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Original Article

# The role of red coloration and song in peacock spider courtship: insights into complex signaling systems

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Research on animal signaling enhances our understanding of links between sensory processing, decision making, behavior, and evolution. Studies of sexually-selected signals may be particularly informative as mate choice provides access to decision patterns in the way that courtship leads to an easily observable behavioral output in choosers, i.e., mating. Male peacock spiders have some of the most elaborate and varied courtship displays known among animals. Particularly striking to human observers is the diversity of red, orange, and yellow ornaments that males exhibit across the genus. The primary objective of our research was to investigate how these visual ornaments interact with vibratory songs to affect female mating behavior of one species, *Maratus volans*. Accordingly, we conducted mating trials under a series of experimentally manipulated vibratory and lighting conditions. Contrary to expectation, chromatic characteristics of longer wavelength ornaments are not driving female mate choice decisions, despite their extensive presence on male fans. Instead, our results suggest that contrast is important to females. Additionally, we found that vibratory signals were not necessary and did not increase mating rates. Our study demonstrates the intricacies inherent in complex signaling systems.

*Key words*: **biotremology, multimodal signals, peacock spider, sexual selection, vibrational signaling, visual signaling.**

## BACKGROUND

For many animal systems, the manner in which females evaluate male courtship signals is unknown (Rosenthal 2017; Rosenthal et al. 2017). Empirical work is needed to improve upon existing models for decision making in mate choice, but designing experiments to elucidate male traits of interest to females is difficult. This is especially true for complex signals spanning multiple modalities (multimodal signals), where it is difficult to tease apart the role of each type of signal. However, in systems where male courtship displays are characterized by multimodal signals, determining how females assess different signaling modalities is critical to understanding how sexual selection shapes male phenotypes.

The challenges of studying multimodal signals are further compounded by the inherent subjectivity of observing animal signals through a human lens (Kokko 2017), especially when our knowledge of the perceptual capabilities of the animal in question is limited. Displays and features that stimulate our eyes and ears grab our attention such that we forget that prominent features to human observers might not be those most salient to the focal organism. In fact, the most relevant components of signals may escape our notice entirely. For example, many animals utilize visual features that are invisible to us, such as polarization (Chiou et al. 2008; Foster et al. 2014), and UV coloration (Hausmann et al. 2003; Hogg et al. 2011; Xu and Fincke 2015; Cronin and Bok 2016). Additionally, the bulk of our planet's animal diversity is composed of species that utilize modes of communication either nearly or completely imperceptible to humans, including substrate-borne signals (Cocroft and Rodriguez 2005; Hill 2008; Hill and Wessel 2016), water-borne signals (Aiken 1985; Patek 2001; Sueur et al. 2011; Ladich 2015; Parmentier et al. 2017), near-field particle signals (Heidelbach et al. 1991; Santer and Hebets 2008; Cator et al. 2009; Shamble et al. 2016), and/or chemical signals (Carde´ and Millar 2004). Even in systems where we understand something about the physiological capabilities of animals and can measure the pertinent signals, it is still easy to draw erroneous conclusions about how different aspects

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of these signals are utilized and processed. For example, recent work on mantis shrimp overturned the existing assumption that these exceptionally colorful stomatopods also have remarkable color discrimination abilities (Thoen et al. 2014). This study, like so many others, highlights the necessity of behavioral data to test hypotheses about signal use across taxa.

Peacock jumping spiders of the species-rich *Maratus* genus present an ideal system for examining the role of complex signaling traits in female choice of mates. During courtship, a male peacock spider will unfurl colorfully-patterned flaps attached to his abdomen (Hsiung et al. 2017), which he waves at a female in coordination with an ornamented third pair of legs (Girard et al. 2011). The extensive use of visual signals by male peacock spiders is not surprising because jumping spiders (Family: Salticidae) are widely considered visual specialists and have many adaptations that allow them to approach the physical limit of optical resolution for their compact size (Land 1969; Land 1985; Zurek et al. 2010; Nagata et al. 2012; Zurek and Nelson 2012; Caves et al. 2018). Behaviorally, visual traits have been demonstrated to play an important role in courtship of many jumping spiders (Jackson 1981; Forster 1982; Uhl and Elias 2011; McGinley et al. 2015; Peckmezian and Taylor 2015). In *Maratus volans*, male visual (waving of abdominal flaps and the third pair of legs) and vibrational (rate of vibratory songs) displays were shown to predict mating success (Girard et al. 2015), although it is not known if/how male coloration contributes to this outcome. Studies of the effects of color in other species of jumping spiders have generated equivocal results (Lim et al. 2007; Taylor and McGraw 2013; Taylor et al. 2014). Moreover, physiological studies investigating color vision in salticids indicate that there is interspecific variation in the number and spectral sensitivities of photoreceptors, although most are believed to be UV-green-sensitive dichromats (DeVoe 1975; Yamashita and Tateda 1976; Blest et al. 1981; Nagata et al. 2012; Zurek et al. 2015; Morehouse et al. 2017).

In addition to complex ornaments and displays, *Maratus* males employ vibratory songs during courtship, as do males in several other groups of jumping spiders. Some genera use simple substrate-borne vibrations (*Phidippus* (Elias et al. 2010, 2014)) while others evolved more complex vibratory songs (*Habronattus* (Maddison and Stratton 1988; Elias et al. 2003; Elias et al. 2012), *Saitis* (Gwynne and Dadour 1985), and *Maratus* (Girard et al. 2011)). The few studies that have examined the impact of vibratory signals on female mate choice determined that these signals are essential for males to achieve copulation (Elias et al. 2005, 2006; Sivalinghem et al. 2010) and reduce female aggression (Wignall and Herberstein 2013; Xiao et al. 2015). Although previous work on *M. volans* identified several aspects of male vibrational signals that predict mating success, elements of motion displays by males explain more than twice the variance in mating success as any aspect of vibrational signals, suggesting that visual signaling modalities are dominant in this species (Girard et al. 2015). To date, however, no studies of *Maratus* have examined the impacts of vibrational and visual signals in isolation or how these 2 courtship elements interact in combination to affect mating. Is the presence of both modalities required for mating success (Partan and Marler 1999, 2005; Hebets and Papaj 2005)? Instead, perhaps each modality can compensate for the other in diverse signaling environments (Heuschele et al. 2009; Gordon and Uetz 2011; Gray et al. 2014; Partan 2017).

Here, we examine how interactions between different signal modalities affect mate choice by female *M. volans*. In particular, we focus on vibrations and long wavelength (LW) visual ornaments (575–700 nm). We chose to manipulate LW ornaments because LW sexual ornaments are only found in few jumping spider groups (Maddison and Hedin 2003; Zurek et al. 2015; Leduc-Robert and Maddison 2018) and exemplify one of the major axes of visual signaling diversity across the *Maratus* genus (Girard and Endler 2014). To explore the impact of LW visual signals and assess the relative contributions of visual and vibratory signals to female mate choice, we compared patterns of male mating success under various vibratory and lighting conditions. We predicted that if *M. volans* females were selecting males based on chromatic properties of their long-wavelength ornaments, then manipulating the reflection patterns of long-wavelength ornaments would significantly decrease mating rates. Furthermore, we predicted that manipulating vibratory environments would have a significant but smaller effect as was suggested in a recent study (Girard et al. 2015). In addition to generating new insights into the mate choice decisions of females, our analyses reveal how interactions between signaling modalities may vary across taxa, thereby highlighting the importance of assessing multiple sensory modalities when evaluating the impact of female choice on signal evolution.

# METHODS

## Study animals

*M. volans* specimens were collected from 4 locations (Royal National Park, Ku-ring-gai Chase National Park, Muogamarra Reserve, and Wyrrabalong National Park) around Sydney, New South Wales from 15 September to 11 November 2015 and 13 September to 11 November 2016. Live spiders were brought back to the laboratory, where they were housed individually with leaf litter from their environment and kept on a natural 14:10 light:dark cycle. Spiders were fed a diet of fruit flies (*Drosophila melanogaster*) and occasionally pinhead crickets (*Acheta domestica*). Only females that were collected as juveniles and that matured in the lab were used in this experiment so that we could ensure their virgin mating status. Female *M. volans* females likely only mate once in their lifetime and become highly aggressive when they have mated (Girard et al. 2015).

## Experimental design

To assess the effects of vibratory and visual cues on female mating decisions, we used a 2 × 2 factorial design to conduct mating trials under variable vibratory and lighting conditions. In order to modify the reflected chromatic properties of male signals, trials were conducted in chambers with 1 of 2 illumination types (Figures 1 and 2): broadband (full spectrum light: FS, 400–700 nm) or lighting with longer wavelengths removed (minus red spectrum light: MRS, 400–575 nm); a more detailed description of the illumination chambers is provided in the "experimental manipulations" section below. Under each type of lighting, we also varied the vibratory environment of our mating arenas (again, see "experimental manipulations" section below for more details). The 2 mating arena types used in our trials either propagated all male signaling frequencies (vibration: V) or attenuated all vibrations (no vibration: NV). Our 4 treatments were thus labeled as follows: full spectrum-vibration (FS/V), full spectrum-no vibration (FS/NV), minus red spectrum-vibration (MRS/V), and minus red spectrum-no vibration (MRS/NV). This design allowed us to distinguish between the importance of vibratory signals and LW chromatic signals in dictating female mating behavior.

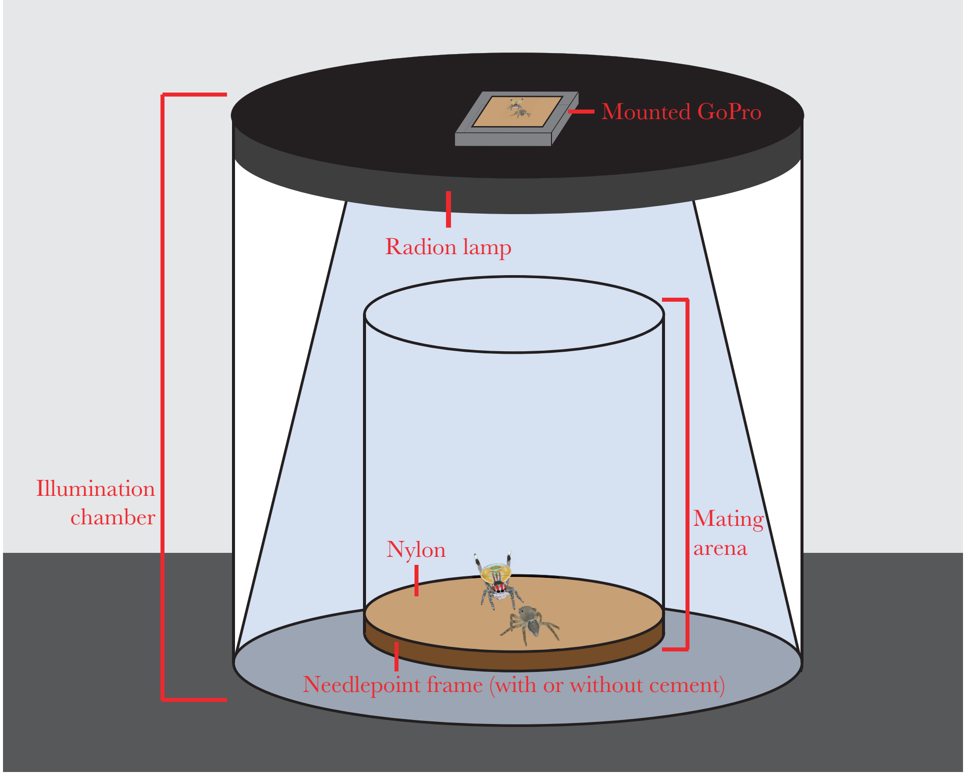

**Figure 1**
Experimental set-up.

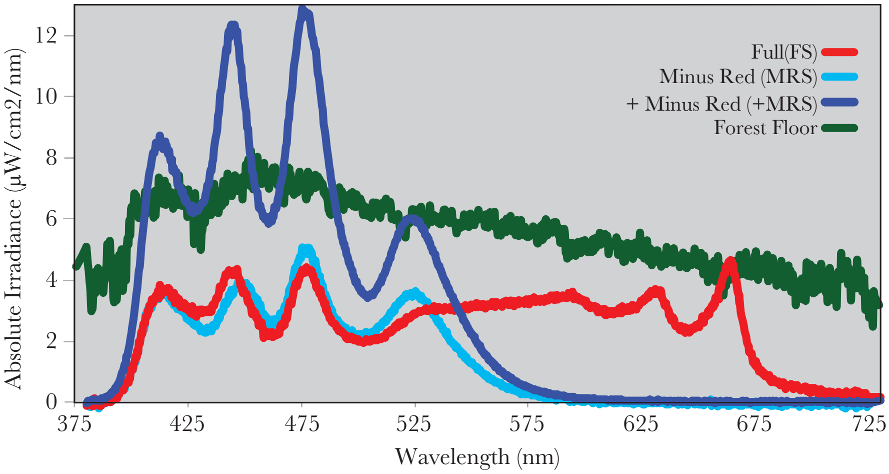

**Figure 2**
Irradiance spectra across natural and experimental conditions: lighting conditions (at noon) of the natural environment of *M. volans* (green); experimental lighting condition for the FS light treatment (red); experimental lighting condition for the MRS light treatment (light blue); experimental lighting condition for augmented brightness minus red spectrum (+MRS) light treatment (dark blue).

By truncating the longer wavelengths of the visible spectrum for our MRS treatments, we greatly reduced the total level of lighting in the arenas compared to the FS treatments (Figure 2); the latter were 1.76 times brighter. To address this potential confounding factor, once initial mating trials were completed we conducted a fifth manipulation to test whether the differences in mating rates detected in the first experiment were related to the color composition of the lighting environment or the overall brightness of the chamber illumination. In this additional treatment, the MRS condition was the same in terms of wavelength range (400–575 nm) but the brightness (area under irradiance curve for the FS treatment; Figure 2) was adjusted to be similar to that of the full spectrum treatment (Figure 2, increased brightness: +MRS); vibrations were not manipulated and thus we labeled this treatment +MRS/V. For spectra of the different treatments measured as photon flux, see Supplementary Figure S1, in the Supplementary Material.

## Mating trials

Mating trials proceeded as follows: 2 to 3 weeks postmaturation (determined by the appearance of female genitalia (Foelix 1996)), each female was randomly paired with a mature male and assigned to one of the treatment groups. Immediately prior to each trial, vibratory arenas were placed inside the cylinders (30.45 cm height, 25 mm diameter), which were then covered with blackout cloth to ensure that our setups were completely sheltered from all other ambient light. All mating trials ($N$ = 175, 35 for each treatment) were conducted between 09:00 and 17:00 Australian Eastern Daylight Time (AEDT); temperature in the arena was monitored using ibuttons (Maxim Integrate Thermochron *i*Button) to ensure that all experiments were run under approximately the same ambient temperature (26.0 ± 1.04 °C, mean ± SE). Trials were allowed to run for 15 min (we ensured that all males courted during this time) and we recorded interactions between the pairs using a Go Pro (Hero 4) mounted to the top of each lighting chamber. In between use, our arenas and chambers were cleaned with 85% ethanol to remove any potential chemical cues remaining from previous trials. Whenever possible, females were paired with males collected from the same population (only 16/175 females were paired with males from a different collection location). All males and females were only used once.

We used a single-choice assay because of the natural history of the organism as well as experimental constraints. The relative low density of *Maratus* individuals makes it more likely the females assess males individually and not simultaneously. This is especially the case when males are fan dancing during the later stages of display (Girard et al. 2011). Additionally, because we wanted to directly measure copulation success, we elected to use single-choice assays to avoid the complicating factor of male–male interactions. Similar assays have been used in many studies of jumping spiders with comparable natural history (Clark and Biesiadecki 2002; Elias et al. 2005; Hebets and Maddison 2005; Sivalinghem et al. 2010; Taylor and McGraw 2013).

## Experimental manipulations

We used irradiance measurements (obtained with a Jaz – Combo-2 spectrometer, CC-3-DA cosine corrector, Ocean Optics Inc.) from the shady understory of Eucalyptus forests, *M. volans'* native habitat, to approximate, to the best of our abilities, the spectrum and brightness of natural illumination conditions. Absolute irradiance measurements were taken on a sunny cloudless day (at 12 pm AEDT), 12 October 2015, during *M. volans* peak activity at one of our collecting sites (Muogamarra Reserve site). The illumination characteristics of our control treatment (FS—see below) fell within naturally occurring variation in natural lighting.

Light treatments were created using Radion XR15w Pro lamps which consisted of tunable arrays of LED's across a broad spectrum of wavelengths. Six cyan (490–520 nm) LED's were used to augment the light provided by these lamps and help smooth the middle (green) part of each spectrum. LED arrays were mounted inside lighting chambers made from cardboard cylinders (radius = 12.5 cm, height = 30.48 cm) spray-painted matte white. The removal of the LWs from ambient illumination strongly affected color patches that reflect light in the 575–700 nm portion of visible spectrum (yellow, orange, and red ornaments; Figure 3, Supplementary Figure S2). These treatments affected existing ornamentation patterns in several ways. First, the removal of LWs changed the chromatic properties of the reflectance of ornaments (primarily yellow, orange, and red ornaments). Second, this treatment effectively removed any existing patterns of chromatic contrast and replaced this with a pattern of achromatic contrast. Our +MRS treatment had the additional effects of 1) increasing the amount of light reflected off of short wavelength ornaments and 2) further increasing the achromatic contrast between short and LW ornaments. While we were not able to recreate the UV portion of sunlight, all treatments were equal in this regard and thus should have affected female behavior equally in all trials.

In the treatments that allowed vibratory communication by males (FS/V and MRS/V, +MRS/V), our arenas consisted of nylon fabric stretched over a circular wooden needlepoint frame (diameter: 10 cm). Nylon was used as the signaling substrate because it passes relevant frequencies with minimal distortion (Elias and Mason 2014). The arena for our nonvibration treatment groups (FL/NV and MRS/NV) used wooden needlepoint frames filled with cement. Nylon fabric was also stretched over these frames to replicate the background color and texture of the vibratory arenas; because the nylon was directly in contact with the cement, however, it was unable to move freely and thus drastically attenuated vibrational signals (Figure 4). Both treatment types were surrounded with white Teflon sheets to prevent spiders from leaving the arena. To remove any effects of potential vibrational noise in the room during our trials, we always ran similar vibration treatments concurrently. For example, FS/NV trials were run simultaneously with MRS/NV trials and FS/V trials were run simultaneously with MRS/V trials.

## Measuring male color:

In order to understand which color patches of male *M. volans* would be affected by our lighting manipulations, we used a SOC710 hyperspectral imaging system (Surface Optics Co., USA) with 128 channels (bands) to collect spectral data from male fans. Pinned specimens of dead male *M. volans* were imaged under a broadband 800W tungsten halogen photographic light (StudioPRO). The camera was operated using a PC laptop and the Lumenera software v.6.3.0 provided by the manufacturer. The integration time for image capture was 300 ms, which was determined to work best with our illumination levels. The raw hyperspectral image cube (hypercube) generated by the system's CCD sensor was calibrated to express camera responses for each pixel in radiance units ($\text{mW}\cdot\text{cm}^{-2}\cdot\text{nm}^{-1}\cdot\text{sr}^{-1}$) using a dark image reference file (recorded immediately after photographing each spider), and a calibration file provided by Surface Optics. Absolute reflectance data (this imaging system detected wavelengths between 380 and 750 nm) for each pixel location was then reconstructed using the manufacturer's spectral radiance analysis software, which automatically divided each radiance spectrum by the light reference spectrum to produce a normalized reflectance for our data. The light reference consisted of a pixel sample area from a Munsell grey N5 panel that was positioned next to the focal spider in every photo. See (Garcia et al. 2015) for similar methods.

For all individuals imaged ($N$ = 21), 2 nonoverlapping pixel samples within each color patch on a male (Figure 3a) were selected for analysis. When possible, the samples analyzed were sized to be approximately 10 × 10 pixels, although some samples (e.g., patch F in Figure 3a) were necessarily smaller. Finally, all spectral data were exported into Excel where samples were averaged within and then across individuals ($N$ = 21) to generate Figure 3b. Predicted reflectance of fans in each of our lighting conditions (Figure 2) is presented in Supplementary Figure S2.

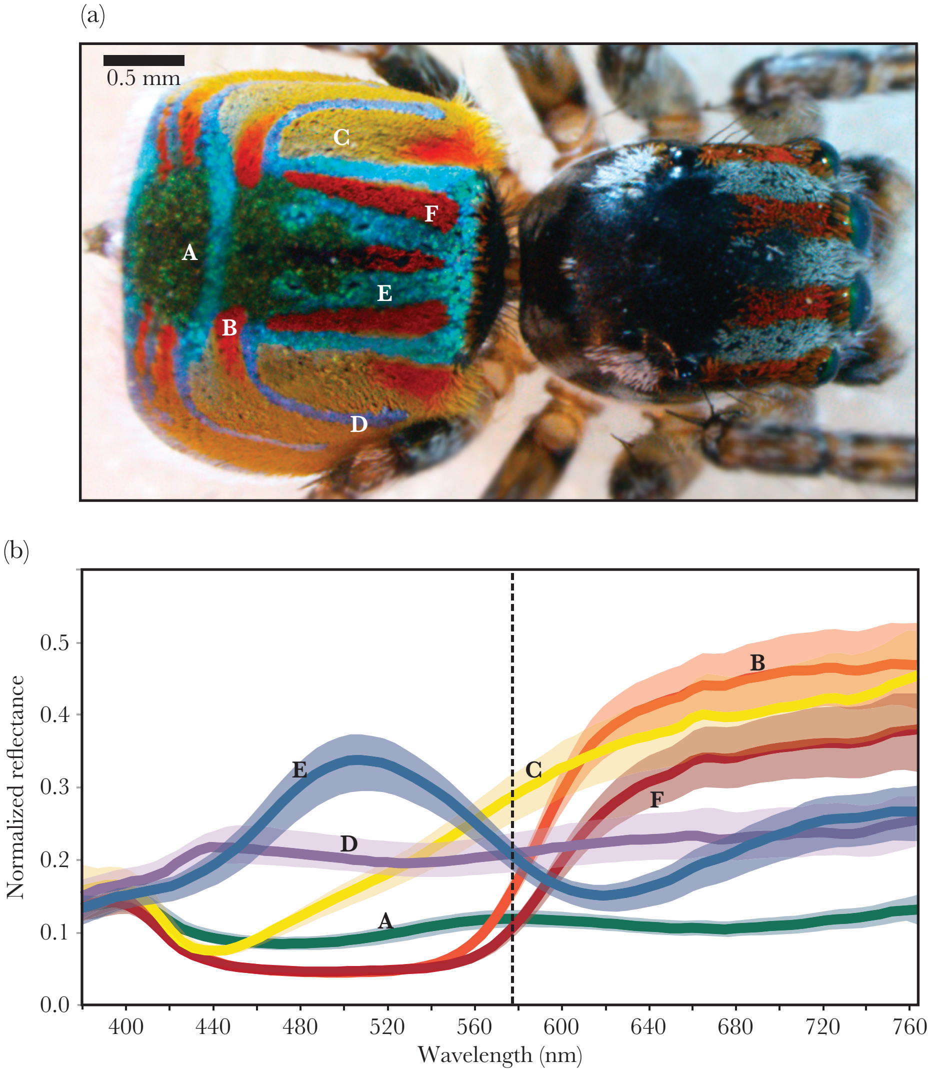

**Figure 3**
*M. volans* fan ornamentation coloration. (a) color patches lettered A–F correspond to reflectance curves A–F in (b). Wavelengths to the right of the dotted line in (b) are those that were removed in our MRS treatments. Data shown is averaged for $N = 21$ individuals, and the shaded region around each curve reflects standard error for each wavelength.

## Scoring behavior

We constructed ethograms for both males and females. We then used the JWatcher Video software package (Blumstein et al. 2010) to score each trial from the original 4 treatments. During our trials, males spent time 1) moving around the arena, 2) still, orientated towards females, or 3) performing courtship behaviors towards females (Girard et al. 2011, 2015). For the purposes of our analysis, we scored behavior after both animals orientated to each other. For males, we recorded the proportion of time spent engaged in visual displays such as fan dancing (opisthosomal fan flaps opened and moving back and forth laterally, Figure 3) or leg waving (third pair of legs extended and waved up and down) (Girard et al. 2011). To quantify the proportion of time that males spent vibrating, we identified this behavior based on the abdominal movements of males (Girard et al. 2011) that were visible on recordings. Both visual and vibratory courtship displays are important for male mating success (Girard et al. 2015); thus, we wanted to examine whether male behavior was similar across treatment groups or if there were any differences in male courtship under separate lighting and vibratory conditions that would account for any differences we saw in mating rates. For females, we recorded the proportion of time spent oriented at males, as well as any instances of lunges and abdomen wiggling (see Girard et al. 2015). All 3 of these female behaviors correlate with female mating receptivity, positively in the case of orientation, and negatively with lunges or abdomen wiggling (Girard et al. 2015). For pairs of spiders that mated, we also scored latency to mate and mating duration.

## Statistical analyses

Statistical analyses were performed using JMP (v.13.0.0, SAS Institute Inc.). To examine differences in mating rates across treatments, we used a nominal logistic regression, with treatment group as a fixed effect and population, temperature, trial date and time as random effects. For pairs that mated during one of the original 4 treatment groups, we used 1-way analysis of variance (ANOVA) to determine if treatment type affected latency to mate or copulation

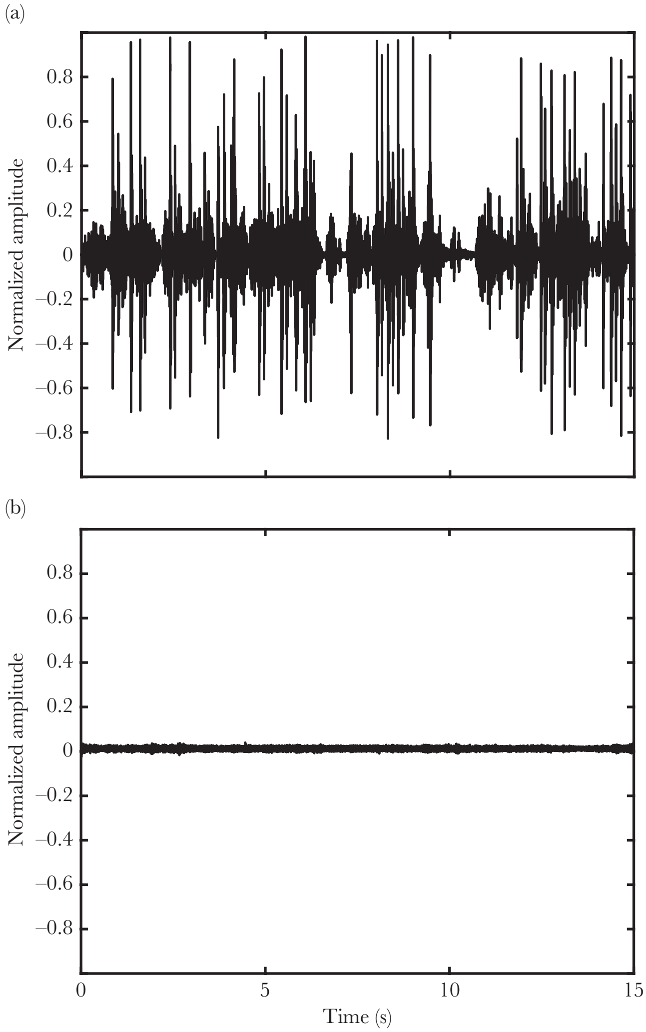

**Figure 4**
Waveforms of *M. volans* vibratory displays in both the (a) Vibration treatment and (b) No-Vibration treatment arenas. These waveforms accompany Supplementary Videos S1 and S2 provided in the Supplementary Data section.

duration. We also used 1-way ANOVA to determine if male behavior was consistent across lighting and vibrational regimes and to assess whether female behavior changed under different treatments. Finally, we used unpaired *t*-tests (assuming unequal variances) to investigate whether the same aspects of male and female behavior that were previously found to be correlated with mating success (male: visual and vibratory display effort as well as vibrational vigor; female: aggression;) (Girard et al. 2015) were important in our study. Similarly, we used 2 separate general linear models (GLMs), each with a normal probability distribution and identity link, to examine whether latency to mate or copulation duration was predicted by these same behaviors.

## RESULTS

We completed a total of 175 mating trials, 86 (49.1%) of which ended with a male successfully copulating with a female. Population of origin, temperature, trial date, and time had no significant effect on mating rates and thus these parameters were dropped from all subsequent analyses.

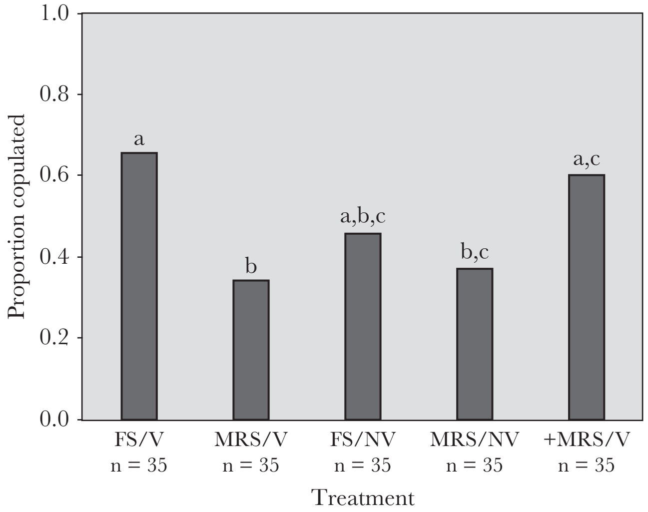

**Figure 5**
Proportion of males that mated in each experimental treatment (full spectrum–vibration, minus red spectrum–vibration, full spectrum–no vibration, minus red spectrum–no vibration, augmented brightness minus red spectrum–vibration). Letters above bars indicate significant statistical differences between treatment groups.

As predicted, the number of successful copulations differed significantly among the 5 treatment groups (Figure 5; $\chi^2$ = 10.76, df = 4, $P$ = 0.03, $N$ = 175). Of the original 4 treatment groups, FS/V had the greatest mating rate (65.7%); this rate was significantly higher than that for both reduced spectrum (MRS) treatment groups (MRS/V: $\chi^2$ = 7.03, $P$ = 0.01; MRS/NV: $\chi^2$ = 5.78, $P$ = 0.02), which had mating rates of 34.3% and 37.1%, respectively. Between MRS treatments, there was no significant difference in mating rate for trials with and without vibratory signals (MRS/V vs. MRS/NV; $\chi^2$ = 0.06, $P$ = 0.80). The final treatment group (FS/NV) did not differ significantly from any of the other treatment groups (MRS/NV: $\chi^2$ = 0.94, $P$ = 0.33; FS/V: $\chi^2$ = 2.11, $P$ = 0.15; MRS/V: $\chi^2$ = 1.48, $P$ = 0.22). Interestingly though, this FS/NV treatment had a mating rate (48.6%) that was intermediate to the FS/V and both MRS treatments, suggesting that there may be some reduction in female receptivity when vibrational signals are reduced.

Surprisingly, overall brightness levels appeared to be a major factor impacting mating rates during our trials and not the specific chromatic characteristics of the ambient illumination, suggesting a role for contrast in mate choice. Specifically, the increased brightness of the +MRS/V treatment versus the MRS/V treatment resulted in a significantly greater number of copulations ($\chi^2$ = 4.70, $P$ = 0.03). We observed a 60% mating rate in our +MRS/V treatment, which is comparable to the mating rate we observed in the FS/V treatment group.

For the subset of spiders that did mate during trials, we found no significant difference across the original 4 treatments with respect to the latency to mate ($F_{3,62}$ = 1.69, $P$ = 0.18) or the duration of copulations ($F_{3,61}$ = 0.16, $P$ = 0.92). However, regardless of treatment, we found that both the proportion of time that males spent displaying visually (Girard et al. 2011) and the proportion of time spent vibrating predicted mating latency ($\chi^2$ = 39.85, df = 59, $P$ < 0.0001), with a negative relationship between the amount of time engaged in both signal types and the interval to mating. The amount of time that males spent fan dancing also predicted copulation ($F_{3,134}$ = 17.269, $P$ < 0.0001, Figure 6). Together, these data

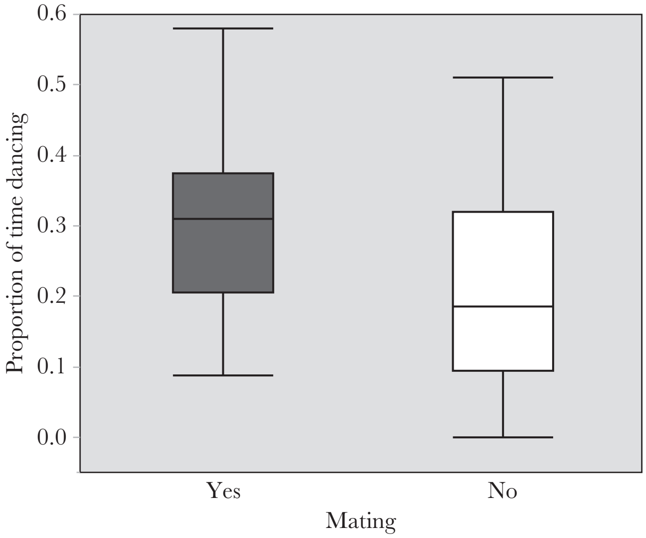

**Figure 6**
Proportion of time males spent dancing during mating trials relative to copulation success: Across treatments (FS/V, FS/NV, MRS/V, and MRS/NV), males that mated (dark grey) spent more time dancing than males that did not (white).

suggest that successful males spend a greater proportion of time engaged in courtship displays, which is consistent with previous data for this species (Girard et al. 2015).

We found no significant difference in the proportion of time that males engaged in visual ($F_{3,134} = 0.30$, $P = 0.82$) or vibrational ($F_{3,134} = 1.28$, $P = 0.28$) signaling across the original 4 treatment groups. Looking at only the short wavelength lighting treatments (MRS/V and MRS/NV), however, revealed a significant difference in the proportion of time that males spent vibrating (Figure 7: $F_{1,67} = 3.099$, $P = 0.04$), with males vibrating more on arenas with the nylon substrate than on those that dampened vibrations using concrete. This suggests that males may alter their activity in response to their substrate or in response to female behavior when vibrations are present.

Lastly, the proportion of time that females spent oriented ($F_{3,134} = 1.06$, $P = 0.37$) in the male's direction, the number of lunges toward males ($F_{3,134} = 0.90$, $P = 0.44$), and the occurrence of abdomen wiggling ($F_{3,134} = 1.653$, $P = 0.18$) did not differ significantly with respect to treatment. However, across the original 4 treatments, females that mated during our trials performed significantly fewer lunges than females that did not mate (Figure 8: $F_{3,134} = 17.03$, $P < 0.0001$).

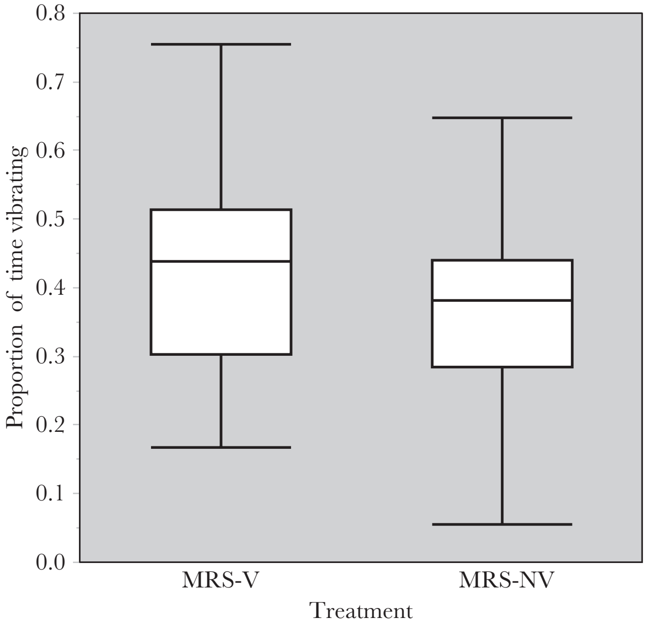

**Figure 7**
Proportion of time males spent vibrating in MRS treatments. Males in the vibration treatment spent significantly more time vibrating than those in the no-vibration treatment.

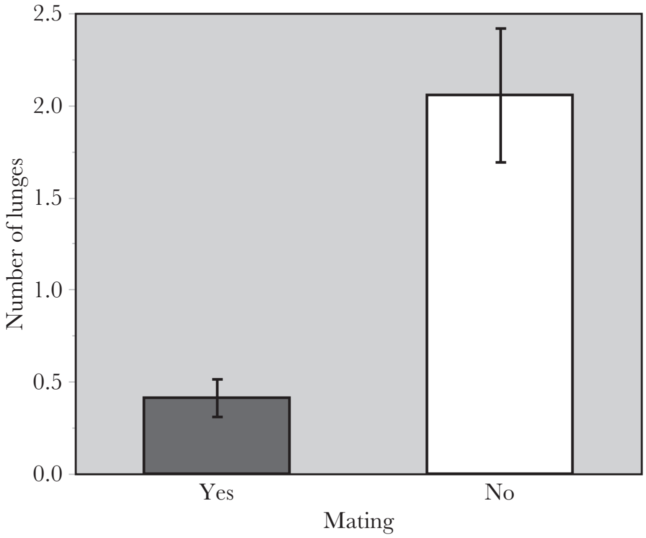

**Figure 8**
Number of aggressive attempts made by females relative to mating success: across the treatments (FS/V, FS/NV, MRS/V, and MRS/NV), females that mated (dark gray) were less likely than females that did not (white) to make aggressive lunges at males.

## DISCUSSION

In systems where complex displays spanning many modalities are involved, it remains a great challenge to elucidate which male traits are important to female mating decisions. Contrary to expectation, our data indicate that chromatic aspects of LW signals play a relatively minor role in mate choice. While there was a significant decrease in mating rates in our MRS treatment groups as compared to our FS treatments, the increase in mating we saw with our +MRS/V treatment suggests that other aspects of male visual signals other than long-wavelength chromatic properties are the focus of female attention. While we cannot rule out the effects of light intensity on mating behavior, our overall mating rates in the FS treatment were similar to mating rates in arenas with bright, broad spectrum illumination (Girard et al. 2015) suggesting that our FS treatment was a proper control for this study. We also observed that attenuating vibratory signals did not significantly affect mating rates. However, we found evidence that vibrations may be useful in some contexts, supporting the idea that vibratory signals may serve to complement visual signals. The proportion of time that males invested in courtship did not differ across our treatment groups, suggesting that differences in mating rates were based on female responses to male signals.

## Why do males have long-wavelength visual signals?

LW signals make up the immense diversity of male ornamentation across *Maratus* (Girard and Endler 2014) and are fairly unique across jumping spiders. We thus hypothesized that chromatic characteristics of LW fan ornaments (e.g., hue, chroma, and saturation) were likely important to female peacock spiders, as they are to females of other species (Houde 1987; Hill 1990; Kodric-Brown and Nicoletto 2001; Blows et al. 2003). If the long-wave color signals (e.g., reds, oranges, yellows) that are so prominent on male peacock spider fans are not used by females in mate choice, why do males invest in the production of these signals?

One possibility is that females are evaluating overall fan pattern and not the specific color components of the fan. Contrasting patterns have been shown to be important for many species (Fuller 2002; Heindl and Winkler 2003; Morrongiello et al. 2010; Barry et al. 2015; Cole and Endler 2015; Franklin et al. 2017; Gaskett et al. 2017). Moreover, research has illustrated that although choosers may assess individual visual components, overall patterning plays a larger role in mate choice (Blows et al. 2003; Grether et al. 2004; Endler and Mielke 2005; Gumm and Mendelson 2011; Cole and Endler 2015). Under this hypothesis, the long-wave chromatic components of *Maratus* fans function to establish the contrast between adjacent ornament patches (chromatic or achromatic contrast). Chromatic contrast patterns are formed via the interaction of neurons comparing the response of different photoreceptors (opponency, see Cronin et al. 2014). While we cannot say anything about how patterns of chromatic contrast are perceived in *Maratus,* because the sensitivity of photoreceptors is unknown (Vorobyev and Osorio 1998; Cronin et al. 2014), luminance differences between the long and short wavelength ornaments (e.g., E vs. F in Figure 3 and Supplementary Figure S2) are minimal. This suggests a role for chromatic contrast. In our manipulations removing LWs, effectively turning a presumed chromatic contrast pattern into achromatic contrast (relative luminance) pattern, did have an effect on female mating rates, however, this effect disappeared when the achromatic contrast between patches was increased in our enhanced illumination (+MRS) treatment. Taken together, our data thus support the hypothesis that *Maratus* use both patterns of chromatic and achromatic contrast under different lighting conditions.

While several animals have been demonstrated to use chromatic and achromatic contrast patterns for distinct tasks (Giurfa and Vorobyev 1998; Kelber et al. 2003; Osorio and Vorobyev 2005), recent work has been accumulating that achromatic and chromatic vision can interact (Lind and Kelber 2011; Kelber and Henze 2013; Schnaitmann et al. 2013; Olsson et al. 2018). For example, studies in blue crabs and guppies have shown that both chromatic and achromatic cues are used in mate choice (Baldwin and Johnsen 2012; Cole and Endler 2015). Red, yellow, and orange signal components, similar to those focused on in our study, may be especially important in creating a contrast with the mottled brown/green background of the forest floor (Lovell et al. 2005; Arenas et al. 2014) and/or between adjacent blue/green ornaments. Contrast between LW signals and green/blue backgrounds in their natural environment have been used to explain the prevalence of these ornaments in aposematic coloration across taxa (Ruxton et al. 2004). Assessment of color patterns and plasticity in the way color patterns are assessed may be an adaptation to heterogeneous light environments (Endler 1993; Warrant and Johnsen 2013; Cole and Endler 2015).

Although reliance on patterning/contrast may explain the apparent lack of importance of long-wave chromatic information in our study, other explanations are possible. First, females may be selecting males purely based on the brightness of their ornaments. In this scenario, females assess the chromatic properties of the "blue" ornaments due to their increased brightness, whereas in the FS treatment, females assess the brightness of "red" or "blue" ornaments. Manipulations of the short wavelength components are needed to address this hypothesis. Second, neural mechanisms may compensate for the absence of LWs such that females still perceive red coloration in the absence of the associated wavelengths (color constancy: (Neumeyer 1998; Balkenius and Kelber 2004; Chittka et al. 2014). Some ornaments, particularly those in the "yellow" portion of the spectrum reflect both long and short wavelength light and may allow for discrimination/assessment under the increased light levels in the MRS+ treatment. Accordingly, the decreased mating rates observed during MRS treatments without enhanced illumination may have resulted from poor signal contrast in low light levels. In any case, our data demonstrate that females are unlikely to select males based on variation in chromatic properties of LW reflections. Third, it is possible that the lighting environment of the MRS treatment (but not the FS and +MRS treatments) affected female willingness to mate, regardless of the males they encounter or their behavior. Light environment impacts on mating behavior have been observed in experiments (see Endler 1991; Rosenthal et al. 2018) and anthropogenically impacted environments (see Swaddle et al. 2015). Finally, while our results suggest that chromatic properties of LWs are relatively unimportant in mate choice, they may be used in other contexts such as foraging, learning and navigation (Hempel de Ibarra et al. 2001; Hoefler and Jakob 2006; Jakob et al. 2007; VanderSal and Hebets 2007; Peckmezian and Taylor 2015; Taylor et al. 2016); future work is needed to explicitly test these hypotheses.

## Role of vibratory songs in mating success

Similar to our findings for the chromatic features of LW visual signals, our data suggest that vibrations do not play a crucial role in female willingness to mate. This finding is consistent with previous research (Girard et al. 2015) indicating that even though vibratory signaling predicts copulation, this effect is much smaller than for visual signals. Males may alter their use of vibrational signals in response to the substrate, vibrating more only when signals can be effectively transmitted (Heuschele et al. 2009; Gordon and Uetz 2011; Gray et al. 2014; Patricelli et al. 2016; Partan 2017). This shift in signal use may allow an animal to compensate for reduced efficacy in signal transmission in one sensory modality, for example, by increasing the amount of time spent vibrating under low light condition. Similar results are reported for other types of spiders (Gordon and Uetz 2011; Sullivan-Beckers and Hebets 2014), possibly driven by high costs inherent in vibrational signaling in spiders (Kotiaho et al. 1998; Ahtiainen et al. 2005; Hoefler 2008; Elias et al. 2014). In peacock spiders, males tend to produce more substrate-borne vibrations when females are not attentive to visual displays, which results in females reorienting themselves toward males and thus presumably paying more attention to visual displays (Girard et al. 2015). Thus, we suggest that the interaction between vibratory and visual signals in our study species is not static but varies in response to the environmental conditions in which courtship occurs.

# CONCLUSIONS

Animal courtship displays are complex and often involve multiple signals that employ more than one sensory modality. Presumably females evaluate more than one signal when making mate choice decisions. Recent models suggest that multiple signals evolve when different signals convey distinct types of information and thus serve distinct functions (Ay et al. 2007; Bro-Jørgensen 2010; Wilson et al. 2013). With regard to peacock spider signals, which employ multiple sensory modalities (i.e., vibratory and visual signals), we hypothesize that each modality may have unique functions and represent different axes of overall variation in courtship behavior based on this and other studies ((Girard et al. 2011, 2015; Girard and Endler 2014). Vibratory songs may function to draw a female's attention across long distances, when the female is not oriented toward a male (Girard et al. 2011; Girard et al. 2015), or when lighting conditions are less than ideal (this study). Once a female is attentive to a male, contrast patterns on the fan may become more important (this study), possibly to enhance contrast with the background environment or potentially as a signal of species identity (not examined). Finally, it is possible that motion (dancing) is assessed as a signal of mate quality given that males that dance at higher rates are preferred as mates (Girard et al. 2015). Thus, although dancing is also a visual signal, it may function quite differently from color-based signals. More generally, we suggest that the evolution of complex signals in this and other species, is driven by the need for different types of information (species identity, mate quality, and multiple messages) and for maximal signal transmission in less than optimal environments (use of LWs, behavioral compensation, and redundant backups) (Candolin 2003; van Doorn and Weissing 2004, 2006; Hebets and Papaj 2005; Bro-Jørgensen 2010; Elias et al. 2011; Wilson et al. 2013; Herberstein et al. 2014). Complex signals thus evolve to meet the myriad of challenges inherent with fluctuating, heterogeneous abiotic and biotic environments, signal production and effective transmission in these environments, and the variation in mate choice that this engenders. Future studies are needed to investigate this hypothesis directly. As many have stated, trying to understand an organism that is unlike ourselves is the biggest challenge to animal behavior research (Nagel 1974) but also one of the most meaningful as we seek to understand the natural world.

# SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Girard et al. (2018).

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