The role of male body size in mating success and male–male competition in a false widow spider

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In many animals, body size is correlated with reproductive success. Selection sometimes generates striking differences in body size between males and females (i.e. sexual size dimorphism, SSD). SSD is common in spiders (Araneae), and is typically explained by selection for larger, more fecund females and rapidly maturing, and consequently smaller, males. Within a species males and females also often vary in body size. In the false widow spider, *Steatoda grossa*, females are larger than males and males trade body size for rapid development and early maturation. Moreover, males vary considerably in body size, suggesting that under certain conditions there may be advantages to large size. Here, we tested the role of male body size on mating success under noncompetitive and competitive mating conditions (i.e. male–male competition) in *S. grossa*. We found that body size did not influence mating success or copulation duration under noncompetitive conditions, but that larger males were more successful at obtaining access to females under competitive mating conditions. Additionally, we found that total copulation duration was significantly lower when a rival male was present. Our results show a large male advantage under male–male competition, which we suggest may contribute to the high variation in male body size observed in *S. grossa*. We further suggest that the reduced copulation duration observed under competitive mating conditions may have potential ramifications for male and female reproductive success and we discuss how patterns of selection acting on male body size might limit the extent of SSD in this species.

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Body size is a key phenotypic trait influencing mating and reproductive success in many animal species (Andersson, 1994; Andersson & Iwasa, 1996). For females, larger body size is often positively correlated with the number of eggs a female is able to produce or the size of the eggs she produces, and thus larger females enjoy a fecundity advantage (Head, 1995; Honěk, 1993; Roff, 1993; Shine, 1988). In contrast, larger male body size is frequently attributed to sexual selection (i.e. selection arising from differences in reproductive success resulting from the competition for access to gametes for fertilization; Andersson, 1994; Shuker & Kvarnemo, 2021). For example, larger males may gain greater mating success because they outcompete smaller males during direct male–male contests for access to females (Arnott & Elwood, 2009). Larger males may also have higher fitness because they are more successful at defending females or resources important for reproduction (Moore et al., 2009; Shuster & Wade, 2019), because females prefer larger males (Charlton et al., 2007; Lank & Smith, 1992) or because large male body size is positively correlated with endurance and thus the amount of time invested in gaining matings (Ospina-L. et al., 2017). Alternatively, selection may favour a smaller body size if small males have greater success in scramble competition for mates because they are more mobile, more agile or can maintain longer search times due to higher energy efficiency (Blanckenhorn et al., 1995; Crompton et al., 2003; Kelly, 2020).

At the same time, male body size may be constrained by trade-offs with other traits that contribute to fitness. One such trade-off is that between size at maturity and the time taken to reach sexual maturity (i.e. development time): larger body sizes can be obtained

by extending the period of growth (Blueweiss et al., 1978). However, longer development times can also incur costs, such as an increased risk of predation or parasitism (Benrey & Denno, 1997; Blanckenhorn, 2000; Fordyce & Shapiro, 2003; Stamps, 2007; Uesugi, 2015). Male body size may also be linked to survival in some animal taxa (Alcock, 1996). For example, larger individuals may be more susceptible to predation if they are less agile or manoeuvrable, they are more visible to predators (le Roux et al., 2019) or they face increased mortality risk if they require more food and resources are limited (Blanckenhorn, 2000). Thus, body size can impact fitness in a variety of ways.

Understanding how selection acts on body size has been of particular interest in animals exhibiting sexual size dimorphism (SSD). SSD is a common phenomenon in the animal kingdom, but in some taxa the size difference between males and females can be extreme. Such extreme SSD (ESSD) is prevalent in many spider families, where females are much larger than males (Head, 1995; Vollrath & Parker, 1992). ESSD may be the result of selection for larger and more fecund females, selection for reduced male size or a combination of the two (Coddington et al., 1997; Head, 1995; Prenter et al., 1999; Uhl et al., 2004; Vollrath & Parker, 1992). At the same time, male–male competition over access to females appears to be an important driver of large body size in many spiders (reviewed in Elgar, 1998). Several studies have shown that large males usually outcompete smaller males during direct contests or that larger males can occupy a favourable position on the female's web and prevent smaller rivals from accessing the female (Dodson & Schwaab, 2001; Foellmer & Fairbairn, 2005; Golobinek et al., 2021; Hoefler, 2007; Maklakov et al., 2004; Rittschof, 2010; Schmitt et al., 1992). Importantly, however, the advantages of large body size for male mating success may be influenced by variation in the local operational sex ratio (OSR) (Dodson et al., 2015; Vollrath & Parker, 1992). For example, at increasingly male-biased OSR, the form of male–male competition can switch from interference competition to scramble competition (Weir et al., 2011). Under scramble competition, small male size may be advantageous. For example, small males may be better able to locate receptive females because they mature sooner (i.e. selection for protandry, Danielson-François et al., 2012), or because they are better able to climb (i.e. gravity hypothesis, Moya-Laraño et al., 2002) or disperse (i.e. bridging gravity hypothesis, Corcobado et al., 2010). Additionally, it has been posited that small body size may be favoured because smaller males are better able to avoid sexual cannibalism or because they have lower metabolic requirements enabling them to spend more time and energy searching for females (Foellmer & Moya-Larano, 2007). Thus, selective pressures acting on male body size in spiders may be complex. Yet, compared to many other taxonomic groups (e.g. insects, fish, anurans, mammals), the role of male body size in mating success remains relatively unexplored in spiders (see Andersson, 1994).

In this study we investigated the potential role of male body size in determining mating success and copulation duration in a false widow spider, Steatoda grossa (Araneae: Theridiidae). This is a synanthropic, cosmopolitan species that is frequently found living in buildings and in close association with humans, and it reproduces year round (Nentwig et al., 2022). Female S. grossa appear to be sedentary, living and reproducing in their cobwebs, as is common in many comb-footed spiders (family Theridiidae; Knoflach, 2004). Webs of adult virgin females disseminate a sex pheromone that attracts adult males (Scott et al., 2018), and females show a preference for building webs in sites that already contain cobwebs of conspecifics, perhaps as this indicates microhabitat suitability (Fischer et al., 2019). In contrast to females, male S. grossa appear to be relatively more mobile and spend their time actively searching for females. Importantly, S. grossa exhibits

pronounced SSD, with adult female body mass being 5–10 times greater than adult male body mass (Harvey, 2022; Wilczek et al., 2017). As in other spider taxa, the pronounced SSD observed in S. grossa indicates a fitness advantage for large female size and small male size (Foellmer & Moya-Larano, 2007). Indeed, SSD in S. grossa may be, at least in part, due to fecundity selection in females and selection for early maturation in males (i.e. protandry) resulting in reduced male body size, as is postulated for other spider taxa (Prenter et al., 1999; Vollrath & Parker, 1992). Males of S. grossa indeed mature earlier than females, and rapid development time trades off against size at maturity, resulting in small male body sizes of typically less than 15 mg (Harvey, 2022). In that study, small male size was argued to be favoured due to reduced predation risk and earlier access to females, and it was suggested that rapid development is more important than larger male body size in this species (Harvey, 2022). Yet, despite the apparent importance of rapid development and early maturation for male S. grossa, male body size is highly variable in this species (Fischer et al., 2020; Harvey, 2022). For example, male body mass varies with food availability: mature virgin males weigh 7–35 mg (Harvey, 2022). Moreover, male body mass varies considerably even when males are raised under identical conditions in the laboratory (see Appendix and Figs A1, A2).

Given selection for rapid maturation, the observed variation in male body size is surprising and suggests that additional selection pressures may be acting on male size, or alternatively that selection on body size is lacking, in this species. We therefore examined the potential role of body size in male mating success and copulation duration. Specifically, we tested for an association between male body size and both mating success and copulation duration under noncompetitive and competitive mating conditions. Given the lack of information on the mating system of this species, we have refrained from making specific predictions concerning the potential role of male body size in mating success when matings occur under noncompetitive conditions. In contrast, given the prevalence of large male advantage under male–male competition (Hoefler, 2007; Rittschof, 2010), we predicted that male body size may influence mating success under competitive mating conditions. Specifically, we predicted that large males would outcompete small males and thus gain the greater share of mating opportunities.

METHODS

Spider Collection and Maintenance

Several hundred juvenile and adult male and female spiders were collected from the buildings and grounds of Wageningen University & Research (51.9863°N, 5.6680°E) and the Netherlands Institute of Ecology (51.9876°N, 5.6706°E) in Wageningen, The Netherlands, during 2019 and 2020. All field-collected juvenile spiders were reared in the laboratory in petri dishes (8 cm diameter) until their final moult. Upon reaching adulthood, males were transferred to individual petri dishes, while females, which are several times larger, were transferred to individual plastic boxes (11 × 11 cm and 6 cm high). These adults were then mated to produce an F1 laboratory cohort. Matings were established by placing a male in a female's home container, and pairs were created using individuals from different locations to minimize the chance of inbreeding. Mated females typically produced an egg sac approximately 2–3 weeks after mating. In addition, some field-collected female spiders produced egg sacs. Egg sacs from both the field-collected females and the laboratory crosses were transferred into individual petri dishes (8 cm diameter) until hatching (ca. 30–40 days later). After hatching, spiderlings were separated into individual petri dishes (8 cm diameter) with a damp cotton ball (ca.

1 cm diameter). The spiderlings were provided with two to three freshly killed (by freezing) fruit flies (*Drosophila melanogaster*) once every 1—2 weeks, then after two to three moults, they were given five to six freshly killed *Drosophila hydei* fruit flies (which are larger than *D. melanogaster*) every 1—2 weeks. Once spiderlings had moulted to L3, they received one small house cricket, *Acheta domestica*, nymph every 1—2 weeks. Fruit flies and crickets were obtained from commercial retailers. Finally, when females reached adulthood, they were transferred to individual plastic boxes, where they constructed a web, and were provided with one late-instar *A. domestica* nymph weekly. In contrast, males remained in their individual petri dishes and, because adult males eat little food, were only provided with live *D. hydei* flies once every 2 weeks. Adult males and females were subsequently used for the mating experiments (described below). All spiders were maintained at 22 ± 2 °C, 16:8 h light:dark cycle with 50% relative humidity.

Mating Experiments

We performed mating trials under two conditions: (1) a noncompetitive mating scenario (i.e. one male/one female, $N = 47$) and (2) a competitive mating scenario (i.e. two males/one female, $N = 34$). All mating trials were conducted with virgin males and females that had moulted to adulthood 2—4 weeks prior to the experiment. Mating trials were performed in the female's housing container after ensuring that the female had successfully constructed a web. Prior to the mating trials, adult males were narcotized for ca. 10 min using CO_2 and were weighed to the nearest 0.001 mg using a Mettler Toledo Microbalance MT5 (Columbus, OH, U.S.A.). Once the males became active again, they were introduced into the plastic container with the adult female. Mating trials were conducted in the laboratory during the day at room temperature; unlike most species of true widow spiders in the genus *Latrodectus*, which are nocturnal, light does not affect courtship and copulation behaviour in *S. grossa* (Scott et al., 2018). Successful copulations typically included one to four distinct copulatory bouts, which we defined as the period between the successful insertion of the male's pedipalp into one of the female's epigynes and its subsequent removal. Following a copulatory bout, males frequently repeat their courtship behaviour, which, when the female is receptive, can lead to an additional copulatory bout. Typically, males appear to alternate the use of their left and right pedipalps between successive copulatory bouts. Upon successful palp insertion, the male habitually 'lifts' the body of the female and both sexes remain quiescent until mating is terminated. Spiders were observed for 90 min or until the palp was removed. Thereafter, males were removed from the female's box and returned to their original petri dishes. In some instances, observations exceeded 90 min. Specifically, when males and females were in copula at the end of the 90 min period, observations were continued until the mating terminated naturally.

In the noncompetitive mating experiment, males were randomly assigned to a female trial. In each trial, we observed male courtship behaviour and recorded the duration of all copulatory bouts (i.e. the period between pedipalp insertion and removal). We then summed the duration of copulation across all copulatory bouts to obtain total copulation duration for each mating. Males were selected randomly in this experiment. In these trials, average male body mass was 20.5 ± 9.2 mg (range 7.2—53.9 mg).

For the competitive mating experiment, two size-mismatched males (one 'small' and one 'large') were simultaneously introduced, at the same location, into the female's home container. To select male pairs for the competitive mating experiment, we randomly selected males from the population that were visually size-mismatched (see Fig. A2). We then weighed males to ensure

the two males indeed differed in size. Importantly, the two male rivals always differed considerably in size (mean $\pm$ SD large:small male body mass ratio $= 2.5 \pm 0.7$, range 1.7—5.0). Males classified as 'small' averaged 11.2 ± 3.1 mg (range 5.3—16.1 mg), while males classified as 'large' averaged 27.3 ± 7.6 mg (range 13.9—47.9 mg). Each pair was then assigned randomly to a female for a competitive mating trial. In these trials, we recorded (1) the duration of each copulatory bout, (2) the identity of the successful male (i.e. 'large' or 'small') in each copulatory bout, and (3) the total number of fights between males observed across the entire mating trial. We defined a fight as any direct interaction between the males. These interactions were characterized either by the males facing one another and extending their first two pairs of legs to 'push' against the other male, or by the unmated male making physical contact with the mating male's body. Such interactions often resulted in the two males 'tussling' or holding each other tightly with their legs contracted. We then summed the duration of copulation across all copulatory bouts (regardless of male identity) to obtain the total time a female spent in copula.

Statistical Analysis

For noncompetitive mating trials, we assessed the relationship between copulation duration (s) and male body mass using a linear model, using data from successful trials (i.e. trials in which there was a copulation, $N = 45$ of 47 trials) only. Under competitive mating conditions, six trials did not result in a copulation. We therefore tested whether the body mass ratio of competing males (large:small male size) or the number of fights between males differed between unsuccessful and successful trials using permutation tests. Next, considering only successful competitive mating trials, and given that we predicted that larger males would win more matings, we used a one-tailed binomial test to determine whether mating success of large males was greater than expected by random chance. We then tested for an effect of male body mass ratio on the number of fights occurring during a trial using a linear model. Additionally, we examined the relationship between total copulation duration and the number of fights using a linear model, with copulation duration as the dependent variable and both the number of fights, male body mass ratio and their two-way interaction as predictor variables (using data from successful trials only). The nonsignificant interaction term ($F_{1,30} = 0.14$, $P = 0.73$) was removed from the model.

Next, we combined data from the two mating scenarios (noncompetitive and competitive matings) and compared female mating success (i.e. whether or not a female successfully mated) between the two scenarios using a binomial proportion test. Finally, we compared total female copulation duration (using data from successful trials only) between the two mating scenarios using a Mann—Whitney U test. All values given are mean $\pm$ SD. All statistical analysis was performed using R 4.1.3 (R Core Team, 2023) and RStudio (RStudio Team, 2020), and model assumptions were examined using the package DHARMa (Hartig & Lohse, 2022).

Ethical Note

All spiders were maintained under standard rearing conditions, using offspring from field-collected individuals and egg sacs. Although we did not require any institutional or governmental agency review for this species, we made every effort to conduct all our work in accordance with the ASAB/ABS standards for the use of invertebrates in research. All field collections and laboratory experiments were performed with the aim of minimizing any negative effect on the wellbeing and behaviour of the animals and the source population. We gently moved males between their home

petri dish and the female's container using brushes, and back again by gently grasping them with forceps. Competition among males for mating access to females is a common occurrence in many spiders, and following mating experiments all spiders were placed back into the laboratory population and reared under standard housing conditions with access to sufficient food.

RESULTS

Across all mating experiments, average male body mass was 19.8 ± 9.6 mg (range 7.2−53.9 mg). We observed a ritualized and hierarchal courtship sequence typically consisting of five sequential behaviours. (1) Approach and stroking: the male approached the female and used his forelegs to 'stroke' the female. (2) Web reduction: the male moved around and used his chelicerae to cut the female's silk threads. (3) Web building: the male added fresh silk near the female. (4) Vibration: the male was positioned with second and third leg pairs folded underneath his body, which was vibrated rapidly. At this point, the female, if receptive, moved towards the male and oriented her body vertically in the web with the ventral surface of the abdomen facing the male. (5) The male approached the female, similar to step (1). Finally, copulation occurred when the male successfully inserted one of his pedipalps into the female's epigynum. At this point the male clasped the female with his pedipalp and physically raised her body. Typical matings included three to four pedipalp insertions/copulatory bouts, after which mating was terminated naturally and males no longer showed interest in the females. All males in our experiments showed ritualized courtship behaviours except for one pair of males in the competitive mating condition because they were continuously engaged in conflicts.

Under noncompetitive mating conditions, 96% of males (45 of 47 trials) were successful in obtaining copulations with the female. In the two trials in which males failed to mate, body mass did not appear to play a role in the male's failure (male body mass: 31.0 and 11.8 mg; failed trials 1 and 2, respectively). In addition, male courtship behaviour did not appear to influence mating success in these two cases, as both males exhibited typical courtship behaviour (J. A. Harvey, personal observation). Across all successful mating trials, average total copulation duration was 45.5 ± 17.4 min, and the average number of copulatory bouts per mating trial was 2.3 ± 1.0. Finally, total copulation duration was not influenced by male body mass under noncompetitive mating conditions ($F_{1,43} < 0.001$, $P = 0.98$).

Under competitive mating conditions, 28 of 34 trials resulted in successful copulation, with an average total copulation duration of 25.17 ± 16.5 min. Successful and unsuccessful trials did not differ in either the body mass ratio of the competing males ($z = 0.88$, $P = 0.38$) or the number of fights between the competing males ($z = 0.47$, $P = 0.67$). Considering only trials that resulted in a successful mating, large males 'won' significantly more in terms of gaining access to females than expected by chance (one-tailed binomial test: $P < 0.001$). In 25 of 28 successful trials, the larger male was the only male to successfully copulate. In one of the trials, the smaller male was the only male that achieved a copulation, whereas in the other two trials, the smaller male achieved a single copulation, while the larger male always achieved a greater number of copulatory bouts during a trial (number of copulatory bouts for large versus small males: seven versus one and four versus one). Fighting was commonly observed between males and across all trials males engaged in an average of 8.8 ± 6.1 fights. The number of fights, however, was not influenced by male body mass ratio ($F_{1,32} = 0.96$, $P = 0.34$). Similarly, female copulation duration was not influenced by male body mass ratio ($F_{1,25} = 0.003$, $P = 0.96$),

nor was it influenced by the number of fights occurring between the competing males ($F_{1,25} = 1.22$, $P = 0.29$).

Comparing mating success across the two mating scenarios, we found that the presence of a male competitor did not significantly influence mating success (i.e. successful copulation; 96% versus 82%, noncompetitive and competitive mating conditions, respectively; proportion test: $\chi_1^2 = 2.61$, $P = 0.11$). However, total female copulation duration was significantly reduced under competitive mating conditions compared to noncompetitive mating conditions (Mann−Whitney test: $W = 249$, $P < 0.0001$; Fig. 1).

DISCUSSION

In this study, we showed that male body size in *S. grossa* does not impact male mating success or copulation duration under noncompetitive mating conditions. However, under competitive mating conditions, larger males won contests significantly more often. Interestingly, when males competed for mating opportunities, small males did not appear to avoid conflict, but instead male−male interactions typically escalated into physical fights regardless of how much larger 'large' males were. These fights were characterized by males facing each other and spreading their first appendages as widely as possible to exaggerate their size to their opponent, possibly acting as a form of intimidation, and frequently escalated into physical tussles between rivals. We also found that copulation duration was reduced when matings took place in the presence of a rival male. Finally, we observed a highly ritualized courtship behaviour in *S. grossa*, consistent with previous descriptions in this species (Knoflach, 2004; Scott et al., 2018) and with courtship behaviours observed in a range of spider taxa (e.g. Fisher & Price, 2019; Schmitt et al., 1992; Wignall & Herberstein, 2013).

Under noncompetitive conditions, male body size did not appear to influence mating success or copulation duration in *S. grossa*, which is consistent with findings in several spider taxa (Kotiaho et al., 1996; Schäfer et al., 2008; Schneider, 1997). Although we did not explicitly test female choice here, the lack of a relationship between male body size and mating success suggests that precopulatory female choice (at least for body size) is perhaps absent or minimal in this system. Our findings do not exclude the possibility that other male traits may play a role in female choice in this system (e.g. acoustic, vibratory, tactile or chemical signals; Huber, 2005), as they do in other spider species (e.g. Wignall & Herberstein, 2013). However, we found that almost all virgin females accepted the first male they encountered. Under conditions
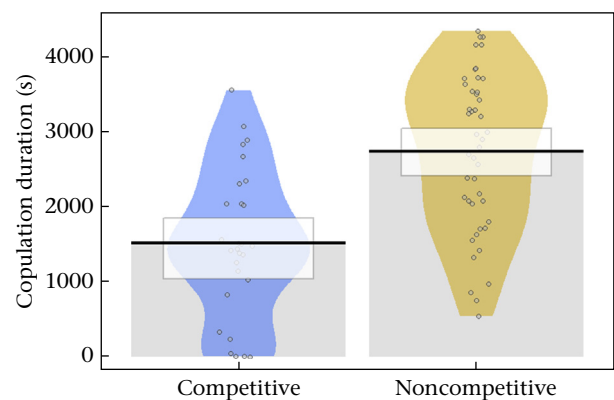
Figure 1. The difference in total copulation duration of females under competitive and noncompetitive conditions presented in violin plots. Circles show the data. The solid line is the median. The bean shape represents density. The box indicates a 95% confidence interval.

in which male encounter rate is low (Andrade, 2003) and given the potential costs of choosiness (e.g. the risk of remaining unmated; Kokko & Mappes, 2005), females may be under strong selection to accept the first male they encounter to ensure their reproductive success.

Under competitive conditions, we found that larger males gained a competitive advantage in direct contests for access to mates, which suggests that sexual selection via male–male competition may be important in *S. grossa*. Large male advantage under male–male competition has also been observed in the closely related Mediterranean black widow spider, *Latrodectus tredecimguttatus* (Golobinek et al., 2021) and indeed a number of spider species (reviewed in Elgar, 1998; Dodson & Schwaab, 2001; Foellmer & Fairbairn, 2005; Hoefler, 2007; Maklakov et al., 2004; Rittschof, 2010; Schmitt et al., 1992; but see Neumann & Schneider, 2015). Thus, our study contributes to a body of literature showing large male advantage in a range of different spider families. Intriguingly, a previous study of *S. grossa* suggested that selection for rapid development was more important than increasing male body size (Harvey, 2022). Despite this, some males in this species are relatively large (>50 mg), and our findings suggest that this may be due to sexual selection for larger size under competitive scenarios.

We found that the presence of a rival male reduced total copulation duration. Although we did not examine reproductive success in terms of offspring production in the current study, our findings may have implications for male or female fitness. Specifically, reproductive success may be correlated with copulation duration if males that copulate longer transfer more sperm (Snow & Andrade, 2004) or if copulation duration positively affects the number of sperm stored by a female (Bukowski & Christenson, 1997). This pattern has been confirmed in several species of arachnids (Andrade, 1996; Austad, 1982; Cohn, 1990; Kiss et al., 2019; Schneider et al., 2006; Schneider & Lesmono, 2009), although in some species the relationship between sperm transfer and copulation duration is nonlinear (Snow & Andrade, 2004; Szirányi et al., 2005). Alternatively, if sperm transfer takes place early during copulation, extended copulation duration may reflect a form of physiological mate guarding, which may be important for the transfer of substances that ensure fertilization or render females nonreceptive to other males (e.g. seminal fluid proteins, insertion of mating plugs). Scott et al. (2018) showed that males never obtain copulations with previously mated females, suggesting that they may be monandrous or at least unreceptive to additional matings in the short term, although to what extent this is caused by male-derived substances transferred during copulation is unknown. Regardless, under both scenarios, a shorter copulation duration may result in the production of fewer offspring.

The factors driving intra- and intersexual differences in body size in animals include sexual conflict and a range of ecological factors such as predator-induced early mortality, variable exposure to abiotic stresses such as heat and ease of finding mates (Blanckenhorn, 2000). In spider taxa, female-biased SSD is commonly observed in many species and reaches its zenith in families such as the Araneidae and Theridiidae. For instance, the body mass ratio of females to males in the genera *Trichonephila* and *Latrodectus* may be 50 to 1 or even greater (Cheng & Kuntner, 2014; Kleinteich & Schneider, 2010; Kuntner & Coddington, 2020). In Australian redback spiders, *Latrodectus hasselti*, large males were more successful than smaller males in competition for females, but small males still had 10 times higher fitness than larger males because of their significantly faster development time to adulthood (Kasumovic & Andrade, 2009), supporting the 'first come, first served' hypothesis. This competitive advantage is apparently a major factor driving ESSD in *L. hasselti* and perhaps other widow spiders.

It is also important to recognize that SSD appears to be most exaggerated in web-building spiders, where the ecology of adult males and females generally differs significantly. By contrast, SSD appears to be only marginal in many, although not all, nonweb-building spider species in the Lycosidae, Pisauridae, Salticidae, Zoropsidae and other cursorial ambush-feeding spiders where both sexes have significantly overlapping niches. Variation in SSD is therefore generated by multiple biotic and abiotic selective forces acting on each sex, although broadly speaking SSD in spiders appears driven by fecundity selection for large female size and selection for small male size (Foellmer & Moya-Larano, 2007). Compared to other closely related spiders in the Latrodectinae (i.e. widow spiders) that display ESSD (Kuntner & Coddington, 2020), in *S. grossa* SSD is less pronounced. This may be due to lack of selection for morphological or behavioural traits that influence mate location (e.g. climbing ability and dispersal, Moya-Laraño et al., 2002; Corcobado et al., 2010; Grossi & Canals, 2015), low levels of sexual cannibalism (Elgar & Fahey, 1996) and lower mortality of immature spiders in urban habitats with a low predation risk. In females, selection for large body size is generally correlated with increased fecundity (Head, 1995), whereas for males, we suggest that large male size is advantageous in male–male competition, which may occur more frequently in urban habitats where these spiders are most abundant and immature survival is higher.

Different forms of male courtship behaviour have been demonstrated across many phylogenetically unrelated groups of vertebrates and invertebrates (Reynolds, 1996). This reveals evolutionary convergence among many animals in the differing roles played by males and females in reproduction. Females usually invest much more in reproduction than males, and hence selection has been geared towards female choosiness for fitter males. In spiders, courtship behaviour can be influenced by the presentation of nuptial gifts, such as prey, from the male to the female (Stålhandske, 2001), colourful displays in species with good vision (Girard et al., 2011) or, as in *S. grossa* and widow spiders, a combination of multiple physical and tactile cues (Fischer et al., 2020; Knoflach, 2004; Scott et al., 2018; Sivalinghem & Mason, 2021). Complex courtship behaviours in spiders have been little studied in most taxa, and should be the focus of future research, along with how balancing selection on reproduction and survival generates variation in body size of males in different spider families.

Author Contributions

Data Availability

Declaration of Interest

The authors declare no conflicts of interest.

Acknowledgments

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Appendix

Steatoda grossa males exhibit considerable variation in body size, even when under identical conditions in the laboratory and measured after maturity (Fig. A1, $N = 115$). The visual difference between small and large males is immediately apparent when two individuals are compared (Fig. A2). This approach to visual comparison of body size was used to select size-mismatched males for our competitive mating trials (see Methods).
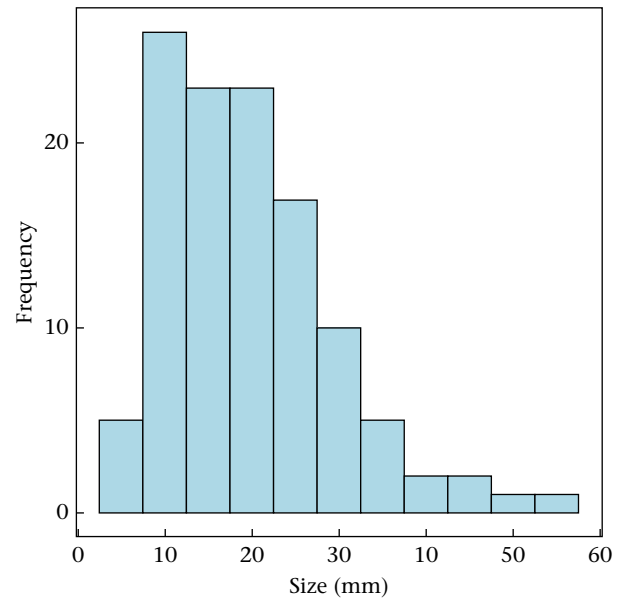
Figure A1. The body mass distribution of 115 males reared under identical conditions in the laboratory (mean ± SD: 19.82 ± 9.61 mg; range 5.3–53.9 mg).

Figure A2. Variation in male body size in *S. grossa*. These two males were randomly selected from the spider rearing; both males are mature and of similar age (9–10 months) and were raised and maintained under identical laboratory conditions and feeding regimes (large one = 27.5 mg, small one = 5.2 mg). Photo: Mark Hillaert.