



Male mate choice in a sexually cannibalistic widow spider

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Males of the brown widow spider, *Latrodectus geometricus* (Theridiidae), invest energy in courtship displays and are often cannibalized after mating; accordingly, partial sex role reversal is expected. In this species, subadult females are able to mate and produce viable offspring. In contrast to mature females, these subadult females do not cannibalize their mates after copulation. Nevertheless, when given a choice, males preferred mature over subadult females and older over young mature females. We found no benefit for males in mating with the females of their choice. Older females were significantly less fecund than young mature females, and were not more fecund than subadult females. We tested possible advantages in mating with cannibalistic (mature) females, such as an increased probability of plugging the female's genital duct or longer copulations, or disadvantages in mating with subadult females, such as higher remating risk. None of these explanations was supported. Thus, we lack an adaptive explanation for male preference for mature older females. We suggest that older females produce more pheromone to attract males and that males are thus misled into mating with older, more aggressive and less fecund females.

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Both females and males are known to be choosy to different degrees in selecting mates, depending on the species and factors such as the parental investment of each partner (Trivers, 1972), the sex ratio of the available mating partners (Emlen & Oring, 1977) and the variation in quality among available mates (Owens & Thompson, 1994; Parker, 1983).

Even though sexual selection is considered to act more strongly on males, in a variety of taxa there may be a reversed sex role, in which males are choosy and females compete for males (Clutton-Brock, 2009; Eens & Pinxten, 2000), or only partially reversed if males, or both sexes, are selective, but females do not compete for males directly (Edward & Chapman, 2011). For example, Gwynne and Simmons (1990) showed that, when food is scarce, katydid females competed for males and the nutritious spermatophores that they produce. Other notable examples are two wolf spider species, *Allocosa alticeps* and *Allocosa brasiliensis*, in which females actively search for males waiting in their burrows. The females initiate a courtship display at the entrance of the males' burrows and males either accept or reject them (Aisenberg, Costa, González, Postiglioni, & Pérez-Miles, 2010).

Choosy females may gain direct benefits such as paternal care and nutritional nuptial gifts (Lehmann & Lehmann, 2016) and indirectly from 'good genes' (Bertram et al., 2016). Males are expected to benefit from mating selectively if they invest heavily in parental care (Trivers, 1972) or in courtship and mating (Edward & Chapman, 2011; Petrie, 1983; Scharf, Peter, & Martin, 2013), or if female quality varies, such that males are able to distinguish better quality or more fecund females. The benefits for a male of being choosy should outweigh the costs of searching (Edward & Chapman, 2011) and mate assessment (Dewsbury, 1982; Petrie, 1983).

While female preference for males is often based on the male's secondary traits (display and ornaments, Darwin, 1871), in most cases the key factor determining the male's mate choice is the female's potential fecundity (Bonduriansky, 2001; Fitzpatrick, Berglund, & Rosenqvist, 1995). Phenotypic indicators of potential female fecundity (e.g. age, body size, mating status) are often subtle and are assessed by males either directly or by means of pheromones or other cues produced by the females.

Maternal age has been found to influence growth and survival of different fish species, for example. Larvae from older black rockfish, *Sebastes melanops*, grow faster and survive starvation longer than the larvae of younger fish (Berkeley, Chapman, & Sogard, 2004). Larval survival, some disease resistance and larval growth in

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Atlantic cod, *Gadus morhua*, increase with maternal age (Hansen, Puvanendran, & Banger, 2015).

Female age is particularly important for relatively short-lived organisms such as most arthropods. In many arthropods, older females are selected against by males, owing to the negative effect on various traits of the offspring. Maternal age has been found to have a negative effect on egg size in Lepidoptera (Wasserman & Asami, 1985) and in the cockroach *Nauphoeta cinerea* (Moore & Harris, 2003). It also has a negative effect on offspring viability, as in *Drosophila serrata* (Hercus & Hoffmann, 2000), and in the oleander aphid, *Aphis nerii* (Zehnder, Parris, & Hunter, 2007).

In spiders, as in many other taxa, female mating status and pattern of male sperm precedence strongly affect male choice (Bonduriansky, 2001). Studies of male mate choice in spiders have found that males favour virgin females, in an attempt to avoid sperm competition. A few of the many examples are St Andrew's cross spider, *Argiope keyserlingi* (Herberstein, Schneider, & Elgar, 2002), the wasp spider, *Argiope bruennichi* (Schulte, Uhl, & Schneider, 2010) and the widow spider, *Latrodectus hesperus* (MacLeod & Andrade, 2014). The first male to mate may avoid sperm competition by plugging the female's genital duct and preventing access by additional males. Plugs are often formed by males adding secretory substances into or over the female's genital opening after sperm transfer (Parker, 1998), but can also be devised by males leaving copulatory organs that break off partly or completely during copulation in the genital duct of the female. Plugging this duct with part of the copulatory organ is common among widow spiders, for example *Latrodectus curacaviensis* (Bhatnagar & Rempel, 1962), *Latrodectus mactans* (Abalos & Baez, 1963) and *Latrodectus revivens* (Berendonck & Greven, 2002), and occurs also in other spider genera, for example *A. bruennichi* (Nessler, Uhl, & Schneider, 2006) and the nephilid spider *Herennia multipuncta* (Kuntner, Kralj-Fiser, Schneider, & Li, 2008).

Mate choice critically depends on the ability to discriminate between qualities of potential mates. Chemical signalling is a common mode of intersexual communication in many arthropod taxa, which can be used as a means of assessing a mate, as well as being a common form of long-distance sex attractant (Roelofs, 1995; Wyatt, 2003). In many spider species, the female remains in her web while adult males travel in search of mates, while females may communicate with potential mates over long distances. These chemical signals (pheromones) pass through a noisy chemical background, and are often complex and species specific. Males discriminate between virgin and mated females by means of pheromones deposited on the web, on dragline silk or on the female's body surface (Anava & Lubin, 1993; Herberstein et al., 2002; Papke, Riechert, & Schulz, 2001; Perampaladas, Stoltz, & Andrade, 2008; Riechert & Singer, 1995; Roberts & Uetz, 2005; Stoltz, McNeil, & Andrade, 2007). Discrimination may result from quantitative or qualitative differences in pheromones produced by females based on their mating status (Papke et al., 2001; Riechert & Singer, 1995; Stoltz et al., 2007) or postmating inhibition of pheromone production by females (Perampaladas et al., 2008; Riechert & Singer, 1995; Stoltz et al., 2007). For example, male redback spiders, *Latrodectus hasseltii*, were more active on extracts from webs of virgin females than on extracts from webs of just-mated females. Moreover, males were less active on extracts from webs of just-mated females than on extracts from webs of the same females 3 months after they had mated (Perampaladas et al., 2008). Male *L. hesperus* respond differently to silk-borne pheromones extracted from webs of females depending on whether they were well or poorly fed. This may indicate quantitative or qualitative differences in pheromones produced by females, based on their nutrient status, maybe affecting their fecundity (Baruffaldi & Andrade, 2015).

Mate search can be risky and energetically costly. For example, after their final moult vagabond males of many spiders do not catch prey, but rely on nutrients stored as juveniles (Foelix, 2011), increasing the cost of energy depletion and mortality due to exhaustion (Kasumovic, Bruce, Herberstein, & Andrade, 2006). In addition, mortality rates, due to predation of actively searching males, can be relatively high (Kasumovic et al., 2006). Therefore, even though male choosiness decreases the probability of mating with inappropriate females, it is also likely to increase searching time, and thereby male mortality rate (Kasumovic et al., 2006). Accordingly, males are expected to discriminate a female's quality from a distance (Stoltz et al., 2007).

Another reason to be choosy is the risk of sexual cannibalism. This is a widely documented phenomenon in spiders (Prenter, MacNeil, & Elwood, 2006), occurring in many genera, including widow spiders (*Latrodectus*, Theridiidae; Andrade, 1996; Biaggio, Sandomirsky, Lubin, Harari, & Andrade, 2016; Harari, Ziv, & Lubin, 2009; Segoli, Arieli, Sierwald, Harari, & Lubin, 2008). In some species, cannibalized males contribute to female reproductive success (e.g. in the fishing spider, *Dolomedes triton*; Johnson, 2001), but this may not be the case generally (Fromhage, Uhl, & Schneider, 2003). The small size of *Latrodectus* males relative to females suggests that they do not provide nutritious benefit to the female; therefore, the parental investment by which the male provides himself as nutrition for the female seems unlikely (Andrade, 1996; Segoli et al., 2008). Male *L. hasseltii* show a somersault behaviour, in which the male places the dorsal surface of his abdomen onto the female's mouthparts during copulation; sexual cannibalism in this species prolongs copulation duration, thereby enabling the male to fertilize more eggs (Andrade, 1996). Similar self-sacrifice behaviour occurs in the brown widow spider, *Latrodectus geometricus* (Biaggio et al., 2016; Segoli et al., 2008). Male *L. geometricus* invest time and energy when courting adult females (Harari et al., 2009; Segoli et al., 2008). Courting activities include vibrating, and removing portions of, the female's web, followed by contact courtship that involves adding threads around the female and vibrating on her (Biaggio et al., 2016; Harari et al., 2009; Knoflach & Van Harten, 2002; Segoli et al., 2008). However, males of both species can also mate with subadult females (females in their final juvenile instar), resulting in the production of viable eggsacs following the females' final moult to adulthood. Courting display towards subadult females is significantly shorter than with adult females; the males do not somersault and are rarely (if ever) cannibalized (Biaggio et al., 2016), and consequently may survive to mate again with another female.

Here we hypothesized that males of *L. geometricus*, when given the choice, would prefer to court and mate with subadult females based on the notable benefits they can obtain. To test this hypothesis, we assessed the courting effort and survival outcome of males introduced to females that varied in their age and reproductive status and tested male mate choice accordingly.

METHODS

Natural History and Mating Behaviour

Latrodectus geometricus (Theridiidae) has a worldwide distribution, found mainly in drier and warmer regions (Garb, Gonzalez, & Gillespie, 2004; Knoflach & Van Harten, 2002; Levy & Amitai, 1983), and is associated with human habitats. Like other species of the genus, it is characterized by an extreme female-biased sexual size dimorphism (Knoflach & Van Harten, 2002; Segoli et al., 2008). Mated females can produce an eggsac as early as 1 week after mating, and multiple eggsacs over their lifetime; spiderlings emerge several weeks after oviposition.

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