Natural variation in condition-dependent display colour does not predict male courtship success in a jumping spider

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ARTICLE INFO

In many animals, males display costly, condition-dependent ornaments to choosy females. Indicator models of sexual selection predict that females should choose mates based on natural variation in such traits. In *Habronattus pyrrithrix* jumping spiders, males have conspicuous, condition-dependent red faces and green legs that they display to cryptically coloured females during courtship. In a correlational study using field-collected spiders, we paired individual males with virgin females in the laboratory and found that natural variation in male coloration did not predict mating success (likelihood of copulation) or levels of female aggression. Rather, mating success was best predicted by male body condition. We then conducted an outdoor experiment under natural sunlight where we gave both virgin and mated females the choice between two simultaneously courting males, one with his facial coloration experimentally reduced and the other that received a sham treatment. Again, we found no relationship between male coloration and courtship success. Our previous studies have shown that the presence (versus absence) of red facial coloration improves courtship success, but here we found no evidence that more subtle natural variation in this trait has any effect on success. We discuss these findings in the context of complex signalling and species recognition in *Habronattus*. While many studies report negative results for condition-dependent quality signalling alongside positive ones, few discuss the implications of negative results. We argue that, as empirical data accumulate, we should move towards asking why some condition-dependent traits are consistently important to females while other equally condition-dependent traits are either ignored, or only matter in certain contexts.

In many animals, males engage in costly behaviours or display elaborate ornaments to females during courtship interactions (reviewed in Andersson, 1994). Indicator models of sexual selection posit that these elaborate traits, due to the costs associated with their production or maintenance, can honestly signal the individual quality of the bearer (Andersson, 1982). Empirical work supporting this idea has grown over the years and there are now countless examples showing that natural variation in costly courtship signals that females find attractive is correlated with different aspects of male quality, such as nutritional condition (e.g. calling in field crickets: Scheuber, Jacot, & Brinkhof, 2003), health status (e.g. scent marks in house mice: Zala, Potts, & Penn, 2004), ectoparasite load (e.g. bowerbird bowers: Doucet & Montgomerie, 2003), physical strength (e.g. dancing ability in humans: Hugill, Fink, Neave, & Seydel, 2009), foraging ability (e.g. nuptial gifts in scorpionflies:

Missoweit, Engels, & Sauer, 2007), parental ability (e.g. courtship rate in damselfish: Knapp & Kovach, 1991) and cognitive ability (e.g. song complexity in zebra finches: Boogert, Giraldeau, & Lefebvre, 2008).

Because of the costs associated with producing or maintaining colourful ornaments, studies of animal coloration have been at the forefront of work on honest signalling (see reviews in Andersson, 1994; Hill & McGraw, 2006a, 2006b). For example, many animals use carotenoids to produce elaborate red, orange or yellow colours, or use melanin to produce black and brown colours; variation in both of these pigment types can signal various types of information relevant to prospective female mates (e.g. Candolin, 2000; Hill & Montgomerie, 1994; Mateos-Gonzalez, Quesada, & Senar, 2011; McGraw, 2007; McGraw & Hill, 2000; Minias, Kaczmarek, Wlodarczyk, & Janiszewski, 2014). In addition to pigmentary colours, there is also growing evidence that females prefer elaborate structural colours that are linked to attributes of male quality (e.g. Doucet & Montgomerie, 2003; Kemp & Rutowski, 2007; McGraw, Mackillop, Dale, & Hauber, 2002; Siefferman & Hill, 2003).

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Jumping spiders (Salticidae) are an excellent group to examine whether variation in condition-dependent coloration affects mating success. Jumping spiders have excellent vision (e.g. Blest, Hardie, McIntyre, & Williams, 1981; Harland & Jackson, 2000; Land, 1969; Williams & McIntyre, 1980), including the ability to distinguish between different colours in various contexts (e.g. Jakob, Skow, Haberman, & Plourde, 2007; Nakamura & Yamashita, 2000; VanderSal & Hebets, 2007). In many of the more than 5000 species of jumping spiders (Platnick, 2013), males display brightly coloured ornaments to dull and inconspicuous females during complex courtship (e.g. Maddison, 1995; Oxford & Gillespie, 1998), and evidence suggests that some of these traits have been driven by sexual selection (Masta & Maddison, 2002). The condition dependence of such colours has been well documented; several aspects of coloration that are displayed to females during courtship contain reliable information about male diet and age (Lim & Li, 2007; Taylor, Clark, & McGraw, 2011; Taylor & McGraw, 2013).

Surprisingly, however, the idea that this naturally occurring condition-dependent variation in male colour might affect male mating success (a crucial and explicit prediction of indicator models) has yet to be tested in jumping spiders. Initial studies of a few species, using broad manipulations that obliterated colour signals completely, suggest that colour influences courtship success. For example, work done with two UV-reflecting salticid species (Cosmophasis umbratica and Phintella vittata) has shown that blocking out UV light affects mate choice decisions, suggesting that the presence (versus absence) of UV coloration is important in courtship signalling (Li et al., 2008; Lim, Land, & Li, 2007; Lim, Li, & Li, 2008). In Habronattus pyrrithrix (the same species examined in the present study), previous work has shown that removing male red facial coloration using make-up reduces courtship success of males displaying in bright sunlight (Taylor & McGraw, 2013). While these studies are useful for determining the context in which colour is important (i.e. courtship), they do not disentangle hypotheses about species recognition, where we expect only the presence of a trait (versus its absence) to be important to females, from hypotheses about quality signalling, where we expect females to pay close attention to more subtle, natural variation in the trait.

The goal of the present study was to test the hypothesis that natural variation in male display coloration in H. pyrrithrix mediates mate choice. Per the indicator model, we predicted that the most elaborate expression of condition-dependent male coloration (i.e. larger, redder facial patches and darker green legs; Taylor et al., 2011) would be preferred by females. We first tested this idea correlationally by pairing field-collected males and virgin females in a mating success study in the laboratory to determine whether colour variation among males predicted the likelihood of copulation. Because male red facial coloration is sensitive to juvenile diet, with males reared on high-quality diets maturing with larger, redder facial patches (Taylor et al., 2011), this colour patch seems like the most likely candidate to signal a male's nutritional status or foraging ability; thus, in a second study, we focused solely on this red coloration. Outdoors, under natural sunlight, we gave both virgin and mated females the choice between two simultaneously courting males, one with his facial coloration experimentally reduced and the other that received a sham treatment (while his natural red facial coloration remained intact), and we measured courtship success of both males. Because female spiders of different mating status (i.e. virgin versus mated) are expected to show different levels of choosiness (e.g. Jackson, 1981), using only virgin females is common practice in jumping spider mate choice experiments (e.g. Clark & Biesiadecki, 2002; Elias, Hebets, & Hoy, 2006; Elias, Hebets, Hoy, & Mason, 2005; Lim et al., 2008; Taylor & McGraw, 2013). However, male

H. pyrrithrix interact with and actively court both virgin and mated females in the field (L. A. Taylor, personal observation), and thus inclusion of both classes of females increases the likelihood that our experiment will capture ecologically relevant levels of choosiness. Moreover, cannibalism in this species is common in the field (Taylor, 2012) and has obvious implications for male fitness; thus, the inclusion of mated females, which are typically more aggressive than virgins (Taylor, n.d.), allows us to consider more thoroughly both male courtship success and the aggression a male receives from choosy females.

Despite dozens of similar studies in other organisms (predominantly in birds; see Hill & McGraw, 2006b), this is the first study to directly manipulate jumping spider colour patterns within natural levels of variation to test the hypothesis that condition-dependent colours function as quality-indicating sexual signals. Expanding this large body of empirical work to lesser-known taxa (e.g. jumping spiders) allows us to test broadly held generalities that may provide novel insights for the field.

METHODS

Study Species

Habronattus pyrrithrix Chamberlin 1924 is found throughout southern California and Arizona, U.S.A., south to Sinaloa, Mexico (Griswold, 1987). In Phoenix, Arizona they are quite common and found at high densities in riparian areas, grassy backyards and agricultural areas (L. A. Taylor, personal observation). Similar to other Habronattus species, male H. pyrrithrix engage in complex courtship display repertoires consisting of both visual and substrate-borne components (e.g. Elias, Maddison, Peckmezian, Girard, & Mason, 2012; Taylor et al., 2011). Courtship typically begins when a male waves his front legs at a female from several centimetres away, while approaching in a zigzag fashion (stage 1 of courtship; Fig. 1a). Displaying males orient their red faces and green legs directly towards females, such that these colours are generally not visible from above (L. A. Taylor, personal observation). If the female does not retreat or attack the male, he will continue to approach until he is within a few millimetres of the female's face, where he abruptly stops, extends his first pair of legs straight up, and begins the substrate-borne component of the display (stage 2 of courtship; Fig. 1b). This substrate-borne component consists of complex, multicomponent vibrations that are coordinated with various motions of ornamented appendages (for additional detail on the complexity of these vibrations, see Elias et al., 2012). Both of these stages are highly variable in length and appear to depend both on the female's response (e.g. remaining stationary, attacking the male, or hopping away) and on the male's persistence (L. A. Taylor, personal observation). In stage 3 of courtship, the male extends his front legs and gently taps the female's carapace; if the female does not retreat or attack, the male typically proceeds to mount and copulate with her (Fig. 1d).

In the field, males typically court all females they encounter, including both virgin and mated conspecifics as well as females of other Habronattus species (Taylor, 2012, n.d.). Some females will allow males to copulate, some simply escape a male's advances by hopping away, and some show considerable aggression towards males; cannibalism is common in both the field and laboratory (Taylor, 2012, n.d.). Agonistic display between males is uncommon in Habronattus (Cutler, 1988; Richman, 1982); in H. pyrrithrix, males will occasionally wave their legs in the direction of other males, but these displays are rare and short in duration, lasting only a few seconds, compared with displays for females that can continue for hours (L. A. Taylor, personal observation).

Figure 1. Stages of male courtship in *Habronattus pyrrithrix*. (a) Stage 1: the male waves his legs as he approaches the female in a zigzag fashion. (b) Stage 2: the male (right) has successfully approached and stopped directly in front of the female (left) and is now performing a display that consists of both visual and substrate-borne components. (c) Stage 3: the male gently taps the female's carapace with his front legs. (d) The male proceeds to mount and copulate.

Correlational Mate Choice Study

The goal of our correlational mating success study was to determine whether naturally occurring variation in male display coloration explains variation in male mating success. Many mate choice studies in jumping spiders involve exposing a single female to multiple potential mates that are physically isolated from one another and from the female and then assessing female choice based on differential receptivity behaviours of the female (e.g. Cross, Jackson, & Pollard, 2007; Li et al., 2008; Lim et al., 2008). However, to our knowledge, there is no known behaviour other than copulation or a female's willingness to let a male approach and make contact with her that reliably signals receptivity in *Habronattus* (L. A. Taylor, personal observation; see also Masta & Maddison, 2002). For this reason, most mate choice studies with *Habronattus* involve presenting a single male to a single female and assessing mating success by directly observing whether or not copulation occurs (e.g. Elias, Hebets, et al., 2006; Elias et al., 2005; Hebets & Maddison, 2005; Masta & Maddison, 2002); thus, we used this approach for the correlational mating success study.

In June 2007, we collected 21 mature adult males and 21 penultimate females (in their final instar, just prior to sexual maturity) from Queen Creek, Arizona (Maricopa County, 33°13′29″N, 111°35′34″W). We housed spiders individually at approximately 28 °C in clear plastic cages (10.16 × 10.16 × 12.86 cm) with an artificial green plant (Ashland Fern Collection, Michael's Stores, Irving, TX, U.S.A.) provided for enrichment (Carducci & Jakob, 2000). Fluorescent laboratory lighting was supplemented with full-spectrum light (30 W

compact full-spectrum light bulbs, Mercola, Hoffman Estates, IL, U.S.A.) positioned in metal clamp light fixtures directly above the spider cages. Additional light bulbs were positioned in the corners of the room (26 W Daylight CFL bulbs, General Electric, Fairfield, CT, U.S.A.). All lights were on a 14:10 h 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 set-up is provided as Supplementary material (Fig. S1). Three times per week, spiders were fed crickets (*Acheta domesticus*) that approximated the spiders' own body mass; this feeding regime resulted in spiders with body condition indices that were comparable to those observed in the field (Taylor, n.d.).

Upon moulting to sexual maturity, we randomly paired each female with a male. Trials began between 0800 and 1100 hours when females were between 13 and 29 days postmaturity. Just before each trial began, we weighed spiders to the nearest 0.0001 g with a digital scale and photographed them next to a size standard. From digital photographs, we measured each spider's carapace width using Photoshop software (Adobe Systems Inc., San Jose, CA, U.S.A.). Because the carapace width of *H. pyrrithrix* is fixed at maturity, while the abdomen stretches with feeding, we used the residuals of a regression of body mass on carapace width as an estimate of body condition that is uncorrelated with body size and is a common metric of estimating condition in spiders (e.g. Jakob, Marshall, & Uetz, 1996; Taylor et al., 2011).

At the start of each trial, the randomly paired male was introduced into the female's cage and we videotaped all interactions for the first hour. After the hour-long videotaped trial, males and females were housed together for an additional 48 h to give them

additional opportunities to court and mate. We then removed the male and fed the female in excess (approximately three times her own body weight in crickets daily) for 2 weeks to allow her to lay eggs if she had mated. We confirmed the fertility of all eggs by monitoring them and allowing them to hatch. From the videos, we recorded the levels of female aggression directed towards males (i.e. number of attacks). We quantified mating success by recording whether or not females laid fertile eggs (leading to hatching spiderlings). In our data from more than 100 laboratory matings of virgin female *H. pyrrithrix* within this specific age range, we have never seen a female copulate with a male and not go on to lay fertile eggs within 2 weeks on this feeding regime (Taylor, n.d.). Thus, we are confident that the presence of fertile eggs (and hatching spiderlings) is a reliable metric of mating success for the 48 h trial (see also Taylor & McGraw, 2013).

At the conclusion of each mating trial, male spiders were euthanized by placing them in the freezer where they were stored until colour analysis. Colours were quantified following methods described in Taylor et al. (2011). Briefly, we used a reflectance spectrophotometer (USB2000, Ocean Optics, Dunedin, FL, U.S.A.) coupled to a modified Leica DMLB2 fluorescence light microscope fitted with a 40× quartz objective lens (Leica Microsystems, Wetzlar, Germany) and illuminated with a full-spectrum Leica 75 W xenon arc lamp (Leica Microsystems). Reflectance measures were taken in a dark room and relative to a Spectralon diffuse reflectance white standard (Labsphere Inc., North Sutton, NH, U.S.A.). This setup allowed us to quantify the minute colour patches on the male's red faces and green front legs (ca. 0.4 and 0.5 mm in width, respectively) that are too small to measure accurately with standard spectrophotometry equipment. Unfortunately, the optics of the microscope cuts out a portion of the UV spectrum and so this instrument only provides spectral data from 375 nm to 700 nm. In some jumping spider species, UV reflectance appears to be important in communication (Li et al., 2008; Lim et al., 2007; Lim et al., 2008), and thus we must use caution when excluding considerable UV reflectance from our analysis. However, in a previous study, we confirmed that, while reflectance does extend into the UV for the green legs, there are no UV peaks (Taylor et al., 2011); thus, the benefit of using an instrument that allows precise and repeatable measures on minute colour patches that dominantly reflect long-wavelength light far outweighs the disadvantage of excluding some UV wavelengths.

In quantifying male colours, we focused specifically on five colour metrics that were found to be condition dependent in a previous study; this allowed us to test the a priori prediction that females should assess variation in these specific condition-dependent traits during mate choice (Taylor et al., 2011). We took the average of two reflectance measures from each male's red facial patch and from each of the male's green front legs. From these spectral data, we calculated (1) the hue of the red face (the wavelength corresponding to the inflection point of the red curve), (2) the red chroma of the face (the proportion of total reflectance between 600 and 700 nm) and (3) the brightness (mean reflectance) of the green front legs. In addition, because male faces are relatively large surfaces that are only partially ornamented with red scales, we also measured the size of the red patch on male faces, by photographing each male in a standardized, face-front position through a Leica MZ 125 stereo microscope at 50× magnification using a Spot Insight 11.2 digital camera (Diagnostic Instruments, Sterling Heights, MI, U.S.A.; image resolution 1600 × 1200 pixels) and Image-Pro Express software (Media Cybernetics, Silver Spring, MD, U.S.A.). All photos were taken using the same light and camera settings. We used Photoshop software (Adobe Systems Inc.) to calculate the total area of red scale coverage on each male's face. Because larger males had larger patch sizes, we calculated both (1) total patch area and (2) a 'relative patch size index' using the residuals of a regression of patch area on carapace width (Taylor et al., 2011).

At the conclusion of the study (after all eggsacs hatched), females and spiderlings were released where they were originally collected.

Colour Manipulation Experiment

Because the results of our correlational study in the laboratory suggested that natural variation in male coloration was unrelated to mating success (see Results), we went on to explore this idea further using a colour manipulation experiment under circumstances in which we might expect colour signalling to be most prominent. Specifically, we presented both virgin and mated females with two simultaneously courting males (one of which had his facial coloration experimentally reduced) and we ran all trials outdoors under natural sunlight. Because a male's red facial coloration is consistently condition dependent in field-collected individuals (see Results; see also Taylor et al., 2011), reflects the quality of an individual's juvenile diet (Taylor et al., 2011), and, at least in some contexts, acts as a signal in courtship interactions (Taylor & McGraw, 2013), we currently have the most evidence that red colour, as opposed to other ornaments, contains reliable information relevant to mate choice. Thus, we focused on this colour ornament for the present experiment. Our rationale for including both virgin and mated females was that it would ensure that our study would encompass the broadest possible range of ecologically relevant variation in both female choosiness and female aggression. While it is unclear how many times females can mate in the field, we have found in the laboratory that mated females are more reluctant to mate and also more aggressive than virgins (L. A. Taylor, personal observation). In the field, *H. pyrrithrix* are found in high abundance and males will frequently encounter and actively court any female they encounter, regardless of mating status (Taylor, n.d.). Because all of the spiders were collected at the same time, mating status in our study was naturally confounded with female age; virgin females (collected in their penultimate stage of development) were likely to be younger than the mated females that were collected after they had matured.

As described above, to interpret female choice in a simultaneous mate choice experiment with *H. pyrrithrix*, males must be allowed to approach and make contact with females, and thus cannot be physically isolated from them. Thus, the best methodology for simultaneous choice tests in this species is to place two males and one female into an experimental chamber where all three can interact freely (see Taylor & McGraw, 2013). Consequently, because our experimental design did not prevent males from seeing and interacting with one another, we could not completely disentangle male–male competition from female choice per se. However, when two males are courting the same female, they typically direct their displays at the female simultaneously, rather than towards one another (L. A. Taylor, personal observation); thus, we expected that any major effect of colour manipulation in our experiments would result from responses of the female, rather than from interactions between males.

In March 2011, we collected 42 mature adult male spiders and 21 female spiders from the same population described above. Of the females, 10 were mature upon collection and appeared to be gravid, while 11 were in their final (penultimate) instar just prior to sexual maturity, ensuring that they were virgins. We housed these spiders in the laboratory (as described above) for 1 month before the trials began, which allowed putatively gravid females to lay eggs (to confirm that they had indeed already mated) and allowed penultimate females to reach maturity. Because our previous studies suggested that both male size and body condition

consistently predicted mating success (see Results; see also Taylor & McGraw, 2013), we wanted to eliminate variation associated with size and condition as much as possible to attempt to identify effects of male colour per se. The month-long period of housing males in the laboratory on a constant diet (see above) aimed to reduce variation associated with body condition as much as possible. To ensure that our month-long housing of male spiders did not negatively impact their motivation to mate, we compared male courtship effort in this experiment with males in an observational pilot study conducted earlier in the same season; in the pilot study, two males (between 2 and 8 days after collection) were paired with virgin females (see Results). To further reduce size-related variation between two males in a trial, we paired males by body size such that the mean ± SD difference in carapace width between the males in each pair was only 0.052 ± 0.089 mm.

Males in a pair were randomly assigned to either the colour manipulation group or the sham-treated control group. Males in the colour-manipulated group had their red facial coloration experimentally reduced so that it closely matched the mean reflectance curve of the 10 least colourful males from this same population in a previous study (Taylor et al., 2011; see Fig. 2a, c). To reduce male coloration (namely, chroma; Fig. 2a), we applied a mixture of water and black liquid eyeliner (Colour: 'Perversion', Urban Decay Cosmetics, Costa Mesa, CA). We also applied additional eyeliner along the edges of the facial patch to reduce the size of the red area to approximate the mean of the 10 smallest patch sizes from a previous study (Taylor et al., 2011). On sham-control males, we applied the same amount of eyeliner and water to an equivalent area on the top of their carapace just behind their anterior median eyes, while their red facial coloration was left intact (Fig. 2b). On the day before

mating trials, we anaesthetized males with carbon dioxide for approximately 5 min while we performed colour manipulations. After waking up from anaesthesia, males were offered a cricket to confirm that they had recovered fully and were capable of capturing prey. To confirm that our colour manipulation did not affect courtship activity or motivation, we recorded the latency for males to begin courting and the overall courtship effort of each male during trials. In comparing the courtship latency and effort between males in this study and males in a previous nonmanipulative observational study with a similar design (i.e. two males introduced into the cage of a virgin female), we found no evidence that either our colour manipulation or sham treatment had any significant effect on male behaviour (see Results).

Before a trial began, we moved the female's cage outdoors to allow her to acclimate for 1 h. All trials were run in full sunlight between 0900 and 1500 hours, when the mean temperature was 26–32 °C. These outdoor trials were run in a riparian habitat on the campus of Arizona State University where H. pyrrithrix is found in high abundance (L. A. Taylor, personal observation), thus providing natural light and natural vegetation to serve as background colours. Irradiance data collected in this outdoor area is provided as Supplementary material (Fig. S1). At the start of the first phase of the trial, the two males were weighed (to determine current body condition, as described above) and placed in the female's cage in immediate succession, in random order. All interactions were videotaped for 40 min.

From the videos, we used the freeware program Cowlog (Hänninen & Pastell, 2009) to quantify the latency of each male to begin courting and the overall time spent courting. Results from previous studies indicated that the males' approach distance to
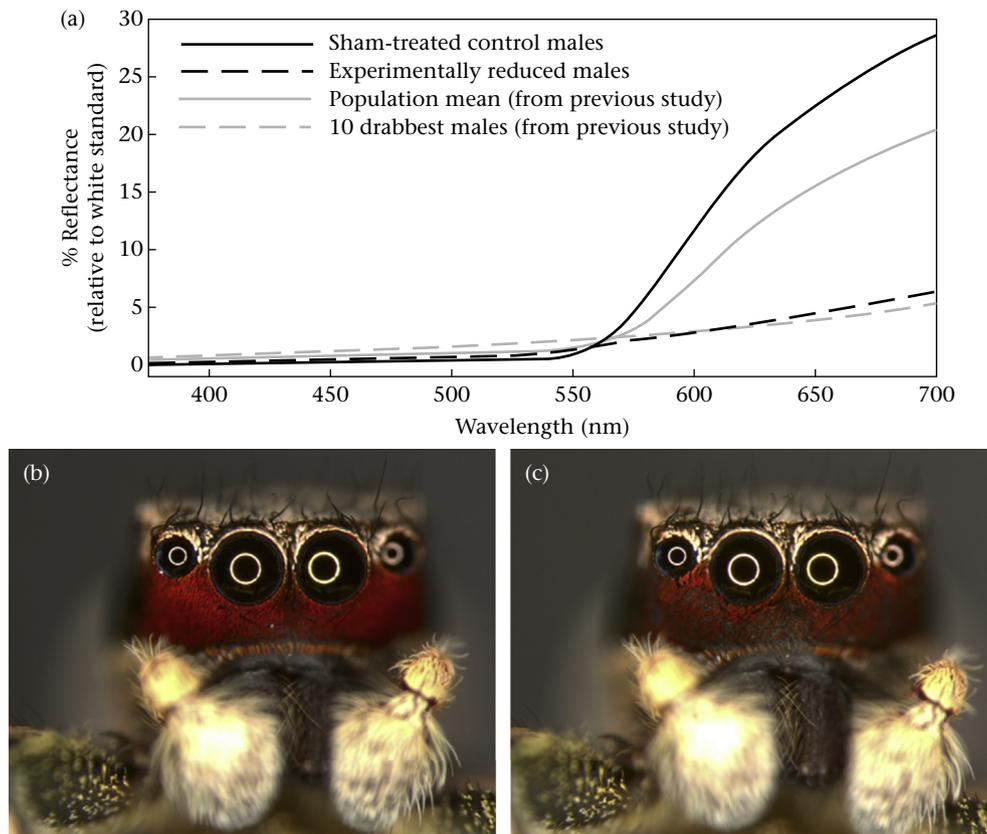

Figure 2. Experimental colour manipulation used to reduce the size and colour of the red facial patch of male *Habronattus pyrrithrix*. (a) Spectral properties of sham-treated control males and colour-manipulated males, compared with the population mean and the 10 drabbest males from a previous study (Taylor et al., 2011). (b) The intact red facial coloration before colour manipulation. (c) The facial coloration of the same male after experimental manipulation (i.e. colour reduction).

females was an excellent predictor of mating success (i.e. males that were able to get closer to females were more likely to proceed through all stages of courtship and eventually copulate, leading to fertile eggs; see Taylor & McGraw, 2013). Because having two simultaneously courting males seemed to distract the female and extend the latency to copulation (L. A. Taylor, personal observation), we found low levels of copulation in this experiment, comparable to previous studies (Taylor & McGraw, 2013). Thus, we used the mean distance that males approached females over the course of the trial as an estimate of courtship success (see Taylor & McGraw, 2013). We also recorded the number of attacks by females on each male and all instances of copulation.

At the conclusion of the colour manipulation experiment, males were euthanized by placing them in the freezer. Females and hatchlings were released to the population where they were originally collected.

Statistical Analyses

Correlational mating success study

First, to corroborate previous findings on the condition dependence of male colours, we used linear regression to examine the relationships between a male's body condition at collection and colour variables that were found to be condition dependent in previous experiments (specifically, the hue, red chroma and size of the red facial patch and brightness of the green legs; Taylor et al., 2011). We then used logistic regression to examine whether these colour variables predicted successful copulation, and we used linear regression to determine whether they predicted levels of female aggression. We also used logistic regression and linear regression, respectively, to determine whether either male size or male body condition predicted copulation success and levels of female aggression.

Colour manipulation experiment

First, to confirm that our manipulation of facial coloration did not adversely affect male behaviour, we used ANOVA to determine whether treatment groups (colour manipulated versus sham control) differed in the latency for males to begin courting or in their total courtship effort (amount of time spent courting over the course of the trial). Furthermore, to confirm that our overall treatment procedure (including both sham and control treatments as well as the month-long period that males spent in the laboratory) did not adversely affect male behaviour, we used a t test to compare the behaviour of all males used in this study with the behaviour of untreated field-collected males used in an observational pilot study with a similar design. We used logistic regression to confirm that the approach distance of males to females predicted a male's likelihood to reach stage 2 of courtship, which is required for achieving successful copulation (see Fig. 1).

To test the focal hypothesis of our study, we used mixed-model nested ANOVAs to determine whether male colour treatment, female mating status (virgin or mated), or their interaction affected courtship success (the males' approach distance to females) or levels of female aggression. Because each pair of males was tested simultaneously with a single female, female ID was included as a random factor, nested within female mating status. Because both male size and body condition affect courtship and mating success in *H. pyrrithrix* (see Results; see also Taylor & McGraw, 2013), we also ran mixed-model nested ANCOVA as above, but with the addition of male size and condition as covariates. Finally, to examine whether the size difference between the two males influenced the outcome of interactions, we ran a second ANCOVA (as described above), but with the difference in size between the two males included as a covariate.

Because males were more successful when courting virgin females than when courting mated females (see Results), we also examined whether this pattern might be related to male courtship effort. We used mixed-model nested ANOVAs to determine whether female status predicted a male's latency to begin courting or his total courtship effort. Again, because each pair of males was tested simultaneously with a single female, female ID was included as a random factor, nested within female mating status.

In light of the surprising finding that females were more aggressive towards larger males in better condition (see Results), we examined the idea that female aggression is an inherent risk associated with proceeding through courtship. Specifically, we used ANOVA to determine whether males that were successful at proceeding to stage 2 of courtship received more aggression from females during the courtship process than males that did not progress to stage 2. Because two males were paired with each female, we included female ID as a random factor in the model.

All data met assumptions of parametric statistics, with the exception of female aggression data (for both the correlational study and the colour manipulation experiment); these data were thus rank-transformed prior to analyses (Iman & Conover, 1979). To aid in the interpretation of negative results, we include effect sizes and 95% confidence intervals around those effect sizes, where appropriate. Small effect sizes with narrow confidence intervals that encompass zero indicate the strongest support for the null hypothesis (i.e. no effect) (Colegrave & Ruxton, 2003; Nakagawa & Foster, 2004). All statistical analyses were conducted using SAS 9.2 and JMP 10 (SAS Institute, Cary, NC, U.S.A.).

RESULTS

Correlational Mating Success Study

As in our previous study, males in better condition had larger, redder facial patches (hue: $F_{1,19} = 4.63$, $R^2 = 0.20$, $P = 0.045$; red chroma: $F_{1,19} = 6.43$, $R^2 = 0.25$, $P = 0.02$; absolute face patch size: $F_{1,19} = 5.73$, $R^2 = 0.23$, $P = 0.03$; relative patch size: $F_{1,19} = 9.93$, $R^2 = 0.34$, $P = 0.005$). However, in contrast to previous studies, the brightness of the male's green legs was not related to his body condition ($F_{1,19} = 1.01$, $R^2 = 0.05$, $P = 0.32$).

Eleven out of 21 males (52.4%) copulated during trials, leading to fertile eggs. Aspects of condition-dependent male red facial coloration (hue, chroma, size) did not significantly predict successful copulation (Table 1) or affect rates of female aggression (hue: $F_{1,19} = 0.23$, $R^2 = 0.01$, $P = 0.64$; red chroma: $F_{1,19} = 0.30$, $R^2 = 0.02$, $P = 0.59$; absolute face patch size: $F_{1,19} = 1.69$, $R^2 = 0.08$, $P = 0.21$;

Table 1
Results of logistic regression for the correlational mate choice study examining the effects of a male's colour metrics, body size and body condition on his likelihood of successful copulation

	χ^2_1	P	Effect size (log odds ratio)	Lower 95% CI for effect size	Upper 95% CI for effect size
Hue of red face	0.73	0.39	−1.35	−4.87	1.74
Red chroma of face	0.64	0.43	−1.57	−6.73	2.24
Absolute face patch size	0.08	0.78	−0.63	−5.58	3.98
Relative face patch size	0.02	0.89	−0.24	−3.74	3.18
Brightness of green legs	2.74	0.10	−2.43	−5.89	0.43
Body condition	4.15	**0.04**	−4.91	−11.65	−0.16
Body size	0.08	0.78	−0.52	−4.41	3.20

Significant P values are shown in bold. Note that small effect sizes with narrow confidence intervals encompassing zero indicate the strongest support for the null hypothesis (i.e. no effect) (Colegrave & Ruxton, 2003; Nakagawa & Foster, 2004).

relative patch size: $F_{1,19} = 0.71$, $R^2 = 0.04$, $P = 0.41$). Similarly, aspects of male green leg coloration also did not predict successful copulation (Table 1) or affect levels of female aggression (leg brightness: $F_{1,19} = 0.41$, $R^2 = 0.02$, $P = 0.53$).

Males in better condition were significantly more likely to copulate (Table 1, Fig. 3), but male size had no effect on this measure of mating success (Table 1). Neither male condition nor size affected female aggression (condition: $F_{1,19} = 0.31$, $R^2 = 0.02$, $P = 0.58$; size: $F_{1,19} = 1.03$, $R^2 = 0.05$, $P = 0.32$).

Colour Manipulation Experiment

Our experimental colour manipulations had no detectable adverse effects on male behaviour, as there were no differences between the colour-manipulated and sham-treated groups in the latency for males to begin courtship ($F_{1,40} = 1.99$, $P = 0.17$) or the total time that males spent courting ($F_{1,40} = 0.07$, $P = 0.80$). Furthermore, in comparing male behaviour in this experiment with the results of a previous nonmanipulative observational study with a similar design (i.e. two field-collected males between 2 and 8 days postcollection introduced into the cage of a virgin female), we found no differences in either latency to begin courting or total time spent courting (latency: $t_{54} = 1.04$, $P = 0.30$; effort: $t_{54} = 1.58$, $P = 0.12$). As in previous studies, a male's approach distance to the female was a strong predictor of the male's ability to proceed to stage 2 of courtship ($\chi^2_1 = 12.55$, $P = 0.0004$).

Males were significantly more successful in courting virgin females than mated females, but a male's colour treatment had no effect on his success (Fig. 4, Table 2). Neither female mating status nor male colour treatment affected levels of female aggression (Table 2). When male size and condition were included as covariates, these factors had no effect on male courtship success (Table 3). Surprisingly, though, females were more aggressive towards males in better condition and also tended to be more aggressive towards larger males (Table 3).

Males began courting virgin females more quickly ($F_{1,21} = 30.96$, $P < 0.0001$) and devoted more total time to courting virgins ($F_{1,21} = 4.57$, $P = 0.044$) than they did mated females. Males that

proceeded to stage 2 of courtship ($N = 16$ out of 42) tended to receive higher levels of aggression from females than males that did not proceed to stage 2 ($F_{1,20} = 4.12$, $P = 0.056$).

DISCUSSION

In both a correlational study and a colour manipulation experiment with *H. pyrrithrix*, male colour variables that are consistently condition dependent across studies had no effect on female mate choice. First, using field-collected spiders, we paired individual males with virgin females in the laboratory and found that natural variation in male red facial and green leg coloration did not predict mating success (likelihood of copulation) or levels of female aggression. Rather, mating success was best predicted by male body condition. We then went on to conduct an outdoor experiment under natural sunlight, where we gave both virgin and older mated females the choice between two simultaneously courting males, one with his facial coloration experimentally reduced and the other that received a sham treatment. Again, we found no relationship between male coloration and courtship success. Previous studies in this species have shown that the presence (versus absence) of male red facial coloration improves male courtship success (Taylor & McGraw, 2013), but here we found no evidence that natural variation in this trait has any effect on success.

Patterns of Condition Dependence

Consistent with our previous study on the condition dependence of coloration in *H. pyrrithrix* (Taylor et al., 2011), field-collected males in better condition had larger and redder patches of colour on their faces. In that study, we also found that the brightness of a male's green front legs correlated with body condition in the field, yet that pattern did not hold up in the present study. Unlike red face coloration, which is dependent on juvenile diet (Taylor et al., 2011), the brightness of a male's green legs is dependent on male age (Taylor, 2012). Because the present correlational study was conducted earlier in the season (early June) than the previous study (in July and August), it may be that
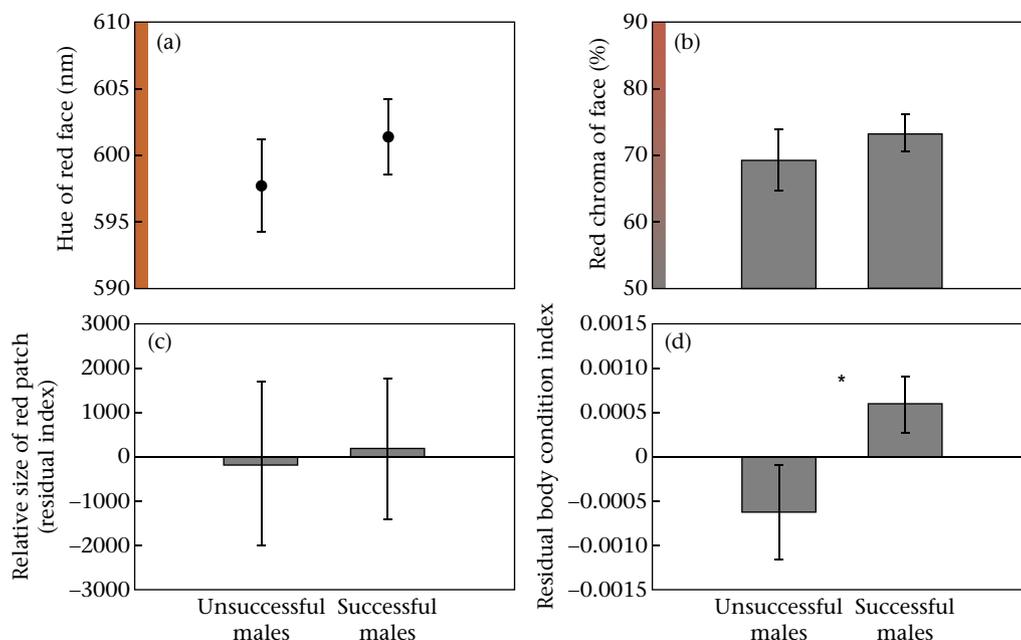

Figure 3. Comparisons of colour variables (a, b, c) and body condition (d) between *Habronattus pyrrithrix* males that did and did not copulate during the correlational study. An asterisk indicates a significant difference between groups.
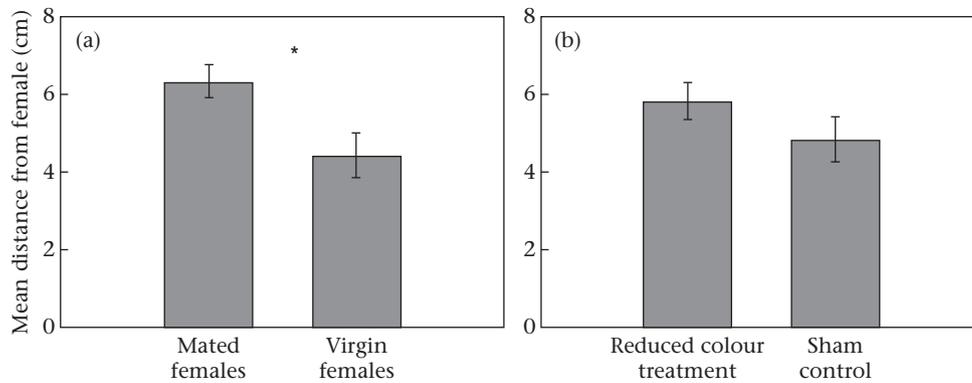
Figure 4. Courtship success of male *Habronattus pyrrithrix* (mean approach distance to females) (a) when courting virgin and mated females and (b) when the male's red facial coloration was experimentally reduced or not experimentally reduced (sham-treated) in the colour manipulation experiment. An asterisk indicates a significant difference between groups.

the population earlier in the season included mostly recently matured (i.e. young adult) males. Later in the season, as more males mature, we would expect to see larger variation in age among mature males. Our colour data are consistent with this idea; the mean leg brightness observed in this study (mean = 21.0% reflectance) was on the darker end of the range found previously (range of male leg brightness = 11.79–48.89% reflectance; Taylor et al., 2011), suggesting that these males were relatively young. Unlike the green leg coloration, once a male's red facial coloration is expressed at maturity, it does not change with age (Taylor, 2012). Juvenile diet seems to be responsible for variation in red facial coloration (Taylor et al., 2011), which may explain why this pattern has been more consistent among field studies. In some systems, the condition dependence of particular display traits varies with environmental heterogeneity; such traits may only provide useful information under relatively poor conditions, when not all individuals can afford to invest in them (Vergara, Martinez-Padilla, Mougeot, Leckie, & Redpath, 2012). Because the red coloration examined here has been found to be consistently condition dependent in this population, it might be a particularly good candidate for a reliable signal of quality in this species (e.g. Andersson, 1982).

Predictors of Mating Success

Contrary to our hypothesis, our correlational study revealed that natural variation in male red facial and green leg coloration did not predict mating success. When we manipulated red facial coloration in our simultaneous choice test, again male coloration had no effect on courtship success; males whose red facial coloration was experimentally reduced were just as successful at approaching females as sham-treated control males. As in previous studies with *H. pyrrithrix* (Taylor & McGraw, 2013), males in our correlational study that were in better condition were more likely to copulate; this pattern of condition improving success holds up for other groups of ground-dwelling spiders (e.g. Gibson & Uetz, 2008). In the colour manipulation experiment, we deliberately reduced variation in male body size (by ensuring that paired males were similar in size) and condition (by keeping males on a constant diet in captivity for 1 month), yet we still saw no effect of colour on courtship success.

There are several possible explanations for our finding that male ornamental coloration is less important for male mating success than other morphological traits. First, males in the genus *Habronattus* engage in extremely elaborate and complex courtship

Table 2
Results of mixed-model nested ANOVA and ANCOVAs for the colour manipulation experiment examining the effects of male colour manipulation and female mating status on mean male approach distance to females over the course of the trial

	df	F	P	Effect size (partial Ω^2)	Lower 95% CI for effect size	Upper 95% CI for effect size
ANOVA						
Treatment	1,19	1.33	0.26	0.008	<0.001	0.19
Female mating status	1,19	5.55	**0.03**	0.098	<0.001	0.32
Treatment*female mating status	1,19	1.89	0.19	0.021	<0.001	0.21
Female ID (nested within mating status)	19,19	0.43	0.96	<0.001	<0.001	0.04
ANCOVA						
Treatment	1,17	0.91	0.35	<0.001	<0.001	0.17
Female mating status	1,17	1.00	0.33	<0.001	<0.001	0.17
Treatment*female mating status	1,17	0.99	0.18	0.023	<0.001	0.22
Female ID (nested within mating status)	19,17	0.39	0.97	<0.001	<0.001	0.006
Male body condition	1,17	2.08	0.17	0.025	<0.001	0.22
Male body size	1,17	0.20	0.66	<0.001	<0.001	0.12
ANCOVA						
Treatment	1,18	1.17	0.29	0.004	<0.001	0.19
Female mating status	1,18	5.31	**0.03**	0.093	<0.001	0.35
Treatment*female mating status	1,18	1.96	0.18	0.022	<0.001	0.23
Female ID (nested within mating status)	19,18	0.41	0.97	<0.001	<0.001	<0.001
Difference in size between focal and partner males	1,18	0.17	0.69	<0.001	<0.001	0.12

Significant *P* values are shown in bold. Note that small effect sizes with narrow confidence intervals encompassing zero indicate the strongest support for the null hypothesis (i.e. no effect) (Colegrave & Ruxton, 2003; Nakagawa & Foster, 2004).

Table 3
Results of mixed-model nested ANOVA and ANCOVAs for the colour manipulation experiment examining the effects of male colour manipulation and female mating status on levels of female aggression (i.e. number of attacks) directed towards courting males

	df	F	P	Effect size (partial Ω^2)	Lower 95% CI for effect size	Upper 95% CI for effect size
ANOVA						
Treatment	1,19	0.13	0.72	<0.001	<0.001	0.11
Female mating status	1,19	0.01	0.94	<0.001	<0.001	0.04
Treatment*female mating status	1,19	0.43	0.52	<0.001	<0.001	0.14
Female ID (nested within mating status)	19,19	0.86	0.63	<0.001	<0.001	0.31
ANCOVA						
Treatment	1,17	0.27	0.62	<0.001	<0.001	0.13
Female mating status	1,17	1.25	0.28	0.006	<0.001	0.19
Treatment*female mating status	1,17	0.09	0.76	<0.001	<0.001	0.10
Female ID (nested within mating status)	19,17	1.36	0.27	0.14	<0.001	0.48
Male body condition	1,17	6.40	**0.02**	0.11	0.0014	0.34
Male body size	1,17	3.48	0.08	0.06	<0.001	0.27
ANCOVA						
Treatment	1,18	0.05	0.83	<0.001	<0.001	0.08
Female mating status	1,18	0.01	0.94	<0.001	<0.001	0.04
Treatment*female mating status	1,18	0.10	0.75	<0.001	<0.001	0.10
Female ID (nested within mating status)	19,18	0.94	0.55	<0.001	<0.001	0.35
Difference in size between focal and partner males	1,18	2.83	0.11	0.04	<0.001	0.24

Significant *P* values are shown in bold. Note that small effect sizes with narrow confidence intervals encompassing zero indicate the strongest support for the null hypothesis (i.e. no effect) (Colegrave & Ruxton, 2003; Nakagawa & Foster, 2004).

displays consisting of various combinations of brilliant colours (e.g. Taylor et al., 2011), motion (e.g. Elias, Land, Mason, & Hoy, 2006), and substrate-borne components (e.g. Elias et al., 2012; Maddison & Stratton, 1988). One hypothesis to explain the evolution of complex signals is that each signal component contains different information, or that they contain similar information but act as backups when other signal components are more difficult to transmit (reviewed in Hebets & Papaj, 2005). If this is the case, it may be that the suite of information presented is very complex, and thus the effect of any one component of the display (such as facial colour) on a female's overall mate choice may be subtle. Examining these traits in isolation might make subtle effects difficult to detect. Alternatively, it could be that colour itself is not a preferred trait, but that it functions to modulate assessment of other parts of the male's complex display. For example, in courting *Schizocosa* wolf spiders, the presence of substrate-borne vibrations alters the female's visual attention; females only pay attention to visual aspects of the display in the presence of vibrations (Hebets, 2005). Future work in *H. pyrrithrix* should examine the combined and interactive effects of the various signal components (e.g. colour, motion and vibration).

A third explanation is that variation among females in their preferences for different display traits obscures overall, general preference patterns for any one trait, such as red facial colour. Studies of the complex displays of bowerbirds suggest that there are age-specific differences in the male traits that females use in mate assessment (Coleman, Patricelli, & Borgia, 2004). Similarly, in buntings, there is extreme temporal variation in female mate choice, with females preferring different traits from year to year, presumably depending on their specific needs in a changing environment (Chaine & Lyon, 2008). In both cases, it has been argued that such variation in female preferences may have driven male signal complexity (Chaine & Lyon, 2008; Coleman et al., 2004). If similar female preference variation is responsible for the complex displays in *Habronattus*, significant preferences for any one trait such as red facial coloration again may be difficult to detect in a single year or study. Because previous work has shown that female choosiness, preference and aggression change with mating status in other jumping spiders (e.g. Cross et al., 2007; Jackson, 1981), in our experiment we included both virgin and mated females, which allowed us to include the broadest possible range of both

choosiness and aggression that males might experience in the field. While we found no evidence of an interaction between female mating status and female preference for male red facial colour, there are other factors that might create variation in female preferences that should be explored in this system. In wolf spiders, female preferences are shaped by the females' experience with males before they mature (Hebets, 2003). Given the evidence for flexibility in courtship strategies of many species of jumping spiders (e.g. Cross, Jackson, & Pollard, 2008; Jackson, 1977, 1992; Jackson & Macnab, 1991; Jackson & Willey, 1995) and their ability to modify many aspects of their behaviour through experience and learning (reviewed in Jakob, Skow, & Long, 2011), it would be interesting to examine how female experience might create variation in colour preferences in *H. pyrrithrix*.

Finally, it may be that the brilliant colours of male *H. pyrrithrix* aid females in species recognition rather than acting as a quality signal; this idea is consistent with the results of both the present study and previous work (see Taylor & McGraw, 2013). While male colour is not a requirement for successful copulation, the presence of a male's red facial patch improves his success if he is courting in the sun (Taylor & McGraw, 2013). In some populations, multiple species interact at high rates; for example, in one population in Phoenix, Arizona, we found that individuals were just as likely to encounter a heterospecific as they were to encounter a conspecific, yet males approached and courted every female, regardless of her species (Taylor, 2012). Under such circumstances, interspecific communication is likely to be extremely important with strong selection pressure on clear and unambiguous species recognition signals. Theoretical work, dominated by consideration of signalling in better-studied taxa such as birds, predicts that species recognition signals should not evolve to be particularly costly, condition dependent or elaborate, as they only need to allow prospective mates to be differentiated from a limited number of other possible species (reviewed in Dale, 2006). Yet male *Habronattus* might challenge this rule, given that the recognition costs subsume both survival and reproduction; the need to identify themselves clearly to females from a safe distance and to reduce their risk of cannibalism might shift the costs and benefits in favour of extremely conspicuous, elaborate species recognition signals.

Our study also revealed interesting patterns in male behaviour. Males courted every female to some extent in every trial. Even in

the field, *H. pyrrithrix* males typically court every female that they encounter, including heterospecifics (Taylor, 2012). In our colour manipulation experiment, we monitored male courtship effort to confirm that our treatments were not affecting a male's motivation to court and, interestingly we found that, while male colour treatment did not affect a male's courtship effort, males began courting virgin females more quickly than they did older mated females and also invested more time overall to active courtship with virgins. There is growing evidence that males of some species of jumping spiders show preferences for some females over others (Cross et al., 2007; Hoefler, 2007). In *Phidippus clarus*, mature males cohabit with and guard immature females before they mature; these males show a preference for larger females that mature sooner (Hoefler, 2007). In *Evarcha culicivora*, both males and females actively engage in courtship, and males prefer larger females as mates (Cross et al., 2007). In the present study, because males were introduced into the cages of females, it is possible that cues from female silk provided information to males about female mating status and/or age (e.g. Hoefler, 2007). Because mated female jumping spiders are often choosier than virgin females (Jackson, 1981) and because males of some species deposit mating plugs over the copulatory organs of females after mating (Jackson, 1980), choosing to prioritize time courting virgin, rather than mated, females may be advantageous. Even when males court indiscriminately, future work should examine subtle choices that males may make about where to focus their courtship effort. In addition, all of the males included in our study were collected as adults and thus likely came into the laboratory with a variety of different experiences. While there is no evidence yet that male jumping spiders modify their courtship behaviour with experience, we know that jumping spiders show a remarkable capacity for learning in other contexts (Jakob et al., 2011); an interesting next step would be to examine how such learning might influence male courtship.

An interesting and unexpected finding uncovered in this experiment was that females actually show higher, rather than lower, levels of aggression towards males that are in better condition, and that larger males also tended to receive higher levels of aggression from females (although these effects were relatively small). Multiple studies have now shown that female *H. pyrrithrix* prefer to mate with bigger males in better condition (correlational study; see also Taylor & McGraw, 2013). Why then should these presumably 'preferable' males elicit higher levels of aggression from females? Perhaps female aggression is simply a part of the courtship process that males must endure to progress through courtship. We show here that, regardless of colour treatment, males that are able to successfully proceed to stage 2 of courtship (where they are within millimetres of the female's face; see Fig. 1b) receive higher levels of aggression than males that are not able to make it to this stage. If these attacks are attempts at cannibalism by females, this suggests that progressing through courtship might be inherently risky for males. It may be that, when two males are courting simultaneously, larger males are more willing to incur such risks, as they may be harder for females to cannibalize. Or perhaps these nonfatal attacks directed towards females are not missed cannibalism attempts, but are rather an additional way that females assess a male's quality.

In summary, our results indicate that, while there is indeed variation in courtship and mating success among male *H. pyrrithrix* (i.e. not all males copulate, and there is variation in how effective males are at approaching females and proceeding through the stages of courtship), this variation was not predicted by aspects of condition-dependent red facial coloration. Throughout the honest signalling literature are numerous examples of studies in which suites of condition-dependent colour variables are tested as quality indicators (e.g. see reviews in Hill, 2006; Santos, Scheck, &

Nakagawa, 2011; Senar, 2006). While many of these studies report negative results alongside positive ones (e.g. see meta-analysis data in Santos et al., 2011), most discussions in the literature focus only on the specific results that support their hypotheses, glazing over the importance of the tests that do not. As a result, numerous cases of traits that are strongly condition dependent but do not affect female choice are reported, but go comparatively unnoticed in the literature. If hypotheses and predictions are indeed generated a priori, then nonsignificant results that do not support hypotheses should be just as important to our overall understanding of the importance of quality signalling as the significant results that do support them. Multiple meta-analyses have revealed that the ways in which results on a particular topic are reported (i.e. publication biases) change as paradigms in behavioural ecology shift (Alatalo, Mappes, & Elgar, 1997; Poulin, 2000; Simmons, Tomkins, Kotiaho, & Hunt, 1999). We argue that, as the evidence for condition-dependent quality signalling continues to accumulate, we should move towards understanding why some condition-dependent traits matter to females while others are ignored by females or only matter in certain contexts. This approach may help us better understand the complex factors that shape the brilliant and often costly ornaments that males display.

Supplementary Material

Supplementary material for this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2014.05.005.

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