



Courtship and male ornaments as honest indicators of immune function



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Having an effective immune system can be very costly, sometimes at the expense of other important life history traits, including reproduction. This trade-off can be exaggerated in males of species that have costly sexual signalling, where condition-dependent components of the signalling system reflect the health status of the bearer. It is therefore vital for a male to be able to adequately balance the costs of activating the immune system successfully while also expressing high-quality sexual signals. We examined males of the brush-legged wolf spider *Schizocosa ocreata* to see whether static condition-dependent components of sexual signalling in adult males are indicative of health status (immune stress response, encapsulation) and whether female preference for these traits is influenced by infection. After experimental ingestion of a bacterial pathogen (*Pseudomonas aeruginosa*), symmetry of male foreleg tuft (a secondary sexual trait) was found to predict the intensity of the subsequent infection, such that males with more asymmetrical tufts had higher levels of bacteria in the haemolymph. Females were equally likely to mate with infected and uninfected males in mating trials, but females that mated with infected males had bacteria in their haemolymph and on their body surface. Males that engaged in courtship had significantly lower encapsulation responses than males that did not engage in courtship, but among those males that courted, larger tuft size indicated a higher encapsulation response even after energetically costly courtship. These results indicate that females may be able to use static sexual signalling traits to examine a male's overall health, but females do not appear to discriminate against males who are actively infected, even though there is a direct cost to the female via the transfer of male infection.

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Organisms across all taxa must cope with assault from a variety of parasites and pathogens. While it is advantageous for an individual to have a broadly effective immune system, there is often a complex balance between the ability to successfully execute an immune response and simultaneously express costly sexually selected traits, such as male secondary sexual characters. A broad generalization of the immunocompetence handicap hypothesis (ICHH) predicts that only high-quality males will be able to allocate resources to both immune system activation and the development of these condition-dependent traits (Folstad & Karter, 1992; Simmons, 2011). These types of sexual traits are therefore thought to enforce signalling honesty, since low-quality males cannot withstand the costs of both mounting an immune response and investing resources into sexual signalling (Folstad & Karter, 1992; Grafen, 1990; Zahavi, 1975). Consequently, females that

select males with more exaggerated signalling traits may receive indirect fitness benefits via successful offspring (Sheldon & Verhulst, 1996; Westneat & Birkhead, 1998). While there is evidence that females gain indirect fitness benefits by selecting for a trait that indicates heritable immunocompetence (Cotter & Wilson, 2002; Fellowes, Kraaijeveld, & Godfray, 1998; Ryder & Siva-Jothy, 2001), there may also exist direct benefits to the female as well. If a condition-dependent trait is indicative of an individual's immune capacity, then it could signal a male's current state of infection, such that a female may be able to avoid an infected male and hence the risk of infection (Able, 1996; Houde & Torio, 1992; Loehle, 1997; Milinski & Bakker, 1990).

Many studies in both vertebrates (Duffy & Ball, 2002; Garvin, Dunn, Whittingham, Steeber, & Hasselquist, 2007; Griggio, Zanollo, & Hoi, 2009; López & Martín, 2005; Møller, 2002; Mougeot, 2008) and invertebrates (Ahtiainen, 2004; Lawniczak et al., 2007; Rantala, Jokinen, Kortet, Vainikka, & Suhonen, 2002; Ryder & Siva-Jothy, 2000; Simmons, Zuk, & Rotenberry, 2005) have found a positive correlation between sexually selected traits and some aspect of immune function, suggesting that female mate

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preference may be acting as a selective pressure that influences the ability of males to withstand such trade-offs between sexual signalling and immunity. However, some species have sexual displays that are complex, sometimes consisting of multiple signalling modalities that may each reflect different types of information (Candolin, 2003; Johnstone, 1996; Møller & Pomiankowski, 1993). In some cases, static (fixed) and dynamic traits may correlate with separate aspects of male quality (Møller & Pomiankowski, 1993). While each signal may convey information on different temporal aspects of male condition, all traits combined should be expected to reflect overall male quality, since females would be receiving a more complete assessment of males rather than just relying on a single trait (Doucet, 2003; Loyau, Saint Jalme, Cagniant, & Sorci, 2005; Martín, Amo, & López, 2008; Møller, 2002).

The brush-legged wolf spider *Schizocosa ocreata* has a multimodal sexual signalling system, with both visual (foreleg ornaments and leg-tapping displays) and vibratory (stridulation and percussion) components. Females prefer males with larger foreleg tufts, greater courtship display rates and higher-amplitude vibratory signals. The foreleg ornaments (tufts of bristles) are fixed at sexual maturity and are indicative of past condition (Uetz, McClintock, Miller, Smith, & Cook, 1996; Uetz, Papke, & Kilinc, 2002; Uetz, Roberts, Wrinn, Polak, & Cameron, 2009) whereas behavioural displays (courtship vigour) are more dynamic and prone to fluctuate with current male condition (Gibson & Uetz, 2012). There is also some evidence in *S. ocreata* that past male condition reflected in these traits may include exposure to parasites and pathogens. Males infected in the laboratory as juveniles had more asymmetrical foreleg tufts at maturity, as well as decreased courtship vigour and lower mating success than control males, indicating that infection is causing some level of developmental stress that results in lower-quality condition-dependent traits (Gilbert, Karp, & Uetz, 2016). Additionally, males infected as juveniles had higher encapsulation rates (one measure of immune function) at maturity than control males, suggesting that resources may be allocated away from investment in sexual signals and into immune function (Gilbert et al., 2016).

While these results suggest that there is some type of life history trade-off occurring in at least one condition-dependent modality expressed by this species, it remains to be examined whether infection as an adult has an impact on male signalling quality and effort. Because foreleg tufts are fixed after moulting to sexual maturity, infection as an adult would be expected to affect only the more dynamic components of the signalling system, such as courtship vigour. As a consequence, females may not be able to assess male infection status as accurately, since it is unlikely that active infection (exposure as an adult) would be reflected in fixed traits (i.e. leg tufts). It is currently unknown whether dynamic signalling modalities can potentially indicate to a female that the male signaller is currently infected. In this study, we examined relationship(s) between immunity and multimodal sexual signalling in several ways: (1) by infecting adult males and looking at the impact of infection on courtship, performance and mating success; (2) by investigating the potential for transfer of infection during copulation to assess the potential fitness consequences of mating with an infected male and (3) by testing whether the expression of an adult indicator trait (foreleg tuft size) is related to immune response (Fig. 1).

METHODS

Study Species and Care

All spiders were captured as juveniles from a deciduous leaf litter forest at the Cincinnati Nature Center (Clermont County, OH,

U.S.A.) in August 2014. Spiders were housed individually in opaque deli dish containers on a 13:11 h light:dark cycle, provided access to water ad libitum and fed on a consistent schedule of two to three crickets (*Acheta domesticus*, approximately 3.2 mm in length) twice per week. Spiders were kept in separate opaque containers except during mating trials. We examined all individuals postmortem for the presence of parasites (nematodes, insect larvae) and excluded infected individuals from our analysis to rule out the possibility of immunosuppression outside of the experimental treatment. All spiders used in the following experiments were 7–12 days postmaturity.

Experimental Infection

Infection methods were modified from Gilbert et al. (2016). One week after moulting to sexual maturity, males were subjected to oral ingestion of the bacterial pathogen *Pseudomonas aeruginosa* (strain PA-14). This pathogen occurs naturally in the environment in which these spiders are found and has been found in the haemolymph of a few individuals at very low levels (Gilbert & Uetz, n.d.). All stocks were kept in Copan Cryovials at -80°C and grown on Luria broth media (1.0% Tryptone, 0.5% yeast extract, 1.0% NaCl, 1.5% agar). All plates containing bacteria were cultured daily approximately 18 h prior to use in the experiments and were discarded within 24 h after culturing. Spiders ($N = 60$) were withheld water for 24 h to encourage complete consumption of a 1 μl droplet of sterile water containing 600 colony forming units (CFUs) of bacteria as determined by McFarland turbidity standards (McFarland, 1907). Any spider not observed drinking the full amount of water was dismissed from further experiments. Control groups ($N = 50$ males) were withheld water for 24 h, then given a 1 μl droplet of sterile water only. Following exposure, spiders were returned to a clean housing container and resumed a normal diet and ad libitum access to water.

Mating Trials

We placed infected males ($N = 20$, within 1 h of infection) and control males ($N = 20$) individually into a round plastic arena (diameter: 15.5 cm, height 7.2 cm) lined with filter paper. After a 2 min acclimation period, we placed a virgin adult female ($N = 40$) in the centre of the arena and allowed each pair 5 min to begin mating. Pairs that did not mate within 5 min were removed from the arenas ($N = 8$). In cases of successful mating ($N = 32$), copulation was allowed to proceed until natural separation of mating pairs (2–10 h).

Courtship vigour and mating success

All behaviour trials were recorded using a Sony camcorder (model HDV-XR260V) and scored blindly at a later date for male courtship displays (leg waves, leg taps, body bounce) to get an approximation of male courtship vigour (number of courtship displays per second) and overall mating success (Delaney, Roberts, & Uetz, 2007; Kaston, 1936; Montgomery, 1903).

Transfer of infection

After allowing mated pairs to separate naturally, we immediately quantified (within 10 min) *P. aeruginosa* CFUs on the body surface and in the haemolymph of surviving (noncannibalized) males ($N = 25$ total, 15 infected and 10 control) and females ($N = 25$ total).

Quantification of bacterial presence

To determine levels of *P. aeruginosa* infection on the body surface and in the haemolymph of treated *S. ocreata* at the conclusion

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