

Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*

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Abstract

Sexual selection, through female choice and/or male–male competition, has influenced the nature and direction of sexual size dimorphism in numerous species. However, few studies have examined the influence of sperm competition on size dimorphism. The orb-web spider *Nephila edulis* has a polygamous mating system and extreme size dimorphism. Additionally, the frequency distribution of male body size is extremely skewed with most males being small and few large. The duration of copulation, male size and sexual cannibalism have been identified as the significant factors determining patterns of sperm precedence in spiders. In double mating trials, females were assigned to three treatments: either they mated once with both males or the first or the second male was allowed to mate twice. Paternity was strongly associated with the duration of copulation, independent of mating order. Males that were allowed to mate twice not only doubled the duration of copulation but also their paternity. Small males had a clear mating advantage, they copulated longer than large males and fertilized more eggs. Males of different sizes used different tactics to mate. Large males were more likely to mate through a hole they cut into the web, whereas small males approached the female directly. Furthermore, small males usually mated at their first attempt but large males required several attempts before mating took place. There was no obvious female reaction towards males of different sizes.

Introduction

Patterns of sexual dimorphism in dioecious organisms depend on the relative strengths of a variety of selection pressures (Andersson, 1994; Møller, 1994). For example, selection may favour large female size if this ensures greater fecundity, parental care or dominance in contests over resources. Typically, sexual selection is thought to influence sexual size dimorphism in the context of female choice and/or male–male competition, and most studies have focussed on the benefits of large body size (Blankenhorn, 2000). Thus, large male body size may be

favoured if females prefer larger males, or larger males dominate in physical contests over females (Andersson, 1994). Under conditions of scramble competition, sexual selection may favour small body size if smaller, early emerging males are more likely to find females than later males (Andersson, 1994). However, multiple mating by females allows sexual selection to persist after mating has taken place (Møller, 1998). If females store sperm from several mating partners, then these sperm may directly compete for fertilization inside the female. Numerous studies have identified an extraordinary diversity of mechanisms by which males attempt to ensure that the eggs of their mating partners are not fertilized by rival males (see Birkhead & Møller, 1998). However, the relationship between sperm competition and male body size is still poorly understood (Simmons & Siva-Jothy, 1998).

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In many invertebrates, the outcome of sperm competition may resemble a lottery, in which the fertilization success of each male is a function of the relative quantity of his sperm in the female sperm-storage organ at the time of fertilization (Parker, 1998; Simmons & Siva-Jothy, 1998). Greater fertilization success can then be achieved by either delivering more sperm and/or displacing the sperm of rival males (Simmons & Siva-Jothy, 1998). However, females often play an active role in this process, favouring the sperm of one male over another by selective uptake or storage of sperm (Eberhard, 1996, 1998). Male body size explains variation in paternity in several terrestrial invertebrates (Parker, 1970; McLain, 1985; Lewis & Austad, 1990; Watson, 1991; Simmons & Parker, 1992; Otronen, 1994). In general, larger males have a greater share of paternity than their smaller rivals (but see Archer & Elgar, 1999). This may arise because the larger males fill the spermatheca of the female more extensively than smaller males, thereby leaving less volume for the smaller males (Simmons & Siva-Jothy, 1998) and/or females may preferably store and use the sperm of larger males. Alternatively, larger males may be able to monopolize females when these are most receptive. Thus, selection may favour larger body size in species where sperm competition is intense.

The mating systems of spiders are often promiscuous, with both males and females mating with more than one partner (Elgar, 1998), and therefore multiple copulations may increase a male's share of paternity. Although mating plugs (Masumoto, 1993) and a reduction in female receptivity following copulation (see Elgar, 1998) have been reported, the patterns of variation in paternity suggest that sperm competition occurs in many spider families. The proportion of eggs fertilized by the second mate (P_2) of a multiple-mating female increases with the duration of copulation in spiders (e.g. Austad, 1982; Cohn, 1990; Andrade, 1996; Fahey & Elgar, 1997; Elgar *et al.*, in press; J.M. Schneider & M.A. Elgar, unpublished observations). This suggests that longer and/or multiple copulations allow males to deliver more sperm (e.g. Elgar, 1995), or that the duration of copulation influences the uptake and storage of sperm (e.g. Bukowski & Christenson, 1997; see also Christenson & Cohn, 1988). Orb-weaving spiders are also promiscuous, with several males often found on the webs of single females. Nevertheless, several genera of these spiders are characterized by diminutive males and large females (Elgar, 1991), even though relatively larger males of these species are thought to have a higher mating success (e.g. *Nephila clavipes*; Vollrath, 1980). The evolution of the extreme sexual size dimorphism in this taxon is puzzling, given this mating advantage for larger males. Indeed, explanations for the evolution of this pattern of sexual size dimorphism are controversial (Elgar, 1991; Vollrath & Parker, 1992; Head, 1995; Elgar & Fahey, 1996; Coddington *et al.*, 1997; Prenter *et al.*, 1997, 1998).

The female golden orb-weaver *Nephila edulis* is a large spider that builds a relatively permanent web. Mature males can be less than 10% of the size of a mature virgin female, and several males may cohabit on the webs of both penultimate and mature females. The reproductive tract of female *N. edulis*, like all entelegne spiders, is bilateral with two genital pores covered by a sclerotized plate called the epigynum, two sperm ducts and two receptacula seminis where the seminal fluid is stored. Males use secondary genital structures (pedipalps) for mating, which must be filled with sperm and then inserted into the female genital opening. In some spiders, the copulating male alternates between left and right palp without releasing the female, whereas the copulating male of most orb-web spiders typically inserts one palp, then releases the female and courts her again before inserting his other palp. However, almost 100% fertilization is achieved by a single insertion in *N. plumipes* and *Argiope keyserlingi* (M.A. Elgar, J.M. Schneider & M.E. Herberstein, unpublished observations; J.M. Schneider, M.L. Thomas & M.A. Elgar, unpublished observations). The practice of multiple insertions in these species is therefore curious since courtship is typically time-consuming and in some species involves the risk of sexual cannibalism (Robinson & Robinson, 1980; Elgar, 1992).

Here, we investigate the sources of variation in paternity and mating behaviour of *N. edulis*. In particular, we explore the relationship between body size and sperm competition by examining whether male size affects the frequency and duration of copulation and paternity. We also contrast the mating systems of *N. edulis* with the closely related, sexually cannibalistic *N. plumipes* in order to draw conclusions about the evolutionary significance of sexual size dimorphism in the presence and absence of sexual cannibalism.

Methods

Females of *N. edulis* are found in the drier woodland regions of eastern Australia, including both tropical and temperate regions. Although the spiders are quite common in these places, they are not found in the large aggregations that are typical of the closely related *N. plumipes* (Elgar, 1989). Sub-adult female and both sub-adult and adult male *N. edulis* were collected in February and March 1999 from several populations around Euroa, northern Victoria. The females were housed in individual cups until adulthood, when they were transferred to separate Perspex frames (100 × 75 × 20 cm), in which they built typical orb-webs. The females were watered and fed around eight blowflies *Lucilia cuprina* (Diptera) at least 3 days per week. Females were measured and weighed shortly after every moult. We used callipers to measure the length of the tibia-patella of leg I, and the maximum width of the cephalothorax (to the nearest 0.02 mm). The female was immobilized by covering her with Glad-Wrap (plastic

film). Males were collected as adults or sub-adults from the webs of females, and were maintained in the laboratory in individual cups (250 mL) on a diet of *Drosophila* (Diptera) and blowflies. The weight and length of the tibia-patella of leg I (to the nearest 0.02 mm) of each male was recorded several hours before its mating trial.

We staged matings by gently placing a male in the lower edge of the female's web, using a small paintbrush and, typically, he traversed the web to the hub. We noted the time when he reached the edge of the web and when he arrived at the hub. We introduced several flies into the web, as the initiation of courtship and mating in *N. plumipes* is more likely to occur if the female has just captured a prey item (e.g. Elgar & Fahey, 1996). The male usually proceeded to attempt to copulate with the female shortly after she had captured a prey item.

The males of *N. edulis* use two different mating tactics. In one, the male crawls onto the female's body from the same side of the web to which she is hanging, whereas in the other he remains on the other side of the web and copulates through a hole in the web that he had previously cut. Males did not always succeed in copulating at the first attempt, and we counted the number of attempts a male made until he copulated successfully. The reactions of the females towards approaching males were classified into one of three categories: (a) no reaction; (b) low aggression, in which the female tugged the web a few times and (c) high aggression, in which the female tugged the web intensively and rushed at the male. We recorded the time at which copulation commenced, and the time when the male removed his pedipalp and returned to the web or when he was caught and consumed by the female.

Patterns of paternity were determined using standard double-mating trials (following Parker, 1970). Mature males were randomly assigned to either normal (N) or irradiated (I) treatments; males in the latter were irradiated with a dosage of 10 krad from a cobalt- γ -emitter. The proportion of developed eggs was then used to calculate P_2 , the proportion of eggs fertilized by the second male. Females were randomly assigned to one of four treatments, which varied the order and composition of the two kinds of male mating partners. Thus, each female was provided with either: (a) a normal male and then an irradiated male (NI); (b) an irradiated male and then a normal male (IN); (c) two irradiated males (II) (which controls the sterilization success) or (d) two normal males (NN) (which controls the number of undeveloped eggs in a normal clutch). Following the standard method of calculating P_2 , the proportion of eggs hatched in the two treatments was corrected for the proportion of eggs hatched in the NN (0.84) control and in the II control (0 eggs hatched). The second male was always placed with the female at least 30 min after the first mating had occurred. However, not every female re-mated, and it was sometimes necessary to exchange the male or to repeatedly introduce him to the web for a

few days. There was a significant difference in the P_2 values between the IN (mean $P_2 \pm SE = 0.38 \pm 0.07$) and the NI (mean $P_2 \pm SE = 0.67 \pm 0.07$) treatments ($\chi_{84}^2 = 14.99$, $P < 0.0001$) suggesting that some nonfertilized or undeveloped eggs were wrongly assigned to the sterile male. However, the order of the sterile and normal males was reversed and paternity of first and second males was underestimated with the same probability. The mean of the distribution should thus not be affected although more noise (symmetrical) is added to the data, making it perhaps more difficult to detect significant relationships.

Mating in *N. edulis* typically occurs in the following way. The male mounts the female and drums on her epigyne with his pedipalps, sometimes briefly inserting a pedipalp. He then inserts one of his pedipalps for a much longer period, sometimes removing it briefly and then usually inserting the same pedipalp. Eventually, he removes his pedipalp and walks off the female. He may then re-mount the female and repeat the behaviour, either using the same or a different pedipalp. We defined a copulation bout as the period of time from when the male commenced inserting his pedipalp to when he walked off the female. We examined the relationship between paternity and frequency of copulation bouts by allowing some males within the above treatments, NI and IN to make either one or two copulation bouts. We randomly assigned females to mating trials in which the first male had two copulation bouts and the second male one, and vice versa. Nine females had only a single copulation bout with each male.

Mated females remained in their frames, where they were watered and fed around eight blowflies on at least 3 days per week. The mated female laid an egg sac about 35 days later, and this was removed and placed in a separate sterile plastic container with a perforated lid. The vials containing the egg sacs were placed in an incubator (25 °C). Eggs were preserved in alcohol after 1 month or once the eggs began to hatch (typically indicated when the egg sac felt soft). The hatchlings and undeveloped eggs were subsequently counted under the microscope.

Data were inspected for normality and transformed where appropriate. We used nonparametric tests for those data for which we could not obtain normal distributions. The data were analysed using JMP 3.2.2 (SAS Institute) for the Macintosh. Means are given $\pm SE$, unless specified otherwise.

Results

Less than 10% of the males that mated with a virgin female were cannibalized by the female, compared with 9% of males that mated with a mated female. There was no significant difference between males that were cannibalized and those that escaped in either the duration of copulation (first mate: Wilcoxon-test: $\chi^2 = 0.82$,

	First mate		Second mate	
	Cannibalized	Survived	Cannibalized	Survived
Male body mass (g)	0.013 ± 0.016 <i>n</i> = 5	0.035 ± 0.004 <i>n</i> = 87	0.015 ± 0.01 <i>n</i> = 8	0.028 ± 0.003 <i>n</i> = 83
Copulation duration (s)	280.8 ± 87.76 <i>n</i> = 5	199.3 ± 21.16 <i>n</i> = 86	406.5 ± 124.2 <i>n</i> = 8	268.7 ± 36.3 <i>n</i> = 82

	<i>n</i>	Mean	SE	Median	Maximum	Minimum
Virgin females						
First copulation	91	203.7	20.55	145	786	8
Second copulation	43	207.2	43.9	83	1403	6
Total copulation	91	301.7	34.8	202	1710	12
Mated females						
First copulation	90	185.5	26.4	100	1523	7
Second copulation	39	220.9	39.9	111	1073	8
Total copulation	90	280.9	34.9	131	1523	7

$P > 0.36$; second mate: $\chi^2 = 3.12$, $P > 0.07$) or in male body mass (first mate: $\chi^2 = 1.88$, $P > 0.17$; second mate: $\chi^2 = 3.37$, $P > 0.06$; Table 1).

Duration of copulation and paternity

The mean total duration of copulation was roughly doubled if the male was allowed to make two copulation bouts (Table 2). The duration of the first and second copulation bout of the same male were positively correlated when the male mated with either a virgin ($r_s = 0.53$, $P < 0.0003$) or mated female ($r_s = 0.34$, $P < 0.04$). There was no significant difference in the total duration of copulation (the first and second copulation bouts were summed for males that had two bouts) of males that mated with either virgin or mated females ($t_{1,179} = 0.42$, $P > 0.67$; Table 2).

The proportion of eggs fertilized by the second male, P_2 , was not normally distributed; both extremes of the distribution were more common than values around 50% (Fig. 1). This pattern persists if the data for the two treatments (either the first or the second male had two copulation bouts) are inspected individually. The mean P_2 when both males had only one copulation bout was 0.66 (SD = 0.56, median = 0.83, $n = 8$), which was not significantly different from 0.5 (Wilcoxon-signed-rank = 7, $P > 0.3$). In general, paternity was positively correlated with the duration of copulation (Table 3), and it clearly increased if the male was able to have two copulation bouts. The median paternity of a male mating with a virgin female was 0.24 (mean ± SE, 0.33 ± 0.07, $n = 46$) if he had a single copulation bout and 0.78 (mean ± SE, 0.64 ± 0.07, $n = 40$) if he had two copulation bouts ($F_{1,84} = 9.99$, $P < 0.003$). A similar pattern emerged for males mating with mated females: males

Table 1 Mean (±SE) body mass and duration of copulation of males that were cannibalized or survived mating as the first or second mate of a female.

Table 2 The durations of copulations (s) of first and second copulation bouts of either virgin or mated females. 'Total copulation' are the statistics for the absolute copulation duration of particular males irrespective of whether they had one or two copulation bouts. The frequency distribution of the duration of copulation was significantly different from normal, with brief copulations being more common.

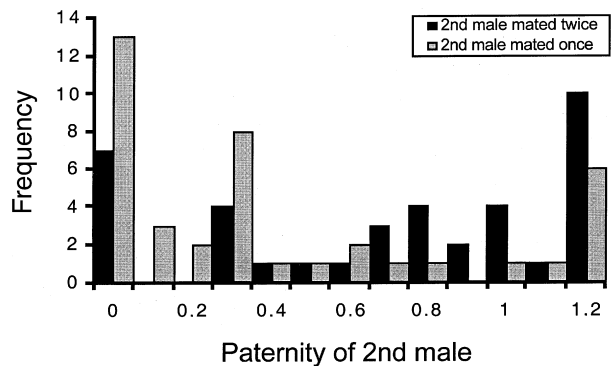


Fig. 1 The distribution of P_2 values. The dark bars indicate the experiments where the second male was allowed to mate twice whereas the first male copulated once. The lighter bars show P_2 for females that copulated twice with their first and once with their second mate.

that had a single copulation bout had a median paternity of 0.23 (mean ± SE, 0.41 ± 0.07, $n = 48$) compared with a median paternity of 0.76 (mean ± SE, 0.67 (0.07, $n = 38$) for males that had two copulation bouts ($F_{1,84} = 6.81$, $P < 0.002$). Cases where the first and the second male had only one copulation bout are incorporated in the above analyses.

Body size, mating behaviour and duration of copulation

The distribution of body mass of males was skewed, with a relatively large number of smaller males (Fig. 2). This distribution suggests that selection may favour smaller males. This may be mediated by the influence of body

Table 3 Spearman correlation coefficients between the duration of copulation and male body mass and paternity of the focal male (P_1 or P_2).

	Correlation coefficient			<i>n</i>
	<i>n</i>	Male mass	Paternity	
Virgin females				
First copulation duration	91	-0.57***	0.32*	86
Second copulation duration	43	-0.20	0.56**	40
Total copulation duration (sum _{virgin})	91	-0.62***	0.43***	86
Mated females				
First copulation duration	90	-0.62***	0.53***	85
Second copulation duration	39	-0.19	0.53**	38
Total copulation duration (sum _{mated})	88	-0.60***	0.59***	85
(sum _{mated}) - (sum _{virgin})	88	-0.63***	0.61***	83

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

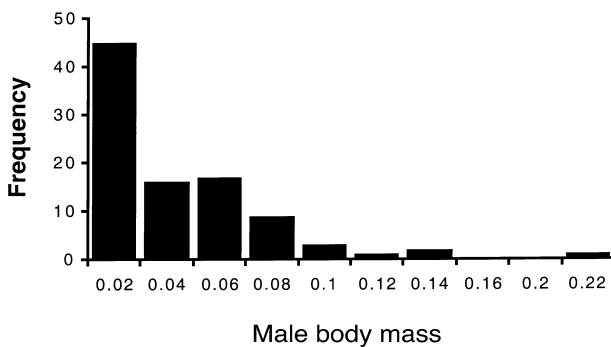


Fig. 2 Distribution of male body mass (g).

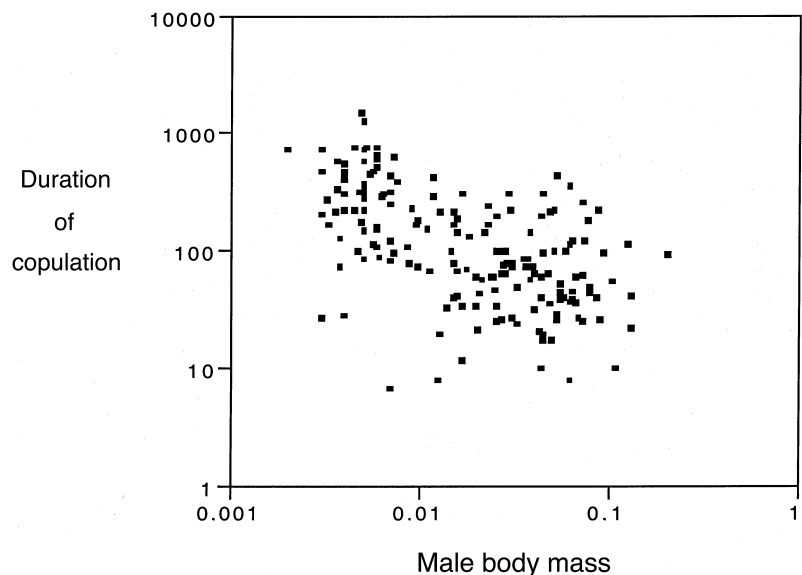
size on the duration of copulation. Smaller males generally copulated longer than large males (Fig. 3), and the duration of copulation was negatively correlated with male body size for both individual and combined copulations (Table 3). There was also a direct positive

association with being small and gaining paternity. Body mass of the first male was significantly correlated with paternity (P_1) ($n = 86$, $r_s = -0.3$, $P < 0.004$) as was the mass of the second male (P_2) ($n = 86$, $r_s = -0.27$, $P < 0.011$).

Male mating strategies were influenced by their body size. Males that walked directly onto the body of the female were significantly smaller than males that copulated through a hole that they cut in the web (virgin females: first copulation, $F_{1,63} = 21.4$, $P < 0.0001$; second copulation, $F_{1,24} = 8.69$, $P < 0.008$; mated females: first copulation, $F_{1,56} = 8.3$, $P < 0.006$, second copulation, $F_{1,18} = 1.5$, $P < 0.24$) (Fig. 4).

Females were rarely aggressive towards males (Table 4); 60–70% of all male approaches did not elicit a visible reaction from the female. There was no relationship between female aggression and male body mass (Table 4), but male size influenced their ability to initiate copulation. Small males were more likely to copulate at their first attempt, whereas larger males were

Fig. 3 The relationship between male body mass (g) and the duration of copulation (s) plotted on a log-log scale. Data from all males are pooled irrespective of whether they mated once or twice.



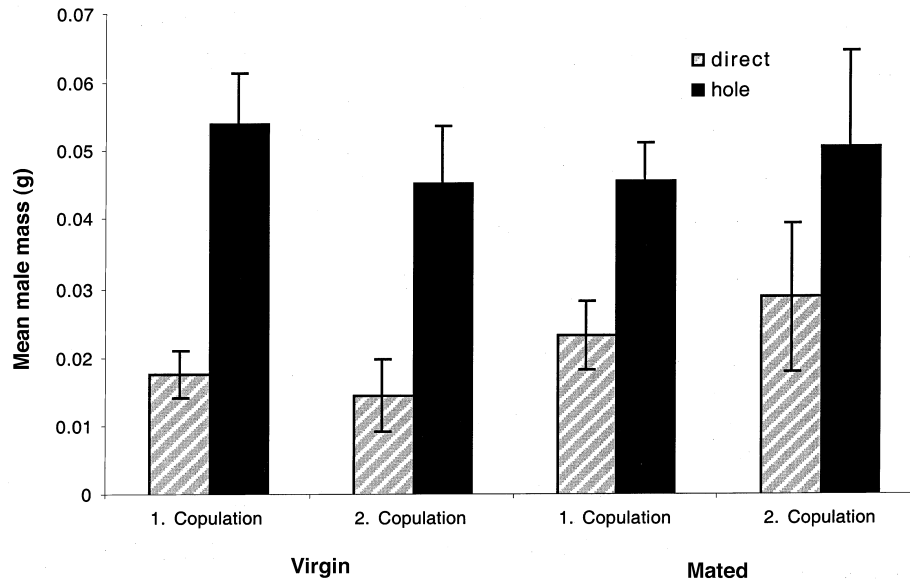


Fig. 4 Mean body mass with standard errors of males that mated directly from the body of the female (grey bars) or through a hole in the web (black bars). Data are separated for 1 and 2 copulations of males that mated with virgin or mated females.

Table 4 Female reaction towards an approaching male was classified into four categories of either no, mild or high aggression and the fourth category of aggression that prevented mating never occurred. Relative frequencies are given in percentages and true frequencies in parentheses. The last column gives results of a Wilcoxon-rank sum test between the rate of aggression of the female and the body mass of the male. None of the values is significant.

Aggression	No. (%)	Mild (%)	High (%)	χ^2 with male mass
First male, first copulation	61 (55)	29 (26)	10 (9)	2.73
First male, second copulation	74 (32)	16 (7)	9 (4)	1.60
Second male, first copulation	77 (70)	15 (14)	8 (7)	2.64
Second male, second copulation	62.5 (25)	27.5 (11)	10 (4)	0.91

more likely to mate after two or more (up to 36) attempts to copulate (virgin female: first copulation, $t_{1,90} = -2.1$, $P < 0.04$; mated female: first copulation, $t_{1,89} = -2.7$, $P < 0.009$).

Discussion

Paternity in *N. edulis* is a direct function of the duration of copulation. When two males compete over paternity, the male that mates the longest or most frequently gains the larger share of paternity. Curiously, small males copulate longer than large males and thus fertilize relatively more eggs. Cannibalism is infrequent in this species (see also Uhl & Vollrath, 1998) and females rarely show aggressive behaviour towards males. Nevertheless, large males

require more attempts to achieve a successful copulation than small males.

Paternity is expected to correlate with the duration of copulation when either sperm transfer or sperm uptake is a function of time. The mechanism of sperm competition may be similar to that described for many insect species (Simmons & Siva-Jothy, 1998). Males that copulate longer, transfer more sperm and thus should fertilize a greater proportion of eggs (see Parker, 1998). The relative number of sperm transferred per male would thus determine paternity. However, in the sister species, *N. plumipes*, the number of sperm stored by the female was independent of the duration of copulation (J.M. Schneider & M.A. Elgar, unpublished observations). An alternative mechanism is internal courtship and cryptic female choice (Eberhard, 1996, 1998). Sperm transfer occurs early in copulation in several spiders (e.g. Brown, 1985), and sperm uptake or storage by the female may depend on the performance of the male during mating. The longer a male courts the female internally after sperm has been transferred, the more of his sperm will be used for fertilization (see also Bukowski & Christenson, 1997). Both mechanisms may result in a mating system in which the males enjoy greater fertilization success by mating repeatedly, and females may exert mate choice by selectively allowing repeated copulations. However, which sex controls the length of copulation and what internal mechanism determines the success of a male requires further investigation.

Males employ one of the two mating strategies that depend upon their body size. Smaller males climb directly onto the body of the female from her side of the web. In contrast, larger males remain on the web, on

the opposite side to the female, and mate by cutting a hole in the web through which they gain access to her. They usually touch the females with several legs, but do not climb onto her. These male behaviours suggest different requirements for successful copulations of males of different sizes. Large males may have more difficulty initiating mating, as indicated by the high number of unsuccessful mating attempts. The less competent larger males sometimes failed to cut a large enough hole in the web, or attempted to mount the female, which was impossible because of their size. Small males may be more successful in approaching or mating unnoticed (see Elgar & Fahey, 1996). Alternatively or additionally, females may actively prefer copulation attempts of small males.

Explanations for the evolution of the extremely small size of males, typical in the genus *Nephila*, are controversial. One suggestion is that diminutive males may be favoured by selection through sexual cannibalism, if females do not detect small males or their size provides little nutritional value (Cambridge, 1871; Darwin, 1871; Elgar, 1991; Elgar & Fahey, 1996), but this argument clearly does not apply to *N. edulis*. Vollrath & Parker (1992) argue that the extreme sexual size dimorphism in these spiders is a result of the sex ratio bias that arises from differences in male and female life-styles. A female bias may occur in species with relatively sedentary adult females and more mobile adult males that suffer higher mortality as a result of their mate searching behaviour. The female biased sex ratio relaxes selection by male-male competition for larger male size and thus selection for protandry will favour diminutive males (Vollrath & Parker, 1992). Coddington *et al.* (1997) use phylogenies to argue that small male size arises from selection favouring evolutionary changes to larger female body size rather than smaller male body size. Further comparative studies support the idea that sexual size dimorphism is largely driven by variation in female rather than male size (Prenter *et al.*, 1997, 1998). However, the question remains why male body size did not also increase with female body size. Whatever the evolutionary progression, selection must have either favoured smaller male body size and/or suppressed any increase in male body size. Our data, which reveal that smaller males have a mating advantage in sperm competition, add a novel aspect to this debate.

Considerable size variation in males is a characteristic of *N. edulis* (see also Uhl & Vollrath, 2000). Why is this variation maintained, despite a directional selective advantage through sperm competition and female choice? Several selection pressures that favour large male body size have been identified: larger males may be at an advantage when several males on the web compete for access to the female (Vollrath, 1980; Elgar & Fahey, 1996); large males may live longer and hence have more time to search for mates (Vollrath & Parker, 1992) and large males may produce more sperm,

enabling them to charge their palps more often and fertilize more females. The relative strength of these various selection pressures may explain the distribution of male body sizes (Elgar & Fahey, 1996; Prenter *et al.*, 1998).

The importance of opposing selection pressures is further highlighted by the comparison of *N. edulis* with its sister species *N. plumipes*. These almost indistinguishable species occur sympatrically and have similar ecological and life-history attributes. However, the coefficient of variation in body sizes of *N. edulis* is 104% for males (28.2% for females), whereas males vary in size by only 31.7% (the mean body mass is smaller than in *N. edulis*) in *N. plumipes*. The major difference between the two species is that females of *N. plumipes* are highly sexually cannibalistic. Smaller males are less likely to be cannibalized than larger males (Elgar & Fahey, 1996; J.M. Schneider & M.A. Elgar, unpublished observations), although there is no evidence that smaller males enjoy greater fertilization success. Males of *N. plumipes* are very unlikely to inseminate more than two females because of the high rate of cannibalism and physical damage that occurs to the male mating organ in most matings. The combination of low average and small variation in mating success will significantly reduce the competitive advantages for large males, thereby relaxing selection on large body size and may thus explain the absence of large males in this species. The variation in this genus starkly illustrates the risks of generalizing findings from studies of a single species.

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