

Article

# Male mate choice as differential investment in contest competition is affected by female ornament expression

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## Abstract

High male mating effort and high variation in female quality select for male mate choice, which may be expressed as differential investment of reproductive effort based on female value. Male reproductive effort includes investment in direct contest competition with rival males for access to females, yet variation in male–male contest behavior is rarely examined in the context of male mate choice. We examine such male response to variation in female body size, reproductive state, and female-specific ornamentation in the striped plateau lizard, *Sceloporus virgatus*. We housed lizards in trios of 2 size-matched males and one female for 5 days, such that all 3 lizards were physically isolated and the males could see the female but not each other. We then placed males simultaneously into the female's cage and scored the interaction. Male–male aggression was not significantly affected by female body size, reproductive state, nor ornament color, but was influenced by ornament size which reliably signals the phenotypic quality of the female and her offspring. In the presence of larger-ornamented females, males engaged in more male–male aggressive display behavior more quickly, and performed fewer high-intensity contact behaviors but were equally likely to escalate to this riskier level of fighting. Our data suggest that males adjust their energetic investment during intrasexual competitive interactions in response to variation in the contested female which, assuming males gain direct or indirect benefits from their strategic allocation of reproductive effort, fits the modern understanding of male mate choice.

**Key words:** aggression, female-specific ornaments, intrasexual competition, lizards, resource quality, sexual selection

Female-biased parental investment and male-biased potential reproductive rates have long been understood to select for female mate choice and male–male mate competition (Trivers 1972; Clutton-Brock and Vincent 1991; Andersson 1994). However, such “typical” expressions of sexual selection do not preclude the expression of male mate choice and female–female mate competition in the same species (Kraaijeveld et al. 2007; Edward and Chapman 2011) and choosiness is not necessarily negatively correlated to competitiveness within a sex (Preston et al. 2005; Bel-Venner et al. 2008; Candolin and Salesto 2009). Indeed, mate choice expressed by competitive males is now well-documented across a variety of polygynandrous animals and appears to be selected by high male mating

effort, high variation in female mate quality, and low search costs (Dewsbury 1982; Johnstone et al. 1996; Bonduriansky 2001; Edward and Chapman 2011; South et al. 2012).

Male mate preferences may be expressed as a rejection of females below some threshold (Johnstone et al. 1996; Barry and Kokko 2010), but such rejection behavior is not required (Olsson 1993; Bonduriansky 2001; Reading and Backwell 2007; Wong and Svensson 2009; Edward and Chapman 2011). Rather, males may express preferences as differential investment of their reproductive effort (i.e., time and/or energy in courtship, mate guarding, sperm allocation, and interactions with rival males; Bonduriansky 2001; Edward and Chapman 2011) in response to the perceived quality of

potential female mates. Male mate choice is often based on female characteristics such as receptivity (Rowland et al. 1991; LeBas and Marshall 2000; Ruiz et al. 2008), unfamiliarity (Tokarz 1992; Orrell and Jenssen 2002), and phenotypic indicators of fecundity like body size (McLain and Boromisa 1987; Olsson 1993; Reading and Backwell 2007; Wong and Svensson 2009; Ancona et al. 2010). For instance, male chameleons are more likely to court receptive vs. non-receptive females (Kelso and Verrell 2002) and invest more time guarding larger, more fecund females (Cuadrado 1998). Males are expected to gain direct benefits from such choice by maximizing the number of females inseminated and/or the number of offspring produced (Edward and Chapman 2012). Males may also bias reproductive investment based on female traits that signal viability and offspring quality, such as female ornaments (Amundsen et al. 1997; Whiting and Bateman 1999; Weiss 2002; Torres and Velando 2005; Weiss et al. 2009; Swierk et al. 2013), providing opportunities for indirect benefits of male mate choice. While theoretical models predict that indirect benefits of male choice will be weak in strictly polygynous species (Servodio 2007; South et al. 2012), these benefits are likely stronger when specifics of mating system and natural history limit the potential number of mates a male can have (Bonduriansky 2001).

For some species, the potential number of mates is limited and mating investment per female is high because territorial males must sequentially and repeatedly court a small number of familiar, sedentary females that overlap their territory in distinct patches during an extended pre-mating period prior to attaining copulation (Smith 1985; Olsson 1993). Decisions to be made include who to visit when, and how much reproductive effort to expend during a given visit (Orrell and Jenssen 2002; Ruiz et al. 2008). Because reproductive effort spent visiting and courting one known female is effort that cannot be spent on another, selection may favor males that are responsive to variation in female fecundity, receptivity, and/or quality over males that allocate their reproductive effort indiscriminately across these familiar females. This scenario, in which males allocate their reproductive effort across repeated interactions with a relatively small number of known and readily located potential mates, has not been fully considered by models of sequential mate choice (Fawcett and Johnstone 2003; Härdling and Kokko 2005; Barry and Kokko 2010). However, the benefit of discriminating among these females may increase as the male's capacity to exclusively mate with all available females decreases (Edward and Chapman 2011) due to, for instance, short and synchronous ovarian cycles among females in the population, female home ranges that overlap with multiple territorial males, positive relationships between investment in a given female and likelihood of paternity, and/or sperm limitation (Dewsbury 1982; Olsson 1993; Abell 1997; Kelso and Martins 2008; Edward and Chapman 2011). Note that such discrimination among familiar females does not preclude a male from courting an unfamiliar female if he happens to come across one.

Many territorial lizards express the above natural history characteristics, including the striped plateau lizard, *Sceloporus virgatus*. *Sceloporus virgatus* females each produce one clutch per year during a brief and synchronous breeding season, with matings occurring during a 2-week period that is preceded by a prolonged courtship period (Rose 1981; Weiss 2002). As capital breeders (Bonnet et al. 1998), females are selected to be sedentary during the period of egg development, and do not engage in active mate searching (e.g., vitellogenic females are 8 times more likely than males to be inactive and are rarely seen traveling; Rose 1981). In contrast, territorial males sequentially visit females whose home ranges overlap his own (Rose 1981); on average, a given male's territory overlaps with 4.4 females (Abell

1999a). However, males do not have exclusive access to females; on average, a given female's territory overlaps with 3.9 different males (Abell 1999a), females are courted by multiple males (median = 4 males; Smith 1985), and clutches can have mixed paternity (Abell 1997). The most likely sire is the male who maintained the closest spatial relationship with the female (Abell 1997). The amount of courtship, repeated across multiple days throughout the pre-mating period, also has an important influence on female acceptance of a mate (Smith 1985; Kelso and Martins 2008). Thus, to maximize their chance of paternity, males need to invest significant time and energy, both of which are limited, in each female. Sperm also may be a limited resource as up to 10% of mated females produce clutches with one or more unfertilized eggs (Abell 1999b; Weiss et al. 2009), indicating possible sperm depletion or poor sperm viability. Thus, *S. virgatus* males have high mating effort per female and low capacity to mate with all available females, 2 factors selecting for male mate choice (Dewsbury 1982; Edward and Chapman 2011).

Here, we ask whether *S. virgatus* males express mate choice by strategically modulating their aggressive interactions with rival males in response to female reproductive value. Although the value of a contested resource is well known to affect contest behavior (Parker 1974; Enquist and Leimar 1987; Arnott and Elwood 2008), this is rarely studied in the context of male mate choice. However, male-male aggression has been shown to vary with female mating status, readiness to mate, body size, and body condition (Verrell 1986; Dick and Elwood 1990; Bridge et al. 2000; Hoefler et al. 2009; Xu et al. 2012). If this responsiveness to female reproductive value optimizes the allocation of male reproductive effort, it should be considered in our modern understanding of male mate choice (Bonduriansky 2001; Edward and Chapman 2011). When male contest behaviors allow females to detect quality differences among male opponents and thereby influence female choice (Wong and Candolin 2005; Hämäläinen et al. 2012), strategic male-male aggressive behavior may play a similar role to strategic male courtship behavior, which is a much better studied aspect of male mate choice. Certainly as we expand our conceptualization of male mate choice to include decision-making during male-male aggression, the evolutionary effects of male mate choice, male-male competition, and female mate choice will blur (Edward and Chapman 2011).

In *S. virgatus*, male-male contests most often occur within 2 m of a female (Smith 1985); thus, the aggressive displays of *S. virgatus* males could serve as signals of male quality to both opponents and potential female mates. Costs of aggressive display behaviors maintaining signal honesty include restricted aerobic metabolism and increased lactate production during lateral compression, increased predation risk, and decreased survival (Marler and Moore 1988; Cooper 1999; Brandt 2003). Winners of these encounters tend to be larger, are closer to the center of their territory, and have invested more effort in the courtship of the contested female relative to losers (Smith 1985). As well, the male that predominates in courtship and maintains the closest spatial relationship to a given female is most likely to mate with her (Smith 1985; Abell 1997). However, no physical characteristics have been shown to reliably predict male mating success [except for an effect of body size found only among small yearling males (Abell 1997), which we exclude from our study].

Female characteristics informing male mate choice decisions may include her fecundity, readiness to mate, phenotypic quality, and offspring viability. In *S. virgatus*, the former varies significantly, from 3 to 18 eggs/clutch, and may be assessed by female body size (Vinegar 1975a; Smith et al. 1995; Abell 1999b). The latter information can be assessed via female-specific orange ornamentation that

develops on the throat during vitellogenesis, peaks near the time of ovulation, and fades during the month-long gravid period when females carry fertilized eggs in the oviducts (Weiss 2002). Dynamic changes in ornament color allow for the assessment of readiness to mate (Weiss 2002), whereas the size of the ornament is a better indicator of female phenotypic quality, age, and the quality of her offspring (Weiss 2006, 2016; Weiss et al. 2009, 2013; Goldberg et al. 2017; Table 1). Males maintain closer spatial relationships to and tend to more intensely court females painted to express dark orange ornaments than females painted to express pale orange or no orange color (Weiss 2002). If mate choice by *S. virgatus* males is also expressed via strategic investment in competition, we predict male–male aggression will positively correlate to female phenotype. Responsiveness to female body size or ornament color may suggest direct benefits of mate choice, optimizing mate and/or offspring number, whereas responsiveness to female ornament size may suggest additional indirect benefits of choice, optimizing offspring quality.

## Materials and Methods

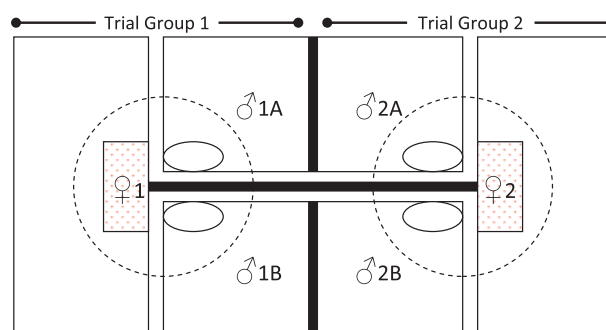
*Sceloporus virgatus* individuals (102 males and 51 females) were collected by noose from 22 May to 15 June in dry streambeds and surrounding plateaus near the Southwestern Research Station (SWRS) in Cochise County, Arizona, USA. All animals were collected within 3.5 km of each other along various forks of the Cave Creek drainage and are considered to be one genetic population. On the day of capture, we measured each lizard's body size (snout-to-vent length; SVL; measured to the nearest 0.5 mm), counted ectoparasitic mites, and toe clipped lizards for permanent identification.

Lizards were housed on an east-facing screened porch of SWRS's Live Animal Holding Facility (LAHF) in trial groups comprised of 2 males and 1 female ( $n = 51$  groups). Males of a trial group were size matched [average difference in SVL =  $0.6 \pm 0.1$  (SE) mm] and randomly assigned to a female with alteration to ensure all members of a given trial group were collected at least 100 m apart from each other on the same day. Lizards were housed in glass terraria

( $50.8 \times 27.9 \times 33.0$  cm) arranged as shown in Figure 1. This arrangement allowed visual contact between the female and each male of a trial group, but prevented visual contact between males. Each lizard had access to a dirt substrate for burrowing, a basking perch, and a heat lamp on a 14:10 light cycle. Animals were fed 2 small crickets every other day, and water was provided *ad libitum*. After 5 days of captivity in this arrangement, the lizards took part in a behavioral trial; afterward, we confirmed female reproductive state as vitellogenic (with ovarian follicles) or gravid (with oviductal eggs) via a small incision on the ventral side of anesthetized females and then closed the incision with surgical adhesive. The following day, we released lizards to their site of capture.

## Behavioral trials

Behavioral trials ( $n = 51$ ) were conducted every other day from 27 May to 20 June. All trials were conducted between 09:30 and 13:30 in a dedicated LAHF room (mean ambient temperature =  $27.9 \pm 0.2^\circ\text{C}$ ).



**Figure 1.** Housing arrangement of *Sceloporus virgatus* trial groups. Animals of a given trial group (e.g., ♀1, ♂1A, and ♂1B) were housed such that females could see both males but males could not see each other. Terraria are represented by thin black lines, opaque dividers by thick black lines, brick perches by rectangles with dots, PVC pipe perches by ovals, and the location of the light source by the dashed circle.

**Table 1.** Correlates of *Sceloporus virgatus* female-specific ornamentation

Female characteristic	Ornament size	Ornament color	
		Brightness or value	Wavelength or chroma
Body size	$P^a X^b P^c$	$X^a X^b X^c$	$P^a X^b X^c$
Body condition	$P^a X^b$	$X^a X^b$	$X^a X^b$
Mite load	$N^a X^b X^c$	$X^a X^b X^c$	$N^a X^b X^c$
Corticosterone	$N^d$	$X^d$	$N^d$
Age	$P^e$		$X^e$
Clutch size	$X^a N^b$	$X^a X^b$	$X^a P^b$
Average egg mass	$P^a X^b$	$X^a X^b$	$P^a X^b$
Yolk antioxidant concentration	$P^f$		$P^f$
Yolk antioxidant total content	$P^f$		$X^f$
Offspring body condition	$P^g$	$X^g$	$X^g$
Offspring sprint speed	$P^g$	$P^g$	$X^g$

P, significant positive relationship; N, significant negative relationship; X, no relationship; italics indicate near statistical significance ( $0.05 < P < 0.10$ ). The symbol is placed between the columns for brightness and wavelength when a general “color score” was utilized in analyses.

<sup>a</sup>Weiss (2006).

<sup>b</sup>Goldberg et al. (2017).

<sup>c</sup>Present study.

<sup>d</sup>Weiss et al. (2013).

<sup>e</sup>Weiss (2016).

<sup>f</sup>Weiss et al. (2011).

<sup>g</sup>Weiss et al. (2009).

Approximately 10 min before the start of a trial, we moved the female's tank into the observation room, wrapped it in brown paper, provided a clean basking brick and a heat lamp, and placed males in separate transport containers. To start the trials, the 2 opponent males were simultaneously placed into the stimulus female's tank as far from the female as possible. The animals were allowed to interact freely for 20 min and the interaction was videotaped from behind a blind.

Videotapes were scored by M.D. for the number of and latency to perform low-, mid-, and high-intensity behaviors by the 2 male opponents (see ethogram, Table 2). In general, interactions began with low-intensity headbob and push-up displays, some interactions escalated to mid-intensity fullshow and face-off displays, and peak aggression was demonstrated by risky high-intensity behaviors involving physical contact: charges, bites, and bite holds. Because headbobs are used in multiple contexts by lizards (Martins 1993), including both aggression and courtship, we were unable to assess whether a given male headbob was directed toward the opponent male or the stimulus female; however, given that courtship-specific displays (i.e., jiggles; Vinegar 1975b) were very rare during our trials, we opted to analyze all male headbobs in the context of male-male aggression. In contrast, the intended receiver of charges, bites, and bite holds was obvious; thus, we were able to separately score and analyze these high-intensity contact behaviors performed by males to females in attempts to gain a copulation grasp.

For each intensity category, the number of behaviors performed during a trial was negatively correlated to the latency to perform the first behavior (all  $P \leq 0.002$ ). Therefore, to generate independent response variables, we used principal component analysis (PCA) with varimax rotation via the psych package in R (R Core Team 2016; Revelle 2017) and extracted the rotated component scores. The 6 measures of male-male aggression (total number of low-, mid-, and high-intensity behaviors and the latency to the first low-, mid-, and high-intensity behavior) per trial were reduced to 2 varimax-rotated components with eigenvalues  $>1$  (Table 3). Trials with large Component 1 scores had large numbers of low and mid aggression behaviors with low latencies; the scores are referred to as "male-male display behavior." Trials with large Component 2 scores had high levels of high aggression behaviors with low escalation latencies to these risky behaviors; these scores are referred to as "male-male contact behavior."

Similarly, the number of high-intensity behaviors directed by males to the stimulus female and the latency to the first high-intensity behavior were reduced to one principal component that explained 85% of the variation in the full dataset. The principal component was loaded positively by the number of behaviors and negatively by the latency to the first behavior; the scores (PC1) are referred to as "female-directed behavior." Behavior performed by the female was rare, so although it was scored, it is not used in any statistical analysis.

## Female ornamentation

We quantified each female's ornament expression on the day of her behavioral trial. To measure ornament size, we photographed each female's left color patch using an Olympus C-5050 ZOOM 5 megapixel digital camera set to macro mode with a superbright zoom F1.8 lens. Female position relative to the camera and external lighting were standardized, and a ruler was included in each photograph for calibration. We used the "Color Range" function of Adobe Photoshop 4.0 with a custom-made color selection file to select orange pixels and used the National Institute of Health's ImageJ (1.42q) to quantify the area of that selection in  $\text{mm}^2$ .

To measure the ornament color, we used an Ocean Optics USB 2000 spectrometer (integration time = 500 ms, average = 5, boxcar = 5) with a PX-2 xenon light source and a Spectralon white standard. The probe was placed directly above the female's left patch at a standardized distance and we captured 3 reflectance spectra from each female at 0.32 nm increments. We calculated ornament "brightness" as the mean reflectance from 577 to 700 nm (inclusive of yellow-to-red wavelengths) averaged across the 3 spectra of a given female. In addition, we calculated the wavelength of maximum reflectance (from 577 to 700 nm) and analyzed the median value across a female's 3 spectra.

## Data analysis

Statistical analyses were performed using R 3.3.1 and R Studio. We used  $t$ -tests, Mann-Whitney  $U$ -tests, and Chi-squared tests, as necessary, to assess whether there were morphological differences among individuals involved in trials that did ( $n = 39$ ) and did not ( $n = 12$ ) result in the expression of male-male aggressive behavior. We used stepwise regression to examine whether male aggressive behavior was affected by female body size (female SVL, and the SVL difference between the sexes), reproductive state (categorized as vitellogenic or gravid), and ornament expression (size, brightness, and wavelength of maximum reflectance). Only final models are

**Table 3.** Loadings of varimax-rotated components of a PCA with measures of male-male aggression

Behavior	Component 1	Component 2
Low-intensity behaviors (LOW)	0.90	0.17
Mid-intensity behaviors (MID)	0.86	0.05
High-intensity behaviors (HIGH)	0.20	0.79
Latency to LOW	-0.61	-0.45
Latency to MID	-0.75	-0.05
Latency to HIGH	0.01	-0.89
% variance	42.0	27.5
Eigenvalue	2.87	1.30

**Table 2.** Ethogram of aggressive behavior modified from Weiss and Moore (2004)

Intensity category	Behavior	Description
Low	Head bob	Lowering and raising of the head using the neck
Low	Push-up	Lowering and raising of the head by flexion and extension of legs
Mid	Fullshow hold	Lateral compression of the body and dewlap extension in the absence of pushups
Mid	Fullshow display	Lateral compression of the body and dewlap extension while performing pushups
Mid	Face-off	Two individuals performing fullshow behavior within 2 body lengths of each other, typically in an anti-parallel orientation
High	Charge	Rapid movement toward another individual
High	Bite	Rapid opening and closing of mouth toward or against skin of another individual
High	Bite hold	Clamping down with mouth on another individual, who often struggles to break free



**Table 4.** Morphological characteristics (mean  $\pm$  SE and total range) and reproductive state of individuals in trials with ( $n=39$ ) and without ( $n=12$ ) male–male aggressive behavior

Trait	With aggression	Without aggression	Range
Average male SVL (mm)	56.9 $\pm$ 0.2	56.7 $\pm$ 0.4	55.0–60.5
SVL difference between paired males (mm)	0.6 $\pm$ 0.1	0.7 $\pm$ 0.3	0–3
Female SVL (mm)	63.1 $\pm$ 0.4	63.3 $\pm$ 0.6	60–68
SVL sex difference (mm)	6.2 $\pm$ 0.4	6.7 $\pm$ 0.9	0.5–12.0
Ornament size (mm <sup>2</sup> )	6.5 $\pm$ 0.9	6.1 $\pm$ 1.9	0.01–29.6
Ornament brightness (% reflectance)	50.3 $\pm$ 2.5	54.9 $\pm$ 5.1	26.6–82.9
Ornament peak wavelength (nm)	627.2 $\pm$ 11.1	641.2 $\pm$ 6.9	577–700
% vitellogenic (vs. gravid)	77% (30 of 39)	58% (7 of 12)	

presented. We confirmed that forward and backward selection resulted in the same final model, and verified all variance inflation factors (VIFs) were under 10 to avoid issues of multicollinearity (max VIF = 3.5). The number of fullshows and female-directed behavior were both ln-transformed [ $\ln(1+x)$ ] to meet model assumptions.

To investigate the possible signal value of ornament components (size, brightness, and peak wavelength), we used regression models with backward stepwise selection. The original models included the following predictors: female body size, mite load, and reproductive state. Orange area was ln-transformed [ $\ln(1+x)$ ] to meet model assumptions.

## Results

We compared morphological measurements of individuals in trials that did and did not result in aggressive behavior from at least 1 male (Table 4). These 2 types of trials did not differ in the average body size of the 2 male opponents ( $t_{49}=0.52$ ,  $P=0.608$ ), the size match of the opponents ( $W=232$ ,  $P=0.971$ ), female body size ( $t_{49}=0.34$ ,  $P=0.733$ ), the size difference between the males and the stimulus female ( $t_{49}=0.56$ ,  $P=0.577$ ), female ornamentation (ornament size:  $t_{49}=0.19$ ,  $P=0.851$ ; brightness:  $t_{49}=0.87$ ,  $P=0.390$ ; peak wavelength:  $t_{49}=1.01$ ,  $P=0.319$ ), nor female reproductive state (vitellogenic or gravid;  $\chi^2=1.59$ , Monte-Carlo simulated  $P=0.282$ ). Trials without male–male aggression ( $n=12$ ) are not included in further analyses.

### Male–male aggression

Component 1, which describes male–male display behavior, was significantly and positively predicted by the size of the female ornament ( $\beta_{\text{unstd}}=0.054$ ,  $\beta_{\text{std}}=0.318$ ,  $F_{1,37}=4.16$ ,  $P=0.049$ ,  $R^2=0.10$ ; Figure 2A); no other predictors remained in the final model. One female with a very large ornament had high influence on the regression model (Cook's distance = 1.9). Removing this female did not affect the interpretation, though the model is strengthened ( $\beta_{\text{unstd}}=0.104$ ,  $\beta_{\text{std}}=0.471$ ,  $F_{1,36}=10.25$ ,  $P=0.003$ ,  $R^2=0.22$ ). Thus, females with large ornaments incited more male–male aggressive displays more quickly than did females with small ornaments.

We also directly analyzed the total number of fullshow behaviors, as this is the behavior that involves lateral compression and is known to serve as an endurance handicap signal in other phrynosomatid lizards (Brandt 2003). Orange area was the only variable to remain in the model and marginally positively influenced the number of fullshows performed ( $\beta_{\text{unstd}}=0.047$ ,  $\beta_{\text{std}}=0.312$ ,  $F_{1,37}=4.00$ ,  $P=0.053$ ,  $R^2=0.10$ ; Figure 2B).

As above, data from the female with a very large ornament emerged as having high influence on the regression (Cook's distance = 2.5). Repeating the analysis after excluding this female strengthened our conclusion ( $\beta_{\text{unstd}}=0.099$ ,  $\beta_{\text{std}}=0.501$ ,  $F_{1,36}=12.03$ ,  $P=0.001$ ,  $R^2=0.25$ ).

Component 2, which describes male–male contact behavior, was significantly predicted by a final model that included ornament size, body size, and reproductive state of the female ( $F_{3,35}=3.38$ ,  $P=0.029$ , adjusted  $R^2=0.16$ ; Table 5A). In the presence of a large-ornament female, opponent males had significantly lower Component 2 scores (meaning fewer male–male contact behaviors and greater latencies) relative to those in the presence of a small-ornament female ( $P=0.024$ ; Figure 2C). Stimulus females with larger body sizes tended to incite more male–male high-intensity contact behaviors than did smaller females ( $P=0.066$ ; Figure 2D). There was no significant effect of reproductive state ( $P=0.135$ ).

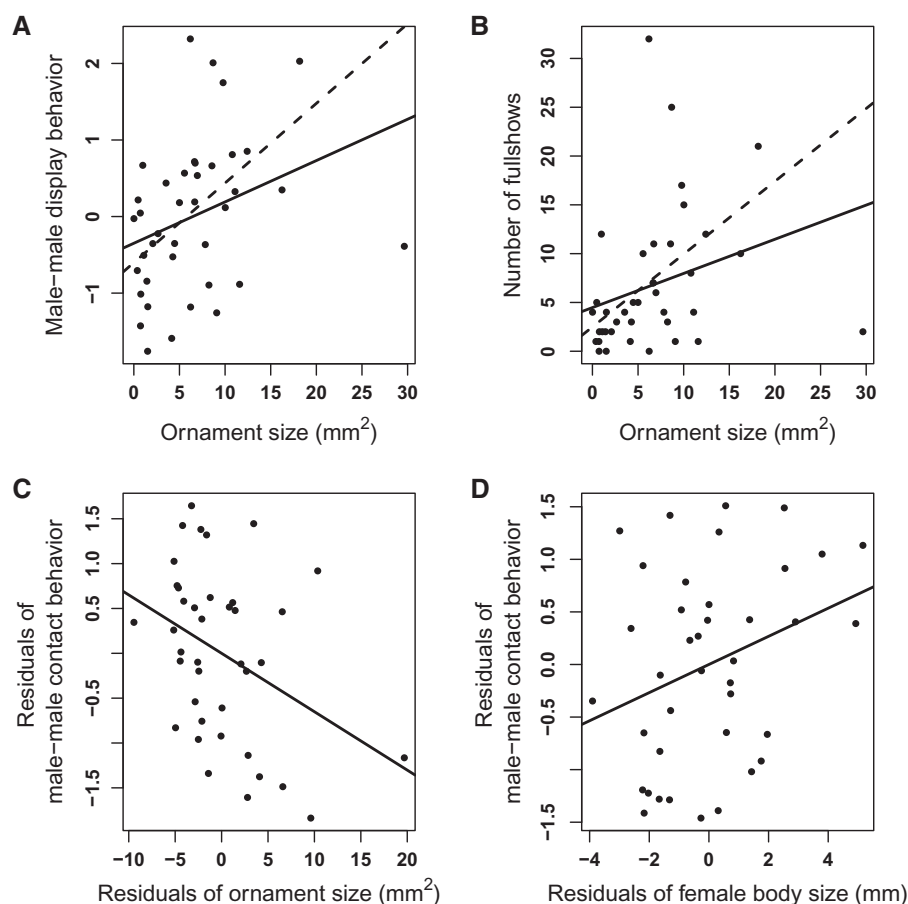
We ran a post hoc logistic regression to determine whether ornament size affected the likelihood of escalating to male–male contact behaviors (in contrast to the number and latency of these behaviors), and no significant effect was found ( $P=0.240$ ). Thus, relative to contests in the presence of small-ornament females, contests in the presence of large-ornament females were equally likely to escalate to risky contact behaviors, but it took longer for this to occur and therefore fewer contact behaviors were performed during the 20 min trial. Overall, 59% of trials with male–male aggressive behavior escalated to higher risk contact behaviors between males.

### Female-directed behavior

Of the 39 trials with male–male aggression, 46% included female-directed high-intensity contact behaviors that we interpreted as copulation attempts. PC1, which describes the number of contact behaviors directed toward the female and the latency to such behavior, was significantly predicted by a final model that included female body size and the size difference between the males and the stimulus female ( $F_{2,36}=3.52$ ,  $P=0.040$ , adjusted  $R^2=0.12$ ; Table 5B). Males more frequently and more quickly attempted copulation with females that were more similarly sized to themselves ( $P=0.016$ ), and tended to do the same toward large females ( $P=0.113$ ). This suggests that the underlying factor is actually male body size. In a post hoc analysis, PC1 scores of larger males were significantly higher than that of smaller males ( $\beta_{\text{unstd}}=0.250$ ,  $\beta_{\text{std}}=0.377$ ,  $F_{1,37}=6.13$ ,  $P=0.018$ ,  $R^2=0.14$ ).

### Female ornament

We assessed the possible signal value of ornament size, brightness, and peak wavelength to assess why ornament size may be a more



**Figure 2.** Effect of female characteristics on male–male aggressive interactions. (A and B) There is a significant positive influence of female ornament size on male–male display behavior ( $P=0.049$ ) and a similar trend when isolating the number of fullshows ( $P=0.053$ ). The dashed lines show regression lines after removal of an influential data point ( $p_A=0.003$ ,  $p_B=0.001$ ). (C and D) Partial regression plots show the effect of female ornament size ( $P=0.024$ ) and body size ( $P=0.066$ ) on male–male contact behaviors when controlling for other model parameters.

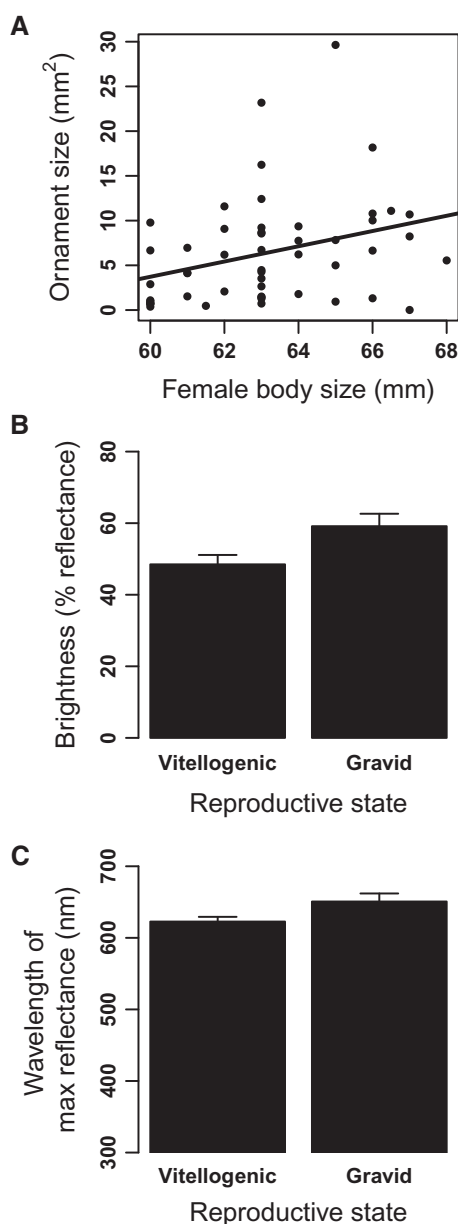
**Table 5.** Unstandardized and standardized coefficients from multivariate regressions concerning (A) male–male ( $F_{3,35}=3.35$ ,  $P=0.030$ ) and (B) male-to-female ( $F_{2,36}=3.52$ ,  $P=0.040$ ) high-intensity contact behaviors

Model predictor	Unstandardized coefficient	Standardized coefficient	<i>P</i>
(A) Male–male contact behaviors			
Ornament size	−0.065	−0.384	0.024
Female body size	0.134	0.306	0.066
Reproductive state: Gravid	−0.550		0.135
(B) Female-directed contact behaviors			
Female body size	0.191	0.431	0.113
Sex difference in body size	−0.257	−0.672	0.016

salient signal to males than ornament color. Ornament size was positively related to female body size ( $\beta_{\text{unstd}}=0.128$ ,  $\beta_{\text{std}}=0.344$ ,  $F_{1,49}=6.58$ ,  $P=0.013$ ,  $R^2=0.12$ , Figure 3A); this pattern remained significant ( $P=0.032$ ) when we instead used relative ornament size (ornament size/body size). Brightness and peak wavelength of the ornament were only predicted by reproductive state (brightness:  $F_{1,49}=4.95$ ,  $P=0.031$ ,  $R^2=0.09$ , Figure 3B; peak wavelength:  $F_{1,49}=4.83$ ,  $P=0.032$ ,  $R^2=0.09$ , Figure 3C). Gravid females had brighter and more red ornaments than did vitellogenic females.

## Discussion

Aggressive behavior between male striped plateau lizards was influenced by the stimulus female's ornament size, but was not significantly influenced by the ornament color, body size, nor reproductive state. In the presence of large-ornamented females, aggressive male–male display behavior was performed more quickly and more frequently. Given the overall explanatory power of the statistical models was moderate to low, there are surely additional unmeasured factors involved in mediating these encounters such as



**Figure 3.** Possible signal value of ornament size, brightness, and peak wavelength. (A) Ornament size was positively related to female body size ( $P=0.013$ ), whereas (B) ornament brightness ( $P=0.031$ ) and (C) peak wavelength ( $P=0.032$ ) were predicted only by reproductive state. Relative to vitellogenic females, gravid females had brighter and redder ornaments.

potential chemical cues of female mating status and individual differences among males in mate choice preferences, recent win/loss history, jaw morphology/strength, and neuroendocrinology. Males may benefit from performing more male–male aggressive displays if females exploit the displays to assess male quality and use this information when making their own mate choice decisions (Wiley and Poston 1996; Candolin 1999; Wong and Candolin 2005; Aquiloni et al. 2008; Chan et al. 2008; Hämäläinen et al. 2012), which seems likely for *S. virgatus* (e.g., Smith 1985) but needs to be tested directly. If so, males may be selected to accept the costs of prolonged aggressive display behavior in the presence of higher quality females. This hypothesis suggests that male mate choice, male–male competition, and female mate choice may all affect the evolution of male

contest behavior; the relative roles of these forces remain to be determined.

Alternatively, *S. virgatus* males may be incited to escalate more quickly to risky contact behaviors and express more of these behaviors in the presence of small-ornament females, as these females may be further from ovulation (Weiss 2002) and perhaps may be more likely to be unmated. Given that reproductive state was not significant in any model examining male–male aggression, we find this latter hypothesis to be less supported than the former. It is more likely that males escalated to contact behaviors more quickly with small-ornamented females simply because they spent less time and energy engaged in display behaviors during these 20 min trials; ornament size did not affect the likelihood of escalation, but rather the timing of it.

It is noteworthy that male–male aggressive behavior was unresponsive to female body size and reproductive state as these are common targets of male mate choice due to their association with fecundity (Olsson 1993; Bonduriansky 2001; Reading and Backwell 2007; Ruiz et al. 2008; Edward and Chapman 2011, 2012). However, we did find a trend for more male–male contact behavior in the presence of larger females, perhaps indicating a tendency to accept a higher level of risk in the presence of more fecund females. Note that our results are specific to decision-making in the context of male–male aggression and do not inform us about the effect of female body size and reproductive state on other forms of mating investment. For instance, Abell (1997) found that *S. virgatus* males are more likely to maintain close spatial relationships with large females than with small females.

Overall, we conclude that males express differential investment in male–male aggressive displays (i.e., mate choice), in part, by strategically investing more reproductive effort in the presence of females with larger ornaments. In our current cohort of females, ornament size was positively related to body size and was unrelated to mite load and reproductive state. In previous studies, females with larger ornaments have been found to be in better condition with fewer ectoparasitic mites and lower corticosterone levels, are older, produce larger eggs with more yolk antioxidants, and produce offspring in better body condition and with faster sprint speeds (Weiss 2006, 2016; Weiss et al. 2009, 2011, 2013). Differences in the results of this study with Weiss (2006) and Goldberg et al. (2017) (see Table 1) may be due to differences in environmental conditions during those years of study (e.g., Chaîne and Lyon 2008; Sockman 2009; Evans and Gustafsson 2017). Overall patterns suggest that males who are strategically responsive to female ornament size may potentially gain both direct (this and previous studies) and indirect (previous studies) fitness benefits. However, males do not seem to be prioritizing information about fecundity over information about other quality metrics during male–male contests given that female body size itself did not significantly predict male–male aggressive behavior. Future work will strive to disentangle the potential benefits of more vs. higher quality offspring by quantifying the evolutionary fitness implications of *S. virgatus* male mate choice. Of course, it remains possible that males receive no benefit from this differential investment in male contest behavior or benefit from their mate choice via a non-sexually selected mechanism (e.g., West-Eberhard 1983).

The presence of male mate choice based on female ornaments is often assumed to equate to sexual selection on the female trait, though this may not be the case (Edward and Chapman 2011; Fitzpatrick 2015; Fitzpatrick and Servedio 2017). For female ornaments to be sexually selected by male mate choice, females must

benefit from males' responses by increasing the number and/or quality of mates. One commonly invoked mechanism by which females can benefit is a form of "indirect female mate choice" (Wiley and Poston 1996) where females produce signals that incite male-male competition and benefit by gaining higher quality mates (Farr and Travis 1986; Montgomerie and Thornhill 1989; Wong and Candolin 2005). It is therefore surprising that the effect of female ornaments on male-male aggressive behavior is rarely examined directly as we did here [but see Cox and Le Boeuf (1977); Given (1993); Cui et al. (2010); and Xu et al. (2012) for studies of female vocalizations]. Females may also benefit from ornament expression via non-sexually selected mechanisms, including social selection (West-Eberhard 1983); for instance, by motivating a male to fight against a rival male, females may avoid persistent courtship from other males (Abell 1997). As evidence for male mate choice based on female ornaments continues to accumulate, it will be important to also discern if and how male responses benefit females and select for female ornaments (Fitzpatrick 2015).

Males' female-directed behaviors (i.e., charges, bites, and bite holds interpreted as aggressive copulation attempts) were not affected by female ornament expression nor reproductive state, which was unexpected given the effect of ornamentation on *S. virgatus* male-male aggression and the importance of reproductive state on male mate choice in many other species (Bonduriansky 2001; Edward and Chapman 2011). Previous studies suggest that *S. virgatus* males are quite persistent when attempting copulation and are not attentive to female cues at that time (Abell 1997; Weiss 2002). Female-directed behaviors were more frequent when males and females were more closely size matched. Given that *S. virgatus* males are smaller than females, this may indicate "prudent" decisions by the male (Hårdling and Kokko 2005) to avoid attempts at subduing females much larger than they are, as they are unlikely to be successful and could possibly lead to injury. Females have been observed to chase, charge, nip, and head-butt persistent males in the field (Vinegar 1975b; Abell 1997). However, because males' female-directed behavior also tended to be more frequent toward larger females, together the 2 predictors of the model (i.e., smaller size difference and larger female size) suggest that it is actually the body size of the males, and not that of the female, that explains this response. A post hoc model confirmed that larger males were more persistent in their female-directed behaviors than were smaller males, perhaps due to higher resource holding potential, higher chances of success, and lower chances of injury. However, there were no successful copulations during our trials, likely indicative of the high mating investment females require prior to accepting a mate and/or interference from opponent males.

Both male mate choice and female-specific ornaments are well documented in lizards (Tokarz 1992; Olsson 1993; Cuadrado 1998; Whiting and Bateman 1999; Cuadrado 2000; LeBas and Marshall 2000; Kelso and Verrell 2002; Orrell and Jenssen 2002; Weiss 2002; Ruiz et al. 2008; Chan et al. 2009; Swierk et al. 2013; Stuart-Fox and Goode 2014), but the value of lizards as a model system to study these phenomena and their interactions seems underappreciated. Our findings show that *S. virgatus* males strategically modulate their investment in male-male aggressive displays during contests for potential mates on the basis of female ornament size, and not on ornament color, female body size, or reproductive state. Ornament size signals multiple aspects of female phenotype including offspring quality (Table 1) and thus, assuming male aggressive display behavior impacts mating success, males may gain both direct

and indirect benefits from their mate preference. Although our modern understanding of male mate choice encompasses differential investment in male-male competition (as well as in courtship, mate guarding, sperm allocation, etc.; Bonduriansky 2001; Edward and Chapman 2011), little work has empirically examined how male-male aggressive behavior is directly affected by the quality of the female being contested. Male-male aggression is typically considered to be a cost of male mate choice and not an expression of it (Fawcett and Johnstone 2003; Servadio and Lande 2006; Servadio 2007; Mautz and Jennions 2011; Edward and Chapman 2012). While we do not question the costliness of contests, game theory surely predicts an effect of resource quality on fighting decisions (Parker 1974; Enquist and Leimar 1987; Arnott and Elwood 2008) and this requires study in the context of male mate choice. Further, we encourage new theoretical models to consider the mating system of territorial lizards and how a limited pool of familiar, sedentary, and predictably located females who do not engage in active mate searching and who require high mate investment may affect the evolution of mate choice in males, as well as the strength of direct and indirect benefits, and the resulting selective pressure on female phenotype. Model predictions can be tested by taking advantage of the wealth of diversity among lizard natural histories that impact limitations on male mate investment and variation in female mate quality, including differences in breeding season (from short and highly synchronous to long and asynchronous), number of clutches per year (from one to many), clutch size (from fixed to highly variable), female ornament expression (from female-specific to male-like to absent), and more.

## Author Contributions

M.D. and S.L.W. conceived the study design. M.D. conducted the experiment and scored all videos. S.W. conducted the statistical analysis and wrote the manuscript. Both M.D. and S.L.W. edited the manuscript and approved the final version.

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