Sexual selection for increased male body size and protandry in a spider

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Female-biased sexual size dimorphism (SSD) is found in many organisms yet is poorly understood. Spiders in general, and web-building species in particular, typically have strongly female-biased SSD. We investigated the causes of SSD in the web-building spider *Stegodyphus lineatus*. Females are slightly, but significantly, larger than males. Large females are more fecund but the selection pressures on male body size are not clear. Males were introduced on to the webs of virgin and mated females and we also conducted competition experiments between males. Large males did not have longer copulations, nor did they mate more successfully with virgin females than small males did; however, they were more successful with previously mated females and remated more often. They also won more fights, and were more successful at obtaining prey from the female's web. Indiscriminate mating by virgin females, however, conferred a fitness advantage on early maturing males. We suggest that the female's mating strategy selects for protandry, which results in female-biased SSD, despite the selection for large body size in males. Indiscriminate mating by females and a trade-off between time to maturation and male body size may be important in understanding the evolution of female-biased SSD.

Sexual size dimorphism (SSD) is a common phenomenon in the animal kingdom (Ralls 1977; Cabana et al. 1982; Hedrick & Temeles 1989; Shine 1989; Fairbairn 1997). SSD in birds and mammals is usually male biased, that is, males are larger than females (Ralls 1977; Cabana et al. 1982) and cases of female-biased size dimorphism are commonly called 'reversed' (e.g. Hohoff et al. 2002; Sunde et al. 2003). However, female-biased size dimorphism is prevalent among reptiles and invertebrates (Arak 1988; Shine 1989; Fairbairn 1997), and, consequently, occurs more often in nature (Ghislen 1974; Legrand & Morse 2000). Large female body size is advantageous since it positively influences fecundity and offspring quality (Darwin 1871; Reznick 1985; Shine 1988; Stearns 1992; Honek 1993). When male size exceeds that of a female, it is often attributed to strong sexual selection, which favours large males via male–male combat or female choice (Clutton-Brock et al. 1977; Andersson 1994). Nevertheless, sexual selection for large male body size commonly occurs in species where males are the smaller sex (Andersson 1994; Fairbairn & Preziosi 1994; Fairbairn 1997; Blanckenhorn et al. 1999; Kraushaar & Blanckenhorn 2002). What keeps males small? In the present study, we approached this question using an eresid spider *Stegodyphus lineatus* as a model system.

SSD in spiders, where males are usually smaller than females (Head 1995) has been a controversial subject for some time. Extreme size dimorphism is found in some web-building spiders, where females are sedentary (sit-and-wait) predators and males actively search for females. Vollrath & Parker (1992) suggested that male web-building spiders might be smaller than females because of high male mortality during mate search (but see Walker & Rypstra 2003), which lowers the potential for direct male–male competition and favours protandry: early maturation by males. Alternatively, Coddington et al. (1997) maintained that body size dimorphism in spiders is a result of selection for larger and more fecund females rather

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than for smaller males (see also Prenter et al. 1998, 1999). Hormiga et al. (2000) suggested, that although sexual body size dimorphism may usually be a result of selection for increased female size, it can sometimes be a result of selection for reduced male size. Finally, Schneider et al. (2000) found that small males may have higher fertilization success; therefore, sexual selection on male body size may add a new perspective to this debate.

In the web-building cribellate spider *S. lineatus*, females are significantly larger than males, but the dimorphism is not pronounced, with large males being larger than small females (Schneider & Lubin 1998). The variation in body size is larger in males than in females (Schneider 1997), and the largest males can be twice as large as, and eight times heavier than, the smallest ones (A. A. Maklakov, unpublished data). Why are males in this species relatively large and what maintains the variation in male body size? Elgar & Fahey (1996) proposed that sexual cannibalism selects for small male body size in the orb-web spider *Nephila plumipes*, whereas male–male competition provides an advantage to larger males, resulting in considerable size variation. However, male cannibalism by females is common only in some taxa (Elgar & Crespi 1992), and *S. lineatus* is not a sexually cannibalistic species. Sexual conflict may select for increased male body size in *S. lineatus* (Schneider & Lubin 1997, 1998). In this species, males fight with females so that they can destroy the eggsac and force a female to remate. The outcome of these fights is decided by the size of the male relative to that of the female (Schneider & Lubin 1996, 1997). Why then are not all males large?

Small size in males may result from sexual selection. First, in species where females mate with multiple males, small males may have an advantage in sperm competition or may be preferred by the female. For example, in the sexually size-dimorphic *Nephila edulis*, small males copulate for longer and fertilize more eggs than large males (Elgar et al. 2000; Schneider et al. 2000). Second, there may be benefits to protandry, if early maturing males encounter more receptive females than late maturing ones. Indeed, *S. lineatus* females are more aggressive towards males when mated (Erez 1998) or bearing an eggsac (Schneider & Lubin 1997) than when virgin. Thus, females become less available as the season progresses. If the female does mate twice, the sperm is mixed in the spermatheca and each male sires on average 50% of the offspring (Schneider & Lubin 1996). Therefore, second or later males have no advantage over the first male. Since mated females are less receptive, early maturation in males may be advantageous, provided that virgin females mate indiscriminately with regard to male body size. Protandry is usually associated with small male size in species with discrete generations, assuming there is a trade-off between male size and developmental time (Wallace 1867; Darwin 1871; Singer 1982; Zonneveld 1996). Therefore, selection for protandry may result in reduced male body size. Schneider (1997) found that *S. lineatus* males mature on average 16 days earlier than females. This species is characterized by a patchy distribution of individuals (Lubin et al. 1998) and possibly high costs of mate search (Schneider & Lubin 1998), which may further increase the

advantage of early maturation for males. Finally, females lose body mass as a result of the male's presence in their nest (Erez 1998). Males commonly forage on prey caught in the female's web (i.e. sexual kleptoparasitism) and conflicts over access to food may occur. If large males are more successful kleptoparasites, females may prefer smaller males, as it will increase their chances in intersexual competition for food.

Male–male competition is expected to select for large body size but has not been detected in *S. lineatus* (Schneider 1997); however, fierce fights between males were observed in a congener *S. dufouri* (A. A. Maklakov, unpublished data). Females can have more than five male visitors during the season (averages were 1.5 and 2.1 in two populations) and a male may cohabit with a female for up to 18 days (Schneider 1997). This suggests that there is potential for direct interactions between males in the female's nest.

We investigated how sexual selection in the form of female receptivity, male–male competition and sexual kleptoparasitism influences male body size in *S. lineatus* in a series of laboratory, field and semifield experiments. In particular, we asked whether different selective forces favour males of different sizes, resulting in large variation in this trait.

METHODS

Study Species

Stegodyphus lineatus Latreille 1817 (Eresidae) is found in arid and semiarid habitats around the Mediterranean basin. Females are sedentary, whereas males leave their nests after their final moult and wander in search of females. Females are visited by multiple males during the breeding season (Schneider 1997). When two males were paired sequentially with a virgin female, they sired on average 50% of the offspring, suggesting complete sperm mixing (Schneider & Lubin 1996).

Subadult *S. lineatus* ($N = 250$) were collected in their natural habitats in the Negev Desert in Israel in March 2000 and brought to the Sede Boqer Campus of Ben Gurion University. Spiders were kept individually in plastic containers with mesh lids (height 10 cm, diameter 5 cm) and reared to maturity on a diet of desert locusts, *Locusta migratoria*, crickets, *Acheta domestica*, and flour beetles, *Tenebrio molitor*. They received approximately one prey item each twice a week. We alternated different types of food on a weekly basis according to their availability, but at each round all spiders received a single food type. We kept spiders outdoors under natural temperature and light conditions, protected partially against direct sun by a shade cloth. After the final moult to maturity, the spiders were measured and weighed. We measured body size as prosoma width (mm) and calculated size difference by subtracting male size from female size. Prosoma width is a standard measure of body size in spiders, since this part of the body does not change with body condition. This measure has been used successfully in this species by other authors (e.g. Ward & Lubin 1993; Schneider 1997), so we

can compare our results with those of other studies. There is a positive correlation between female body size and clutch size (Ward & Lubin 1993). Females were consumed by their young approximately 2 weeks after hatching. Some of the young were kept in the laboratory for future studies. Adult spiders that were not used in the experiments and excess young were released into their natural habitat.

Mating with Virgin Females

We randomly mated 39 virgin females with 39 virgin males. A male was introduced on to the female's web and we recorded its behaviour along with the female's reaction. Males usually initiated courtship behaviour immediately, resulting in either successful mating or the male entering the nest of the female. In most cases, females remained passive until mating occurred. We considered the following reactions as indications of female aggressiveness: pushing, grabbing or biting a male that was trying to enter a nest and plucking the web upon the introduction of a male. Sometimes, a female rushed out of the nest as if trying to catch a male when we placed it on the web but quickly resumed her original position inside the nest. The latter behaviour was not considered aggressive if other signs of aggression did not follow, since we assumed that the females mistook a male for prey. The behaviour of the pair was observed for 3 h or until copulation had occurred. We left males with females for 5 consecutive days. To investigate the effect of male cohabitation, the pair received three first-instar desert locusts on the second day of the 5-day cohabitation period. We noted the duration of first copulation and the change in male body mass during the 5-day period of cohabitation.

Mating with Mated Females

We paired an additional 39 pairs of virgin males and females following the procedure outlined above. A second male was introduced to each female 5 days after the removal of the first male. The pair was observed for 3 h or until copulation occurred or the male was chased away by the female. Since all males that entered the nest of a virgin female succeeded in mating with her (see Results), we considered nest entering as a successful mating event. If the male succeeded in mating with a female we left it with the female for 5 additional days.

Male–male Competition

Male–male competition experiments were conducted in the field in April–May 2001. Twenty-three male spiders were collected in the field and brought to the laboratory where they were measured, weighed and marked with water-based paint dots on the abdomen. We introduced these males to field nests of *S. lineatus* that contained females and cohabiting males and recorded the behaviour of both intruder and resident males and of the female for 1 h or until one of the males was chased away by the

opponent. After the experiment, all resident males were measured, and 14 of 23 females were brought to the laboratory and monitored for eggsac production to determine if they had mated before the experiment.

'Spider House' Experiment

To test the effect of male body size on male remating success we simulated the field conditions that males experience late in the season when most females are already mated. The experiment examined the ability of males to mate with previously mated females, as well as male survival and ability to locate females. Nests of 23 virgin females, collected as subadults and reared to maturity under the standard procedure described above, were attached to a chicken-wire fence inside the 'spider house', a greenhouse frame (6×14 m) covered with shade cloth, approximately 0.5 m from each other. All females were mated simultaneously to 23 individually marked males of known size that were collected in the field as subadults and reared to maturity. All 23 males were observed mating within 4.5 h and all males stayed with the female at least until the end of the 4.5-h observation session. Males were left unconfined with the females and were free to leave the nest. We checked the interior of the 'spider house' daily to recover males and noted their location (inside or outside the nest) and behaviour (mating or not mating).

Time of Maturation and Male Body Size

Adult females with eggsacs were collected during summer 2000 (June–August), and brought to the Sede Boqer Campus of Ben Gurion University. The females were kept individually in plastic containers with mesh lids (height 10 cm, diameter 5 cm) on a standard diet (see Study species). We recorded hatching date of young and the date when dispersal began. When the majority of spiderlings had left the maternal nest, approximately 2 weeks after the first dispersing individuals, we separated juvenile spiders and placed them in cages covered with fine mesh ($12 \times 12 \times 5.5$ cm). We kept the spiders outdoors in a 'spider house' under natural temperature and light conditions. We fed the spiders once or twice a week depending on the season (there is very little growth during winter) on wild-type fruit flies, *Drosophila melanogaster*, desert locusts, crickets and flour beetles. When males matured the following spring, we noted the date of maturation and measured prosoma width as described above.

Statistical Analysis

Data were analysed with SYSTAT 9 (SPSS Inc., Chicago, U.S.A.). All variables were tested for normal distribution using Kolmogorov–Smirnov one-sample tests before parametric statistics were applied. Frequency data were analysed using tests of independence and Yates correction was applied for small sample sizes. Two-tailed P values are given throughout.

RESULTS

Mating with Virgin Females

All males mated with virgin females. Of 39 virgin females, 25 (64.1%) mated within 3 h of the introduction of a male on the female's web, and the rest mated during the following 5 days of male cohabitation. All females produced eggsacs, all but one of which were viable, thus showing that mating occurred in those cases when it was not observed directly. All males entered nests of virgin females within 3 h. Males that entered female nests but did not mate immediately invariably turned around and positioned themselves inside the nest facing the entrance. No cannibalism, or male–female fights, and almost no female aggression, was observed. In two cases, females plucked the web upon presentation of a male, but nevertheless the males entered the nest and mated with the female. Male body size did not explain whether or not they mated within 3 h (logistic regression: log-likelihood ratio$_1$ = 0.011, N = 39, P = 0.918) nor did it explain the time to mating for the 25 males observed mating within 3 h (linear regression: $F_{1,23}$ = 0.035, $R^2 < 0.001$, P = 0.853).

Mating with Mated Females

Mated females reacted aggressively towards males in 30 of 39 trials (76.9%). In two of nine cases (22.2%), males refrained from entering the nest of a mated female even in the absence of marked aggression. None the less, males often succeeded in mating with aggressive females (50%, N = 30), sometimes after a fight (nine successful matings out of 16 fights; 56.2%). No sexual cannibalism was observed. Large males had an advantage in entering the nests of previously mated females: male mating success (measured as nest entering) increased significantly with increasing male body size (logistic regression: log-likelihood ratio$_1$ = 13.611, N = 39, $P < 0.001$; Fig. 1) and with decreasing body size difference between males and females (log-likelihood ratio$_1$ = 5.558, N = 39, P = 0.018).
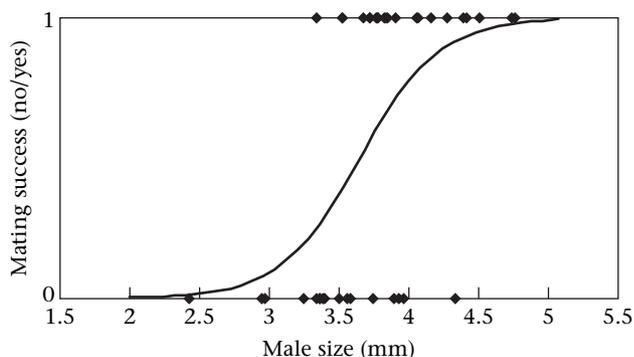

Figure 1. Male body size (mm, prosoma width) as a predictor of male mating success (0 = no mating; 1 = mating) with previously mated females in *S. lineatus*. The function was estimated using logistic regression. Points represent actual data.

First Copulation Duration

Males copulated repeatedly with females, often two or three times after the initial mating. Males were observed copulating with females on the second, third and fourth days of cohabitation, and matings were observed at any time during a 24-h period. Thus, it was impractical to determine the exact number of copulation events and the overall copulation duration during the 5 days of male cohabitation. Instead, we determined the exact duration of the first copulation event for those males that initiated and terminated their first mating within the first 3 h after being placed on the female's web (N = 33). There was no effect of male body size on the duration of the first copulation ($\overline{X} \pm$ SE = 794.1 $\pm$ 76.2 s) for males that mated with virgin females (linear regression: $F_{1,31}$ = 0.017, $R^2 < 0.001$, P = 0.734).

Female Aggressive Behaviour

Virgin females were not aggressive towards their mates (see above). We obtained behavioural data for 75 of 78 virgin females during their first mating. Eight of 75 virgin females showed low-intensity aggressive behaviour towards their first mates, and none of these eight cases escalated into a fight. The rest of the females showed no aggression towards males. The occurrence of aggressive behaviour did not depend on male size (logistic regression: log-likelihood ratio$_1$ = 1.129, N = 75, P = 0.288), or on the body size difference between males and females (log-likelihood ratio$_1$ = 0.355, N = 75, P = 0.552).

Mated females often reacted aggressively towards males (see above); however, their reaction did not depend on male body size (logistic regression: log-likelihood ratio$_1$ = 2.234, N = 39, P = 0.154) or on the body size difference between males and females (log-likelihood ratio$_1$ = 1.223, N = 39, P = 0.286). The occurrence of male–female fights was also not dependent on male size (log-likelihood ratio$_1$ = 0.306, N = 39, P = 0.583), or on the body size difference between males and females (log-likelihood ratio$_1$ = 0.005, N = 39, P = 0.943).

Changes in Male Body Mass

Males that cohabited with females for 5 consecutive days either gained or lost body mass. The body size difference between males and females had a significant effect on whether males lost or gained body mass as a result of cohabitation with the female (Fig. 2). When the body size difference was large, the males lost up to 20% of their initial body mass (linear regression: $F_{1,38}$ = 4.587, R^2 = 0.084, P = 0.039; Fig. 2).

Male–male Competition

Male–male competition in the form of aggressive interactions between the cohabiting resident male and the intruder occurred in 12 of 23 cases (52.2%). In the other 11 cases, the resident male showed no aggression towards the intruder, which successfully entered the nest. The probability of a fight occurring did not depend on the
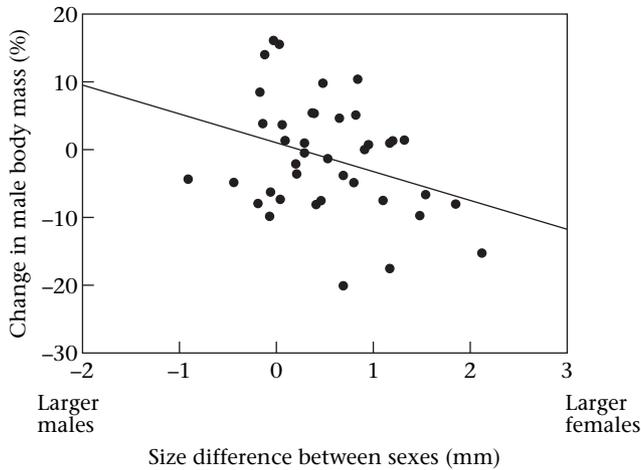
Figure 2. The effect of a 5-day cohabitation period with a female on male body mass in *S. lineatus*. Body size was measured as prosoma width (mm) and relative size difference was obtained by subtracting male size from female size.

Figure 3. The number of females with which males mated in the 'spider house' experiment, where males moved around freely in search of females. Male body size was measured as prosoma width (mm).

relative body size difference between the two males (logistic regression: log-likelihood ratio = 0.058, $N = 23$, $df = 1$, $P = 0.809$) nor did female reproductive status (mated or virgin, $N = 14$ females whose reproductive status was assessed) have an effect on male fighting behaviour (Yates-corrected chi-square test: $\chi_1^2 = 0.984$, $P = 0.321$). Large males were more likely to win the fight: in 11 of 12 cases the larger male chased away a smaller opponent ($\chi_1^2 = 6.75$, $P < 0.01$) whereas residency did not influence the outcome of fights ($\chi_1^2 = 2.08$, NS).

'Spider House' Experiment

All 23 males mated with virgin females in the 'spider house', thus supporting the data from the laboratory experiments (see Mating with virgin females). There was a large variation in overall remating success of the experimental males. Some did not remate at all ($N = 12$), whereas others visited up to four females (Fig. 3). The chance of remating was greater for larger males (logistic regression: log-likelihood ratio$_1 = 9.517$, $N = 23$, $P = 0.002$). This is consistent with the laboratory data that showed that large males were more successful than small ones in entering nests of mated females. This outcome was not merely a result of larger males surviving longer than smaller ones. We recovered as many small as large males and there was no effect of male size on survival (linear regression: $F_{1,21} = 2.321$, $R^2 = 0.057$, $P = 0.143$).

Males that remated stayed longer with previously mated females than with virgin females (Wilcoxon signed-ranks test: $T = 0$, $N = 11$, $P = 0.016$). The duration of male cohabitation period with previously mated females increased with increasing male body size (linear regression: $F_{1,9} = 8.506$, $R^2 = 0.429$, $P = 0.017$).

Time of Maturation and Male Body Size

There was a significant positive relation between the time of maturation (Julian date) and male size (linear regression: $F_{1,33} = 18.281$, $R^2 = 0.337$, $P < 0.001$; Fig. 4).
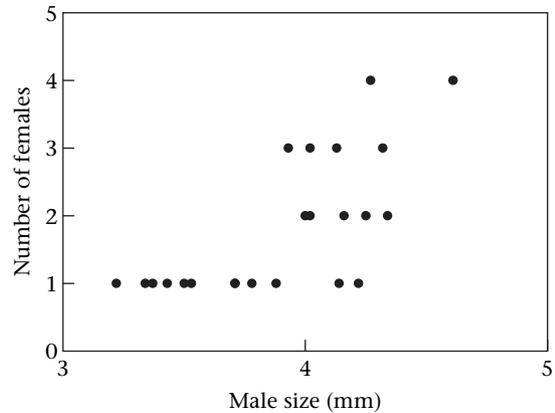
DISCUSSION

Virgin females of *S. lineatus* mated indiscriminately, ruling out the possibility of sexual selection on male body size at this stage. Male body size explained neither the duration of the precopulatory period nor the duration of the first copulation event. Mated females behaved aggressively towards males, irrespective of male size. Larger males were more successful in mating with previously mated females, a result that was confirmed in the experimental simulation of the natural conditions. Although larger males remated more often, they did not survive better than small males. Thus, remating success of large males was not due to an inherently longer adult life span. Our data on male body size and male mating success are similar to Rubenstein's (1987)-data for the web-building spider *Meta segmentata*, which is also characterized by only slightly female-biased dimorphism. However, in *M. segmentata*, males compete directly for access to female webs, which is less common in *S. lineatus*. Nevertheless, it is possible that sexual selection results in increased male body size in both species. Similarly, male mating success in the water strider
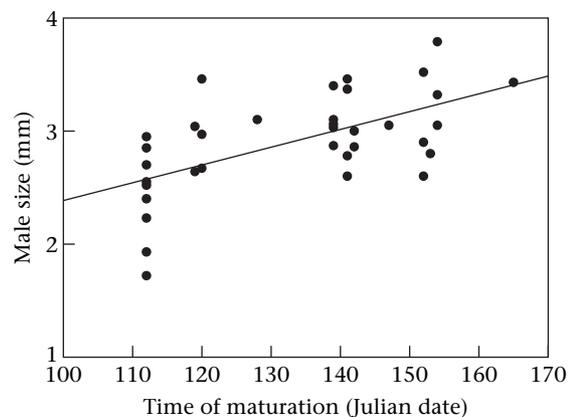

Figure 4. Body size (mm, prosoma width) as a function of maturation date during the season (Julian date) of *S. lineatus* males reared in captivity.

Aquarius remigis is positively related to male body size (Preziosi & Fairbairn 1996, 2000) and sexual selection for larger males is suggested to result in less dimorphic populations (Fairbairn & Preziosi 1994).

Ding & Blanckenhorn (2002) experimentally reversed sexual dimorphism in two species of dung flies (*Scathophaga stercoraria* and *Sepsis cynipsea*) by providing larvae with different rearing environments. Originally, *S. stercoraria* males are larger than females, whereas in *S. cynipsea* females are the larger sex. The prediction was that the phenotypical shift in size dimorphism would affect the relative control over mating in both species. However, this prediction was not upheld, apparently because the sexes control the mating process at different levels in the two species. Ding & Blanckenhorn concluded that the mating systems of these species are, perhaps, long-term consequences of evolutionary shifts in SSD. Nevertheless, there is directional sexual selection for larger males in both *S. cynipsea* (where males are smaller), and *S. stercoraria* (where males are larger; Kraushaar & Blanckenhorn 2002), even though the strength of this selection may vary in space and time (Blanckenhorn et al. 1999). This selection is stronger in *S. stercoraria*, where it is caused primarily by male–male competition, than in *S. cynipsea*, where it is caused primarily by female choice (Parker 1970; Blanckenhorn et al. 2000; Kraushaar & Blanckenhorn 2002).

Male–male competition in the form of aggressive interactions and fights between the resident and the intruding male does occur in this species. In our study, male–male competition favoured large males that won a significant proportion of fights. Nevertheless, only half of all field trials were characterized by agonistic interactions between the males; in other cases the intruder entered the nest without any resistance from the resident male or female. The variation in occurrence of aggressive interactions among males was not explained by female mating status (i.e. virgin or mated), or by the relative body size difference between the males. Males may use different behavioural tactics with respect to their reaction towards conspecifics of the same sex. It is further possible that male fighting decisions depend on the amount of sperm transferred to the female or on the likelihood that the female would remate. Thus, Elgar & Bathgate (1996) showed that male defence of females depended upon the time since mating.

Large body size provides males with a feeding advantage during their stay in the female's nest. Males in our study fed on prey caught by females, and, during the 'spider house' experiment, we observed males and virgin females ($N = 4$) fighting over food items present on the female's web prior to mating. The relative body size difference between a male and a female influenced the body mass gained or lost by a male during the period of sexual cohabitation. Thus, larger males were more successful in gaining access to prey caught in the female's web.

In our experiments both in the laboratory and in the spider house, we observed males mating with females on the first, second, third and fourth day of cohabitation. Thus, it appears that multiple copulations with the same male are a common occurrence. Paternity may be correlated with copulation duration if males that copulate for longer transfer more sperm (Parker 1998; Elgar et al. 2000) or if copulation duration positively affects the uptake of sperm by a female (Bukowski & Christenson 1997). This pattern has been confirmed in several species of arachnids (Austad 1982; Cohn 1990; Andrade 1996). Fahey & Elgar (1997) showed that longer cohabitation affects fertility, and assumed that there is a positive relation between cohabitation duration and copulation frequency. The duration of the cohabitation period in *S. lineatus* increased with male body size in our study, suggesting that sperm transfer and resulting paternity may also increase with male size.

The advantages accruing to large males because of their ability to overcome the resistance of mated females, their success in male–male competition and sexual kleptoparasitism may result in selection for large size in males. Nevertheless, we suggest that indiscriminate mating by virgin females and indiscriminate aggression towards males by mated females provide a fitness advantage to early maturing males, which may outweigh the size advantage. Polyandry is expected to reduce protandry (Parker & Cortney 1983; Zonneveld 1992; Morbey & Ydenberg 2001) but only when mated females are indiscriminately receptive and there is no first-male sperm priority (cf. Legrand & Morse 2000). In *S. lineatus*, female resistance to remating results in behavioural first-male priority and selects for protandry.

Comparing the effect of the time of maturation on male body size under controlled and field conditions may provide a clue to male decision rules with respect to protandry and final body size. Since both large body size and early maturation are generally advantageous for spiders, one may expect a trade-off between them (Vollrath 1987; Schneider 1997). Schneider (1997) found a negative correlation between the time of maturation and male body size in a field population of *S. lineatus* (later maturing males were smaller), suggesting that there is no trade-off between these two factors. However, when we reared spiders in the laboratory under standardized feeding conditions, we observed a positive relation between the time of maturation in the season and male body size. The following simple model may account for the patterns described above.

We suggest that the 'rule of thumb' for males is to mature as early as possible, regardless of size, to reap the benefits of protandry. However, males should grow as large as possible before maturation to win intersexual conflicts, and male–male competition and to be successful kleptoparasites. Early maturing males will include both those males that succeeded in reaching a large size and those that are still small but have sufficient resources to mature into adults. The reduction in male size as the season progresses found by Schneider (1997) is expected because late maturing males will be the ones that were too small and undeveloped to mature at the start of the season. Thus, if males mature as early as possible, late maturing males will be smaller on average than early maturing ones which include both very successful large and less successful small males. Early maturation within the season gives access to virgin females that mate

indiscriminately, which results in a fitness advantage for the first males.

We argue that the benefits of early maturation outweigh those of a large body size and result in protandry and female-biased sexual size dimorphism in this species. However, sexual selection for increased body size in males reduces the difference in body size between the sexes. Historically, two explanations have been proposed to explain the occurrence of protandry: sexual selection for early male emergence and the incidental result of natural selection on male and female body size (Darwin 1871; Wiklund & Fragerstrom 1977; Singer 1982; Vollrath & Parker 1992; Zonneveld 1996). Although these hypotheses are not mutually exclusive, our data are more consistent with the idea that protandry is sexually selected rather than an incidental result of selection on reduced male body size. This is because we found no evidence for direct selection on reduced male body size and because there is a trade-off between development time and male body size at maturity.

Female mating behaviour and the trade-off between time to maturation and male body size may prove crucial to understanding the evolution of female-biased sexual size dimorphism in different taxa. Indiscriminate mating by females confers fitness advantages to early maturing males, since mating with virgin females is usually beneficial. The benefit could derive from first-male priority in sperm competition, loss of receptivity by mated females and reduced fecundity with successive bouts of egg laying (Wiklund & Fragerstrom 1977; Thornhill & Alcock 1983; Wiklund & Forsberg 1991; Wedell 1992), or from early arriving females having higher fecundity (Kleckner et al. 1995). Scramble competition among males is likely to lead to protandry, resulting in males being smaller than females (Singer 1982; Zonneveld 1996). Our results indicate that such selection may be strong enough to produce female-biased dimorphism even when several evolutionary forces select for large male body size.

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