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Contact pheromones mediate male preference in black widow spiders: avoidance of hungry sexual cannibals?

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Males often exercise mate choice when mating frequency is constrained, costs of choice are low and variation in female quality and/or expected paternity can be reliably detected. Across invertebrates, males use sex pheromones to discern female mating status, but there are few demonstrations that information about expected fecundity ('quality') is encoded in pheromones alone. Here we examine whether females' sex pheromones allow males to detect differences in female food intake and mass in two species of widow spiders (*Latrodectus hesperus* and *Latrodectus hasselti*) in which chemicals are deposited by females in silk. Recent work shows that male *L. hesperus* prefer well-fed females, and that these females produce more silk than hungry females. Thus, changes in diet could be mechanistically linked to changes in silk-bound pheromonal signals. We show that unmated females of both species lose more than half of their mass when food is withheld, and silk production is reduced by 48% (*L. hesperus*) to 67% (*L. hasselti*). Males had a significant sexual response to pheromones extracted from the females' silk in both species, although this response was not directly correlated with silk or female mass. In *L. hesperus*, but not in *L. hasselti*, males were less responsive to sex pheromones from food-deprived females compared to well-fed females. While females on good diets provide the benefit of higher fecundity in both species, the risk of being cannibalized by hungry females during courtship exists only in *L. hesperus*. We conclude that sex pheromones alone can provide information about recent female feeding history, possibly reducing the costs of males expressing choice in the field. The species difference in male response also suggests that male preferences in these spiders may depend less on the benefit of seeking a highly fecund female and more on avoiding the cost of risky mating attempts with a likely cannibal.

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A variety of studies now show that male mate choice often co-occurs with intermale competition in species where females invest more in offspring than do males (reviewed in: Bonduriansky, 2001; Edward & Chapman, 2011). As with female choice, the evolution and maintenance of male mate choice is more likely when variation in mate quality is high, the cost of being choosy is low, and when investment in each reproductive opportunity, whether this is via mating effort (investment in securing copulations/fertilizations) or paternal effort (investment in offspring), is sufficient to limit mating frequency (Bonduriansky, 2001; Edward & Chapman, 2011; Jennions & Petrie, 2000). However, mate choice may differ between the sexes in ways that could have important implications for the evolution of choosy males. Mate choice critically depends on the ability to discriminate the relative value of a potential partner, and there may be sex differences in the availability of reliable cues of mate quality. For choosy females, discrimination is often facilitated by ornaments or displays that correlate with male traits and evolve through sexual selection on competing males (Candolin, 2003). In contrast, sexual selection on females is typically weak (Andersson, 1994), so choosy males will often need to discriminate among females for which natural selection tends to favour crypsis over display (Arnqvist & Rowe, 2005). If cues related to female quality are readily discriminable, the cost of being choosy will decrease and the potential fitness benefits required for choice to be a viable tactic will also decrease. Thus, the conditions under which we expect to find male mate choice in nature can be quite variable, and understanding male mate choice requires not only identifying the particular qualities preferred by males (male preferences, Jennions

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& Petrie, 2000), but also which cues males may use to accurately identify preferred females.

Although confidence of paternity is clearly critical for choosy males (reviewed in Edward & Chapman, 2011), male fitness is also limited by the reproductive potential ('quality') of his mates. Considerable theoretical and empirical work confirms that, in terms of male preferences, the most relevant aspect of female quality across taxa is fecundity (or fertility, Bonduriansky, 2001; Edward & Chapman, 2011). At a given risk of sperm competition, the benefits of having a highly fecund mate may be sufficient to favour choice, particularly if being choosy does not in itself cause significant additional restrictions on mating frequency in nature (Edward & Chapman, 2011). Ovum production (maximum fecundity) is often positively correlated with female body mass or size (e.g. amphibians: Verrell, 1985; fish: Kraak & Bakker, 1998; invertebrates: Danielson-Francois, Fetterer, & Smallwood, 2002; Harari, Zahavi, & Thiery, 2011; Johnson, Miles, Trubl, & Hagenmaier, 2014; Lelito & Brown, 2008). Moreover, body mass or size may reflect recent food intake, which can affect the likelihood and timing of reproduction (realized fecundity), with poorly fed females delaying egg laying (Stoltz, Hanna, & Andrade, 2010). While mass, size, and even mating status could be assessed visually in some taxa (e.g. Maxwell, Barry, & Johns, 2010; Maxwell, Gallego, & Barry, 2010), in many others this is not possible and this information would have to be gleaned from alternative modalities (e.g. Allen, Barry, & Holwell, 2012). For example, chemical signals or cues can allow males to assess female fecundity and mating status (e.g. Barry, 2010; Chinta et al., 2010; Foster & Johnson, 2011; Harari et al., 2011; Lelito & Brown, 2008; Maxwell, Gallego, et al., 2010; Prouvost, Trabalon, Papke, & Schulz, 1999) or receptivity (Maxwell, Barry, et al., 2010), and this assessment may be accomplished at a distance, allowing males to assess females prior to heavy investment in courtship (Barry, 2010; Harari et al., 2011; Johansson & Jones, 2007; Maxwell, Barry, et al., 2010; Maxwell, Gallego, et al., 2010; Thomas, 2011), thus significantly reducing the cost of choice. Chemical communication is common in invertebrates, so male mate choice could be widespread if female fecundity and mating status are commonly encoded in sex pheromones, and if male preferences (Jennions & Petrie, 2000) are based on this information (e.g. Gaskett, 2007; Johansson & Jones, 2007; Thomas, 2011). If so, given their diversity, invertebrates may be particularly interesting models for assessing male mate preferences, and for testing general theory regarding the evolution and maintenance of male mate choice.

Here we focus on male assessment of female feeding history, examining whether sex pheromones alone permit male discrimination of mates in two species of 'widow' spiders (*Latrodectus hesperus* and *Latrodectus hasselti*, Araneae: Theridiidae), and consider whether patterns of discrimination can suggest the underlying traits that determine male preferences in these species. In spiders, male choice may be beneficial because mating frequency can be limited by male exposure to high predation risk during mate searching (e.g. *Latrodectus*: Andrade, 2003; Segoli, Arieli, Sierwald, Harari, & Lubin, 2008; *Nephila*: Kasumovic, Matthew, Herberstein, & Andrade, 2007) and courtship (e.g. *Argiope*; Herberstein, Schneider, & Elgar, 2002), in addition to which mating often includes the risk of sexual cannibalism (Huber, 2005). Mate discrimination may be possible in spiders because females produce sex pheromones on their bodies or silk, and these can be used by males to localize potential mates, to trigger courtship and to assess female phenotypes and mating status (Baruffaldi & Costa, 2010, 2014; Gaskett, 2007; Uhl & Elias, 2011). Males of many spider species show variation in courtship intensity in response to silk threads and/or silk extracts of females that vary in mating status (Baruffaldi & Costa, 2010, 2014; Gaskett, Herberstein, Downes, & Elgar, 2004; Roberts & Uetz, 2005; Rypstra, Wieg, Walker, & Persons, 2003; Stoltz, McNeil, & Andrade, 2007). However, most tests for cues of female fecundity and recent feeding history have used the female, her silk, or both to test male responses (e.g. Johnson, Trubl, Blackmore, & Miles, 2011; MacLeod & Andrade, 2014; Schulte, Uhl, & Schneider, 2010). Here we focus on establishing a causal link between male behaviour and pheromonal cues of fecundity or size by manipulating female diet and assaying male responses to silk extracts in the absence of other types of information (see Gaskett, 2007; Schulz, 2013). Responses to sex pheromones are a commonly used proxy for mate preference since such responses mediate mate attraction, courtship and coupling in nature in many invertebrates (Johansson & Jones, 2007; Thomas, 2011).

In recent studies conducted in western black widow spiders (*L. hesperus*) males were found to adjust their mating effort based on web-borne cues of female feeding history (in the laboratory, Johnson et al., 2011), and were preferentially attracted to females and their webs if those females are well fed and unmated (in the field, MacLeod & Andrade, 2014). This shows that males are choosy in nature (MacLeod & Andrade, 2014); that is, they act on preferences in the presence of natural costs (e.g. Jennions & Petrie, 2000). This also suggests that male preferences for heavier females could be mediated by chemical cues. However, in both studies, other cues in addition to chemicals from the silk were present (bodies of prey, and females), leaving it unclear whether chemical cues were responsible for male choice. Here we asked how female mass and silk production is affected by diet, and whether males discriminate between well-fed and poorly fed females based on silk-borne chemical cues (sex pheromones) alone. There are mechanistic links between diet and silk production in *L. hesperus* that may facilitate such discrimination; well-fed females produce more silk and alter the structure of the web relative to starved females (Blackledge & Zevenbergen, 2007). Thus, hungry females may produce less pheromone-laden silk than well-fed females. We also assess whether there is a link between diet and silk volume in *L. hasselti*, a congener in which this has not previously been examined. This is a first step toward asking whether this is a genus-wide response by females to variable food intake.

Male spiders may also be choosy because of the risk of being attacked and consumed by females, and this is particularly true when cannibalistic females typically attack males that are courting ('precopulatory sexual cannibalism', Elgar, 1992, 1998; Elgar & Schneider, 2004; Herberstein et al., 2002; Huber, 2005). In this case, selection to detect and avoid females with a high propensity to cannibalize should be strong (e.g. Johnson et al., 2011; Maxwell, Barry, et al., 2010). This is consistent with patterns of male preference for satiated females reported for praying mantids where the risk of precopulatory cannibalism is high, particularly when females are poorly fed (Lelito & Brown, 2006, 2008; Liske & Davis, 1987). This prediction, however, is not as strong if cannibalism occurs during or after mating and cannibalized males transfer sperm successfully. In this case cannibalized males can still accrue paternity, and in some species, actually have higher paternity than males that are not cannibalized (e.g. *Latrodectus*: Andrade, 1996; *Argiope*: Schneider, Gilberg, Fromhage, & Uhl, 2006).

We were particularly interested in whether male preference for well-fed females (Johnson et al., 2011; MacLeod & Andrade, 2014) is more likely explained by the fecundity benefits of mating with these females, or by the costly risk of being cannibalized by poorly fed females. These hypotheses are not exclusive, and disentangling these possible fitness benefits is challenging. We approached this puzzle by considering how cannibalism and fecundity benefits might affect the maintenance of male preferences in *L. hesperus* and *L. hasselti*. Although sexual cannibalism occurs during courtship

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