

Original Article

Male ornamental coloration improves courtship success in a jumping spider, but only in the sun

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In many animals, males display colorful ornaments to females during courtship, the effectiveness of which depends on the ambient lighting environment. While a variety of hypotheses exist to explain both presence of and variation in such traits, many propose that they function as signals and that their presence is required for or improves successful mating. In *Habronattus pyrrithrix* jumping spiders, males display brilliant, condition-dependent red faces and green legs to drab gray/brown females during courtship. We designed 2 experiments to first test if coloration is required for successful mating and then whether the role of color changes under varying light conditions. In Experiment 1, we paired individual males with virgin females under laboratory lighting and found that blocking either their red or green coloration, or both, had no effect on success (likelihood of copulation, copulation duration, latency to copulation, female aggression, or cannibalism) when compared with sham-treated males. In Experiment 2, we gave virgin females the choice between 2 simultaneously courting males, one with his red coloration blocked and the other that received a sham treatment, and ran trials outdoors in both the sun and the shade. Blocking red facial coloration reduced a male's ability to approach a female, but only when courting in the sun. These results suggest that ornamental coloration is not required for mating in *H. pyrrithrix*, but that red coloration improves success in certain contexts. We discuss implications for the evolution of elaborate, multimodal courtship displays by animals that interact in variable environments.

Key words: animal coloration, courtship, *Habronattus*, mate choice, Salticidae, sexual signaling. [*Behav Ecol*]

INTRODUCTION

Selection for effective communication between potential mates has resulted in elaborate and complex ornaments and behaviors in a variety of taxa. In many animals, courtship occurs in complex, variable, and unpredictable environments, yet the successful transmission of courtship signals depends much on the environmental conditions in which they are sent. For example, the transmission of substrate-borne signals depends on the vibratory properties of the substrate on which they are produced (e.g., spiders: Elias et al. 2004; Hebets et al. 2008; Gordon and Uetz 2011), and the transmission of vocalizations depends on the acoustic properties of the surrounding habitat (e.g., birds: Brown and Handford 2000; frogs: Castellano et al. 2003). The distances between signaler and receiver can also affect the efficacy of different types of signals (e.g., Clark and Biesiadecki 2002). Given this effect of the environment on signal transmission, we might expect that the role and importance of certain traits within a display repertoire will change depending on environmental conditions (e.g., Gordon and Uetz 2011; Wilgers and Hebets 2011).

Many hypotheses have been proposed and tested to explain the functions of traits that are involved in courtship (reviewed in Andersson 1994). Some of these hypotheses make predictions about how receivers will respond to the presence (or absence) of certain display traits. For example, hypotheses positing that such traits function in species recognition (e.g., Couldridge and Alexander 2002), sex/mate recognition (e.g., Lim et al. 2007), or attracting receiver attention (e.g., Clark and Morjan 2001) all predict that the presence of the signal is either required for, or will improve, the chances of successful mating. This is in contrast with other functional hypotheses that make predictions about how receivers respond to natural, more subtle variation in trait expression; such hypotheses posit that such signal variation encodes aspects of individual identity or individual quality to potential mates or competitors (reviewed in Andersson 1994). These 2 broad categories of hypotheses are not mutually exclusive—for example, it is plausible that the presence/absence of a trait might provide important information for species or sex recognition from a distance, while subtle variation in that trait might provide additional information about individual quality as courtship progresses. Because no single experiment can disentangle all of these hypotheses simultaneously, a good starting point is to remove the trait of interest completely and assess behavioral effects on the putative receiver.

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This approach allows us to test some initial predictions of hypotheses about the importance of the trait in species recognition, sex recognition, and attention alterations described above. In addition, such experiments can help us to establish the social or sexual context in which the putative signal likely functions. For example, early experiments that involved blacking out the red epaulets of red-winged blackbirds (*Agelaius phoeniceus*) established their role as an important signal for settling territorial disputes (Peek 1972; Smith 1972). These initial studies provided the foundation for the numerous studies that have followed to probe more deeply into the complex roles that natural variation in these color patches plays in different situations (review and meta-analysis in Yasukawa et al. 2010).

Brilliant colors, because of their production and maintenance costs (e.g., McGraw 2006; Kemp and Rutowski 2007) and their widespread use in animal courtship displays, are good examples of signals that can play important roles in mating (reviewed in Andersson 1994; Hill 2006). Because of the importance of available light in the transmission and perception of color signals (Endler 1991, 1992; Endler and Thery 1996), they are also good examples of traits whose efficacy might vary considerably depending on subtle differences in the ambient environment (e.g., fish: Wong et al. 2007; Heuschele et al. 2009; butterflies: Obara et al. 2008). With the use of modern spectrophotometry, colors (as well as the light environment in which they are transmitted) can be easily quantified and manipulated to tease apart their effects on receivers in both the field and the lab (Endler 1990; Andersson and Prager 2006).

Jumping spiders (family Salticidae) are excellent models for understanding the functions of colorful displays. Their charismatic and colorful courtship has intrigued biologists for years (e.g., Peckham and Peckham 1889, 1890), yet surprisingly little empirical work has been aimed at understanding how male color may influence mating success. Many of the more than 5000 species of jumping spiders (Platnick 2011) are sexually dichromatic and engage in dramatic and colorful courtship displays for potential female mates (e.g., Maddison 1995; Oxford and Gillespie 1998), and certain aspects of these displays, such as male dancing, have been shown to increase female receptivity (e.g., Jackson 1981). Jumping spiders have excellent vision (Land 1969; Devoe 1975; Yamashita and Tateda 1976; Williams and McIntyre 1980; Blest et al. 1981; Peaslee and Wilson 1989; Harland and Jackson 2000), and behavioral experiments indicate that they can discriminate between different colors (blue, green, yellow, and red: Nakamura and Yamashita 2000; red vs. blue: Jakob et al. 2007; red vs. yellow: VanderSal and Hebets 2007). Work done with *Cosmophasis umbratica* and *Phintella vittata* (jumping spiders from Asia) has shown that blocking UV light affects mate-choice decisions, suggesting that UV coloration is playing an important role in courtship signaling in these species (Lim et al. 2007, 2008; Li et al. 2008). To our knowledge, only 1 study, conducted more than 60 years ago, has used direct manipulations of male salticid color patterns (Crane 1949). Crane (1949) painted various male body regions on 5 tropical salticid species; the study was descriptive in nature and results indicated that if male color patterns were altered, females would often still mate with them (Crane 1949). To our knowledge, the present study will be the first to systematically manipulate male color patterns using current color measurement technology and compare mating success with control males using modern statistical approaches.

Males in the genus *Habronattus* are among the most highly ornamented of jumping spiders, with a striking diversity of colorful and sexually dimorphic display traits (Richman 1973, 1982; Griswold 1987; Maddison 1995; Richman and Cutler

1998; Maddison and Hedin 2003). Throughout the genus, male displays consist of various combinations of brilliant colors (e.g., Taylor et al. 2011), motion (e.g., Elias, Land, et al. 2006), and substrate-borne components (e.g., Maddison and Stratton 1988; Elias et al. 2012). Evidence from geographically isolated sky island populations of *Habronattus* suggests that sexual selection is responsible for driving this striking male diversification (Maddison and McMahon 2000; Masta and Maddison 2002), making this an ideal group to examine the functions of color in mating.

Here, we designed 2 experiments to test if brilliant colors of male jumping spiders play a role in mating and whether or not their effectiveness depends on ambient lighting conditions. First, in Experiment 1, we wanted to determine if the presence of condition-dependent display colors are either required for species recognition or improve mating success in *Habronattus pyrithrix*, a sexually dimorphic jumping spider in which males display bright red faces and green legs to dull, drab females during courtship (Figure 1). We paired individual males with virgin females in the laboratory in a 2 × 2 factorial design to examine the effect of blocking either the red facial coloration or green leg coloration, or both, on multiple metrics of mating success and female behavior when compared with sham-treated control males.

After finding that neither of these colors were required for or improved successful mating under laboratory conditions (see Results), we went on to conduct Experiment 2 to examine the sexual significance of red facial coloration more closely under natural lighting conditions, which might give females greater opportunity to fully assess male colors and therefore be more choosy. Specifically, we presented virgin females with 2 simultaneously courting males, one of which had his red facial coloration concealed and the other of which was given a sham treatment. We ran all trials outdoors under



Figure 1

Male courtship in *Habronattus pyrithrix*. (a) Stage 1: male (right) is approaching and displaying his red face and green legs to a potential female mate (left). (b) Stage 2: the male (right) has successfully approached and stopped directly in front of the female (left) and is now performing a display consisting of both visual and vibratory components.

natural light, and each trial was repeated in both the direct sunlight and the shade. In field observations of 2 natural populations of *H. pyrrithrix* in Phoenix, AZ (Maricopa County, USA), densities and interaction rates are high, and we have frequently observed multiple males simultaneously courting females in both the sun and the shade (personal observation). Thus, this design allowed us to extend our study across a range of biologically relevant courtship scenarios.

METHODS

Study species

H. pyrrithrix Chamberlin 1924 is a sexually dichromatic jumping spider in which males display condition-dependent red facial patches and green front legs to inconspicuously colored gray and brown females during courtship (Taylor et al. 2011; Figure 1). The red coloration is contained within body scales on the face (e.g., Hill 1979), whereas the green is present on the surface of the leg cuticle, which is further adorned with white scales (personal observation). The distribution of *H. pyrrithrix* extends from southern California and Arizona south to Sinaloa, Mexico (Griswold 1987). In Phoenix, AZ, they are often found at high densities in leaf litter in natural riparian areas (e.g., cottonwood [*Populus fremontii*], desert willow [*Chilopsis linearis*]) as well as in backyards and agricultural areas; these complex leaf litter and grassy microhabitats create patchy areas of sun and shade in which spiders interact (personal observation).

Like other species of *Habronattus*, courtship is complex (e.g., Richman 1973, 1982; Griswold 1987; Maddison 1995; Richman and Cutler 1998; Maddison and Hedin 2003) and consists of both visual and substrate-borne components (Elias et al. 2012, see also [electronic supplementary material](#) for a video of their courtship behavior). The red faces and green legs of males are oriented toward females during courtship and are generally concealed when the male is viewed from above or from the side (personal observation). Courtship typically begins when a male locates a female from several centimeters away and begins to wave his front legs and expose his red face, gradually approaching in a zigzag fashion (stage 1 courtship, Figure 1a). If the female remains stationary and does not attack or retreat, he will proceed to stage 2 of courtship, in which he approaches to within a few millimeters of the female's face and immediately stops and extends his first pair of legs straight up, nearly perpendicular to the plane of his body (Figure 1b) and initiates the vibratory component of his display (Elias et al. 2012). Both of these stages can last from several minutes to hours, depending on the female's reaction (personal observation). In stage 3 of courtship, the male gently taps the female's carapace with his front legs; if she does not jump away, he typically mounts and copulates (personal observation). Females are often larger than males and courting males are frequently cannibalized prior to copulation in both the field and the lab (unpublished data). Males occasionally display by waving their legs in the direction of other males, but as in other species of *Habronattus* (Richman 1982; Cutler 1988), agonistic interactions are rare and displays typically last for only a few seconds compared with the displays performed for females that can last for hours (personal observation).

Experiment 1: color manipulation and mating success

The goal of Experiment 1 was to determine if the presence of male facial and leg coloration is required for successful mating, and how

they influence various metrics of mating success. We conducted a color manipulation experiment in which we blocked male colors (described in more detail below) and assessed the effects on a male's ability to successfully copulate with a female and also to avoid cannibalism. We focused specifically on the red face and green legs of males because they are condition dependent and clearly displayed to females during courtship (Taylor et al. 2011).

Although standard mate-choice studies in many animals, including some jumping spiders, typically involve pairing a single female with multiple males that are physically isolated and therefore unable to interact with one another (e.g., Cross et al. 2007; Li et al. 2008; Lim et al. 2008), this type of design does not work with *Habronattus*. To our knowledge, there is no known behavior other than copulation (e.g., see Masta and Maddison 2002) or a female's willingness to allow a male to approach and make contact with her (personal observation) that reliably indicates receptivity in any *Habronattus* species. Thus, mating success studies with *Habronattus* typically involve pairing a single female with a single male and measuring "mating success" directly in terms of whether or not copulation occurs (e.g., Masta and Maddison 2002; Elias et al. 2005; Hebets and Maddison 2005; Elias, Hebets, et al. 2006). Thus, this was our approach for Experiment 1.

For Experiment 1, we used lab-reared spiders to minimize variation due to genetics, diet, mating history, and other experience. In July and August 2008, we collected 18 gravid females from Queen Creek, AZ, USA (Maricopa County, 33°13'29.0784"N, 111°35'34.17"W) and brought them back to the lab and allowed them to lay eggs. Throughout the study, we housed all spiders individually in clear plastic boxes (10.16 × 10.16 × 12.86 cm) at approximately 28 °C. Fluorescent laboratory lighting was supplemented with full-spectrum light bulbs (30W compact full-spectrum light bulbs, Mercolla, Hoffman Estates, IL, USA) housed in metal clamp light fixtures positioned directly above the spider cages and the experimental arena. Additional light bulbs were positioned in the corners of the room (26W Daylight CFL bulbs, General Electric, Fairfield, CT, USA). All lights were on a 14:10 light-dark cycle and each cage was fitted with a mesh top to allow adequate light to reach the inside of the cage. Irradiance data from our artificial lighting setup are provided in Figure 2a. Each cage was also provided with an artificial green plant (approximately 10 cm long, Ashland fern collection, Michael's Stores, Irving, TX, USA) affixed to the side of the cage to provide enrichment (e.g., Carducci and Jakob 2000). On hatching and emerging from the egg sac (as soon as spiders were large enough to determine their sex, ca. 2.5 mm), we removed either 4 male or 4 female spiders from each clutch (1 clutch per female) and raised them to maturity in individual cages (as described above) on a constant diet of small crickets (*Acheta domesticus*) amounting to approximately their own body weight 3 times per week. We chose this diet because pilot studies suggested that this diet results in spiders with body condition indices comparable with those collected from the field (unpublished data). Opaque barriers separated the spider cages during rearing so that they could not see and interact with one another.

At maturity, each group of 4 brothers was randomly assigned to an unrelated group of 4 sisters, to which they were paired in the mating success experiment. Because the mothers of these spiders may have mated either singly or multiply in the field, individuals within each clutch may be either full or half siblings. Within each group of 4 brothers, we assigned individuals randomly to 1 of 4 treatments in a 2 × 2 factorial design: 1) red facial color concealed (see below for more details on color manipulations), 2) green leg color concealed, 3) both colors concealed, or 4) neither color concealed (sham control). Individual males were then randomly assigned to a female (unrelated) from their paired clutch, resulting in 36 male-female pairs.

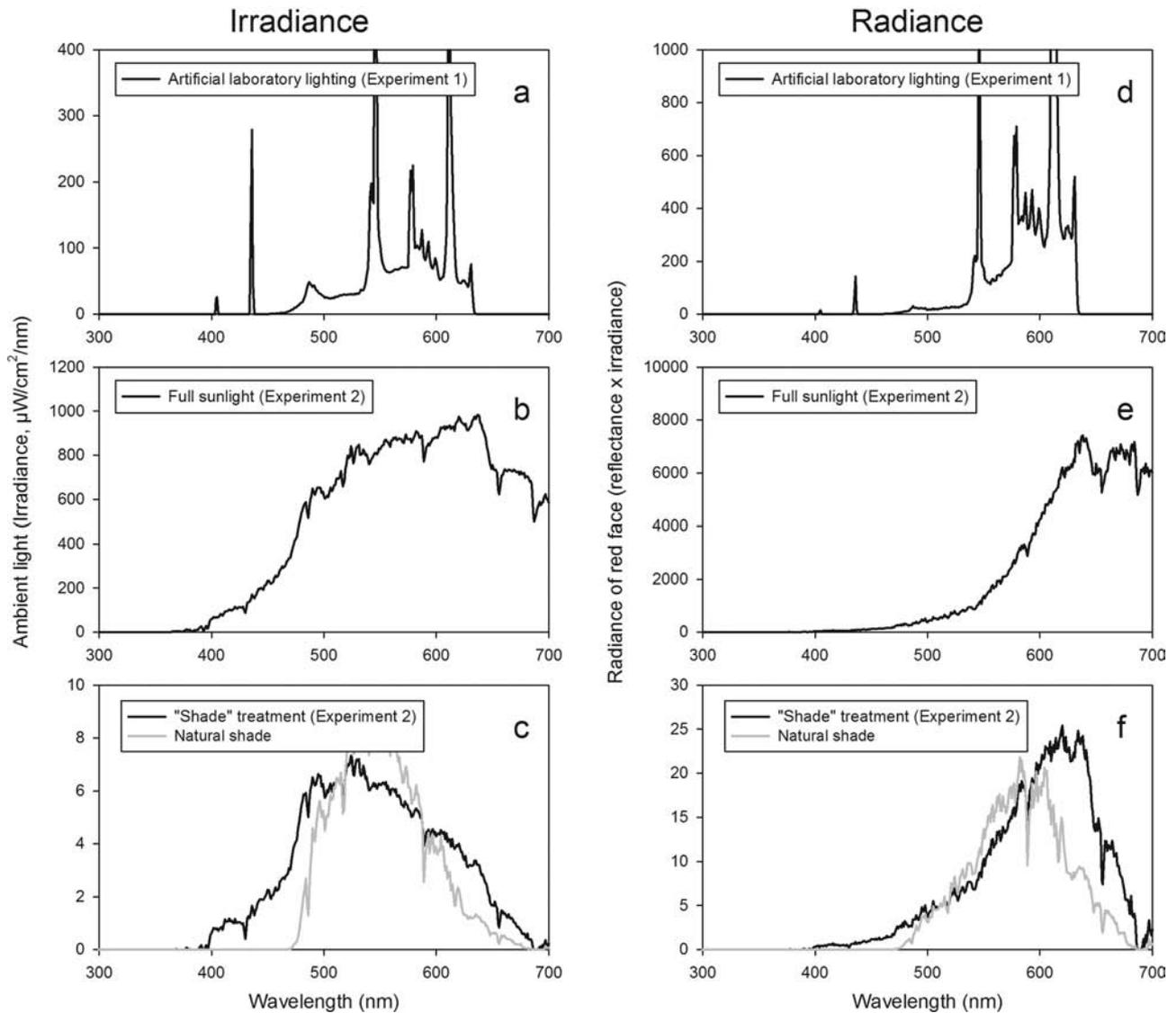


Figure 2

Ambient light (irradiance spectra) of light environments used in this study (a–c) and the estimated radiance of this light when reflected from the red face of a male *Habronattus pyrithrix* (d–f). Artificial lighting (a, d), full sunlight (b, e), and artificial and natural shade (c, f). Irradiance data were collected using a portable spectrometer (USB 2000+) fitted with a cosine-corrected irradiance probe (CC-3) and calibrated with a tungsten halogen light source (LS-1-CAL, all from Ocean Optics, Dunedin, FL, USA). Radiance was estimated by multiplying each irradiance spectrum by the reflectance spectrum of the red face of male *H. pyrithrix* (e.g., see Macedonia 2001; Macedonia et al. 2003). Note that, in natural sunlight (e), the radiance in the red portion of the spectrum (600–700 nm) is higher than in either the shade or artificial light treatments.

We began trials when females were between 10 and 40 days postmaturity. All trials were started between 0800 and 1100 h. Immediately before a trial began, we weighed spiders to the nearest 0.0001 g with an electronic balance (Mettler-Toledo, Columbus, OH, USA) and photographed each spider next to a size standard using a Nikon Coolpix 4500 digital camera (Nikon Inc., Melville, NY, USA). From these photographs, we measured carapace width (just behind the posterior lateral eyes) using Photoshop software (Adobe Systems Inc., San Jose, CA, USA). Because carapace width is fixed at maturity, while the abdomen stretches with feeding, we used the residuals of a regression of mass on carapace width as an estimate of body condition that is uncorrelated with body size and is a common method of estimating body condition in spiders (e.g., Jakob et al. 1996; Taylor et al. 2011).

For each female, we introduced the assigned male partner into the plastic cage in which the female had been raised and videotaped all interactions for the first hour under the laboratory conditions described above. After the 1-h videotaped period, we continued to house the spiders together for an additional 48 h. After the 48-h period ended, we removed the male from the female's cage. Females were then fed in excess (approximately 3 times their body weight in food was provided daily) for 2 weeks to allow them the opportunity to lay eggs. In our experience with >100 laboratory matings of *H. pyrithrix* in this age range, we have never seen a virgin female copulate with a male and not lay fertile eggs within 2 weeks on this feeding regime (unpublished data); thus, we are confident that the presence of fertile eggs is a reliable indicator of mating success during the entire 48-h trial. To confirm that eggs were

fertile, all were allowed to hatch and we recorded whether or not spiderlings emerged.

From the videotapes, we used the freeware program CowLog (Hänninen and Pastell 2009) to record each male's courtship effort (amount of time spent actively courting) and latency to begin courting. We also measured female aggression (number of attacks by females) and whether or not cannibalism or copulation occurred. In instances where copulation did occur in the first hour (11 out of 36), we recorded copulation latency and duration. For the subsequent 48 h, we checked the pair of spiders every 24 h and recorded additional instances of cannibalism.

Color manipulation methods

We concealed the red faces of males by covering the entire red area with black liquid eyeliner (color: "Perversion," Urban Decay Cosmetics, Costa Mesa, CA) (Figure 3a,b), which closely matches the reflectance properties of the underlying black cuticle (Figure 4). On control males, we applied the same amount of eyeliner to an equivalent area on the top of their carapace just behind their anterior median eyes, an area that is not clearly visible to females. For males receiving the leg color manipulation, we covered their green legs with light tan makeup powder (bareMinerals foundation, color: "Light," Bare Escentuals, San Francisco, CA, USA) (Figure 3c), which closely matches the reflectance properties of their other, non-ornamented legs (Figure 4). For control males, we applied the same amount of powder to the same area on the second pair of legs (which are not ornamented and are not displayed to females during courtship). To manipulate their colors, we anesthetized all males with carbon dioxide for approximately 5 min, on the day before their trial began. After waking up from anesthesia, males were offered a cricket to confirm that they had recovered fully and were capable of capturing prey. We compared levels of courtship activity (% time spent courting) and latency to begin courting between treatment groups to confirm that the color manipulation did not affect courtship activity or motivation.

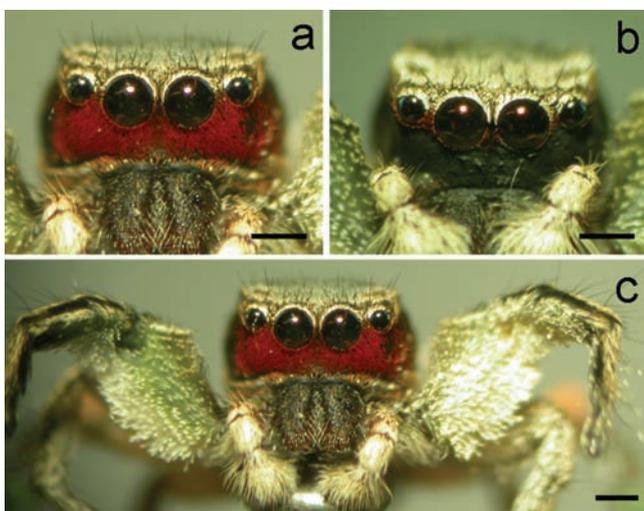


Figure 3 Manipulation of coloration in *Habronattus pyrrithrix*. (a) Premanipulated natural appearance (i.e., red facial coloration intact), (b) red facial coloration concealed with black liquid eyeliner, (c) male with 1 leg that has green coloration intact (left) and the other (right) concealed with foundation powder. Scale bars represent 0.5 mm.

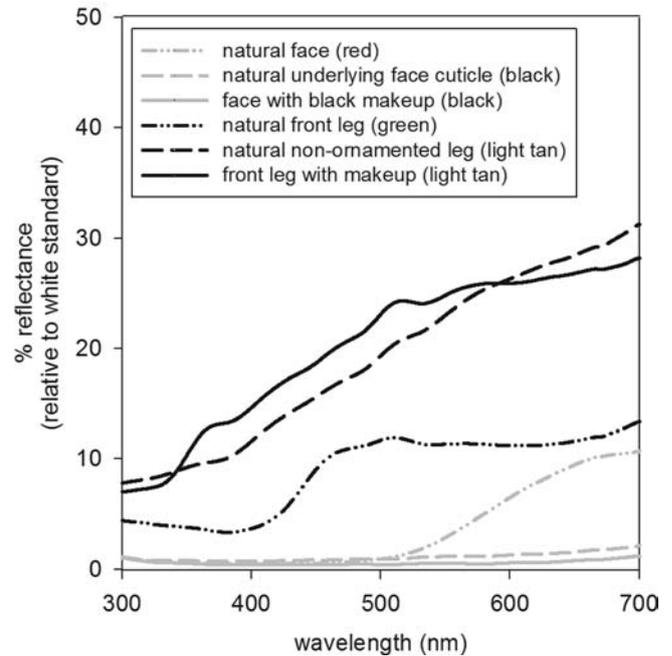


Figure 4 Representative reflectance spectra for the natural and color-manipulated regions of male *Habronattus pyrrithrix* that were the foci of this study.

Experiment 2: simultaneous choice in sunlight and shade

Because our results from Experiment 1 suggested that male colors were not required for successful mating and did not affect any aspect of mating success in the laboratory (see Results), the goal of Experiment 2 was to determine if color would affect male success in a more natural context and whether ecologically relevant variation in the light environment would affect the roles and importance of male color. Specifically, each female was paired with 2 males simultaneously and trials were run outdoors and repeated in both the sun and the shade. Because each female was paired with 2 males simultaneously, we could not manipulate both facial and leg coloration using the same 2×2 factorial design that we used in Experiment 1 (as this would necessitate pairing a single female with 4 simultaneously courting males from different treatments). For this reason, in Experiment 2, we focused on manipulation of the red facial coloration only. We chose to focus on the red coloration rather than the green because red is dependent on juvenile diet (Taylor et al. 2011), and thus we presently have greater evidence that it might contain useful information relevant to mate choice. Furthermore, various degrees of sexually dichromatic red male facial coloration are found commonly across the genus *Habronattus*, appearing independently in multiple species groups and, in some cases, exhibiting striking and unexplained geographic variation (e.g., *H. hirsutus*, *H. americanus*; see Griswold 1987). Thus, experimental studies of red color might provide insights into the function of this particular trait that is relevant to many other species in the genus.

As discussed above, the lack of obvious female receptivity displays in *Habronattus* prevented us from being able to run a typical simultaneous choice test in which females are allowed to view 2 physically isolated males and choose between them. To interpret female "choice" in *H. pyrrithrix*, males must be allowed to approach and make contact with females and the only way to do this was

to place all 3 spiders (1 female and 2 males) into an experimental chamber and allow them to interact freely. Consequently, our experimental design for Experiment 2, and in fact, any possible design that could be used with simultaneously courting males of this species, would not prevent males from seeing and interacting with one another. Thus, our data from this experiment do not allow us to completely disentangle male–male competition from female choice per se. However, when 2 males are courting the same female, males typically direct their displays at the female simultaneously, rather than at the competing male (personal observation), and thus we expect that any major effect of color manipulation that we see in our experiments will be a result of female behavior rather than male–male competition. Despite these expectations, we also quantified male aggression (described in more detail below) as a means of examining possible effects of color on the other male in the trial (see Results).

In contrast with Experiment 1, in which we carefully controlled the relatedness, rearing environment, and experience of all subjects, our approach in Experiment 2 was to perform the experiments under conditions that more closely resembled those in nature. Because there is evidence from multiple taxa that the light environment in which individuals are raised can affect their responses to chromatic cues later in life (e.g., Cronin et al. 2001; Kroger et al. 2003), we used only field-collected spiders for Experiment 2 (from the same Queen Creek population described above). Twenty-four male and 12 female spiders were collected in July and August 2009. Because female mating history affects mate choice in some jumping spiders (e.g., Jackson 1981), females were collected as penultimates (i.e., the developmental stage just prior to sexual maturity) and kept in the laboratory as described above until reaching maturity. It is unclear how many times females can mate; because they are typically reluctant to mate more than once, we used only virgin females in our trials, as is common practice in jumping spider mate-choice experiments (e.g., Clark and Biesiadecki 2002; Elias et al. 2005; Elias, Hebets, et al. 2006; Lim et al. 2008). We have observed male *H. pyrithrix* mating repeatedly, and we are not aware of a limit on the number of times that a male can mate. Males will actively court females regardless of their own mating history (personal observation) and thus we collected males as adults and housed them in the laboratory until experimentation (days in captivity = 33 ± 5.24 [mean \pm SE]). Spiders were housed indoors (using the same cages described above) on a natural light/dark cycle at approximately 30 °C. Natural light was provided from 5 large windows.

We grouped males by collection date, paired them by body size (carapace width), and then randomly assigned each pair of males to a female. Within each male pair, individuals were randomly assigned to 1 of 2 treatment groups. Males either had their red facial coloration blocked or underwent a sham treatment in which their red facial coloration was left intact (following the same methods used in Experiment 1).

When females were between 10 and 28 days postmaturity, we moved their cages outdoors to allow them to acclimate overnight before beginning their outdoor trial the next morning. All trials were run between 0700 and 1100h, when the mean temperature was from 31 to 42 °C. Our field observations indicate that these spiders are typically active and courting throughout the day during this time of year despite the intense heat (unpublished data). Outdoor cages were surrounded by cottonwood (*P. fremontii*) leaf litter to simulate the natural background color of the habitat of these spiders in the field. The location of the trials was in an area that received direct sunlight that could be manipulated with shade cloth

(color: hunter, Springs Creative Products Group LLC, Rock Hill, SC, USA) hanging above. Immediately before the trial began, we took photographs of each spider following the methods described above. We did not have access to an electronic balance at this site, so we estimated mass from photographs by measuring the total area of the carapace and abdomen. Pilot data showed that body area measured this way is highly correlated with body mass in *H. pyrithrix* (linear regression, $F_{1,43} = 62.03$, $R^2 = 0.591$, $P < 0.0001$, unpublished data). This body mass estimate was then used to calculate residual body condition index as described above.

At the start of the trial, the 2 males were placed in random order into the female's cage in immediate succession and all interactions were videotaped. Each trial consisted of 2-h-long periods, one in the sun and the other in the shade. These periods occurred in succession but in random order. The "sunny" period of each trial was conducted with approximately 75% of the cage receiving direct sunlight, while 25% was shaded from above with shade cloth (to provide a retreat from the intense Arizona sunlight). The "shady" period of the trial was conducted in the same location, but with the shade cloth adjusted so that the cage was entirely in the shade. Irradiance data from our "sun" and "shade" treatments are provided in Figure 2b,c.

From the videotapes, we again used CowLog (e.g., Hänninen and Pastell 2009) to quantify the amount of time that each male spent courting and his latency to begin courting. Because we were concerned about keeping the spiders in plastic cages for more than 2 h outdoors in the summer heat of Arizona (average daily high temperature during experiment = 41 °C), and because having 2 simultaneously courting males appeared to distract the female and extend copulation latency, we anticipated (and found) low levels of copulation success during the outdoor trials (only 1 male copulated, during the second phase of his trial). A post hoc analysis of data from Experiment 1 indicated that males that got closer, and remained closer, to females over the course of the trial were more likely to achieve successful copulation; specifically, the mean distance between a male and the female (recorded every 5 min over the entire trial) was an excellent predictor of whether or not a male would copulate in the first hour of the videotaped trial period (11 successful vs. 25 unsuccessful, logistic regression, $\chi^2 = 12.97$, $P = 0.0003$) as well whether he would copulate during the entire 48-h trial period, resulting in fertile eggs (19 successful vs. 17 unsuccessful, logistic regression, $\chi^2 = 19.08$, $P < 0.0001$). Given the robust ability of this distance metric to predict actual copulation success in Experiment 1, we used it as a proxy for courtship success in Experiment 2. Finally, we recorded the number of attacks by females on each male, the number of male attacks directed toward one another, and all instances of cannibalism.

Statistical analyses

In Experiment 1, to confirm that our color manipulations did not have adverse effects on male behavior, we used analysis of variance (ANOVA) to determine if blocking either facial or leg coloration influenced male courtship activity (amount of time spent courting over the course of the trial) or latency for males to begin courting. Next, we used binary logistic regression to determine if facial or leg color manipulation, male body size, male body condition, or female age predicted whether or not a male would mate successfully during the trial (leading to fertile eggs). In cases where copulation occurred in the first hour ($n = 11$), we used analysis of covariance (ANCOVA), with male body size and condition and female age

as covariates, to determine if color manipulations affected male copulation latency or duration. Finally, we used ANCOVA (again with male body size and condition and female age as covariates) to determine if color manipulation had any effect on the number of aggressive attacks that males received from females and binary logistic regression to determine if facial or leg coloration, male body size, male condition, or female age predicted whether or not a male would be cannibalized by females.

In Experiment 2, to again confirm that our color manipulations had no adverse effects on male behavior, we used ANOVA to determine if the average courtship intensity (i.e., time spent courting) and latency to begin courting differed between males with their facial color manipulated and control (sham-treated) males. Because each trial consisted of 2-h-long periods (1 in sun and 1 in shade, in random order), we first used ANOVA to confirm that the order of the trial period (i.e., whether it occurred first or second) had no effect on its outcome. We then went on to use repeated-measures ANCOVA (with male body size and condition as covariates) to determine if color manipulation affected the ability of males to approach females in the 2 different light environments. Because 2 males were paired simultaneously with each female, we included female ID as a random factor in the model. In cases where females cannibalized males ($n = 2$ trials, 1 color-manipulated male and 1 control male, both during the first phase of the trial), we removed the trial from analyses. Because we found a significant interaction between light environment and color treatment ($F_{1,7} = 7.30$, $P = 0.031$, see Table 2), we went on to conduct 2 separate ANCOVAs (1 for each light environment) to more closely examine the effects of male color manipulation on his ability to approach the female in each (using male body size and body condition as covariates). Finally, we used repeated-measures ANCOVA (again, with male body size and condition as covariates and female ID as a random factor) to determine if color manipulation affected the level of aggression (# of attacks) from the female or the partner male.

With the exception of the female and male aggression data (# of attacks), to which we applied a square-root transformation to improve normality, all data met the assumptions of parametric statistics. To aid in interpretation of negative results, we provide

effect sizes and confidence intervals around those effect sizes, where appropriate. Small effect sizes with narrow 95% confidence intervals that encompass zero indicate the strongest support for the null hypothesis (i.e., no effect) (Colegrave and Ruxton 2003; Nakagawa and Foster 2004). All statistical analyses were conducted using SAS 9.2 and JMP 10 (SAS Institute, Cary, NC, USA).

RESULTS

Experiment 1: color manipulation and mating success

Neither face nor leg color manipulation had any effect on male courtship activity ($F_{2,33} = 0.08$, $P = 0.93$) or latency to begin courting ($F_{2,33} = 0.21$, $P = 0.81$).

Copulation that resulted in fertile eggs (i.e., hatched spiderlings) occurred in 19 of 36 trials (~53%). Blocking either the red facial coloration or green leg coloration had no effect on this measure of male mating success (Table 1 and Figure 5a); however, mating success was affected by male size and condition, with larger males in better condition being more likely to copulate (Table 1 and Figure 6). Among the 11 males that copulated in the first phase of the experiment, there was no relationship between color manipulation and a male's latency to copulate ($F_{5,5} = 1.02$, $P = 0.49$) or copulation duration ($F_{5,5} = 0.72$, $P = 0.64$).

Color manipulation had no effect on the number of aggressive attacks by females ($F_{5,30} = 0.79$, $P = 0.57$). Females cannibalized males in 12 out of 36 trials (~33%, including 6 trials where males also successfully copulated), but the probability of cannibalism was not affected by our color manipulation (Table 1 and Figure 5b).

Experiment 2: simultaneous choice tests in the sun and shade

Male color manipulation had no effect on courtship activity (i.e., time spent courting, $F_{1,38} = 0.49$, $P = 0.49$) or latency ($F_{1,38} = 1.58$, $P = 0.22$). The order in which the trial periods in the different light environments occurred (i.e., whether they occurred first or

Table 1

Results of logistic regressions examining the effects of male color treatment (concealed face and/or leg color), male size, male body condition, and female age on the probability of successful copulation (leading to fertile eggs) and on the probability of cannibalism in Experiment 1

	χ^2	df	P	Effect size (log odds ratio)	Lower 95% CI for effect size	Upper 95% CI for effect size
Copulation						
Whole model test	18.29	5	<0.01			
Lack-of-fit test	31.51	30	0.39			
Wald effect tests						
Red facial color	0.06	1	0.81	-0.22	-1.95	1.52
Green leg color	2.55	1	0.11	1.76	-0.40	3.93
Male size	5.57	1	0.02	-6.74	-13.50	-1.90
Male body condition	5.30	1	0.02	-8.61	-17.52	-2.40
Female age	0.13	1	0.72	0.63	-2.72	4.32
Cannibalism						
Whole model test	5.46	5	0.36			
Lack-of-fit test	40.37	30	0.10			
Wald effect tests						
Red facial color	0.74	1	0.39	0.69	-0.85	2.33
Green leg color	0.01	1	0.91	-0.10	-1.70	1.53
Male size	2.99	1	0.08	3.48	-0.23	7.97
Male body condition	0.09	1	0.76	0.74	-4.15	5.64
Female age	1.89	1	0.17	2.07	-0.75	5.29

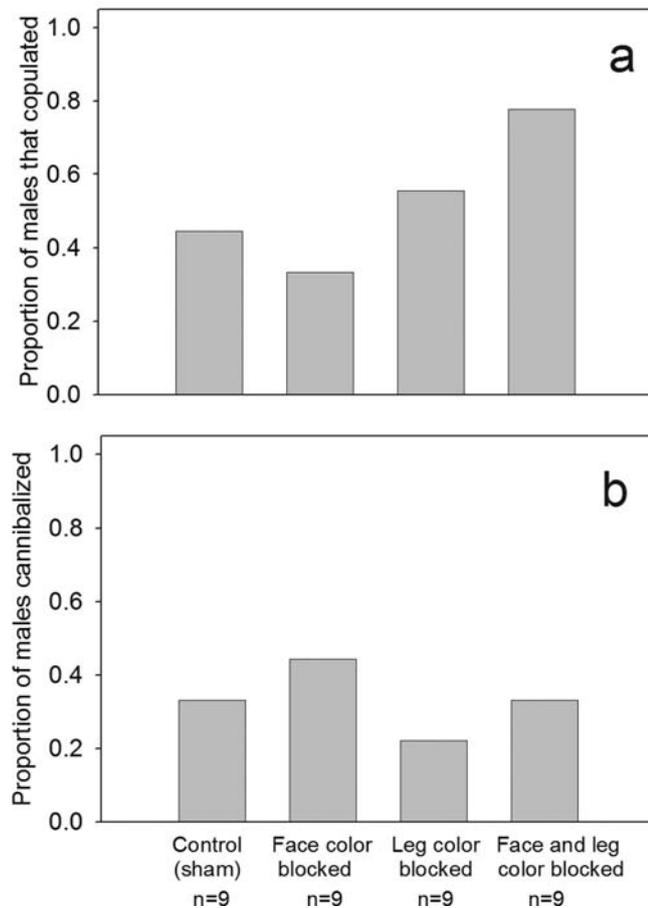


Figure 5 Effect of male color manipulation on copulation success (a) and sexual cannibalism (b) under laboratory conditions in Experiment 1.

second in succession) had no effect on male courtship success (i.e., distance that males were able to get to females, $F_{1,38} = 0.61$, $P = 0.44$).

There was a significant interaction between male color manipulation and light environment on the approach distance of males to females (Table 2). When trials were run in the sunlight, sham-treated males, with their red facial coloration intact, were able to get closer to females than males with their red facial coloration blocked, while neither male size nor condition had any effect on the distance that males were able to get to females (Figure 7a,b and Table 3). In contrast, when trials were run in the shade, there was no effect of color manipulation on the distance that males were able to get to females (Figure 7c and Table 3). Rather, male size (but not condition) was important, with larger males able to get closer to females than smaller males (Figure 7d and Table 3). In some (but not all) trials, females were consistent in their willingness to let males approach during courtship (indicated by a significant effect of female ID; Tables 2 and 3).

Neither color manipulation nor light environment affected levels of aggression that males received from females (light: $F_{1,7} = 0.38$, $P = 0.56$; color manipulation: $F_{1,7} = 2.47$, $P = 0.16$) or from their partner male (light: $F_{1,7} = 0.05$, $P = 0.83$; color manipulation: $F_{1,7} = 1.66$, $P = 0.24$). Full ANCOVA tables are provided as electronic supplementary material (Tables S1 and S2).

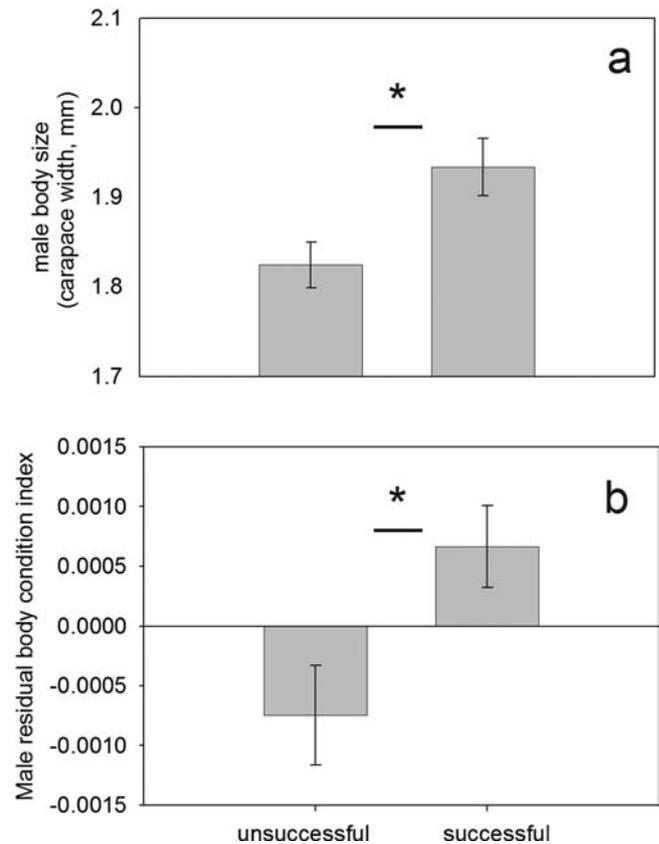


Figure 6 Comparison of male body size (a) and body condition (b) between successful and unsuccessful males in Experiment 1 (mean \pm SEM). Successful males achieved copulation, which resulted in fertile eggs. Asterisks indicate significant differences between groups.

DISCUSSION

Despite being condition dependent in field and laboratory experiments and thus likely candidates for honest mating signals, we found that red facial and green leg coloration of male *H. pyrrithrix* was not required for successful mating. In Experiment 1, blocking either or both of these colors on males in a 2×2 factorial design laboratory experiment had no effect on any metric of mating success. In Experiment 2, we examined the effect of red coloration more closely under more ecologically relevant conditions and found that males with their red coloration intact were better able to approach females, but only when courting in the sunlight. This suggests that color may play different roles in courtship depending on subtle environmental conditions.

Experiment 1

The results of Experiment 1 allow us to rule out the hypothesis that male red and/or green coloration is a required species or sex recognition signal in *H. pyrrithrix*, as these colors were not necessary for successful mating. Just over half of the males in the experiment mated successfully (leading to the production of viable spiderlings), yet this was unaffected by blocking either color. Furthermore, we found no evidence that these colors affected any metric of mating success (time to copulation or copulation duration) or female behavior (aggression or cannibalism), which is surprising given the effort with which males display these colors to females. Overall, our

Table 2

Results of repeated-measures ANCOVA for Experiment 2 examining the effect of color manipulation treatment, body size, body condition, and light environment on the mean distance that males were able to get to females over the course of the trial

	df	F	P
Within-subjects effects			
Light	1,7	2.03	0.20
Light × treatment	1,7	7.30	0.03
Light × size	1,7	2.15	0.19
Light × body condition	1,7	0.07	0.80
Light × female ID	9,7	5.07	0.02
Between-subjects effects			
Treatment	1,7	4.64	0.07
Size	1,7	3.78	0.09
Body condition	1,7	0.57	0.48
Female ID	9,7	3.46	0.06

Because of the significant interaction between treatment and light environment, we went on to run separate analyses for the sun and the shade (see Table 3).

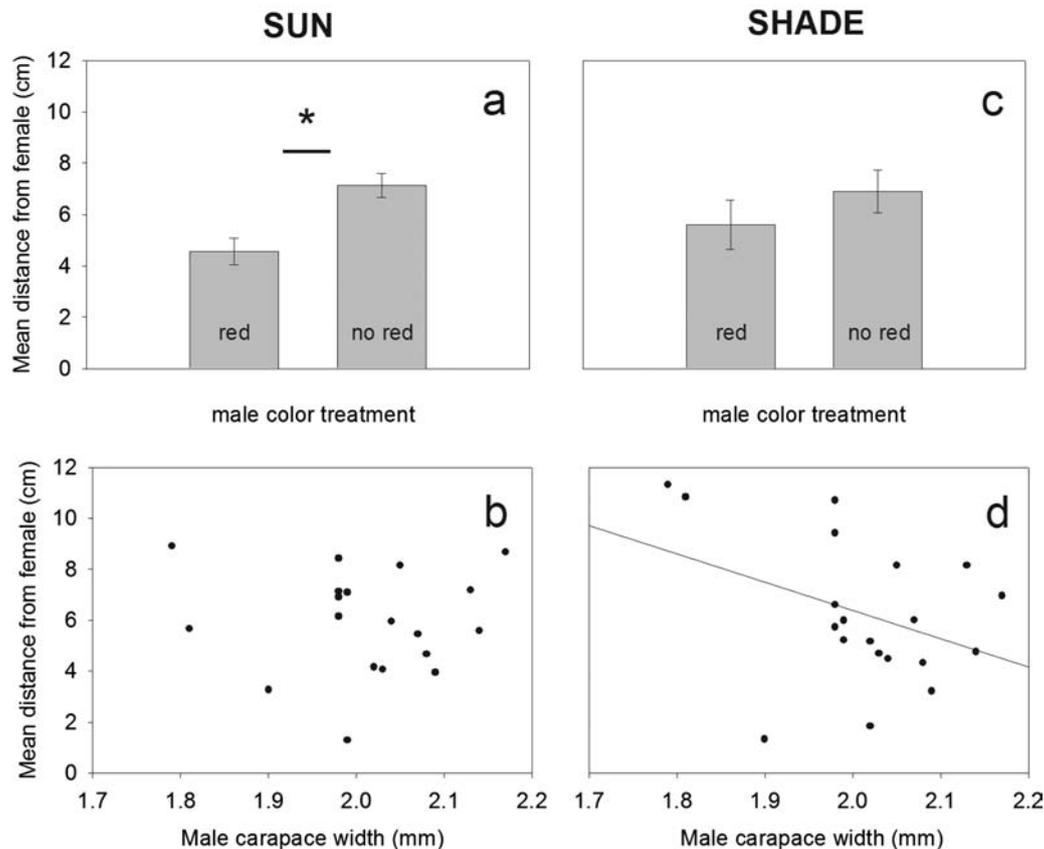
data from Experiment 1 suggest that, even if the colors are used as important signals in some contexts, they are clearly not consistently important in all contexts in which spiders might engage in courtship.

In the field, *H. pyrithrix* males are found courting in a variety of habitats, from open areas in full sunlight to completely

shaded areas beneath the leaf litter (unpublished data). In Experiment 1, we supplemented our laboratory lighting with full-spectrum light bulbs in an attempt to create an environment with irradiance profiles as close to natural light as possible, while maintaining controlled laboratory conditions (see Methods). However, a comparison of irradiance data from this artificial lighting with data from natural Arizona sunlight and shade suggests that all 3 of these light environments differ both in the overall intensity of light as well as the shape of the irradiance spectra, with both shade and our artificial lighting having a relatively low proportion of red light (see further discussion below and Figure 2). Males that mated successfully in Experiment 1 were larger and in better condition than those that were unsuccessful, suggesting that under artificial lighting conditions, females may base their mating decisions on size and condition over male coloration.

Experiment 2

Results from Experiment 2 suggest that red facial coloration may play different roles in courtship depending on the available light where males are displaying. Because ambient light environment affects the transmission of color signals (e.g., Endler 1992, 1993), it is not surprising that the role of red coloration might vary in different lighting environments. Typically, both forest shade (where available light is mostly reflected from vegetation) and woodland shade (where most light comes from the sky, but is outside the path of direct sunlight) are rich in greenish and bluish light,

**Figure 7**

Effect of color manipulation and body size on the ability of males to approach females when courting in the sun (a, b) and shade (c, d) in Experiment 2. The presence of an asterisk indicates a significant difference between treatment groups, and the presence of a regression line indicates a significant relationship between male size and distance from the female.

Table 3

Results of ANCOVA for Experiment 2 examining the effect of color manipulation treatment, body size, and body condition on the mean distance that males were able to get to females over the course of the trial

	df	<i>F</i>	<i>P</i>	Effect size (partial Ω^2)	Lower 95% CI for effect size	Upper 95% CI for effect size
Sun						
Treatment	1,7	8.11	0.02	0.26	<0.001	0.58
Body size	1,7	1.77	0.23	0.03	<0.001	0.36
Body condition	1,7	0.63	0.45	<0.001	<0.001	0.28
Female ID	9,7	1.54	0.29	0.20	<0.001	0.61
Shade						
Treatment	1,7	0.90	0.37	<0.001	<0.001	0.3
Body size	1,7	5.70	0.05	0.19	<0.001	0.52
Body condition	1,7	0.38	0.56	<0.001	<0.001	0.25
Female ID	9,7	5.94	0.01	0.68	0.10	0.86

Due to the significant interaction between treatment and light environment when analyzing the full data set (Table 2), these analyses were run separately for the sun and the shade.

respectively, and relatively low in red light (Endler 1993). In contrast, sunlit areas (including both large and small forest gaps as well as open sky) contain higher proportions of red light (Endler 1993). Irradiance data from our experimental setup were consistent with Endler's (1993) characterization of different light environments; specifically, full sunlight had relatively more red light (600–700 nm) than did our “shade” treatment (Figure 2). Given the lower proportion of red light that occurs in the shade, it might be expected that the color red would be a more effective signal in sun, which is what we found. Indeed, our estimates of radiance (or ambient light that is reflected from a particular surface in a given light environment; e.g., see Macedonia 2001; Macedonia et al. 2003) indicate that more red light would radiate from the red faces of males when viewed in sunlight compared with either shade or our artificial light setup (Figure 2d–f).

H. pyrithrix is abundant in the natural outdoor area in which this study was conducted and thus the variation in lighting environment examined in this study represents relevant ecological conditions. Recent work has demonstrated that spectral sensitivities, particularly in the longer wavelengths, vary widely among salticids (I-Min Tso, personal communication); future work should explore the specific spectral sensitivities of *Habronattus* to better understand how the male's red face would appear to females under different light environments (e.g., Endler 1991).

In the field, *H. pyrithrix* often occur at high densities in sympatry with other abundant species of *Habronattus* (e.g., *H. hirsutus*, *H. hallani*, and *H. clypeatus*; personal observation). Although females of these species are all cryptic in coloration (i.e., gray and brown), the males exhibit striking and conspicuous species-specific display colors (Griswold 1987). Interspecific interaction rates in the field are high (unpublished data), suggesting that males may benefit from signaling their species identity from a safe distance. Although our results demonstrate that a male's colors are not required for copulation, they do suggest that red coloration improves courtship success under certain lighting conditions and are consistent with the idea that the presence of male color may improve species recognition by females (e.g., Lim et al. 2007, 2008).

Implications for multimodal communication in *Habronattus*

In some animals, males can adjust the timing, location, lighting, or visual background of their display to maximize its conspicuousness (e.g., guppies: Endler 1991; forest birds: Endler and Thery 1996;

manakins: Uy and Endler 2004; bustards: Olea et al. 2010). In *H. pyrithrix*, males are unlikely to have this opportunity in the field; they appear to wander in search of females and court them whenever they encounter them (personal observation). Female *H. pyrithrix* are voracious generalist predators that cannibalize males in both the field and the lab (unpublished data) and thus a male's need to begin courtship immediately when he locates a female might reduce his ability to be choosy about his location relative to the available light.

The genus *Habronattus* contains some of the most ornamented species of jumping spiders, with highly complex displays that incorporate color, motion, and substrate-borne components (see Maddison and Stratton 1988; Elias et al. 2003, 2005; Elias, Land, et al. 2006; Taylor et al. 2011). A major question in behavioral ecology is why animals use multiple signals when one signal might suffice and reduce costs (reviewed in Candolin 2003; Hebets and Papaj 2005). A potential hypothesis is that, for animals that court in complex or unpredictable habitats, no single signal component is sufficiently efficacious under all possible conditions; multimodal displays allow different signaling components to act as backups (Johnstone 1996; reviewed in Candolin 2003; Hebets and Papaj 2005). Because male *H. pyrithrix* live in a variety of habitats and have limited control over where and when they display, selection might favor the use of backup signals.

While our study focused on the colors involved in the visual display, *H. pyrithrix* males also produce substrate-borne vibrations as part of their display (Elias et al. 2012). Substrate-borne signals in other arthropods, including spiders, are often linked to body size, suggesting that such signals can convey important information to females (e.g., De Luca and Morris 1998; Gibson and Uetz 2008; Rundus et al. 2011). Interestingly, when in the sunlight, red coloration allowed males to get closer to females, while body size had no effect (see Figure 7a,b). In contrast, in the shade, bigger males were able to get closer to females, regardless of their color treatment (see Figure 7c,d). It is plausible that females rely more on substrate-borne vibratory cues in the shade and rely more on color cues in the sunlight, which would lend support to the hypothesis that these colors and vibratory cues serve as “backups” for each other (Johnstone 1996). An alternative but similar explanation is that male body size itself is simply a “backup” visual cue that females pay attention to when the light environment is less conducive to color signaling (Johnstone 1996).

Recent studies with wolf spiders, whose courtship also involves both visual and vibratory components, support the “backup signal” hypothesis and provide evidence that courting males modify their display depending on the transmission properties of the environment (e.g., Gordon and Uetz 2011; Wilgers and Hebets 2011). Although it was not the focus of the present study, post hoc tests suggest that male *H. pyrrithrix* in this study did not modify aspects of their displays (i.e., latency to begin visual displays, duration of visual display) in the 2 different light environments (unpublished data). Similarly, in a related species of *Habronattus* (*H. dosseus*), males did not modify their displays on different substrates despite clear differences in the attenuation of their vibratory signals on these different substrates (Elias et al. 2004). This suggests that, for *Habronattus*, environmental conditions might constrain the transmission of both the visual and seismic signals. It is important to note that, in our study, experiments were staged in plastic boxes and males courted on the floor and walls of these boxes. Recent work has shown that *Habronattus* vibratory displays are transmitted though plastic in a way that is qualitatively similar to how they are transmitted through wood (Elias DO, personal communication). Thus, although plastic may not be optimal for transmitting vibratory signals, the transmission properties of the plastic boxes used in our experiment likely fall within the natural range of substrates on which we have seen males courting in the field (e.g., leaf litter, sand, rock, twigs, etc.; personal observation). Additional mate-choice studies that manipulate both the light levels and the transmission properties of the substrate will more clearly elucidate the functions and interaction of different display components.

The color red is a common component of male display both within the genus *Habronattus* (Griswold 1987) and across the Salticidae more generally (e.g., face of *Lyssomanes viridis*, Tedore and Johnsen 2012; face of *Evarcha culicivora*, Wesolowska and Jackson 2003; and face and legs of *Saitis barbipes*, Hill 2009). Our results indicate that, in certain light environments (e.g., sunlight), red facial coloration in *H. pyrrithrix* enables males to get closer to females during courtship; approaching females is necessary to achieve successful copulation. The color red has been shown to have interesting and unique effects on receivers in a variety of species; many animals show innate avoidance of red foods in prey choice (e.g., Mastrolta and Mench 1995; Gamberale-Stille and Tullberg 2001; Skelhorn 2011) and red has been argued to be a general signal of intimidation across the animal kingdom (see Pryke 2009). Just recently, Nagata et al. (2012) showed that, in jumping spiders, wavelength-specific light is used in depth perception; when illuminated with red light, objects appear closer to the receiver than when illuminated with green light. During jumping spider courtship, males must approach potentially cannibalistic females, a process during which they must strike a balance between stimuli that attract or provoke females and stimuli that inhibit predation (see discussion in Jackson and Pollard 1997; Nelson and Jackson 2007). The unique psychological effects attributed to the color red (Pryke 2009; Skelhorn 2011) and the unique visual system with which jumping spiders perceive it (Nagata et al. 2012) might make it particularly well suited to helping courting male spiders achieve this balance, and this might explain its prevalence in male jumping spider displays.

Implications for animal behavior studies

Our results suggest that caution should be taken when interpreting the results of behavioral experiments conducted under artificial lighting conditions or even under a subset of possible natural

lighting conditions. Due to logistical constraints, many behavioral experiments must be done under simplified conditions; however, such conditions can adversely affect both the physiology and behavior of many animals (reviewed in Calisi and Bentley 2009). Even when experiments are done outdoors, they are often done under only one lighting regime, yet in our study, the inclusion of both light environments is what uncovered the most interesting patterns.

This study suggests a functional role for the presence of red coloration in the courtship signaling of *H. pyrrithrix* and suggests that this role may vary depending on the environmental context. Recent work on multimodal communication has been taxonomically biased toward vertebrates (Coleman 2009), yet insights into the complex courtship behavior of spiders, in which males must balance the risks of courting females that are also voracious predators, might reveal interesting and unexpected patterns.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behceco.oxfordjournals.org/>

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