



Strong, convergent male mate choice along two preference axes in field populations of black widow spiders



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Strong male mate preferences have been documented in species with otherwise conventional sex roles in the laboratory, and across taxa, male preferences generally focus on indicators of female fecundity and sperm competition risk. However, the few field studies of male choice rarely show equally strong effects. This suggests that costs of choice in nature may make the expression of preferences unlikely, or that interacting assessment cues may lead to unpredictable and variable outcomes in the wild. Field studies are therefore critical for testing whether or not male mate choice is sufficiently strong to exert sexual selection on females. Here we examine male choice in nature in response to two experimentally manipulated cues of female reproductive value. We recorded the attraction of male black widow spiders, *Latrodectus hesperus*, to females in a field enclosure and in a unconstrained natural setting. Stimulus females varied in two ways: sperm competition risk (low–unmated; high–mated) and fecundity (high–fed; low–unfed). Females and their silk were caged to prevent behavioural interactions while allowing the spread of airborne pheromones that attract males. Males in both experiments showed strong, nearly unanimous choice for unmated, well-fed females. In field enclosures, 80% of males made this choice, and wild males made the same choice in 94% of trials. We conclude that male choice in *L. hesperus* is mediated by detection of airborne pheromones, is strong and consistent despite natural costs of mate searching, and is not affected by natural interactions between (sometimes conflicting) cues of female reproductive value. Thus, universal mate choice may exist among males in nature. We propose general features of systems in which this may be likely and discuss implications for the study of sexual selection on females under conventional sex roles.

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Male mate choice will evolve and persist whenever the benefits of choosing outweigh costs of choice. Males are predicted to benefit from mating selectively when polygyny is limited due to male investment in reproduction (parental effort) and/or securing matings (mating effort, sensu Edward & Chapman, 2011), female reproductive value is variable, and the cost of mate assessment is low (Bonduriansky, 2001; Edward & Chapman, 2011). When these conditions are met, males that are able to detect indicators of female reproductive value may compete for mates that would provide high fitness returns on their mating investment (Craig, Herman, & Pack, 2002; Hoefler, 2007) and minimize mating effort expended with less valuable females. Consistent with this, two major axes of male mate preference have been inferred from controlled choice tests in a variety of taxa (Bonduriansky, 2001): in favour of high-fecundity females and in favour of females with low

sperm competition risk (Hoefler, 2007; Hoysak & Godin, 2007; Preston, Stevenson, Pemberton, Coltman, & Wilson, 2005; Reading & Backwell, 2007; Xu & Wang, 2009). These studies suggest sex roles are more labile than expected under the traditional Darwinian paradigm (Bonduriansky, 2001; Edward & Chapman, 2011) since males have strong mate preferences even though they are polygynous, provide no parental care and operational sex ratios are male-biased, conditions that traditionally predict choosy females and competitive males (Bel-Venner, Dray, Allaine, Menu, & Venner, 2008; Bonduriansky, 2001; Jeswiet, Lee-Jenkins, Ramnarine, & Godin, 2011; Preston et al., 2005; Pruitt & Riechert, 2009; Wong & Jennions, 2003). However, the majority of these results are from the laboratory, and while such studies can establish male preferences and probe the ability of males to discriminate among female phenotypes, they cannot establish the frequency or consequence of male mate choice in nature (e.g. Jennions & Petrie, 1997). Thus, the importance of male mate choice in the wild is not yet clear (Edward & Chapman, 2011), and field studies are urgently needed (Maxwell, Barry, & Johns, 2010).

Laboratory studies of preferences may not predict choice in nature for several reasons. First, laboratory-demonstrated male

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preferences are often significantly eroded in the presence of natural costs (e.g. predation risk, cost of mate searching: Booksmythe, Detto, & Backwell, 2008; Head, Wong, & Brooks, 2010; Wong & Jennions, 2003). Second, shifts in preference functions with individual male condition or mating status (Gaskett, Herberstein, Downes, & Elgar, 2004) may not be revealed under controlled conditions. Third, complications introduced by male competition may make it particularly unlikely that preferences translate into universal male mate choice in nature. For example, high-quality, competitive males may monopolize high-quality females (Hoefler, 2007; Yu & Lu, 2010). Less competitive males may avoid the most preferred females and thus forestall competition with higher-quality rivals (Bel-Venner et al., 2008; Candolin & Salesto, 2009) and minimize the risk of rejection (i.e. 'prudent mate choice'; Venner, Bernstein, Dray, & Bel-Venner, 2010). Fourth, males evaluating key aspects of female reproductive value (fecundity and sperm competition risk: Hoefler, 2007; Hoysak & Godin, 2007; Preston et al., 2005; Reading & Backwell, 2007; Xu & Wang, 2009) may resolve these preferences in complex ways under natural conditions that are difficult to mimic in the laboratory. Previous studies have found support for male mate choice in the field for either females with low risk of sperm competition (Herberstein, Schneider, & Elgar, 2002; Jeswiet et al., 2011; Schulte, Uhl, & Schneider, 2010) or for larger females (Barry, 2010; Bel-Venner et al., 2008; Foote, 1988; Maxwell, Barry, et al., 2010; Maxwell, Gallego, & Barry, 2010). However, male choice for multiple criteria has only been found once, in a sexually cannibalistic mantid in which males prefer virgin over mated females, and among virgins, prefer those that are well-fed (Lelito & Brown, 2008).

One possible outcome of male mate choice is sexual selection on females (Clutton-Brock, 2007), particularly for traits that indicate fecundity. Under sex-role reversal, strong mate preferences have been linked to female ornamentation (Rosenqvist & Berglund, 2011) and traits that exaggerate body size (Funk & Tallamy, 2000). However, it is less clear whether male choice can be sufficiently strong or consistent under conventional sex roles (i.e. choosy females, competitive males) to impose selection on females. When operational sex roles are male biased, and males are both choosy and competitive, the risk of sperm competition may drive male choice more than fecundity selection, and so mating biases in nature may not be easily predictable and not consistently linked to female phenotypes. For this reason theory suggests male choice may be variable in nature (Edward & Chapman, 2011) and, therefore, unlikely to impose selection on females. Determining the net effect of male preferences on sexual selection requires simultaneous analysis of variable female fecundity and sperm competition risk, but only a handful of preference studies have tested both aspects of female value together (Callander, Backwell, & Jennions, 2012; Jeswiet, Lee-Jenkins, & Godin, 2012; Lelito & Brown, 2008).

Here we report field experiments examining male mate choice in response to simultaneous manipulations of two predictors of female reproductive value (mating status and size). Using populations of *Latrodectus hesperus* (the western black widow spider), we assessed the attraction of laboratory-reared males in a field enclosure and free-ranging wild males to females that varied in size (fecundity) and mating status (risk of sperm competition). Mating decreases female reproductive value because of decreased confidence of paternity, and perhaps also because of decreased female receptivity and/or increased aggression towards courting males (Andrade, 1996; Contreras-Garduno, Peretti, & Cordoba-Aguilar, 2006; e.g. Schulte et al., 2010). Here we assume sperm competition is the main cost of choosing a previously mated female *L. hesperus*, as no studies to date have tested these other potential costs. As with many web-building spiders, nomadic adult *L. hesperus* males locate sedentary females using airborne

chemical cues released from females and/or their webs (Kasumovic & Andrade, 2004). *Latrodectus hesperus* is a particularly interesting species in which to investigate choice. This species does not demonstrate the ritualized sexual cannibalism seen in other black widow species (Ross & Smith, 1979) and is capable of mating multiple times (E. C. MacLeod, personal observation). This may reduce selection pressure on males to express choosiness. Consistent with this, males do copulate with previously mated females, which are assumed to have higher sperm competition risk, in the laboratory and in the field (where 12–27% of females mate with multiple males; MacLeod & Andrade, 2013). However, we predicted that *L. hesperus* males would be choosy in nature because (1) male mating opportunities may be limited by risky mate searching (as seen in a congener: Andrade, 1996, 2003) and energy- and time-intensive courtship (Ross and Smith 1979), although males are capable of inseminating multiple females (Ross & Smith, 1979), (2) virgin females are reproductively valuable because of first-male sperm precedence (Kaston, 1970; MacLeod & Andrade, 2013) mediated by mating plugs (Foellmer, 2008; Snow & Andrade, 2005; Uhl, Nessler, & Schneider, 2010), (3) larger females are more fecund. Like other animals, poorly fed females tend to be small and of relatively low fecundity (Drapela, Frank, Heer, Moser, & Zaller, 2011; Head, 1995; Uhl, Schmitt, Schafer, & Blanckenhorn, 2004), and in *L. hesperus*, these females are also more likely to attack courting males (Johnson, Trubl, Blackmore, & Miles, 2011). In addition to mate location, chemical cues may also mediate assessment of female reproductive value in *L. hesperus*. Male *L. hesperus* are more responsive to web-based pheromones and cues produced by fed compared to unfed females in the laboratory (Baruffaldi & Andrade, n.d.; Johnson et al., 2011), even though pheromones allow males to detect both types of females (Baruffaldi & Andrade, n.d.). Research on congeners also found that males are able to discriminate mated from virgin females (Andrade & Kasumovic, 2005; Stoltz, McNeil, & Andrade, 2007), although older mated females trigger a stronger male response than recently mated females (Perampaladas, Stoltz, & Andrade, 2008). It is unclear whether males can use chemical cues to discriminate mating status in *L. hesperus*. Given that 12–27% of field-collected females show evidence of polyandry (MacLeod & Andrade, 2013) and males readily court mated females after contacting their webs in the laboratory (E. C. MacLeod, personal observation), it is likely that males can use pheromones to detect once-mated females as well as virgins. If airborne chemical cues provide similar information, males may be able to simultaneously evaluate mating status (sperm competition risk) and body size (fecundity) of multiple potential mates at a distance, which would increase the likelihood of male mate choice.

METHODS

We used two 2×2 choice experiments that crossed female mating status (mated/virgin) and diet (fed/unfed) to determine patterns of male discrimination among females in the field. We ran experiments in two contexts to examine the persistence of male preference when costs to choice were unrestricted (free-ranging males) or reduced (in field enclosures). Costs of choice were expected to be higher on average for free-ranging males compared to males released in an enclosure because free-ranging males would have (1) an increased risk of being exposed to predators (see below), (2) a longer average distance to travel to reach experimental females and (3) a wider (and likely lower) range of initial energy reserves. While we do not expect males to make a priori assessments of these differences in cost, mechanistic responses to these different conditions may be expected to alter the economics of choice and thus alter male decisions.

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