075	68.431	$1.05*10^{-15}$
13	%EstTL+ PatchArea	2	107.962	110.079	71.435	$2.34*10^{-16}$
10	PatchArea	1	108.349	110.464	71.82	$1.93*10^{-16}$
20	ArcR2R4	1	110.22	112.334	73.69	$7.57*10^{-17}$
14	%EstTL + PatchArea + BMres + SVL	4	110.213	112.338	73.694	$7.56*10^{-17}$
11	%EstTL	1	112.722	114.837	76.193	$2.17*10^{-17}$
6	WBCc + *Plasmod*	2	117.61	119.727	81.083	$1.88*10^{-18}$
8	MiteC + HL	2	118.801	120.919	82.275	$1.04*10^{-18}$
1	SVL	1	119.347	121.461	82.817	$7.90*10^{-19}$
5	WBCc x *Plasmod*	2	121.345	123.459	84.815	$2.91*10^{-19}$
3	WBCc + *Plasmod* + MiteC + HL	4	123.608	125.733	87.089	$9.33*10^{-20}$
4	WBCc x *Plasmod* + MiteC + ArcHL	4	132.829	134.958	96.314	$9.26*10^{-22}$

Appendix 1.2. The complete model data for the Akaike's Information Criterion (AIC) of hue. Models are ordered by lowest to highest ΔAIC_i. K describes the number of variables included in each model. RSS is the residual sum of squares. AICc is the AIC score adjusted for small sample size. ΔAIC_i is the difference between the scores of each model from the score of the best model. w_i is the weight of evidence for each model as the best model. The six best-supported models are in bold. Variable abbreviations are found in Table 1.

Models on following page.

Model #	Model	K	RSS	AICc	ΔAIC_i	Wi
18	CapDate + CORT + Patch Size	3	347.334	356.873	0	$4.68*10^{-1}$
2	CORT	1	355.162	358.17	1.297	$2.45*10^{-1}$
17	CapDate + CORT	2	351.923	358.812	1.939	$1.78*10^{-1}$
12	%EstTL + CORT	2	357.742	360.631	3.758	$7.15*10^{-2}$
7	WBCc + *Plasmod* + CORT	3	353.726	363.265	6.392	$1.92*10^{-2}$
9	MiteC + HL + CORT	3	360.262	363.28	6.407	$1.90*10^{-2}$
10	PatchArea	1	403.808	408.171	51.298	$3.40*10^{-12}$
19	CapDate+ PatchSize	2	402.745	409.495	52.622	$1.75*10^{-12}$
13	%EstTL+ PatchArea	2	403.808	410.558	53.685	$1.03*10^{-12}$
16	CapDate	1	408.508	412.872	55.999	$3.24*10^{-13}$
1	SVL	1	410.162	414.525	57.652	$1.42*10^{-13}$
5	WBCc x *Plasmod*	2	410.162	414.525	57.652	$1.42*10^{-13}$
11	%EstTL	1	410.162	414.525	57.652	$1.42*10^{-13}$
20	ArcR2R4	1	410.162	414.525	57.652	$1.42*10^{-13}$
14	%EstTL + PatchArea + BMRes + SVL	4	403.808	415.808	58.935	$7.46*10^{-14}$
6	WBCc + *Plasmod*	2	410.159	416.909	60.036	$4.30*10^{-14}$
8	MiteC + HL	2	410.162	416.912	60.039	$4.30*10^{-14}$
15	%EstTL+ PatchArea + BMRes	3	410.159	419.449	62.576	$1.21*10^{-14}$
4	WBCc x *Plasmod* + MiteC + ArcHL	4	410.162	419.452	62.579	$1.21*10^{-14}$
3	WBCc + *Plasmod* + MiteC + HL	4	410.159	422.159	65.286	$3.12*10^{-15}$

Appendix 1.3. The complete model data for the Akaike's Information Criterion (AIC) of saturation. Models are ordered by lowest to highest ΔAIC_i. K describes the number of variables included in each model. RSS is the residual sum of squares. AICc is the AIC score adjusted for small sample size. ΔAIC_i is the difference between the scores of each model from the score of the best model. w_i is the weight of evidence for each model as the best model. ER is the evidence ratio with respect to the best model. The six best-supported models are in bold. Variable abbreviations are found in Table 1.

Models on following page.

Model #	Model	K	RSS	AICc	ΔAIC_i	Wi
2	CORT	1	250.481	254.87	0	$4.59*10^{-1}$
12	%EstTL + CORT	2	249.018	255.907	1.037	$2.73*10^{-1}$
17	CapDate + CORT	2	245.057	257.046	2.176	$1.55*10^{-1}$
18	CapDate + CORT + Patch Size	3	256.157	259.696	4.826	$4.11*10^{-2}$
7	WBCc + *Plasmod* + CORT	3	255.481	259.98	5.11	$3.57*10^{-2}$
9	MiteC + HL + CORT	3	255.481	259.98	5.11	$3.57*10^{-2}$
16	CapDate	1	294.574	298.937	44.067	$1.24*10^{-10}$
1	SVL	1	295.391	299.391	44.521	$9.87*10^{-11}$
5	WBCc x *Plasmod*	2	295.363	299.726	44.856	$8.35*10^{-11}$
10	PatchArea	1	295.391	299.755	44.885	$8.23*10^{-11}$
11	%EstTL	1	295.391	299.755	44.885	$8.23*10^{-11}$
20	ArcR2R4	1	295.391	299.755	44.885	$8.23*10^{-11}$
19	CapDate+ PatchSize	2	294.574	301.324	46.454	$3.76*10^{-11}$
6	WBCc + *Plasmod*	2	295.296	302.046	47.176	$2.62*10^{-11}$
8	MiteC + HL	2	295.391	302.141	47.271	$2.50*10^{-11}$
13	%EstTL+ PatchArea	2	295.391	302.141	47.271	$2.50*10^{-11}$
4	WBCc x *Plasmod* + MiteC + HL	4	295.363	304.653	49.783	$7.11*10^{-12}$
15	%EstTL+ PatchArea + BMRes	3	295.391	304.682	49.812	$7.01*10^{-12}$
3	WBCc + *Plasmod* + MiteC + HL	4	295.296	307.296	52.426	$1.90*10^{-12}$
14	%EstTL + PatchArea + BMRes + SVL	4	295.391	307.391	52.521	$1.81*10^{-12}$

Appendix 2.1. The complete set of model data for an Akaike's Information Criterion (AIC) of aggressive behavior, as summarized by a principal component of head bobs, push-ups, full show displays, and charges. Models are ordered by lowest to highest ΔAIC_i. K describes the number of variables included in each model. RSS is the residual sum of squares. AICc is the AIC score adjusted for small sample size. ΔAIC_i is the difference between the scores of each model from the score of the best model. w_i is the weight of evidence for each model as the best model. ER is the evidence ratio with respect to the best model. The six best-supported models are in bold. Variable abbreviations can be found in Table 6.

Model #	Model	K	RSS	AICc	ΔAIC_i	Wi
3	SVL + BMRes + BiteForce	3	23.273	27.273	0	$5.37*10^{-1}$
4	SVL + BMRes + BiteForce + CORT	4	22.825	28.865	1.592	$2.42*10^{-1}$
2	BMRes + BiteForce	2	26.548	29.881	2.608	$1.46*10^{-1}$
36	TreatStim + BiteForce	2	17.625	31.625	4.352	$6.09*10^{-2}$
12	CORT	1	30.533	35.733	8.46	$7.81*10^{-3}$
25	CapDate + CORT	2	28.169	36.836	9.563	$4.50*10^{-3}$
20	%EstTL + CORT	2	30.533	39.2	11.927	$1.38*10^{-3}$
11	MiteC + HL + CORT	3	30.53	43.53	16.257	$1.58*10^{-4}$
9	WBCc + *Plasmod* + CORT	3	30.533	43.533	16.26	$1.58*10^{-4}$
37	TreatStim + %EstTL + PatchArea	3	37.903	43.903	16.63	$1.31*10^{-4}$
21	%EstTL + PatchArea	2	39.277	44.991	17.718	$7.63*10^{-5}$
23	%EstTL + PatchArea + BMRes	3	41.446	47.446	20.173	$2.24*10^{-5}$
22	%EstTL + PatchArea + BMRes + SVL	4	44.517	50.917	23.644	$3.94*10^{-6}$
17	PatchArea	1	51.866	54.152	26.879	$7.82*10^{-7}$
29	TreatStim + ColorPC	2	53.612	55.92	28.647	$3.23*10^{-7}$
13	ColorPC	1	54.116	56.401	29.128	$2.54*10^{-7}$
18	PatchArea + Saturation	2	55.387	57.635	30.362	$1.37*10^{-7}$
16	Saturation	1	56.11	58.396	31.123	$9.37*10^{-8}$
35	TreatStim + MiteC + HL	3	53.528	58.528	31.255	$8.77*10^{-8}$
10	MiteC + HL	2	54.645	59.568	32.295	$5.21*10^{-8}$

1	SVL	1	57.478	59.764	32.491	$4.73*10^{-8}$
15	Brightness	1	57.485	59.771	32.498	$4.71*10^{-8}$
30	TreatStim + Saturation	2	58.144	60.451	33.178	$3.35*10^{-8}$
31	TreatStim + Brightness	2	58.748	61.055	33.782	$2.48*10^{-8}$
19	%EstTL	1	57.897	62.754	35.481	$1.06*10^{-8}$
32	TreatStim + Hue	2	61.589	63.896	36.623	$5.99*10^{-9}$
8	WBCc + *Plasmod*	2	61.621	63.928	36.655	$5.89*10^{-9}$
14	Hue	1	61.878	64.163	36.89	$5.24*10^{-9}$
33	TreatStim + *Plasmod* + WBCc	3	61.084	66.084	38.811	$2.01*10^{-9}$
7	WBCc * *Plasmod*	2	61.391	66.248	38.975	$1.85*10^{-9}$
34	TreatStim + MiteC + HL + *Plasmod* + WBCc	5	61.138	66.338	39.065	$1.77*10^{-9}$
5	WBCc + *Plasmod* + MiteC + HL	4	61.977	67.067	39.794	$1.23*10^{-9}$
6	WBCc * *Plasmod* + MiteC + HL	4	70.275	75.475	48.202	$1.83*10^{-11}$
28	CapDate + PatchArea	2	75.698	78.006	50.733	$5.17*10^{-12}$
27	CapDate + ColorPC + PatchArea	3	76.381	78.714	51.441	$3.63*10^{-12}$
24	CapDate	1	79.888	82.174	54.901	$6.43*10^{-13}$
26	CapDate + ColorPC	2	80.133	82.441	55.168	$5.63*10^{-13}$

Appendix 2.2. The complete set of model data for an Akaike's Information Criterion (AIC) of submissive behavior, as summarized by a principal component of retreats and head turns. Models are ordered by lowest to highest ΔAIC_i. K describes the number of variables included in each model. RSS is the residual sum of squares. AICc is the AIC score adjusted for small sample size. ΔAIC_i is the difference between the scores of each model from the score of the best model. w_i is the weight of evidence for each model as the best model. ER is the evidence ratio with respect to the best model. The six best-supported models are in bold.Variable abbreviations can be found in Table 6.

Model #	Model	k	RSS	AICc	ΔAIC_i	Wi
4	SVL + BMRes + BiteForce + CORT	4	26.978	32.978	0	$7.59*10^{-1}$
2	BMRes + BiteForce	2	33.837	37.171	4.193	$9.32*10^{-2}$
3	SVL + BMRes + BiteForce	3	33.818	37.814	4.836	$6.76*10^{-2}$
12	CORT	1	33.897	39.097	6.119	$3.56*10^{-2}$
20	%EstTL + CORT	2	31.161	39.827	6.849	$2.47*10^{-2}$
37	TreatStim + %EstTL + PatchArea	2	25.903	39.903	6.925	$2.38*10^{-2}$
25	CapDate + CORT	2	31.853	40.519	7.541	$1.75*10^{-2}$
11	MiteC + HL + CORT	3	33.897	46.897	13.919	$7.21*10^{-4}$
9	WBCc + *Plasmod* + CORT	3	33.898	46.898	13.92	$7.20*10^{-4}$
36	TreatStim + BiteForce	3	41.166	47.166	14.188	$6.30*10^{-4}$
21	%EstTL + PatchArea	2	42.618	48.332	15.354	$3.52*10^{-4}$
23	%EstTL + PatchArea + BMRes	3	44.832	50.832	17.854	$1.01*10^{-4}$
22	%EstTL + PatchArea + BMRes + SVL	4	47.429	53.829	20.851	$2.25*10^{-5}$
17	PatchArea	1	52.761	55.046	22.068	$1.22*10^{-5}$
29	TreatStim + ColorPC	2	53.612	55.92	22.942	$7.91*10^{-6}$
13	ColorPC	1	54.515	56.8	23.822	$5.10*10^{-6}$
1	SVL	1	57.546	59.832	26.854	$1.12*10^{-6}$
30	TreatStim + Saturation	2	58.144	60.451	27.473	$8.21*10^{-7}$
18	PatchArea + Saturation	2	58.292	60.6	27.622	$7.62*10^{-7}$
31	TreatStim + Brightness	2	58.748	61.055	28.077	$6.07*10^{-7}$