# Sexual cannibalism and sperm competition in the golden orb-web spider *Nephila plumipes* (Araneoidea): female and male perspectives

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Mating systems are frequently shaped by conflicts over reproductive interests between males and females. Sexual cannibalism can be an especially dramatic manifestation of such conflicts. However, the resolutions of this conflict differ among sexually cannibalistic spider species. Cannibalism may be in the interest of both sexes when females consume males as a foraging decision to improve fecundity and/or males sacrifice their bodies to increase fertilization success. In other species, females exert sequential choice of partner by selectively terminating copulation through cannibalism while males fail to obtain a paternity advantage. Here, we investigate the adaptive value of cannibalism in the orb-web spider *Nephila plumipes* where 60% of males do not survive copulation. Virgin females in poor condition are more frequently cannibalistic and more likely to kill large males, but the frequency of cannibalism among mated females is not influenced by these factors. Instead, males that mate with mated females increase their fertilization success by being cannibalized. Cannibalized males generally mate for longer, but longer copulations correspond with increased paternity only in mated females. The amount of sperm from particular males that a female stored was not influenced by any of the measured variables. The number of sperm stored was not related to paternity, nor was there any detectable reduction in sperm number after females had reproduced. Our data suggest that the conflict between the sexes differs between virgin and mated females. Females should always cannibalize a male, but males only gain from cannibalism when mating with mated females, not when mating with virgin females. Interestingly, the frequencies of cannibalism are not different in matings with virgin or mated females. *Key words:* cannibalism, foraging, mating, paternity advantage. *[Behav Ecol 12:547–552 (2001)]*

M ating systems are frequently characterized by conflicts of interest between the sexes, most especially over the frequency of mating. Multiple mating clearly increases the reproductive success of males (Andersson, 1984; Bateman, 1948), but several benefits of multiple mating to females have been recently identified. These include sequential female choice (e.g., Elgar et al., 2000; Tregenza and Wedell, 1998), and producing clutches with genetically more variable and/ or viable offspring (e.g., Shykoff and Schmidt-Hempel, 1991; Watson, 1998; see also Møller, 1998). However, polygamy can create a conflict of interest if the ensuing sperm competition reduces the fertilization success of rival males. An extraordinarily diversity of male adaptations has evolved in order to prevent the sperm of rival males from fertilizing the eggs of the female (Birkhead and Møller, 1998), and these adaptations may act as selective pressures favoring both male and female counter-adaptations.

Sexual cannibalism, in which the female cannibalizes a potential or actual mating partner at around the time of copulation (Elgar, 1992) represents a particularly dramatic manifestation of sexual conflict. The conflict is straightforward if cannibalism occurs before insemination; the female may obtain nutritional benefits, but the male forfeits future reproductive opportunities (e.g., Elgar and Nash, 1988). However, there are both conflicts and congruences of interest between the sexes when cannibalism occurs after the male has inseminated the female (Andrade, 1998; Elgar, 1998). For example,

female and male interests may be similar if his cannibalized soma increases female fecundity, and this paternal investment compensates for any loss of future reproductive opportunities (Buskirk et al., 1984). However, a conflict arises if the female mates with another male and the male shares paternity with this rival male (Elgar, 1998).

This conflict appears to be resolved in favor of both sexes in the redback spider *Latrodectus hasselti* (Andrade, 1996). Experiments involving double matings showed that cannibalized males had a greater fertilization success than males that survived, in part because cannibalized males copulated for longer and also because cannibalistic females were less likely to mate again. Thus, while female *L. hasselti* may improve their fecundity by eating their mates, they may lose complete control over the paternity of their offspring if males can induce females to be unreceptive. However, this pattern may not be general for all spiders if sexual cannibalism allows the female to control the duration of copulation; female *Argiope keyserlingi* delay cannibalizing relatively smaller males, and these males copulate for longer and fertilize relatively more of her clutch (Elgar et al., 2000).

Clearly, any analysis of the adaptive significance of sexual cannibalism must be made from both the female and male perspective. Sexual cannibalism may increase female fecundity, and thus females in poor condition may attempt to cannibalize males more vigorously than females in good condition (Andrade, 1998; Newman and Elgar, 1991). Additionally, larger males may be more attractive prey items than smaller males, and hence more frequently cannibalized. If sexual cannibalism allows the female to control the paternity of her clutch, then there should be an association between cannibalism, copulation duration, and paternity. The benefits of sexual cannibalism to the male depend upon his future mating opportunities, which are expected to be low. A paternal

investment benefit requires that either the female mates once only, or that the cannibalized male fertilizes most of her eggs. Thus, cannibalized males should have a higher paternity than noncannibalized males. Alternatively, sexual cannibalism may be against the reproductive interest of the male, and thus he will always attempt to escape.

The golden orb-web spider *Nephila plumipes* frequently cannibalizes males both before and during copulation (Elgar and Fahey, 1996). This spider, like others in the genus (Elgar, 1991), is highly size-dimorphic, with males less than 5% of the body weight of mature, fecund females. The spider is common along the eastern coastal seaboard of Australia, and usually abundant where it occurs. *N. plumipes* are found in large aggregations, with as many as 10 webs that either share structural threads or are found within 20 cm of another web (Elgar, 1989). The webs of adult and sub-adult females may also contain several mature males (Elgar, 1989; Elgar and Fahey, 1996; Robinson and Robinson, 1980). Here we explore the adaptive significance of sexual cannibalism by conducting staged mating experiments with males and females of known reproductive status.

## METHODS

Sub-adult female and both sub-adult and adult male *N. plumipes* were collected in January and March 1998 from a large single population located in the mangroves at Towra Point, Botany Bay, Australia. Most of the females were housed in separate perspex frames (100 cm × 75 cm × 20 cm), where they built typical orb webs; the remaining females were kept in up-turned plastic cups (1000 ml). The females were watered and fed around 10 bushflies *Lucilia cuprina* on each of 3 days per week. Females were measured and weighed shortly after they matured and again after they had oviposited for the first time. We used callipers to measure the total body length and the width of the cephalothorax across the dorsal eyes. The female was immobilized by covering her with plastic film. Males were collected as adults from the webs of females or as sub-adults from their own webs, which were mostly found near the trunk of mangrove trees. In the laboratory, males were maintained in individual cups (250 ml) on a diet of *Drosophila*. Under a dissecting microscope, males were carefully inspected for species-specific traits and the status of their pedipalps; body length of each male was measured to the nearest 0.5 mm. Most of the males were weighed shortly afterwards.

Patterns of paternity were determined using standard double-mating trials (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 number of eggs fertilized by the second male. Females were randomly assigned to one of four categories, 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 for the sterilization success); or (d) two normal males (NN) (which controls for the number of undeveloped eggs in a normal clutch). The second male was always placed with the female on the day that the first mating had occurred. However, not every female remated the same day, and it was sometimes necessary to exchange the male or to repeatedly introduce him to the web for a few days.

Matings were staged by gently placing a male in the lower corner of the frame, using a small paintbrush. Typically, the male walked up the side of the frame, eventually encountering one of the support threads of the orb web. He then traversed the web to the hub, where he would wait on the opposite side of the female. We noted when the male reached the edge of the web and the hub. Males rarely moved from this location unless the female captured a prey item (Elgar and Fahey, 1996), and so we threw several bushflies into the web. Shortly after the female had captured a fly, and sometimes while she returned to the hub, the male would jump onto her body, run over her a few times and then insert his pedipalp. At that point we started to time the duration of copulation, and checked which pedipalp was inserted into which opening of the female. We recorded the time when either the male removed his pedipalp and jumped off the female, or when the female caught and wrapped him. Some males inserted repeatedly either the same or the other pedipalp and we stopped and restarted timing the duration of copulation accordingly. Repeated insertions happened four times. Typically, a few initial brief insertions precede the one, probably significant, copulation. Insertions were interrupted by pauses of less than 5 s. Males that were captured by the female were immediately removed before the female could feed on them.

Mated females were transferred to separate cups, where they were watered and fed around ten bushflies *L. cuprina* on each of 3 days per week. Another unmated female was then placed in the vacant frame. The mated female laid an egg sac about 35 days later, and this was removed and placed in a separate sterile plastic container that was closed with cotton wool. The vials containing the egg sacs were placed in a large open basin of water in a controlled temperature room (25°C). Eggs hatched 1 month later and were preserved in alcohol. The hatchlings and undeveloped eggs were subsequently counted under the microscope. A number of females died either before they had produced eggs or shortly after they had made their first egg sac (containing eggs). These females were dissected, and we extracted and counted the sperm from each spermatheca, following Bukowski and Christenson (1997). The causes of death are unknown. Most females were found dead in the early morning and were immediately preserved. Since this may not be a random sample of the population, we cannot exclude the possibility of drawing our data from a biased sample.

Data were visually and statistically 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 analyzed using JMP 3.2.2 (SAS Institute) for the Macintosh. Means are given ± standard error, unless specified otherwise. Sample sizes can be different because not all measurements were taken from all spiders.

## RESULTS

We observed a total of 149 matings of *N. plumipes,* of which 79 were with a virgin female and 70 were the second mating of that female. Males were captured and cannibalized in 56% of the matings with virgin females and in 61% of the matings with mated females ($\chi^2 = 0.5$, $p > .47$).

*Cannibalism and body size*
Virgin females that cannibalized males were significantly smaller than females that did not attack males (female body mass, $t_{67} = 3.005$, $p < .004$; female body length, $t_{67} = 2.61$, $p < .012$; female prosoma: $t_{67} = 2.27$, $p < .027$; Table 1). However, there was no significant difference in the size of cannibalistic or noncannibalistic females mating with a second male (female body mass, $t_{60} = 1.207$, $p > .2$; female body length, $t_{60} = 0.89$, $p > .3$; female prosoma, $t_{60} = 0.94$, $p > .3$).

Females were weighed at or shortly after the day of maturation (median = 1 day, upper and lower quartile: 0–3). Most females were mated with their first male within the first 2

**Table 1**

**Body parameters of cannibalistic and noncannibalistic females and of males that were eaten or escaped**

| | First mating | | | | Second mating | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Cannibalism | | No cannibalism | | Cannibalism | | No cannibalism | |
| Female mass (g) | 0.503 | (0.02) | 0.611 | (0.03) | 0.524 | (0.02) | 0.574 | (0.03) |
| Female length (mm) | 18.47 | (0.22) | 19.41 | (0.29) | 18.72 | (0.25) | 19.09 | (0.34) |
| Female prosoma | 4.53 | (0.08) | 4.79 | (0.08) | 4.59 | (0.07) | 4.71 | (0.12) |
| Female condition | 0.110 | (0.003) | 0.126 | (0.005) | 0.113 | (0.004) | 0.120 | (0.005) |
| Male mass (g) | 0.0165 | (0.001) | 0.0133 | (0.001) | 0.0153 | (0.001) | 0.0147 | (0.001) |
| Male length (mm) | 6.18 | (0.10) | 5.68 | (0.12) | 6.07 | (0.10) | 5.83 | (0.14) |

Standard errors are given in parentheses. Statistics are given in the text.

weeks after maturation (median = 7, upper and lower quartile: 4–13). The second male was introduced on the same day but not all mated that day so that the median interval between first and second mating is 1 day (upper and lower quartile: 0–6). The cephalothorax of spiders is a sclerotized body part that does not change after the final molt. Thus, the mass of a female relative to her cephalothorax width can be used as an estimate of her condition when the relationship is linear, which is the case for our range of data. Here we can only estimate condition at the time of maturation. Cannibalistic virgin females matured in a poorer condition than noncannibalistic females ($t_{67} = 2.82$, $p < .007$) but there was no difference in mated females ($t_{60} = 0.98$, $p > .3$). Each female received the same quantity of food in regular intervals and they were also fed during mating trials. Thus, females that received their second male long after their first male may have improved their condition such that its effect on cannibalism was masked. Therefore, we analyzed the relationship between the interval between first and second mating on the likelihood of cannibalism of the second male ($\chi^2 = 0.09$, $p > .7$), and the interval between maturation and first male encounter on the likelihood of cannibalism of virgin females (Kruskal-Wallis Test, $\chi^2 = 0.06$, $p > .8$). If current condition is more important than condition at maturity, we would have expected a reduction in the rate of cannibalism with increasing time.

The size of the male also influenced the outcome of matings. Males that were cannibalized by virgin females were larger than males that avoided cannibalism (male body length, $t_{67}$
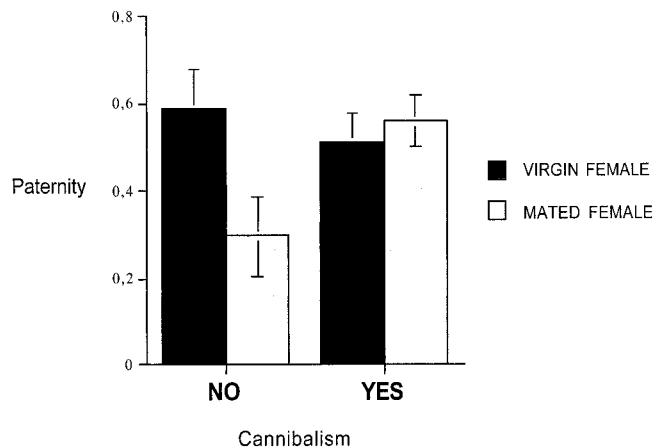


**Figure 1**
Paternity of males that either escaped or were captured by either virgin or mated females. Second mates who were not cannibalized had a reduced paternity compared with second mates that were cannibalized.

$= -3.265$, $p < .002$; male body mass, $t_{39} = -2.415$, $p < .022$; Table 1). However, there was no significant difference in the body size of cannibalized and noncannibalized males that mated with mated females (male body length, $t_{62} = -1.463$, $p > .15$; male body mass, $t_{38} = -0.397$, $p > .6$).

*Cannibalism and paternity*
The double mating experiments revealed that *N. plumipes* has a mixed paternity pattern with a high degree of variation in $P_2$, the proportion of eggs fertilized by the second male. $P_2$ ranged from zero to one, with a median of 0.42 and a mean of $0.46 \pm 0.05$, which was not significantly different from 0.5 ($t = -0.81$, $p > .4$, $n = 33$). The distribution was not significantly different from normal (Shapiro-Wilk Test, $W = 0.94$, $p = .08$).

$P_2$ values, analyzed separately for both treatments, revealed a median of 0.37 (mean = $0.37 \pm 0.08$) for 16 IN females and a median of 0.43 (mean = $0.54 \pm 0.07$) for 17 NI females ($t_{31} = 1.55$, $p > .13$). $P_2$ values were corrected for the 72.8% hatching success in NN controls and 1.17% success in II controls, using the formula suggested by Boorman and Parker (1976). Cannibalism by virgin females had no effect on $P_2$ ($F_{1,31} = 0.56$, $p > .4$). Males that were killed by virgin females sired a mean proportion of $0.51$ ($\pm 0.07$) of the eggs in the first clutch, while males that survived sired $0.60$ ($\pm 0.09$) of the eggs (Figure 1). However, cannibalism by mated females had a dramatic influence on paternity; males that were cannibalized by mated females sired $0.56$ ($\pm 0.065$) of the clutch, compared with only $0.29$ ($\pm 0.081$) for males that survived mating (Figure 1). Two-way analysis of variance revealed that $P_2$ was significantly influenced by cannibalism of the second male ($F_{3,29} = 5.60$, $p < .025$) but not the first male ($F_{3,29} = 0.24$, $p > .6$). The interaction term was not significant ($F_{3,29} = 0.01$, $p > .9$).

Although we introduced a second male into the frame the same day after mating had taken place, the time between first and second matings varied between 0 and 15 days. This is because not every female immediately remated, and some females did not remate for several days. Females that cannibalized their first male were not more reluctant to remate than noncannibalistic females (Kruskal-Wallis Test, $\chi^2 = 0.67$, $p > .4$, $n = 49$). However, $P_2$ increased with the time interval between mating ($r_s = .44$, $p < .011$). Analysis of covariance revealed that cannibalism of the second male ($F_{3,29} = 7.3$, $p < .012$) still explained a significant proportion of the variance in $P_2$ ($r^2 = .28$) when corrected for the mating interval ($F_{3,29} = 4.2$, $p < .049$). However, the results of this multiple analysis may not be reliable because we could not obtain a normal distribution for the mating interval. Finally, $P_2$ was not influenced by the size difference between the two males (differ-
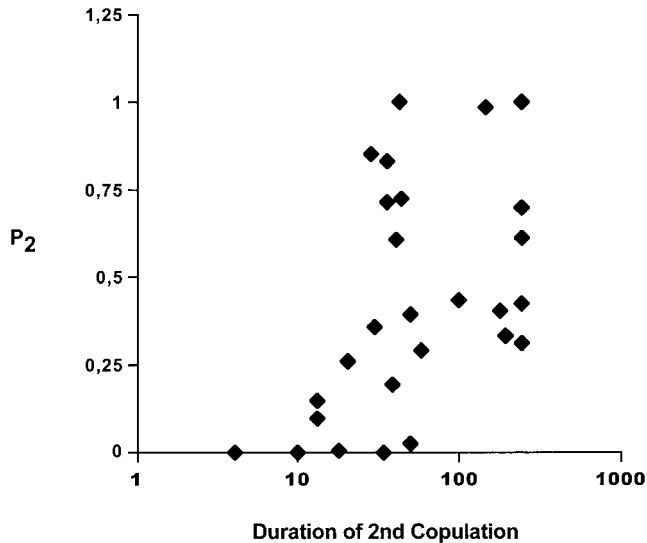
**Figure 2**
The paternity of the second male ($P_2$) on the log of duration of copulation of the second male. Longer copulations are associated with a higher $P_2$.

ence in body mass, $F_{1,13} = 0.05$, $p > .8$; difference in body length, $F_{1,32} = 0.86$, $p > .3$).

*Copulation duration, paternity, and sperm count*
The duration of copulation was measured as the time during which the male conductor was inserted in the female genital opening. The duration of copulation ranged between 12 and 298 s (mean = $57.4 \pm 7.1$, $n = 45$) for virgin females and 2 and 240 s (mean = $53.0 \pm 8.8$, $n = 38$) for mated females. Data for the copulation duration are not normally distributed so we used log-transformed data for parametric statistics.

Cannibalism prolonged the duration of copulation, independently of whether the female was virgin or mated. Males that were cannibalized by virgin females ($n = 26$) copulated for a mean of $74 \pm 11$ s, which was significantly longer than for males that survived (mean = $34.6 \pm 3.7$ s, $n = 19$; ANOVA, $F_{1,43} = 18.1$, $p < .0001$). A similar pattern emerged for males that copulated with mated females (cannibalized males, mean = $77.5 \pm 17.1$ s; noncannibalized males, mean = $33.2 \pm 5.1$; ANOVA, $F_{1,37} = 6.6$, $p < .015$). $P_2$ was not significantly correlated with the duration of copulation of the first male ($r_s = .1$, $n = 26$, $p > .6$), but there was a significant correlation for the second male ($r_s = .55$, $n = 21$, $p < .01$, Figure 2). The difference in the duration of copulation for the two matings did not influence $P_2$ ($r_s = .10$, $n = 18$, $p > .6$).

During mating, males usually inserted their pedipalp in only one genital opening of the female. We were able to relate the number of sperm per spermatheca to a specific male if only one male used that spermatheca. This was the case with 16 first males and 13 second males. We could ascribe unambiguously the content of each spermathecae to either of the two mates for only 12 females. Data were log-transformed before the use of parametric tests. There were between 2640 and 48,840 sperm per spermatheca, with no significant difference in the number of sperm found in the two (paired $t$ test, $t_{28} = -1.56$, $p > .13$) nor any systematic difference in the number of sperm in left or right spermathecae ($t_{56} = -1.2$, $p > .28$). We also found no difference in the absolute number of sperm stored delivered by first (mean = $14424 \pm 2899$, $n = 16$) and second males (mean = $19038 \pm 3842$, $n = 16$; Kruskal-Wallis Test $\chi^2 = 1.0$, $p > .3$). However, pair-wise comparisons revealed a significant linear correlation between the number of sperm stored from the first and second males ($F_{1,11} = 17.39$, $p < .002$), with consistently but not significantly more sperm being stored from the second than from the first male (paired $t$ test: $t_{11} = -2.01$, $p = .07$).

The number of sperm stored in the spermatheca was not influenced by either the body mass or the body length of the first male (mass, $F_{1,8} = 0.66$, $p > .4$; length, $F_{1,15} = 0.014$, $p > .9$), nor by the mass and size of the second male (mass, $r^2 = .21$, $F_{1,9} = 2.1$, $p > .19$; length, $r^2 = .38$, $F_{1,12} = 3.51$, $p < .09$). There were no order effects, since there was no difference between the first and second males in either body mass (paired $t_{82} = -.38$, $p > .7$) or body length ($t_{64} = 0.34$, $p > .7$). The number of sperm per spermatheca was not significantly influenced by whether the first (Kruskal-Wallis Test, $\chi^2 = 0.63$, $p > .4$) or second (Kruskal-Wallis Test, $\chi^2 = 0.34$, $p > .5$) male was cannibalized. Finally, there was no significant correlation between the number of sperm stored in the spermatheca and the duration of copulation of the first mating ($r^2 = .02$, $F_{1,14} = 0.005$, $p > .9$) or second mating ($F_{1,12} = 0.20$, $p > .6$). The difference in the length of copulation of the first and second male was not significantly related to the corresponding difference in sperm per spermatheca ($r_s = .44$, $p > .15$). The number of sperm per spermatheca was not influenced by whether the female had produced her clutch of eggs (Table 2).

## DISCUSSION

Sexual cannibalism in *N. plumipes* appears to be a female foraging strategy, and may also represent a male strategy to improve his fertilization success. For polygamous females, the second male sires a larger proportion of the offspring if he is cannibalized. Although cannibalized males copulate for longer than males that escape, they do not necessarily transfer

**Table 2**

**Comparison of sperm counts between females that had produced one egg sac and females that had no eggs yet**

| | Mean number of sperm per spermatheca | | | |
|---|---|---|---|---|
| | Females without eggs (SE; $n$) | Females with eggs (SE; $n$) | $\chi^2$ | $p$ |
| Left spermatheca | 15,427.5 (4063.2; $n = 8$) | 14,488.6 (2507.9; $n = 21$) | 1.1 | >.29 |
| Right spermatheca | 16,775.0 (3528.0; $n = 8$) | 16,238.1 (2177.6; $n = 21$) | 0.5 | >.49 |
| First male | 13,816.0 (2752.6; $n = 5$) | 15,381.7 (2384.4; $n = 12$) | 0.07 | >.79 |
| Second male | 19,712.0 (2900.8; $n = 5$) | 18,406.7 (4355.1; $n = 12$) | 0.6 | >.46 |

In some cases it was clear which male had mated into which spermatheca but not in all. Therefore sample sizes are much smaller in the second half of the table. Egg laying did not effect the number of sperm stored by a female in a detectable way.

more sperm. Nevertheless, males mating with mated females appeared to transfer more sperm than those mating with virgin females. This suggests that either the male can assess whether a female has mated previously and adjusts the quantity of sperm transferred accordingly, or that the number of sperm stored is under female control.

The evolution of sexual cannibalism should be viewed from the perspective of both males and females, taking into account the possible conflicts and congruences of interests between the sexes. Here we discuss the mating system of *Nephila plumipes* from first the female and then the male perspective.

*Female perspective*
Several lines of evidence suggest that virgin females cannibalize males because of a foraging decision. First, virgin females that mature small and in poor condition are more likely to cannibalize males than females in good condition (see also Newman and Elgar, 1991). Second, large males are more often captured than small males. However, these lines of evidence also raise the question why females are not always cannibalistic. There are several explanations. Smaller males may not be attractive prey items. Andrade (1998) suggested that females of the redback spider *L. hasselti* do not always cannibalize their mates because the nutritional value may not balance the handling costs. This explanation is unlikely for *N. plumipes* because *Nephila* feeds on a variety of prey items, including those that are small (Herberstein and Elgar, 1994) and items that are not immediately ingested are stored in the web for later consumption (Champion de Crespigny et al., 2001). Females may spare preferred males, perhaps to encourage them to mate with them again, or allow them to chase off other suitors. It is difficult to explain why females would then spare the small males that are less able to chase off rivals, at least in a related species (Christenson and Goist, 1979; Vollrath, 1980). Small males may be better at evading the female (see also Elgar and Fahey, 1996), Alternatively, some females, perhaps the large and fat ones, may be less rapacious than others; this may be indicated by the connection between condition at maturation and cannibalistic behavior. Although small females in poor condition may improve their condition from the day of their last molt to the day of mating, they may still be more rapacious than females that matured in a good condition. Size and condition at maturation may reflect habitat quality and may trigger different foraging strategies.

Interestingly, mated females behave very differently from virgin females. Mated females cannibalize males with the same frequency as virgin females, but their success is not related to either their own body parameters or the size of the male. However, possible effects of body condition may be masked by the experimental design because females received various prey items during the mating trials and so they may have been sated by the time the second male was introduced. This is probably unlikely because *Nephila* continues capturing prey indefinitely (see Champion de Crespigny et al., 2001); if sexual cannibalism was purely motivated by female hunger state, we would expect the frequency of cannibalism by mated females to be lower than that of virgins, which is not the case. In addition, there was no relationship between the likelihood of cannibalism and the time that had passed between first and second mating. Finally, males cannibalized by mated females have a higher share of paternity than males that survived whereas this is not the case for virgin females. Perhaps females exert sequential choice of partner, although it is not clear which trait forms the basis of their choice.

*Male perspective*
The benefit of cannibalism to males depends on the likelihood of sperm competition. Males that mate with a virgin

female and are cannibalized may increase her fecundity, but the potential for greater male fertilization success will be reduced if she mates again. Virgin females of *N. plumipes* are likely to remate in natural populations because cannibalistic females are not less likely to remate (cf. Andrade, 1996). Field surveys showed that the webs of adult females typically had more than one male in attendance with some exceeding five males (see also Elgar, 1989; Elgar and Fahey, 1996). The absence of any reproductive benefits strongly suggests that there is no male complicity in sexual cannibalism by virgin females of *N. plumipes*. Instead, sexual cannibalism by virgin females creates an extreme conflict of interest; a male mating with a virgin female should always attempt to avoid cannibalism, since this will allow him to either obtain further copulations or guard her from rival males. The roughly 50% frequency of sexual cannibalism by virgin females suggests that the conflict is not resolved in favor of either sex. Perhaps larger males are more reluctant to mate with smaller, virgin females.

Sexual cannibalism by mated females has a clear effect on male fertilization success. Males that survive copulating with mated females cannot expect to sire more than 30% of the clutch, but this value is doubled if he is captured and eaten. However, the true value of this increase has to be balanced against the probability that he encounters and inseminates other virgin or mated females. It is not possible to comment on the true benefits of cannibalism without these data.

There is no obvious mechanism determining patterns of paternity in *N. plumipes*. In the closely related orb-web spider *N. edulis,* paternity is strongly correlated with the duration of copulation (Schneider et al., 2000). However, while the duration of copulation of cannibalized males was generally longer than that of males that escaped, this translated into greater paternity only for males mating with mated females and increased copulation duration did not result in larger numbers of sperm stored by the female. Furthermore, males mating with nonvirgins either transferred more sperm or their mates stored more of their sperm than that of their predecessor. However, greater sperm numbers did not appear to translate directly into higher paternity. The result is curious and suggests that either the second male manipulates his rival's sperm while he is being cannibalized or that the female exerts some form of sperm choice.

Why are males of *N. plumipes* unable to influence paternity through mating for a longer time or depositing more sperm? One explanation is that the two spermathecae of the female are, in many cases (16 of 27 cases where the side of insertion of both males was observed), filled separately by each male. Thus, the sperm of two rival males may not necessarily mix, and hence may not always compete directly. In this situation, the raffle model of sperm competition (Parker, 1998) may not apply. However, the pay-off for male mating strategies may change dramatically if the female mates with more than two males. In this situation, the third male will usually deposit sperm in a spermatheca that already has sperm, and thus copulation duration and numbers of sperm transferred may be important (see Schneider et al., 2000). Sperm numbers may not be important for fertilization success, which is indicated by the quantity of sperm in the spermathecae of females that had produced a clutch (and thus had used sperm) and those that had not oviposited. However, it is possible that our data of sperm numbers may be biased because we only sampled females that died, rather than obtain a random sample of the population.

Brown (1985) suggested that sperm in the spermatheca require a number of days to become flagellate and capable of fertilizing eggs. For example, females of *Nephila clavipes* that mated shortly after maturation oviposited sooner than females that mated 10 or more days after maturation. One explana-

tion is that males that mate with a mated female shortly before oviposition have a small chance of paternity because their sperm have not had time to capacitate (Brown, 1985). Our results contradict this prediction since the paternity of the second male of *N. plumipes* increased with the time interval between first and second copulation.

Sexual cannibalism may have influenced the dramatic sexual dimorphism in *N. plumipes*. Males that are not captured by females during mating are generally smaller, and these males may also be more likely to avoid cannibalism before mating (see Elgar and Fahey, 1996). In addition, cannibalism quickly reduces the number of males ready to mate and may relax male-male competition. As a consequence, the commonly presumed large size advantage in male-male competition may lose importance (see also Vollrath and Parker, 1992). However, sexual cannibalism cannot be the only factor determining size dimorphism, since *N. edulis* is similarly dimorphic but sexual cannibalism is rare in comparison to *N. plumipes* (Schneider et al., 2000; Uhl and Vollrath, 1998).

The interests of male and female *N. plumipes* differ over sexual cannibalism. Females should always consume a mating partner, whereas males should escape, especially after copulating with a virgin female. The conflict changes for copulations with mated females, who may prefer to exert sequential choice, while males may have an advantage through cannibalism. Interestingly, the observed frequency of cannibalism is similar, even though the nature of the conflict may differ.

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