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

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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).