

# Reproductive success, apparent survival, and ventral blue coloration in male prairie lizards (*Sceloporus consobrinus*)

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## Keywords

coloration; fitness; lizard; mark-recapture; reproductive success; *Sceloporus consobrinus*; testosterone; sexual selection.

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## Abstract

Coloration can evolve in response to selection targeting colorful traits that affect survival or reproductive success. Trait covariation can complicate evolutionary dynamics when selection on covarying traits acts antagonistically. In prairie lizards (*Sceloporus consobrinus*), males exhibit blue ventral patches that are reduced in females. The development of ventral coloration corresponds with increases of circulating testosterone at sexual maturity. Previous work has illustrated that testosterone and coloration covary, such that individuals with higher testosterone have bluer patches. However, testosterone is known to increase mortality in many organisms, including *Sceloporus*, so selection against high testosterone can lead to indirect selection against bluer males. While previous work has suggested that patch coloration does not affect fitness, this has not yet been explicitly tested using estimates of survival and reproductive success. Here, we quantify patch coloration, apparent survival, encounter probability, and reproductive success in a wild population of male prairie lizards to assess the role of patch color variation on fitness. Specifically, we tested how patch coloration affects survival and reproductive success across 2 years. We found that none of the patch phenotypes we measured covaried with fitness, suggesting that neither natural nor sexual selection act, or act very weakly, on patch morphology. We found evidence of sexual selection on body size, such that larger males sired more offspring, likely through increased activity. However, this result was inconsistent, as it was only found in one year. Interestingly, we found that, in both years, bluer males were more likely to sire at least one offspring, suggesting some role of patch coloration in reproduction, although we cannot detect what that role may be. Overall, our study suggests that neither apparent survival nor reproductive success is strong drivers of the evolution of ventral coloration in *S. consobrinus*.

## Introduction

Colorful traits have evolved many times across taxa (Osorio & Vorobyev, 2008) and can affect individual fitness (Andersson, 1994; Hill, 2002). The evolution of color can be in response to natural selection (e.g. Kettlewell, 1973; Mallet & Barton, 1989; Rosenblum, 2006), sexual selection (e.g. Milinski & Bakker, 1990; Siefferman & Hill, 2003), or a combination of the two (Simpson *et al.*, 2020). This is particularly true when selection can act on different components of a colorful trait, such as size or saturation, or when an individual has multiple colorful traits (Møller & Pomiankowski, 1993). Quantifying how both natural and sexual selection act on traits is important for fully understanding the dynamics shaping trait evolution.

Conspicuous or exaggerated traits are often thought to advertise individual quality or condition because of the

associated costs of being visible (Zahavi, 1975). Therefore, the evolution of brightly colored traits is often thought to proceed through female mate choice, where females choose males based on their putatively costly signal. These traits are then passed on to the next generation (specifically to sons in many cases; Hill, 1991) depending on the heritability of the trait. Most quantitative evidence for female mate choice contributing to the evolution of colorful traits is restricted to fishes and birds (e.g. Houde & Endler, 1990; Hill, 2006) despite substantial color variation within other vertebrate taxa. Evidence for female choice in lizards, for example, is relatively scant (Ord *et al.*, 2015). Male color polymorphisms in the side-blotched lizard (*Uta stansburiana*) show clear fitness differences associated with behavioral strategies (Sinervo *et al.*, 2000), while female choice for trait combinations (throat color, dorsal pattern) increases female fitness (Lancaster *et al.*, 2009). However,

there is little evidence for covariance between a continuous color trait and fitness in male lizards. Nonetheless, studies across disparate taxa illustrate female choice as one powerful mechanism by which the diversity of colorful signals can arise.

In this study, we estimate apparent survival and reproductive success as proxies for natural and sexual selection, respectively, in males of a free-living population of prairie lizards (*Sceloporus consobrinus*) to evaluate the evolutionary dynamics of sexually dimorphic abdominal and throat patches. Male prairie lizards have vibrant blue abdominal and throat patches that are greatly reduced, and often absent, in females (Cooper & Burns, 1987; Swierk & Langkilde, 2013). Patch coloration varies continuously, ranging from a vibrant blue to an aquamarine color. Results from correlational studies among morphological traits have suggested that coloration does not affect fitness in *S. undulatus* (Langkilde & Boronow, 2010; Goodlett & Stephenson, 2019), but this has not been directly assessed via estimates of survival or reproductive success in natural populations of *Sceloporus* lizards. Patch development coincides with maturational increases in circulating testosterone, which is necessary to induce blue coloration (at least in the closely related eastern fence lizard, *S. undulatus*; Cox *et al.*, 2005). Testosterone increases melanin within the dermis (Quinn & Hews, 2003), which absorbs long wavelength light not reflected by the superficial iridophore layer (a chromatophore type that can produce a vast array of colors; Scharlt *et al.*, 2016), therefore producing the typical blue color (Morrison & Frost-Mason, 1991; Morrison *et al.*, 1995). In some taxa, melanin can advertise individual quality (McGraw, 2008; Vroonen *et al.*, 2013), so variation in blue that is due to underlying melanin variation could be a target for selection.

At the individual level, morphology, physiology, and performance in *S. consobrinus* are correlated, such that males with higher testosterone concentrations are bluer (Robinson & Gifford, 2019) and bluer males have higher maximum sprint performance (Robinson & Gifford, 2018). Similarly, female *S. undulatus* that display male-typical ornamentation are faster than unornamented females (Assis *et al.*, 2018). While ventral patch coloration has no direct connection to sprinting performance *per se*, the independent connection of each of these traits to testosterone suggests that direct selection on one can lead to indirect selection on the other if they share genetic covariance through hormonal pleiotropy (Arnold, 1983; Hau, 2007; Cox, 2020). In another lizard (the eastern collared lizard, *Crotaphytus collaris*), sprinting performance covaries positively with reproductive success (Husak *et al.*, 2006); if this is similar for the prairie lizard, then reproductive success should indirectly covary with patch coloration. However, increased relative reproductive success in bluer males would also select for higher testosterone which negatively affects survival in *Sceloporus* (Marler & Moore, 1988), largely through increased energy expenditure (Marler & Moore, 1989). Therefore, selection could act against bluer individuals if they cannot survive long enough to reproduce.

Taken together, we have two hypotheses that relate to how natural and sexual selection will act on patch morphology in male prairie lizards. First, for our natural selection hypothesis, we hypothesize that variation in blue patch coloration predicts

variation in apparent survival through the effect of testosterone on coloration (although we do not test for mediation effects of testosterone here). If so, we predict that there will be a negative relationship between apparent survival and patch morphology, such that bluer males have increased mortality. Second, for our sexual selection hypothesis, we hypothesize that blue patch coloration signals individual quality which females use to choose mates. If so, we predict that males with bluer patches will sire more offspring than males with patches that are less blue. Overall, we aim to understand how variation in a continuous trait can shape evolutionary dynamics of a vibrant ornament.

## Materials and methods

We conducted a capture-mark-recapture study at Sylvan Hills Prayer Walk (34.857814, -92.223018, datum = WGS64) in Sherwood, Arkansas from 22 April 2016 to 30 June 2018 on *S. consobrinus* (Fig. 1). This site is approximately 1 hectare in size and comprised of hardwood forest with both artificial and natural forest gaps. Within the 2016 and 2017 breeding seasons (approximately March through June for this population; C. D. Robinson & M. E. Gifford, personal observation), we caught all observed lizards by hand or by a loop of fishing line attached to the end of a telescoping fishing pole. We then assigned each lizard two unique identifiers: a toe clip combination and a bead tag (bead tags were used to facilitate identifying individuals without disturbing them). For toe clips, we removed three toes, with no foot having more than one toe removed. Additionally, due to its presumed importance in climbing and sprinting (M.E. Gifford, unpublished data) we never removed the longest (fourth) toe from either hind limb. Toe clips were preserved in 100% ethanol and stored at 4°C for DNA extractions. Bead tags consisted of four glass beads (two on the left, two on the right; Czech glass beads, Beaded Treasures, Oklahoma City, Oklahoma) sewn into the base of



**Figure 1** Image of a bead tagged male *Sceloporus consobrinus* from Sylvan Hills Prayer Walk, Arkansas. [Colour figure can be viewed at [zslpublications.onlinelibrary.wiley.com](https://zslpublications.onlinelibrary.wiley.com).]

the tail using 20 lb monofilament fishing line. Bead tags were only given to animals above 45 mm snout-to-vent length (SVL); however, animals not assigned a bead tag were not excluded from the study. Our beading method is robust against bead loss. Only one individual who was marked in 2016 and subsequently recaptured in 2017 (26 individuals; 3.8%) lost its tag. No recaptured individuals in 2018 were missing their tag.

For each animal, we measured SVL ( $\pm 0.5$  mm), a proxy for body size, with a clear ruler, body mass with a Pesola spring scale ( $\pm 0.1$  g), and quantified patch morphology (details below). In the summer of 2016, each lizard was measured once. New lizards were captured and measured throughout the breeding season. All previously captured lizards we encountered were visually identified by bead tag or toe clip and recorded as a recapture. During 2016, we captured and marked 97 unique adult lizards (46 male, 51 female) from 22 April to 17 June. In 2017, lizards were caught and remeasured monthly within the breeding season to examine seasonal plasticity for morphology and physiology (Robinson & Gifford, 2019). All measurements were taken by one person (CDR). For selection analyses, we only used the value from the initial measurement in 2017 for an individual to allow for comparisons between 2016 and 2017; initial measurements in 2017 ranged from 23 March to 25 May. In 2017, we captured 105 unique lizards (53 male, 52 female), including 54 individuals originally captured as adults or released as hatchlings in 2016.

### Patch morphology

We quantified patch morphology following Robinson & Gifford (2019). Briefly, we incubated lizards in a VL-36 incubator (Percival Scientific, Perry, IA, USA) at 34°C (field mean body temperature, 2016:  $34.2 \pm 2.3^\circ\text{C}$ ; [Robinson & Gifford, 2018]) for 1 h prior to measurement. We quantified color using an Ocean Optics Flame miniature spectrometer with a X-2 Pulse xenon light source (Ocean Optics, Inc., Dunedin, FL, USA) held perpendicular to the patch, using a probe holder to maintain a consistent 5 mm distance between the light source and lizard. We took three measurements from the left abdominal patch (anterior, middle, and posterior) and one from each throat patch. We averaged within patch type (i.e. abdominal and throat) to obtain representative spectra. Using the pavo package (Maia *et al.*, 2013) in R (version 3.6.3; R Core Team, 2019), we averaged spectra over 5 nm bins (Stuart-Fox *et al.*, 2006), smoothed spectra using locally weighted smoothing, and extracted brightness, saturation, and hue (Montgomerie, 2006; Maia *et al.*, 2013). Brightness represents the total reflectance over the spectral range (Delhey *et al.*, 2003; Siefferman & Hill, 2005; Andersson & Prager, 2006), with higher brightness appearing closer to white (100% reflectance). Saturation is a ratio of the difference between the wavelengths of maximum and minimum reflectance by the total reflectance (brightness) (Smiseth *et al.*, 2001; Andersson *et al.*, 2002; Andersson & Prager, 2006) and represents color intensity. Hue is the wavelength at maximum reflectance (Andersson, 1999; Keyser & Hill, 1999; Andersson & Prager, 2006). Here, blue is

represented as a lower wavelength, so negative relationships with hue imply bluer coloration.

To quantify patch area, we took ventral photographs of each lizard using a Casio Exilim EF-X1 camera after completing spectral measurements. Images were taken with lizards lying on their backs on top of grid paper which was used to calibrate scale. Using ImageJ (Schneider *et al.*, 2012) we quantified area with the freehand tool, drawing around each patch. Because some individuals did not have distinct left and right throat patches (the patches were large and had grown together), we added the two patch measurements together for individuals with distinct patches to obtain one measurement. Although each lizard had distinct abdominal patches, we added left and right abdominal patch measurements together to give a measure of total patch area.

### Reproductive success

To quantify male reproductive success, we captured 51 (2016: 23; 2017: 28) gravid females and brought them to the laboratory at the University of Central Arkansas to collect their eggs. Each female was housed individually in a designated animal space in 45 x 20 x 25 cm (L x W x H) terraria with ~2 cm of sand substrate and a rock for a perch sitting beneath a suspended 40W incandescent bulb, providing a temperature gradient ranging from ~25°C at the front of the cage (room temperature) to ~34°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 and supplied water twice daily by spraying the sides of the cages. To encourage oviposition, we provided a moist 1:1 mixture of sand and peat moss ~6 cm deep in the corner of each enclosure. We placed a small 10 x 20 cm piece of thin opaque plastic over the sand mixture to retain substrate moisture. We visually checked females four times per day for evidence of oviposition. After females laid their eggs, we collected them, immediately weighed them ( $\pm 0.1$  mg), and placed them individually into small plastic cups (59 mL) filled with 35.0 g of fine silica sand and 3.5 g of distilled water. Females were released back to their original site of capture within two days of laying. Eggs were incubated under fluctuating conditions with a mean daily temperature of 27°C (Gifford *et al.*, 2017a,b). Upon hatching, we measured the SVL and mass of each hatchling lizard and collected ~0.5 cm of tail tip. We saved these tips in 100% ethanol and stored them at 4°C for DNA extraction. All hatchlings were released to the location where their mother was first captured as gravid.

We extracted DNA from 79 field caught adult males and 251 hatchlings across 2016 and 2017 using the Qiagen DNeasy Blood and Tissue protocol but substituting Epoch Life Sciences DNA/RNA spin columns. Seven microsatellite loci (Scun3, Scun5, Scun9, Scun11, Scun13, Scun14, and Scun16) were amplified for each individual using primers previously developed for *S. undulatus* (Lance *et al.*, 2009). PCR was performed in 12.5  $\mu\text{L}$  of 10 mM Tris (pH 8.4), 50 mM KCl, 25.0  $\mu\text{g}/\text{mL}$  BSA, 0.4  $\mu\text{M}$  unlabeled primer, 0.04  $\mu\text{M}$  tag

labeled primer, 0.36  $\mu\text{M}$  universal dye-labeled primer, 1.2 mM  $\text{MgCl}_2$ , 0.8 mM dNTPs, 0.5 units JumpStart Taq DNA Polymerase (Sigma-Aldrich, St. Louis, MO, USA), and 20 ng DNA template. Amplification was conducted on an Applied Biosystems GeneAmp 9700 using a touchdown thermal cycling program of 20 cycles of 96°C for 30 s, highest annealing temperature of 65°C (decreased by 0.5°C each cycle) for 30 s, and 72°C for 30 s followed by 20 cycles of 96°C for 30 s, 55°C for 30 s and 72°C for 30 s. Amplicons were run on an ABI-3130xl sequencer with size standards and then scored using GeneMapper v 3.7. Primers Scun11 and Scun16 had null allele frequencies of 27.85% and 28.13%, Scun14 was at 1.66%, and all others were approximately 0%. Observed and expected heterozygosities are presented in Table S1. Number of alleles per locus (4–16 alleles; mean 10.57 per loci) and allelic frequencies varied between microsatellites. To assign paternity, we used the maximum likelihood program CERVUS (version 3.0.7; Marshall *et al.*, 1998; Kalinowski *et al.*, 2007). Parameters included 0.99 potential sires sampled, 0.85 loci typed, and 0.01 loci mistyped. Maternity was known with certainty for each offspring because each female was housed individually. The combination of these seven loci had a combined exclusion probability of 97.7%.

## Statistical analyses

All analyses were performed in R and statistical significance evaluated at  $\alpha < 0.05$ . To estimate the relationships between body size and patch phenotypes on apparent survival ( $\phi$ ) and encounter probabilities ( $P$ ) within the breeding season, we created vectors of 0s and 1s for each individual (2016: 31 males; 2017: 44 males) where each datum within a vector represented whether a lizard was observed (1) or not (0) during a sampling event (i.e. physically recaptured or visually identified via bead tag). There were 19 sampling events in 2016 and 33 sampling events in 2017; 2017 had more sampling events because we were testing for effects of seasonal plasticity as noted above. We assessed assumptions of Cormack-Jolly-Seber (CJS) models using the package R2ucare (Gimenez *et al.*, 2017). Our results indicate that recapture probability was not influenced by when an animal was first marked and that marking an animal did not affect survival. Therefore, no assumptions were violated. We fit CJS models using the *crm* function in the package marked (Laake *et al.*, 2013) to our 2016 and 2017 data independently. Each annual model independently included body size or one of the six color variables (hue, saturation, and brightness of both the throat and the abdomen) as predictors of apparent survival and encounter probability. Predictor variables were fit independently to prevent model over-parameterization. Consequently, we did not include any interaction terms because no model had more than one predictor variable. Because we had no prior information regarding which model would be the best, we tested all possible model combinations (for example of one model combination, the effect of body size on apparent survival and abdominal hue on encounter probability) and then compared competing models using AIC (Burnham & Anderson, 2004). The best models included the one with the lowest

AIC and those with an AIC within two points. Further, to assess only the effects of patch characteristics without body size, we reran these models excluding SVL. For each model, we extracted  $\beta$  coefficients and their associated standard error (SE). Variables were considered significant predictors of apparent survival or encounter probability if their estimate was more than two SE above zero. When multiple models were within 2 AIC points of the best model, we averaged the estimates and SE values.

We estimated sexual selection on body size and patch morphology (color and size) using conventional selection differential analyses. Each year was analyzed separately. In all analyses, we calculated relative fitness (individual male fitness divided by population mean fitness of males) and standardized phenotypes to the population mean in units of standard deviation (Lande & Arnold, 1983; Arnold & Wade, 1984). Area measurements were square root transformed to be comparable to linear measurements. We used total reproductive success (quantified as number of offspring sired per male) to estimate linear and quadratic selection differentials. Linear selection differentials ( $S \pm 1 \text{ SE}$ ) were estimated from a linear regression with reproductive success as a function of each phenotype independently. Quadratic selection differentials ( $C \pm 1 \text{ SE}$ ) were estimated by doubling the slope and standard error from a linear regression including reproductive success regressed against each phenotype plus the phenotype squared (Phillips & Arnold, 1999; Stinchcombe *et al.*, 2008). Statistical significance was examined by running generalized linear models assuming a quasipoisson error distribution to account for overdispersed count data. As an additional analysis, following John-Alder *et al.*, (2009), we dichotomized reproductive success (sired at least one offspring vs. did not sire any offspring) and used ANOVA to test for phenotypic differences between successful sires and males who sired no offspring. While dichotomized reproductive success only has two factor levels, we chose ANOVA over a *t*-test so we could also perform ANCOVA with body size and date of capture as additional explanatory variables in our models. Although dichotomizing fitness loses information by lumping very successful males (those who sired many offspring) with less successful males, it can help us understand whether males that successfully produced any offspring systematically differed from unsuccessful males in any particular traits.

## Results

Using Cervus, we could not assign 9 offspring to a sire across both years. In 2016, 36 out of 46 males (78.2%) were assigned to at least one offspring ( $3.16 \pm 0.47$  offspring/male, mean  $\pm 1 \text{ SE}$ ; maximum 12 offspring). In 2017, 44 males sired offspring, however, some offspring were assigned to males who were caught only in 2016 or to offspring born in 2016 but not captured in 2017, so we cannot calculate a siring percentage.

Output from CJS models is included in the supplementary material (Tables S2–S5). In 2016, each individual was resighted  $3.13 \pm 1.78$  (mean  $\pm 1 \text{ SD}$ ) times (range 1–8). Abdominal saturation best predicted apparent survival; individuals with more

saturated patches had higher apparent survival than individuals with patches that were less saturated. However, the mean estimate from the best models was not greater than 2 standard errors above 0 ( $\beta = 27.282 \pm 16.615$ ) so we cannot conclude that patch saturation is significantly related to apparent survival. Encounter probability was explained equally well by abdominal brightness ( $\beta = -0.078 \pm 0.052$ ), abdominal hue ( $\beta = -0.007 \pm 0.011$ ), throat brightness ( $\beta = 0.039 \pm 0.036$ ), throat hue ( $\beta = -0.006 \pm 0.010$ ), and a null model. None of these variables differed from zero. In 2017, each individual was caught  $4.48 \pm 3.97$  times (range 1–16). SVL was the strongest predictor of encounter probability, and was estimated significantly above 0 ( $\beta = 0.16 \pm 0.023$ ); larger males were more likely to be encountered than smaller males. When SVL was excluded from the model, abdominal saturation was the strongest predictor of encounter probability. Like SVL, abdominal saturation was a significant predictor of encounter probability ( $\beta = 2.594 \pm 0.669$ ), such that males with patches that were more saturated were more likely to be encountered. Survival was equally well explained by a null model as it was by several patch phenotypes, but no estimates differed from zero.

Phenotypic means and variances, to aid in interpreting responses to selection, are presented in Table 1 and correlations between traits are presented in Table S6. In 2016, no trait predicted siring success when using total offspring sired as our

metric of fitness (all  $P > 0.11$ ; Table 2). When dichotomizing reproductive fitness, we found that males with lower abdominal hue (patches that are bluer;  $F_{1,35} = 7.272$ ,  $P = 0.040$ ; Table 3; Fig. 2) were more likely to sire at least one offspring. This relationship was not driven by body size; abdominal hue remained significant after the inclusion of SVL ( $F_{1,34} = 4.379$ ,  $P = 0.042$ ) or date of capture ( $F_{1,34} = 7.300$ ,  $P = 0.010$ ) as covariates in ANCOVA.

In 2017, only body size significantly influenced siring success ( $S = 0.646 \pm 0.296$ ,  $P = 0.025$ ; Table 2; Fig. 3), such that larger males sired more offspring. This pattern held when dichotomizing fitness ( $F_{1,49} = 6.378$ ,  $P = 0.015$ ; Table 3; Fig. 3) and when excluding a male that sired 16 offspring ( $S = 0.606 \pm 0.203$ ,  $P = 0.005$ ; dichotomized fitness:  $F_{1,48} = 5.811$ ,  $P = 0.020$ ). Similar to 2016, males who sired at least one offspring in 2017 had bluer abdominal patches than males that did not sire any offspring ( $F_{1,45} = 4.479$ ,  $P = 0.040$ ; Table 3; Fig. 2), and this remained significant after including body size ( $F_{1,44} = 4.379$ ,  $P = 0.042$ ) or date of capture ( $F_{1,44} = 5.782$ ,  $P = 0.020$ ) as a covariate.

Our results from formal selection analyses (Table 2) should be interpreted with caution. Of the 36 tests, we performed (9 per year each for linear and quadratic selection) only one was significant; for 36 tests at  $\alpha = 0.05$ , there is an expected 1.8 significant results by chance alone, suggesting that our one

**Table 1** Phenotypic means, standard deviations (SD), and standard errors (SE) for *Sceloporus consobrinus*, split by year

	2016			2017		
	Mean	SD	SE	Mean	SD	SE
Snout-to-vent length (mm)	55.533	6.683	0.996	56.549	6.117	0.857
Abdominal hue (nm)	502.095	17.448	2.868	496.241	19.683	2.871
Abdominal brightness (%)	23.468	4.481	0.737	25.130	5.885	0.858
Abdominal saturation	0.951	0.248	0.041	1.040	0.205	0.030
Throat hue (nm)	486.605	17.196	2.790	477.713	15.541	2.267
Throat brightness (%)	16.137	4.053	0.657	21.544	5.794	0.845
Throat saturation	1.343	0.259	0.042	1.179	0.273	0.040
Abdominal patch area (mm <sup>2</sup> )	236.611	94.464	15.744	194.130	74.473	10.749
Throat patch area (mm <sup>2</sup> )	43.669	21.537	3.590	30.620	15.495	2.237

Units are in parenthesis.

Saturation is unitless.

**Table 2** Standardized selection coefficients for linear (*S*) and quadratic (*C*) selection on multiple phenotypes in the prairie lizard (*Sceloporus consobrinus*) in 2016 and 2017 using number of offspring sired (offspring count) as measures of fitness

	2016			Offspring Count			2017			Offspring Count		
	<i>S</i>	SE	<i>P</i>	<i>C</i>	SE	<i>P</i>	<i>S</i>	SE	<i>P</i>	<i>C</i>	SE	<i>P</i>
Snout-to-vent length	-0.106	0.152	0.491	-0.196	0.333	0.548	<b>0.634</b>	<b>0.290</b>	<b>0.025</b>	0.371	0.564	0.876
Abdominal hue	0.020	0.192	0.919	-0.265	0.279	0.359	-0.154	0.307	0.632	-0.591	0.666	0.355
Abdominal brightness	-0.146	0.190	0.446	-0.352	0.228	0.110	0.407	0.302	0.135	-0.159	0.421	0.473
Abdominal saturation	-0.087	0.191	0.651	-0.580	0.339	0.079	0.129	0.307	0.684	-0.246	0.473	0.591
Throat hue	-0.052	0.192	0.787	-0.479	0.287	0.115	0.061	0.308	0.841	-0.098	0.572	0.857
Throat brightness	-0.185	0.189	0.327	-0.196	0.270	0.334	0.150	0.307	0.619	-0.593	0.460	0.174
Throat saturation	-0.006	0.192	0.976	0.444	0.416	0.302	-0.102	0.307	0.733	-0.079	0.428	0.827
Abdominal patch area	-0.772	0.578	0.175	1.131	2.479	0.885	-1.037	2.166	0.615	-2.109	14.57	0.850
Throat patch area	0.071	0.555	0.901	-0.140	2.972	0.961	0.101	0.686	0.885	-1.432	2.409	0.561

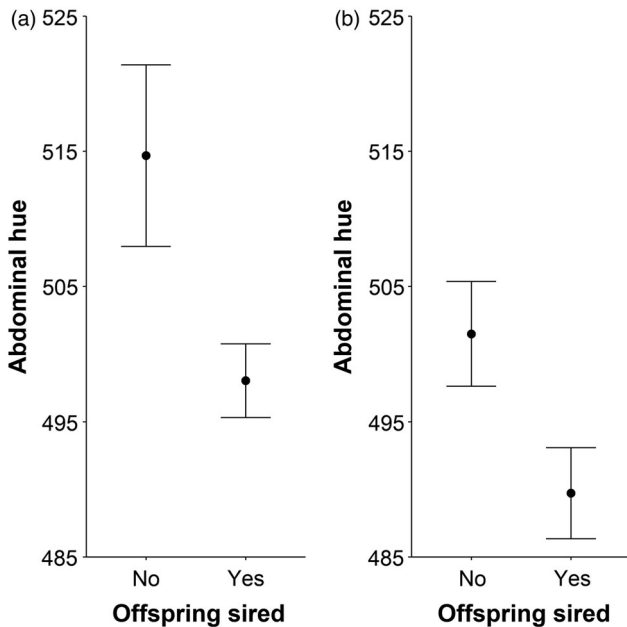
Bolded terms are statistically significant at  $\alpha < 0.05$ .

SE represents 1 standard error.

**Table 3** Output from ANOVA examining the relationship between traits and dichotomized reproductive success (sired at least one offspring vs. sired no offspring) in *Sceloporus consobrinus*

Trait	2016			2017		
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
Snout-to-vent length	0.457	1,43	0.503	<b>6.378</b>	<b>1,49</b>	<b>0.015</b>
Abdominal hue	<b>7.272</b>	<b>1,35</b>	<b>0.011*</b>	<b>4.479</b>	<b>1,45</b>	<b>0.040*</b>
Abdominal brightness	0.056	1,35	0.814	0.327	1,45	0.570
Abdominal saturation	1.168	1,35	0.287	3.935	1,45	0.053
Throat hue	2.439	1,36	0.127	0.623	1,45	0.434
Throat brightness	0.065	1,36	0.800	0.071	1,45	0.791
Throat saturation	1.119	1,36	0.297	3.069	1,45	0.087
Abdominal patch area	0.187	1,34	0.668	3.143	1,46	0.083
Throat patch area	1.098	1,34	0.302	0.387	1,46	0.537

Bolded terms are statistically significant at  $\alpha < 0.05$ .  
 \*Remains significant after inclusion of SVL covariate.  
 Italics are 0.1.

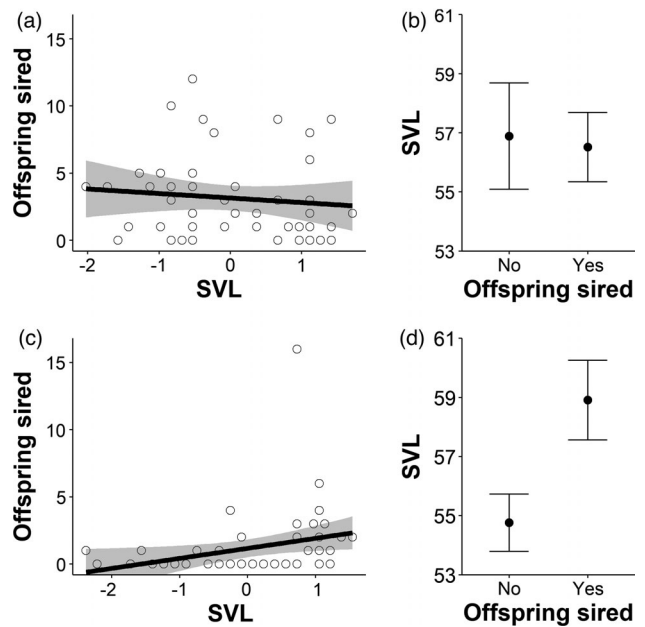


**Figure 2** Relationship between abdominal hue of *Sceloporus consobrinus* and whether males sired at least one offspring in 2016 (panel a) and 2017 (panel b). In both years, males who sired at least one offspring had lower abdominal hue values (were more blue) than those who sired no offspring. Whisker plots are represents by mean  $\pm 1$  SE.

significant result could be the result of a type I error. We believe the results from our dichotomized fitness measure is robust against type I error, however, due to the consistency in abdominal hue predicting siring success.

### Discussion

We found that, across years, male prairie lizards with bluer abdominal patches were more successful siring at least one



**Figure 3** Relationship between body size (SVL) of *Sceloporus consobrinus* in units of standard deviation and offspring in 2016 (panels a and b) and 2017 (panels c and d). In 2016, there was no relationship between body size and reproductive success. In 2017, larger males sired more offspring when examining (c) absolute number of offspring sired or (d) dichotomized fitness. When excluding one male in 2017 who sired 16 offspring, the pattern remains the same. Shaded area represents 95% CI. Whisker plots are represents by mean  $\pm 1$  SE. See Table 1 for standard deviation.

offspring than males with less blue abdominal patches, and this was independent of body size. However, beyond when simply dichotomizing fitness, we could not detect any strong signatures of sexual selection; there were no significant effects of patch phenotypes on male reproductive success, leading us to reject our sexual selection hypothesis. Likewise, there were no clear effects of patch phenotypes on apparent survival, leading us to reject our natural selection hypothesis.

Previously, Ord *et al.*, (2015) highlighted that signal diversity among lizards is strongly influenced by signal efficacy rather than female mate choice. Specifically, the authors concluded, after examining the evolution of colorful throat morphologies across 48 genera, that sexual selection was a weak driver for the evolution of colorful throats (Ord *et al.*, 2015). While our results give some support to the hypothesis that male patch color can influence individual reproductive success in prairie lizards, the evolution of colorful venters in *Sceloporus* as a whole may not have arisen due to effects on reproductive success and instead from abiotic factors selecting for more effective communication. Indeed, shifts in habitat use among species can lead to the loss of ventral coloration (Ossip-Drahos *et al.*, 2016), with shifts away from arboreality facilitating the loss of ventral coloration (Wiens, 1999; Ossip-Klein *et al.*, 2013). Therefore, while the influence of color on reproductive success may not have been the primary driver in the evolution of blue

ventral coloration, it may play a role in the maintenance of blue patches in prairie lizards.

Rather than influencing reproductive success directly, variation in blue patch color could signal quality to other males, helping to establish hierarchies among potential competitors. Male *S. undulatus* (Haenel, Smith & John-Alder, 2003a) and *S. consobrinus* (C. D. Robinson and M. E. Gifford, unpublished data) establish home ranges around the spatial distribution of females. Females, however, often mate with males outside of their home ranges (Haenel *et al.*, 2003b; this study). Even within the breeding season, males are tolerant of other males being nearby and can often be seen within less than a meter of each other. Aggression is typically low, consistent with predictions from the dear enemy effect (Fisher, 1954), except when a female is nearby. When females are present, males become aggressive, which is when traits regulated by testosterone may become important. *Sceloporus* males fight by biting at the abdomen of the opposing male (visible bite scars are sometimes observed, especially on older males), and in some lizard species bite force is influenced by testosterone (Husak *et al.*, 2007; Huyghe *et al.*, 2010). Therefore, when males are of similar sizes and interactions escalate, having a high testosterone level relative to a competitor could provide an advantage. Further, female choice of male traits typically has been shown to be complex. For example, Swierk *et al.*, (2012) demonstrated that in the absence of territorial cues, females use trait combinations, including body condition, head size, and throat patch size, to choose male associates. Therefore, patch phenotypes could be used by males early in the season for conflict resolution and home range establishment but used later in the season by females as a quality assessment tool.

*Sceloporus* lizards typically have low population densities which may limit encounters with potential mates and therefore influence the strength of sexual selection (Arnold & Duvall, 1994). Indeed, Kamath & Losos, (2018) found that in *Anolis sagrei*, mating is related to encounter probabilities. In 2017, the most supported CJS models suggested that body size best predicted encounter probability, and we found significant selection on this phenotype in the same year. Although the significant effect of body size on reproductive success may be a type I error due to the number of tests performed, these independent lines of evidence (covariance between body size and reproductive success; covariance between body size and encounter rate) suggest that body size could be important for female choice in this species, as it is in many other animals (e.g. Price, 1984; Andersson, 1994; Wikelski & Trillmich, 1997; Howard *et al.*, 1998; Aquiloni & Gherardi, 2008). No patch phenotypes were included in any of the best CJS models as variables influencing encounter rates. When body size is excluded from these analyses, leaving only variables that describe patch coloration, abdominal saturation is consistently the best predictor of encounter probability. We found no covariation between abdominal saturation and reproductive success, which may suggest that body size is more important than coloration. However, males with more saturated abdominal patches tended to be more likely to sire at least one offspring (Table 3). Therefore, males with more saturated, bluer patches may be more

active and consequently more successful at acquiring mates, but evidence is limited.

Alternatively, instead of selection for certain phenotypes, there could be no selection against color. The common ancestor of *Sceloporus* likely had colorful patches (Wiens, 1999) and was terrestrial (Ossip-Klein *et al.*, 2013). Arboreal species (like *S. consobrinus*) are less likely to lose their ventral coloration (Wiens, 1999; Ossip-Klein *et al.*, 2013). Some (Holland & Rice, 1998) have suggested that over macro-evolutionary time scales females may lose sensitivity to male traits that initially evolved under sexual selection to prevent suboptimal mating rates (i.e., mating too often; see also Getty, 1999 and Rosenthal & Servedio, 1999). Indeed, repeated years of nondetectable levels of selection on patch phenotypes could lead to the inference that mate choice is relatively unaffected by patch morphology, at least when measured independently. Alternatively, female preference could be slight, such that a much larger sample size is needed to detect signatures of selection (Servedio & Kirkpatrick, 1997). Finally, the maintenance of these signals simply could be for sex recognition (Cooper & Burns, 1987), which is further supported by evidence suggesting that females bearing male ornaments have reduced fitness (Swierk & Langkilde, 2013). Overall, competing models of selection that we cannot directly test here could better explain the patterns we have observed.

One surprising result from this study was the degree of multiple paternity observed within our system. Previous work in *S. undulatus* suggested that few males sire offspring within a given year (Haenel *et al.*, 2003b; John-Alder *et al.*, 2009). In our population of *S. consobrinus*, many males sired at least one offspring and within-clutch multiple paternity were common; all but one clutch between the 2 years of study had multiple sires. Females had, on average,  $4.8 \pm 2.9$  sires per clutch. This could imply that females maximize their own fitness by increasing the genetic diversity of their offspring (Jennions & Petrie, 2000; Yasui, 2001; Calsbeek *et al.*, 2009) or that the strength of selection on male traits via female choice is weak (Arnold & Duvall, 1994). Our data do not necessarily refute the latter but suggest that females have some opportunity to choose potential sires. Further work should assess the effects of genetic diversity on offspring fitness in this system and how it potentially shapes phenotypic selection on patch morphology.

Our study provides tentative evidence for female mate choice in a lizard, which so far has been relatively scant (e.g. Tokarz, 1995; Lailvaux & Irschick, 2006; but see Bleay & Sineru, 2007). While we did not directly assess female mate choice, males with bluer patches were more likely to sire at least one offspring than males with patches that are less blue. However, patch coloration does not covary continuously with reproductive success, so we cannot conclude that there is sexual selection on male ventral coloration. Biotic or abiotic variables not measured in this study, such as environmental variation (e.g. rainfall; Calsbeek *et al.*, 2009) or parasite abundance, could be driving the phenotypic or reproductive variation we observed. For example, variation in parasite infection could influence the appearance of color (Hamilton & Zuk,

1982; Ressel & Schall, 1989; Calisi *et al.*, 2008; Cook *et al.*, 2013; Megía-Palma *et al.*, 2016) or circulating testosterone (Klukowski & Nelson, 2001; Cox and John-Alder, 2007). In years with more parasites, females may assess males differently, resulting in different patterns of selection. Alternatively, sexual selection on patch phenotypes may have become dampened or nonexistent. Further work is needed to better understand the evolution of color patterns in the highly variable *Sceloporus*, both within and among species.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Observed ( $H_o$ ) and expected ( $H_e$ ) heterozygosities for primers used for paternity analyses in *S. consobrinus*.

**Table S2.** Top ten models from CJS models examining the effect of body size (SVL) and patch color on apparent survival ( $\phi$ ) and encounter probability ( $P$ ) within the 2016 breeding season in *S. consobrinus*.

**Table S3.** Top ten models from CJS models examining the effect of patch color on apparent survival ( $\phi$ ) and encounter probability ( $P$ ) within the 2016 breeding season in *S. consobrinus*.

**Table S4.** Top ten models from CJS models examining the effect of body size (SVL) and patch color on apparent survival ( $\phi$ ) and encounter probability ( $P$ ) within the 2017 breeding season in *S. consobrinus*.

**Table S5.** Top ten models from CJS models examining the effect of patch color on apparent survival ( $\phi$ ) and encounter probability ( $P$ ) within the 2017 breeding season in *S. consobrinus*.

**Table S6.** Off-diagonals of correlation matrices for phenotypes within 2016 and 2017 in *S. consobrinus*.