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Diet influences female signal reliability for male mate choice

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Pheromones, arguably the most ubiquitous mode of animal communication, are determined by both genetic and environmental factors. Recent evidence suggests that diet may be an important determinant of pheromone variation, which may both enhance and reduce the reliability of the chemical signal. We investigated experimentally the impact of population origin and diet on chemical signals used in mate assessment by monogynous males of the golden-banded orb web spider, *Argiope trifasciata*. Initial mate preference experiments revealed environmentally determined fine scaling of male mate choice: shortly after their introduction into the laboratory, male spiders preferred females from either their own or a nearby population rather than females from a distant population, suggesting that male choice is driven by phenotype matching, ensuring correct species identity. However, when diet was controlled, males preferred females originating from a distant rather than the same population, allowing males to choose a mate with the most potential genetic benefits. A second set of experiments clearly demonstrated that diet affected the chemical compounds on the surface of the silk threads produced by females, and that males preferred females that had experienced a similar diet. We suggest that phenotype matching strongly influences broad-scale male mating preferences, but it remains to be seen how a combination of genetic and environmental (e.g. dietary) factors influence the relative abundance of these, and perhaps other, mate choice-relevant, silk-bound chemical cues.

Pheromones, chemical signals specifically used to convey information between individuals of the same species, represent arguably the most ubiquitous and ancient mode of animal communication (Bradbury & Vehrencamp, 2011; Wyatt, 2003). Pheromones comprise one or more chemical components, the composition and relative proportions of which are typically species specific and determined by both genetic and environmental factors (Symonds & Elgar, 2008). The latter has important implications for signal reliability (sensu Stevens, 2013): for example, diet affects the composition and thus attractiveness of sex pheromones (Fedina et al., 2012; Rundle, Chenoweth, Doughty, & Blows, 2005), providing a reliable signal of male quality and allowing females to make mating choices that benefit their offspring (Iyengar, Rossini, & Eisner, 2001). Diet similarly affects the cuticular hydrocarbon profile of males, which is used as a reliable signal of quality by female painted crickets, *Gryllodes sigillatus* (Weddle, Mitchell, Bay, Sakaluk, & Hunt, 2012), cockroaches, *Nauphoeta cinerea* (South, House, Moore, Simpson, & Hunt, 2011) and wasps, *Nasonia vitripennis* (Blaul & Ruther, 2011). In these examples, the environmental effects on the signal are directly correlated with the quality of the signaller, but the significance of these effects in the absence of such correlations and their consequences for signal reliability are less widely appreciated (Ingleby, Hunt, & Hosken, 2012).

The role of pheromones in long-range mate attraction and species recognition has been extensively documented, but comparatively less attention has been focused on their involvement in mate choice and sexual selection (Johansson & Jones, 2007). Mate choice may provide the choosing sex with material and genetic benefits (Andersson, 1994), the latter through improved gene combinations (Hettyey et al., 2010; Jennions & Petrie, 2000). These gene combination arguments predict mate choice at the population level (Brown, 1997), in which individuals prefer potential partners from the same or different populations, depending upon the relative benefits of producing genetically diverse progeny (preference for individuals from different populations) or maintaining locally adapted gene combinations

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(preference for individuals from the same population). The reliability of signals that convey information about species identity, mate recognition and mate quality is especially critical in typically monogamous species, for which there are few, if any, opportunities to modify an initial mate choice.

Sit and wait predators, including orb web spiders, are typically opportunistic foragers. In such systems individuals from different populations may have very different diets, depending on the available prey. In cases where pheromone expression is strongly influenced by variation in an individual's diet, this may lead to qualitative differences between populations in pheromone signals (Fornasiero, Dendi, Bresciani, Cecchinelli, & Zuffi, 2011). This could result in individuals discriminating against potential mates from different populations, simply because they are emitting unfamiliar pheromones. Such a scenario would be exacerbated if the selected pheromone acts as a species recognition cue (Johansson & Jones, 2007). For example, theoretically, individuals should benefit from mating with conspecifics from more distant populations as this reduces the potential costs of inbreeding and/or confers indirect benefits through the production of heterozygous offspring (Brown, 1997). However, this scenario requires that individuals from different and particularly distant populations recognize that they are conspecifics, which may not be the case if dietary differences result in (even subtle) changes to pheromones or pheromone blends, resulting in assortative mating between individuals from the same populations in order to avoid the costs of mating with what appear to be heterospecifics (Geiselhardt, Otte, Hilker, & Turlings, 2012).

Male orb web spiders in the genus *Argiope* are typically monogynous, and males are frequently cannibalized after the first insemination and are always cannibalized after the second insemination. Although males that survive the first mating may mate with a second female, most males sire offspring from a single female only (Frornhage, Uhi, & Schneider, 2003; Herberstein, Gaskett, Schneider, Vella, & Elgar, 2005; Schneider & Fromhage, 2010). Judicious mate choice is critically important for monogynous males because their entire reproductive investment rests with a single individual, but it is especially crucial for species in which premating sexual cannibalism occurs, because these males are also at risk of complete reproductive failure (Gaskett, Herberstein, Downes, & Elgar, 2004; Schneider & Fromhage, 2010; Schulte, Uhl, & Schneider, 2010). Accordingly, we expect selection to favour male *Argiope* spiders that can not only accurately discern a high-quality mate but also initially discriminate between the webs of heterospecifics and conspecifics. Mature adult females release volatile sex pheromones (Chinta et al., 2010) that attract both conspecific and heterospecific males (Olive, 1982). Females also deposit contact pheromones onto their web, so initial assessment of a female (species recognition) and her potential value as a mate (mate assessment) should take place at the edge of the web, on the outer silk threads, the safest location for a male as it is the furthest from the potentially cannibalistic female residing in the central hub of the orb.

Female web-based contact pheromones probably provide males with crucial species-specific and possibly individual-quality information about the female. However, environmental variation, such as dietary differences, might interfere with these cues, rendering a male unable to make the 'best choice' regarding his reproductive fitness. Here, we investigated the role of chemical cues in mate assessment by males of the golden-banded orb web spider, *Argiope trifasciata*. Specifically, we addressed three questions: (1) do environmental effects obscure more subtle cues in male choice at the population level; (2) does the surface chemistry of silk threads produced by females change with diet; and (3) are male mating preferences influenced by female diet?

METHODS

Ethical Note

No permits or licences were required for the collection, maintenance or experimentation of animals used in this study. Male and female spiders were collected from wild populations and housed individually in a laboratory environment as described below. No short- or long-term adverse effects were observed from our housing environment, the diet manipulation treatments or to males or females during behavioural assays. Individuals were frozen rather than released after completion of this study as the species is univoltine, and adults would have perished in the wild shortly after release.

We collected juvenile and subadult male and female golden-banded orb web spiders from two sites near Seymour (separated by approximately 5 km) and a third site near Euroa (approximately 49 km from Seymour) in northern Victoria, Australia, during January and February of 2012 and 2013. All spiders were maintained in a climate-controlled laboratory at 24 °C under natural daylight conditions: females were housed in Perspex frames (58.5 × 58.5 cm and 15 cm high) and males in small upturned plastic 200 ml cups (9 cm high). Males and females were fed, each week, two first- and second-instar or three third-instar crickets, *Acheta domestica*, respectively. Unless otherwise stated, all webs were sprayed with a light mist of water twice weekly. We noted the date of the final moult from subadult to sexually mature adult for males and females, and all adults were weighed within 2 days of their final moult.

Male Mate Preference, Female Geographical Origin and Diet

We conducted mate choice bioassays to test whether virgin males distinguish between the silk of virgin females according to their population origin, and whether mate choice can be influenced by diet. Females were placed in clean, individual frames, where they built a web overnight. The female was removed from the web once it had been constructed. Two frames were placed next to one another (approximately 15 cm apart). A support thread from each web was then carefully detached from the side of the frame (ensuring the web remained intact) and wound around the same end of a clean wooden skewer (length 25.5 cm). The skewer was fixed to the bench equidistant between the two frames. A focal male (from the same population as one of the two females) was gently placed at the base of the skewer and allowed to walk up towards the silk support strands. The silk threads from each female web overlapped on the skewer, ensuring the male could touch both before commencing to walk along one of the threads to the web. For each trial, we noted which thread the male traversed.

Each male was tested twice, first with a pair of females that had been collected approximately 3 weeks before from the field (natural diet). We still considered this to be a natural diet background, as males and females had limited exposure to the laboratory environment (and thus constant cricket diet) at this time. It was necessary to wait 3 weeks before commencing mate choice trials to allow males and females to mature. For the second bioassay, each male was tested with a pair of adult females that had been reared on a laboratory, single-prey diet (comprising only *A. domestica* crickets) for a further 5 weeks (average number of days between natural and single-prey diet trials = 35.8 ± 0.9). In both sets of trials the male diet was the same as the female diet, and thus we expected variation in pheromones (either between the sexes or between populations) due to dietary differences would be reduced or now absent. For each trial, males were provided with a choice of silk thread from the web constructed by an adult female from the