# Sexual cannibalism in *Nephila plumipes* as a consequence of female life history strategies

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## Abstract

The evolution of sexual cannibalism has been modelled as both an adaptive and nonadaptive female strategy. Recent evidence from several species suggests a connection between female foraging and sexual cannibalism, but the precise benefits for females have remained obscure. Here, we investigate the difference between cannibalistic and noncannibalistic female *Nephila plumipes* by removing the potential nutritional benefit of cannibalism. Courting and mating males that were killed by a female were immediately removed so that the female could not consume them. Nevertheless, cannibalistic females gained more mass from maturation to oviposition and produced larger first clutches than noncannibalistic females, although cannibalistic females matured at a smaller size and mass than noncannibalistic females. In juvenile instars, mass gain was generally smaller in females that moulted in a good condition but intermoult intervals were shorter. However, the time from maturity to oviposition was not shorter in females that matured in a good condition. Male behaviour did not differ according to the risk of cannibalism. We suggest that sexual cannibalism in *N. plumipes* is a side-effect of an increased foraging vigour of females that matured at a smaller size and body mass. Selection pressure on males to avoid cannibalism may be weak because of limited mating opportunities.

## Introduction

Sexual cannibalism is comparatively common in spiders and several adaptive and nonadaptive explanations for its evolution have been proposed (Elgar, 1992; Johns & Maxwell, 1997; Andrade, 1998). There is accumulating evidence from spiders and other taxa that female body size attributes determine the likelihood of cannibalism suggesting a connection between foraging decisions and cannibalistic behaviour towards males. Newman & Elgar (1991) showed that, in theory, sexual cannibalism can represent an adaptive foraging decision for virgin females, whereas Arnqvist & Henriksson (1997) proposed a nonadaptive explanation where sexual cannibalism is a

result of a genetic correlation between juvenile and adult aggression. Both models are primarily concerned with premating cannibalism, although the logic can be applied to cannibalism during or after mating. An important difference between pre- and post-mating cannibalism is that the second option is less costly for females, whereas premating cannibalism will leave some females unmated (Arnqvist & Henriksson, 1997). An important difference for the male is that premating cannibalism prevents mating, whereas cannibalism during mating can potentially enhance fertilization success even to the point where male suicide is adaptive (Andrade, 1996). In this paper, we focus on sexual cannibalism that occurs during copulation.

Andrade (1998) suggested that sexual cannibalism in red back spiders, *Latrodectus hasselti*, evolved as a foraging strategy that the males subsequently exploited to increase their fertilization success through prolonged copulation. Although females are more likely to cannibalize a male if

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they are in poor condition, Andrade (1996) was unable to detect any direct advantages to the females of male consumption. We found similar results for the cannibalistic Australian spider, *Nephila plumipes* (Schneider & Elgar, 2001) suggesting that sexual cannibalism in this species is also influenced by female foraging decisions.

Many cannibalistic spiders, including *Latrodectus* and *Nephila*, are characterized by an extreme sexual size dimorphism, with males being smaller than typical prey items. The apparently small nutritional benefit of a male, combined with the relatively long time interval between mating and oviposition, suggest that the somatic contribution of a male to fecundity is an unlikely explanation for the evolution of such a dramatic behaviour. Additionally, sexual cannibalism is apparently not obligatory and some males survive copulation. Nevertheless, it is difficult to reject the nutritional-advantage explanation because even if nutritional benefits are not apparent they may still be detectable only in particular conditions, or the male soma may improve the viability of eggs or young spiderlings (e.g. Johnson, 2001). Andrade (1998) suggested that in female widow spiders, the cost–benefit ratio of male killing may differ for females in different nutritional states, such that the handling costs may sometimes exceed the nutritional benefit obtained. This may occur in some spiders but in others, such as *Nephila*, females capture every prey item that is entangled in the web, and store excessive prey (Champion de Crespigny *et al.*, 2001). In any case, the handling costs of sexual cannibalism should be negligible because the female barely moves to capture him.

The adaptive significance of sexual cannibalism in *N. plumipes* has been examined using the double mating, sterile male technique (Schneider & Elgar, 2001; Schneider *et al.*, 2001). We found that females that matured at a small size and in a poor condition were more likely to cannibalize a male and that these females preferred large males as prey over small males (Schneider & Elgar, 2001). There are two possible explanations for these results: the first is adaptive and requires that adding a male to the diet results in a nutritional benefit for the female (nutritional-advantage or feeding opportunism). Alternatively, sexual cannibalism may be nonadaptive and simply reflects female foraging vigour if, following Arnqvist & Henriksson (1997), her size and nutritional state at maturation depends on her onto-genetic feeding history and strongly influences her fecundity (aggressive-spillover; Johnson, 2001). How-ever, the aggressive-spillover explanation predicts that females with an aggressive feeding history should mature large and heavy and be cannibalistic. We reverse that particular prediction and argue that females with a history of low food-availability should increase their foraging effort. Accordingly, sexual cannibalism among females that mature at a small size would be a consequence of their more aggressive and less selective foraging behaviour.

We tested these alternative explanations by allowing the female to kill her mating male but then preventing her from subsequently consuming him. This allowed us to compare the size, weight at maturation and fecundity of cannibalistic and noncannibalistic females. We compared the factors that determine mass gain and moulting decisions in juvenile spiders with those that are responsible for resource accumulation from maturation until oviposition. Additionally, we examined male beha-viour towards females of different size and condition. In *N. plumipes*, most males will only approach a female while she captures or consumes a prey item (Elgar & Fahey, 1996; Schneider *et al.*, 2001). Males vary in their mating vigour (time to attempt copulation) and this may reflect different degrees of caution.

## Methods

Subadult female and both subadult 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. In 1999, 86 juvenile females (mostly three instars from adulthood) were collected from the same site. Juvenile females were used to investigate growth until maturity and were measured and weighed after each moult until maturity. 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 about 10 blowflies *(Lucilia cuprina)* on each of 3 days per week. Females from 1998 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 prosoma across the dorsal eyes. The female was immobilized by covering her with plastic film. Mated females were transferred to separate cups, and other unmated females were then placed in the vacant frames. Females were checked daily for the presence of egg sacs. The egg sacs were removed from the frame 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). The eggs hatched 1 month later and were preserved in alcohol. The hatchlings and undeveloped eggs were subsequently counted under the microscope.

As the date of oviposition could not be foreseen, females were weighed after they had oviposited (the same day). We calculated the mass at oviposition by adding the number of eggs multiplied by a constant to the body mass after oviposition. The constant is the estimated mass of a single egg. We assumed that the mass of an egg is 0.2 mg and the same for every female. We tested this assumption by measuring, under the microscope, the egg diameter of random samples of 15 eggs from 10 first

clutches produced by an additional sample of females collected from the same site in the summer of 1999/2000. The body mass and size of these females fell within the range of the original study population. Mean egg diameter per female varied between 1.75 and 1.95 mm. The coefficient of variation in egg diameter within clutches ranged from 4.5 to 8.9% and was only 3% between females. We conclude that any variation in egg size between females is within the range of variation within females.

The difference between the body mass at two subsequent moults and the difference between mass at oviposition and that at maturation is referred to as the mass gain, and this difference divided by the mass at the previous moult (or maturation for the adult females) was the relative mass gain. Female condition was calculated as female mass at her final moult divided by prosoma width. The prosoma of spiders is a sclerotized body part that does not change after the final moult. Thus, the mass of a female relative to her prosoma width can be used as an estimate of her condition when the relationship is linear, which is the case for our range of data.

Males were collected as adults from the webs of females or as subadults 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*. Males were carefully inspected (using a dissecting microscope) for species identity and the status of their pedipalps (Schneider *et al.*, 2001). The body length of each male was measured to the nearest 0.5 mm and most of the males were weighed shortly afterwards. Some males damage one of their pedipalps during mating by ectomizing the tip of their conductor (Schneider *et al.*, 2001). Of the males used in our experiments, 16 were collected in the field with only one intact pedipalp. Half of these males were used as first and the other half as second mates. Eight of these males were cannibalized and eight survived after mating with an experimental female. Eleven of these males with only one intact pedipalp were the first or second mate of a cannibalistic female and five were mated to noncannibalistic females. Each female in our experiment was courted by at least one male that had two intact pedipalps.

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 move from their position above the hub unless the female captured a prey item (Elgar & Fahey, 1996), and so we kept throwing blow flies into the web until copulation occurred. We counted the number of flies we had to offer until mating occurred. Shortly after the female had captured the 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. Males that were captured by the female were immediately removed before the female could feed on them.

Not all data were available for each mating trial and therefore the sample sizes differ between analyses. All data were inspected for normal distribution. The interval between maturation and oviposition and the intermoult interval of the penultimate instar were inverse-tangent transformed when used with parametric statistics. The intermoult interval of the juvenile instar was square-root, inverse-tangent transformed to achieve a normal distribution. When variances were unequal, nonparametric Wilcoxon tests were used to compare samples.

## Results

### Cannibalism

Males were captured and killed in 62.5% (40 of 64) of the matings with virgin females and in 64.5% (40 of 62 – two females killed their first male whereas the fate of their second male is unclear) of the matings with mated females. Females that killed their first male were typically but not significantly more likely to kill their second male (neither male = 12, first only = 10, second only = 12, both males = 28; $\chi^2_1 = 3.6$, $P = 0.059$). All of the cases in which the female captured and killed the male occurred after mating had commenced; there were no cases of premating sexual cannibalism.

### Cannibalism and female mass gain

Foraging vigour may be reflected by the mass that females gained from maturation to oviposition, as we provided all of the females with very similar amounts of prey but females may have differed in the quantity they consumed. Absolute and relative mass gain from maturation to oviposition were negatively influenced by female prosoma width (linear regression; absolute: $r^2 = 0.17$, $F_{1,42} = 8.51$, $P < 0.01$, relative: $r^2 = 0.29$, $F_{1,42} = 16.89$, $P < 0.001$), by female body mass at maturation (absolute: $r^2 = 0.32$, $F_{1,42} = 19.39$, $P < 0.0001$, relative: $r^2 = 0.45$, $F_{1,42} = 34,23$, $P < 0.0001$), and by female condition at maturation (absolute: $r^2 = 0.30$, $F_{1,42} = 18.2$, $P < 0.0001$, relative: $r^2 = 0.43$, $F_{1,42} = 30.98$, $P < 0.0001$). Thus, females that were heavy and large at maturity accumulated fewer resources than small and light females despite a similar food regime.

The partial effects of different variables can be assessed by multiple regression. We selected condition as the representative variable for both size and weight at maturity. Multiple regression revealed that 45% of the variance in mass gain was explained by female condition, the interval between maturation and oviposition and by cannibalistic tendencies of the female (Table 1).

**Table 1** Multiple linear regression model with the mass gained from maturation until oviposition as response variable ($r^2 = 0.45$, $n = 41$). Coefficients for the linear model, standardized $\beta$, $F$-values and $P$-values are given.
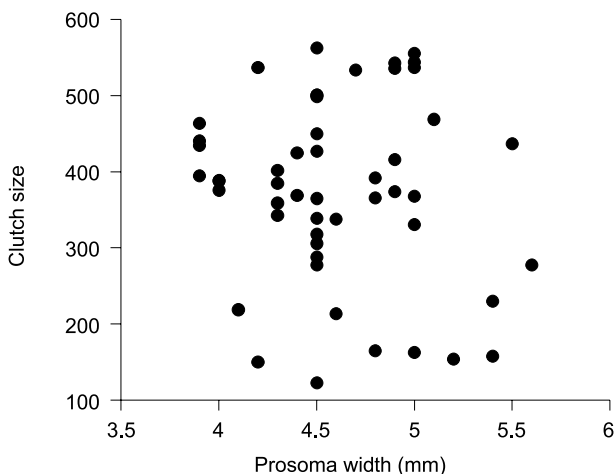
| | Coefficient | $\beta_{mass\ gain}$ | $F_{mass\ gain}$ | $P$ |
|---|---|---|---|---|
| Cannibalism | −0.057 | −0.265 | 4.253 | 0.046 |
| Interval between maturation and oviposition | 0.005 | 0.360 | 7.180 | 0.011 |
| Female condition | −3.618 | −0.601 | 18.68 | 0.0001 |
| Intercept | 0.304 | | | |

**Table 2** Life-history variables (mean ± SE) of females that killed one or two males (cannibalistic) and females that did not kill a mate. Sample sizes are given in brackets. Not all data are available for every female, therefore sample sizes vary.

| Females | Cannibalistic | Noncannibalistic | $t_1$ |
|---|---|---|---|
| Mass at maturity (g) | 0.507 ± 0.018 (50) | 0.671 ± 0.064 (8) | 3.168** |
| Prosoma width (mm) | 4.555 ± 0.062 (55) | 5.044 ± 0.152 (9) | 2.985** |
| Condition (g mm$^{-1}$) | 0.112 ± 0.003 (55) | 0.133 ± 0.008 (9) | 2.500* |
| Interval between maturation and oviposition (days) | 43.87 ± 1.897 (46) | 47.80 ± 4.069 (10) | 0.875 |
| Absolute mass gain | 0.190 ± 0.022 (36) | 0.021 ± 0.072 (5) | −2.617* |
| Relative mass gain | 0.430 ± 0.063 (36) | 0.075 ± 0.111 (5) | −2.024* |
| Clutch size | 388.42 ± 17.0 (43) | 293.0 ± 37.32 (9) | −2.325* |

*$P < 0.05$, **$P < 0.01$.

Cannibalistic females (those that killed, but did not eat, one or both males) gained significantly more mass than noncannibalistic females (Table 2) and the noncannibalistic females were significantly heavier at maturation than the cannibalistic females. These relationships remained significant when they were corrected for the other variables in the multiple regression.

Noncannibalistic females matured around a mean of day 59 (SE = 3.2) of the year and thus about 14 days later than cannibalistic females that moulted around day 45 (SE = 1.0) (Wilcoxon test, $\chi^2_1 = 16.43$, $P < 0.0001$, $n = 63$).

## Cannibalism and female fecundity

The number of eggs in the first clutch was not a function of either female mass at maturity (linear regression, $r^2 = 0.03$, $F_{1,49} = 1.36$, not significant), or prosoma width ($r^2 = 0.02$, $F_{1,49} = 0.76$, not significant; Fig. 1), a relationship that is common in other spiders. About 50% of the females laid a second clutch, but the combined number of eggs was also not related to the above variables ($P > 0.05$ for all regressions). The body mass

of females after their first oviposition positively predicted the size of the second clutch (linear regression, $r^2 = 0.15$, $F_{1,26} = 4.62$, $P < 0.05$) suggesting that females can save body reserves for a second reproductive event. However, the mass after the first oviposition of females that laid two clutches did not differ from that of females that laid only one clutch ($t_{58} = -0.117$, not significant).

Cannibalistic females (those that killed one or both males) laid larger clutches than noncannibalistic females ($t_{50} = -2.33$, $P < 0.05$; Table 2). Thus, females that killed their partner gained more weight and laid more eggs than those that did not kill their partner, although the cannibalistic females were prevented from consuming their victim.

Multiple regression revealed that four variables explain 43% of the variation in clutch size (Table 3). The model is not improved by including prosoma width or the day of maturation. As expected, body mass at maturation is an almost significant predictor of clutch size, when other influences are controlled. Nevertheless, the relatively stronger influence of the other factors suggests that clutch size is determined by complicated interactions of various parameters.



**Fig. 1** The size of the female as prosoma width plotted against the number of eggs in her first clutch.

**Table 3** Multiple linear regression model on the size of the first clutch ($r^2 = 0.43$, $n = 41$). Coefficients for the linear model, standardized $\beta$, $F$-values and $P$-values are given.

| | Coefficient | $\beta_{clutch\ size}$ | $F_{clutch\ size}$ | $P$ |
|---|---|---|---|---|
| Cannibalism | −54.06 | −0.290 | 4.269 | 0.046 |
| Female mass at maturation | 299.45 | 0.347 | 3.877 | 0.057 |
| Interval between maturation and oviposition | −10219.1 | −0.390 | 6.939 | 0.012 |
| Absolute mass gain | 486.83 | 0.571 | 11.427 | 0.002 |
| Intercept | 15906.45 | | | |

## Female growth until maturity

Female body mass at maturity was a linear and positive function of her size and condition at the previous moult and the mass gained during the intermoult interval. These three variables explain 99.8% of the variance in body mass (Table 4). Body size (prosoma width) at maturation is determined by the same variables, which explain 83% of the variance. In both cases, the model was not improved by adding the intermoult interval or body mass at the previous moult.

Absolute and relative mass gained during the penultimate and adult instar was not significantly influenced by prosoma width at the previous moult. Mass gain was a function of body size, expressed as prosoma width, only in the ante-penultimate instar (Table 5). However, body mass at moulting negatively influenced the subsequent mass gain through all instars (at least in a multiple regression). Thus, relatively heavy females (for their prosoma width) accumulate fewer resources until the next moult, possibly because their stores are already filled from the previous instar (Table 5). Generally, spiders can optimize growth through mass gain and the timing of the next moult. Females that had a higher mass gain also had shorter intermoult intervals, but this correlation disappeared in the adult instar when the time until oviposition was compared (Table 5). Females that were relatively heavy at maturation (for their prosoma width) take longer to lay their eggs than light females, but prosoma width has the opposite but nonsignificant effect: large maturing females may oviposit slightly earlier than females that were smaller (Table 5). These relationships are reversed when intermoult intervals in the juvenile and penultimate instars are considered.

## Male behaviour and female size

In 61 first matings, 11 males (18%) mated without waiting for the female to catch a fly, 32 (52%) mated after the female had captured one fly, 13 (21%) after she captured two flies and the remaining five matings occurred after she had captured three or more flies. The proportions were similar in the 45 observed second matings; 20% of the males ($n = 9$) mating without a fly, 56% mating after one fly was captured and 18% after two flies were captured. Only three matings took place after three or four flies had been captured. Matings with cannibalistic and noncannibalistic females did not require

**Table 4** Multiple linear regression model on female body mass at maturity as response variable. Penultimate prosoma width (size) and condition as well as the mass gained in the previous instar explain 99.8% of the variation ($n = 84$). Coefficients for the linear model, standardized $\beta$, $F$-values and $P$-values are given.

|  | Coefficient | $\beta_{adult\ mass}$ | $F_{adult\ mass}$ | $P$ |
|---|---|---|---|---|
| Prosoma width at penultimate moult | 0.049 | 0.173 | 457.96 | 0.0001 |
| Condition at penultimate moult | 4.499 | 0.503 | 3989.8 | 0.0001 |
| Mass gain | 0.992 | 0.788 | 16983.49 | 0.0001 |
| Intercept | −0.213 | | | |

**Table 5** Multiple linear regression models on the influences of female mass and size (prosoma width) after the previous moult on the absolute and relative mass gain until after the following moult and on the intermoult interval. In the lower section of the table, correlation coefficients between mass gain and the intermoult intervals are given. In the adult instar, the following moult is replaced by the appearance of the first clutch. Juvenile instar is the instar prior to the penultimate moult. There are some unpublished data on even earlier moults that support the assumption that the juvenile instar is representative for earlier ones. Given are coefficients of the linear model, standardized coefficients ($\beta$) and $F$-statistics.

|  | Juvenile instar | | | Penultimate instar | | | Adult instar | | |
|---|---|---|---|---|---|---|---|---|---|
|  | Coefficient | $\beta$ | $F$ | $r$ | $\beta$ | $F$ | $r$ | $\beta$ | $F$ |
| Response variable: absolute mass gain | | | | | | | | | |
| Female mass | −0.719 | −0.603 | 26.039*** | −0.698 | −0.557 | 10.628** | −0.61 | −0.621 | 8.995** |
| Female prosoma | 0.105 | 0.681 | 33.228*** | 0.146 | 0.654 | 14.659*** | 0.024 | 0.076 | 0.134 |
| Intercept | −0.169 | | | −0.279 | | | 0.38 | | |
| Response variable: relative mass gain | | | | | | | | | |
| Female mass | −10.25 | −0.874 | 74.374*** | −4.435 | −0.688 | 18.993*** | −1.67 | −0.648 | 12.101** |
| Female prosoma | 0.579 | 0.383 | 14.289*** | 0.254 | 0.222 | 1.981 | −0.024 | −0.029 | 0.024 |
| Intercept | 0.201 | | | 0.857 | | | 1.375 | | |
| Response variable: intermoult interval (or interval from moult to oviposition) | | | | | | | | | |
| Female mass | −0.92 | −0.77 | 9.15** | −0.136 | −0.53 | 7.44* | 0.019 | 0.575 | 7.29* |
| Female prosoma | 0.04 | 0.37 | 2.12 | 0.016 | 0.36 | 3.32 | −0.004 | −0.339 | 2.54 |
| Intercept | 1.27 | | | 1.47 | | | 1.55 | | |
| Correlations with intermoult interval (or interval from moult to oviposition) | | | | | | | | | |
| Mass gain | −0.385* | | | −0.0655 | | | 0.123 | | |
| Relative mass gain | −0.045 | | | 0.093 | | | 0.139 | | |

*$P < 0,05$, **$P < 0.005$, ***$P < 0.001$.

different numbers of flies (median is 1.5 for the second mates of noncannibalistic females and 1 for the other matings; *first mate*: $\chi^2_3 = 2.05$, $n = 57$; *second mate*: $\chi^2_3 = 3.9$, $n = 45$). First males were presented to noncannibalistic females on average 1.9 ± SE 0.36 days and to cannibalistic females 1.9 ± 0.12 days after maturation ($\chi^2_1 = 0.0$, $n = 56$). The interval between maturation and first mating was not correlated with the number of flies required until copulation ($r_s = -0.07$).

Males waited for up to 5 h at the hub of the web without attempting copulation (median *first mate*: 79 min, median *second mate*: 60 min). However, as soon as a fly was thrown into the web, most males jumped onto the female within the next minute [median *first mate*: 2 min (0–5), median *second mate*: 1 min (0–5)]. There is too little variation in male behaviour to permit further analysis.

First matings that occurred without a fly were not with heavier ($t_{56} = 0.79$) or larger (prosoma width) females ($t_{56} = 1.47$) nor was there such a relationship in second matings ($t_{40} = 0.55$, $t_{40} = 0.28$; Table 6). Furthermore, we could not detect an influence of male body mass on the likelihood of mating before the female had caught a fly (logistic model: *first mate*: $\chi^2_1 = 1.87$, $n = 32$; *second mate*: $\chi^2_1 = 0.14$, $n = 29$; Table 6). The likelihood of postmating cannibalism was not influenced by whether the female was or was not consuming a prey item (*first mate*: $\chi^2_1 = 1.95$, $n = 59$; *second mate*: $\chi^2_1 = 0.55$, $n = 43$).

## Discussion

Females of *N. plumipes* differ in size and body mass at maturation and not all females are sexually cannibalistic. Cannibalistic females matured at a smaller body size and mass and had more eggs in their first clutch than noncannibalistic females. These results could be interpreted as revealing direct benefits through the consumption of males, and thus support the nutritional-advantage explanation of sexual cannibalism (e.g. Buskirk *et al.*, 1984). However, the females in our experiment were able to kill the male but we prevented them from subsequently eating him. Thus, cannibalism *per se* may be relatively unimportant in the process of resource accumulation. Instead, sexual cannibalism in this species may be a simple consequence of an increased foraging vigour of females that matured at a small size and in a poor condition. Noncannibalistic females may follow a different growth strategy, perhaps they have one more instar. This interpretation is supported by the observation that noncannibalistic females matured later than cannibalistic females.

The nutritional-advantage hypothesis (Buskirk *et al.*, 1984), which predicts a direct benefit of male consumption, is unlikely to explain the evolution of sexual cannibalism in this species. However, the underlying mechanism may apply, if there is a small cost to sexual cannibalism and the nutritional value of the male is greater for smaller than larger females. Accordingly, the benefits of cannibalism will outweigh the costs for smaller than larger females, and thus cannibalism is expected to be more likely among smaller than larger females. However, consuming males does not appear to be a strategy in itself but rather a side-effect of a more general difference in the cost–benefit ratio of foraging effort for females that mature in different conditions.

Although prosoma width remains the same after maturation, body mass can change drastically in the period between maturation and oviposition. Nevertheless, it is unlikely that our data were influenced by any short-term periods of food deprivation because all of the females in our experiments received the same amount of food during the entire observation period, and the interval between maturation and mating did not differ between cannibalistic and noncannibalistic females. Additionally, stored food pantries (see Champion de Crespigny *et al.*, 2001) were present in the webs, suggesting that females were not food limited. Nevertheless, experiments with large differences in food availability for all size classes are necessary to clarify the role of hunger, independent of female condition at maturation, and the likely interaction between size and mass at maturity (past experience) and food availability (current experience) (Spence *et al.*, 1996).

These data highlight the importance of incorporating an experimental approach to investigating the fecundity effects of sexual cannibalism. Several studies have examined whether the addition of a male to the diet of a female increases her size or reproductive output (Birkhead *et al.*, 1988; Elgar & Nash, 1988; Andrade, 1996; Arnqvist & Henriksson, 1997; Fahey & Elgar, 1997; Elgar *et al.*, 2000;

**Table 6** Female mass at maturation and male mass (mean ± SE) for copulations that took place before a fly were given (0 flies) or after one up to four flies were captured by the female. Cannibalism shows the proportion of all matings that ended with the male being cannibalized. Sample sizes are given in brackets, they differ because not all data are available for each mating.

|  | 0 Flies | One fly | Two flies | 3–4 Flies |
|---|---|---|---|---|
| Female mass (g) (first mating) | 0.573 ± 0.047 (*n* = 11) | 0.538 ± 0.023 (*n* = 31) | 0.479 ± 0.054 (*n* = 13) | 0.582 ± 0.063 (*n* = 5) |
| Female mass (g) (second mating) | 0.563 ± 0.046 (*n* = 9) | 0.515 ± 0.032 (*n* = 24) | 0.589 ± 0.071 (*n* = 8) | 0.496 ± 0.056 (*n* = 3) |
| Male mass (g) (first mating) | 0.0174 ± 0.002 (*n* = 4) | 0.0136 ± 0.001 (*n* = 18) | 0.0141 ± 0.002 (*n* = 8) | 0.0178 ± 0.002 (*n* = 3) |
| Male mass (g) (second mating) | 0.0143 ± 0.002 (*n* = 6) | 0.0137 ± 0.001 (*n* = 17) | 0.0179 ± 0.002 (*n* = 5) | 0.0228 (*n* = 1) |
| Cannibalism (%) (first mating) | 81.82 (*n* = 11) | 62.50 (*n* = 32) | 61.54 (*n* = 13) | 40 (*n* = 5) |
| Cannibalism (%) (second mating) | 66.67 (*n* = 9) | 68 (*n* = 25) | 25 (*n* = 8) | 33.33 (*n* = 3) |

Johnson, 2001). However, most of these studies relied on natural variation in cannibalism rather than specifically adding a male to the female's diet (e.g. Elgar & Nash, 1988; Fahey & Elgar, 1997) or preventing her from consuming her victim (e.g. Birkhead *et al.*, 1988). Clearly, data from those experiments in which male consumption is not randomly allocated across females are difficult to interpret if it is not known whether sexual cannibalism and female foraging voracity are linked.

Females that moulted with a relatively large body mass gained less mass until their next moult than females that moulted in a poor condition. This result may be because of the constraints of moulting. Females in good condition may not be able to convert all of their resources into growth of the sclerotized body parts because expansion of these structures is limited (Higgins & Rankin, 1996; Hutchinson *et al.*, 1997 and references therein). As a consequence, females with a rich feeding history may carry accumulated resources into the following instar, thereby allowing them to moult again sooner. The negative correlations between body mass and mass gain with intermoult interval in the juvenile instar are consistent with this explanation. However, there is no significant correlation for penultimate instar females between mass gain and time to reach maturity, although the penultimate intermoult interval is predicted by body mass.

In contrast, the effects of size and weight change after maturation, and the timing of oviposition is not related to mass gain. Surprisingly, females that were heavy for their size took longer to lay their first clutch. Thus, it appears that once a female has reached maturity with a given body condition, she cannot increase her fitness by reducing the time until oviposition. Neither stored nutrients from previous moults (apparent as mass at maturity) nor a maximal mass gain after maturation will positively affect the timing of oviposition.

Females that matured in a good condition oviposited later and their mass gain was smaller than females in poor condition, despite the longer time taken to oviposit. Accordingly, there is no advantage to aggressive foraging for large females, and they may benefit by reducing their foraging efforts or prey intake. Assuming there are trade-offs between foraging effort and other fitness relevant traits, less vigorous foraging may even have advantages. For example, Higgins (2001) showed that rapid growth (mass gain) in the congener *N. clavipes* has a physiological cost that reduces survival. However, only juvenile spiders were used in her study and mortality occurred shortly before or during the next moult. Thus, the relevance of these costs of rapid growth for adult females that do not moult again is not known.

In addition, aggressive foraging may not help heavy females increase their fitness by producing larger first clutches. This is because the positive influences of mass gain and mass at maturity on clutch size are compromised by the negative effect of the interval between maturation and oviposition. Females that mature heavy

for their size can maximize clutch size only through the total mass gained until oviposition and not through the rate of mass gain. The mass a heavy female can gain is further limited by the amount of resources already stored from previous moults. Consequently, it may be beneficial for heavier females to gain mass more slowly.

Females can produce several clutches, although the average number of clutches in the field is not known. Perhaps females choose between alternative reproductive strategies of either investing a major part of their resources in their first clutch or investing relatively less in their first clutch in order to retain resources for subsequent clutches. The relative contributions to first and subsequent clutches may vary along a continuum, rather than representing a bimodal distribution. Females that mature above a certain body size and condition may be more likely to produce multiple clutches. This is suggested by the positive correlation between body mass after oviposition and the number of eggs in the second clutch. However, only half of the females in our study survived to lay a second clutch, and body mass was not a predictor of the appearance of additional clutches. This may be a laboratory artefact. Females were transferred to cups after they had produced their first clutch, and this may have compromised their survival, independently of their size and/or condition. Mortality may have masked differences in the likelihood of producing second and third clutches. An alternative explanation, that there is an upper limit to clutch size that the larger females may have already met, is unlikely. This explanation predicts a distribution of clutch sizes that does not exceed a particular maximum, and our data do not remotely fit such a curve (Fig. 1).

In theory, males might assess the risk of being killed through the size and mass of the female they are courting. Males of *N. plumipes* typically approach the female cautiously and usually attempt copulation while she is feeding on a prey item (Robinson & Robinson, 1980; Elgar & Fahey, 1996). In our study, most males waited until the female had captured at least one prey item before attempting to mate. If males adjust their behaviour to the risk of cannibalism, they should have been more likely to attempt copulations with nonfeeding females that were also larger and heavier. However, this was not the case, and the probability of post-mating sexual cannibalism was not related to the number of flies placed in the web before mating occurred. Presumably, the male's strategy of attempting to mate when the female is feeding evolved to reduce the risk of premating cannibalism, and the success of this strategy may be reflected by the rarity of premating cannibalism in *N. plumipes* (Elgar & Fahey, 1996).

In *N. plumipes*, sexual cannibalism by females appears to be a consequence of their life-history strategy. A hypothesis proposed for the evolution of premating cannibalism in the fishing spider (Arnqvist & Henriksson, 1997) similarly predicts that the foraging voracity of juveniles

and cannibalism should be linked. However, the hypothesis assumes that high foraging voracity of juveniles results in large and heavy maturing females and that those females also tend to be cannibalistic – a prediction not supported by our data. Our interpretation simply reverses the causation, so that cannibalistic females are characterized by a history of poor feeding that forces them to be less selective foragers. At this point, the basal mechanism of the nutritional-advantage hypothesis is incorporated.

Our preliminary interpretation is that female *N. plumipes* mature at some constitution and with varying foraging experiences. Their subsequent foraging vigour will be determined by these parameters as will their reproductive strategy. As a consequence, females with high vigour will cannibalize their mates. Males do not appear to adjust their behaviour to the risk of post-mating cannibalism. Perhaps they benefit indirectly from being cannibalized because these females produce more eggs in their first clutch, thereby increasing potential paternity, and cannibalized males increase their share of paternity when they mate with previously mated females (Schneider & Elgar, 2001). Males of *N. plumipes* damage their genital structure during mating and as they are paired, males can expect a limited mating success even if they survive copulation (Schneider *et al.*, 2001). Thus, the costs of post-mating cannibalism for males may be rather small. If the costs and benefits are balanced, selection for a male counter adaptation against sexual cannibalism may be weak. Then high frequencies of sexual cannibalism can persist without providing a measurable benefit to females.

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