Behav Ecol Sociobiol (1997) 40: 127–133

Babette F. Fahey · Mark A. Elgar

Sexual cohabitation as mate-guarding in the leaf-curling spider *Phonognatha graeffei* Keyserling (Araneoidea, Araneae)

Received: 2 February 1996 / Accepted after revision: 27 October 1996

Abstract The leaf-curling spider *Phonognatha graeffei* incorporates a twisted leaf into the central hub of its orb-web that is used as a retreat. This species is unusual among orb-weaving spiders because males cohabit in the leaf retreat with both immature and mature females, mating with the former shortly after the female molts. Cohabitation appears to be a form of mate-guarding because cohabiting males respond agonistically to rival males that venture onto the web, and their behaviour depends upon the reproductive status of the female; males defending immature females are more aggressive than those defending virgin, adult females. Males copulate with previously mated females for significantly longer than with virgin females. Females may cannibalise cohabiting males, which occurs independently of whether the female has been deprived of food. Females that cannibalise a single male do not have a higher fecundity than non-cannibalistic females.

Key words Male-male competition · Mate-guarding · Orb-weaving spiders · Sexual cannibalism · Sperm competition

Introduction

The potential for multiple mating by females is responsible for the extraordinary diversity of mechanisms males utilise to secure their reproductive investments against rival males. Mate-guarding, in which the male attempts to prevent other males from copulating with his mate, is a particularly widespread mechanism (Thornhill and Alcock 1983; Birkhead and Møller 1992; Alcock 1994; Andersson 1994). Males may guard females from other males before and/or after copulation has taken place, with the timing apparently depending upon patterns of sperm precedence and the duration of female receptivity. Pre-copulation mate-guarding of immature females is likely in species in which the first male to mate secures the most fertilisations, whereas post-copulation mate-guarding is likely if the last male has sperm precedence (Ridley 1983; Alcock 1994).

The timing and duration of pre-copulation mate-guarding in species with first male sperm precedence will depend upon the length of time females are receptive, and the expected encounter rate of males with unguarded, virgin adult females (Parker 1974; Ridley 1983). There may be little, if any, pre-copulation mate-guarding if males are likely to encounter many receptive, virgin females that are not guarded by other males. If, however, males expect to encounter very few virgin, adult females that are not guarded, selection may favour males that guard immature females against rivals (Parker 1974), and mate with them as soon as they attain sexual maturity. Successfully guarding an immature female ensures that the male will be the first to mate with her and hence fertilise the majority of her eggs. In contrast, a mature female may have already mated and hence her value, in terms of the expected reproductive success of the male, will be lower if males are unable to distinguish between virgin and mated adult females. In which case, males may guard immature females more vigorously than mature females (Austad 1984). While mate-guarding affords the advantage of fertilising most of the eggs of the female, it may also attract several costs, including loss of foraging opportunities and greater exposure to predators (Parker 1974).

Both pre- and post-copulation mate-guarding occur in spiders (e.g. Austad 1984; Jackson 1986; Watson 1990; Dodson and Beck 1993; Eberhard et al. 1993), and the former appears to be common among orb-weaving spiders (e.g. Robinson and Robinson 1980; Miyashita

B.F. Fahey[1] · M.A. Elgar (✉)
Department of Zoology, University of Melbourne,
Parkville, Victoria 3052, Australia

Present address:
[1] Department of Anthropology, Harvard University,
Cambridge, MA 02138, USA

1993; Elgar and Fahey 1996). Male orb-weaving spiders usually attain sexual maturity before females, and these adult males do not build webs but rather seek mating opportunities. After locating the web of a female, the male may remain at the centre or edge of the orb-web, interact aggressively with other males, and attempt to copulate with the female shortly after she attains sexual maturity (Robinson and Robinson 1980). While this behavior increases the probability that the male is the first to mate, remaining in close proximity to the female may also increase the risk of cannibalism, which is common in orb-weaving spiders (Elgar 1992).

The leaf-curling spider *Phonognatha graeffei* is an orb-weaving spider that is ubiquitous throughout eastern Australia (Main 1976). Leaf-curling spiders build webs among shrubs in both lightly wooded areas and suburban gardens. They are easily recognised by the curled leaf that is incorporated into the central hub of the web and used by the resident spider as a retreat (Thirunavukarasu et al. 1996). Males are smaller (5 mm in length and *c*. 20 mg) and mature earlier than females (8 mm in length and *c*. 60 mg at sexual maturity but increasing to over 260 mg before ovipositing). Sexually mature males may share the leaf retreat with either immature or mature females. Females oviposit about 4 weeks after mating, depositing up to 200 eggs into an egg sac that is sealed in a dead leaf.

Here, we describe the patterns of cohabitation in *P. graeffii*, and examine whether this behavior represents a form of mate guarding. In particular, we investigate whether the vigor of male guarding behavior depends upon the reproductive status of females, and what factors determine the outcome of any contests between males. We also evaluate the risk to males of sexual cannibalism by females and the potential benefits of this behaviour to females.

Materials and methods

Immature male and female *P. graeffei* were collected in early January from a coastal population at Sandringham, Port Phillip Bay, Victoria. The spiders were maintained in individual containers with a moist atmosphere and fed three to five blowflies *Lucilia cuprina* (Diptera) each week. Maintaining females in this way allowed us to be certain of the mating status of each female.

Courtship and mating trials were carried out in perspex mating frames (40 × 50 × 10 cm) with removable panels. Females of known reproductive status (immature, adult virgin or mated) were weighed, placed in the mating frame and allowed to build a web. Small pieces of paper littered the floor of the frame, and the female incorporated one of them into the web to use as a retreat. If necessary, parts of the paper retreat were carefully cut away so that it was possible to observe the behaviour of the spiders inside the retreat. A male of known reproductive status was weighed and placed at the base of the mating frame. The trial was abandoned if courtship had not commenced within an hour of the male being placed in the mating frame. We recorded the behaviour of both the male and female, and the onset and duration of copulation bouts. Copulation was deemed to commence when the male grasped the abdomen of the female with his forelegs, and inserted a pedipalp into her genital opening. Copulation consisted of a series of alternate pedipalp insertions, each lasting a few minutes. We defined the duration of copulation as the time from when the male made his initial palpal insertion until he withdrew his palp for the final time, just prior to releasing his grasp on the female and separating from her.

Mating trials involved both adult virgin and mated females. A male mating with a virgin female was allowed to cohabit with the female until the following day, after which he was removed and a second male was introduced. We recorded the courtship and copulation behaviour of the female and both the males, and the onset and duration of copulation bouts.

We examined whether the duration of cohabitation influenced female fertility by comparing the proportion of eggs from which spiderlings emerged of females that associated with males for different durations. Males were allowed to mate with virgin females and then removed from the courtship frame after either (1) 1 h of copulation, (2) 24 h of cohabitation, or (3) several days of cohabitation. We also collected mature females from field populations in order to obtain estimates of female fertility under natural conditions. We assume that the different periods of cohabitation reflect differences in the duration and/or frequency of copulation, since pairs copulate frequently while cohabiting. Females were maintained in isolation after mating, fed flies *ad libitum*, and allowed to oviposit. The eggs were then separated from the egg-sac, counted and incubated in vials within a humid perspex box. The hatchlings were counted and removed as they emerged, thereby preventing intra-brood cannibalism.

The duration of post-copulation cohabitation was recorded for males placed with either immature females; virgin, mature females; or mated females. Males paired with an immature female usually cohabited until she moulted, and then they mated. We monitored each pair every day after mating had taken place and noted the position of the male on the web. A male was defined as "cohabiting" if he was sharing the retreat with the female.

We examined whether cohabitation is a form of mate-guarding by recording the response of cohabiting "resident" pairs of different reproductive status to male intruders. A male was introduced into a web of either an immature or mature virgin female and allowed to enter the leaf retreat and cohabit with the female. After 24 h, another male was introduced at the base of the mating frame and allowed to venture onto the web. We then recorded the behaviour of both the defending and intruding males. In separate trials, we placed a second female at the base of the mating frame with a web and pair of cohabiting spiders, and recorded which spider responded to the female intruder.

The relationship between female fecundity and sexual cannibalism was examined by comparing the fecundity (number of eggs in the clutch) of females under different diets and cannibalism frequencies. Females were assigned randomly to one of three cannibalism treatments: cannibalism of a male immediately after mating; cannibalism of a male three weeks after mating; or no cannibalism. Each male was chilled before being given to the female, which facilitated her ability to capture him. Following mating, females were assigned randomly to one of two dietary regimes, consisting of either one fly per day or one fly every 3 days, and maintained in small containers until they oviposited. The eggs were removed from their protective silk sac and counted.

We examined whether sexual cannibalism was influenced by the nutritional state of the female by comparing the frequency of cannibalism among well-fed and food-deprived pairs. Pairs of males and females were allowed to mate and then assigned randomly to one of two treatments; one group of spiders were food-deprived for one month while the other group were fed daily. All pairs were monitored each day, and we recorded any incidence of cannibalism.

All statistical analyses were performed using SYSTAT 5.2 (Wilkinson 1992). Data were log-transformed in order to normalise their distributions. Non-parametric tests were used if normal distributions were not obtained by transformation. Unless stated otherwise, values given are means ± SE and the null hypothesis was rejected if the α-level was less than 0.05.

Results

Courtship and copulation

After locating the web, the male approached the leaf retreat from the lower part of the orb-web. The resident female usually tugged on the web when she detected the vibrations of the male, and the male responded by rapidly flexing his abdomen up and down. These abdominal flexions continued as the male made his way towards the leaf retreat, and he often paused for several minutes during this time. The reproductive status of the female had no effect on the frequency with which females tugged on the web (Table 1). However, males reached the leaf retreat of immature females more quickly than of mature virgin females and took the longest time to reach mated females (Table 1).

The male entered the leaf retreat from the top, positioned himself below the ventral surface of the adult female, grasped her abdomen with his front two pairs of legs and inserted his pedipalps alternately into the genital opening of the female, tapping on her epigynum between insertions. Copulation consisted of a series of consecutive pedipalp insertions, each of which lasted a few minutes, and was terminated when the male released his grasp on the female and separated from her. An analysis of covariance revealed that the duration of copulation for males mating with previously mated females was significantly longer (136.58 ± 8.42 min, $n = 18$) than that for males mating with virgin females (100.85 ± 5.15 min, $n = 43$; $F_{1,57} = 7.978$, $P < 0.008$), but was not influenced by either male weight ($F_{1,57} = 0.354$, $P > 0.5$) or female weight ($F_{1,57} = 0.143$, $P > 0.5$), or any of the interactions among these factors and covariates ($P > 0.07$ in all tests).

Duration of cohabitation and defence against intruders

Adult males released into frames with sexually mature females entered the leaf retreat and proceeded to copulate shortly afterwards. Males released into frames with penultimate instar females similarly entered the leaf retreat, remaining there with the immature female. Mating then occured within a day after the female moulted into her final, adult instar. Males stayed with the female for several days after mating before leaving the web. Males that moved off the web usually remained at the extremities of the mating frame or left it if the frames were opened, and it seems likely that, under natural conditions, males do not return to a female after leaving her web. Therefore, we estimated the duration of post-copulation cohabitation, under laboratory conditions, to be the number of days spent by a male sharing the female's retreat prior to moving to the extremities of the mating frame. There was no significant difference in the mean duration of post-copulation cohabitation between males that had mated with recently moulted females (1.6 ± 0.9 days, $n = 11$), virgin mature females (0.4 ± 0.1 days, $n = 16$) or mated females (1.3 ± 0.4 days, $n = 17$; Kruskal-Wallis test statistic = 4.506, $df = 2$, $P > 0.1$).

The reproductive status of the female influenced the behaviour of both defending and intruding males. In general, males competing over immature females had higher frequencies of both abdominal flexions and web-tugs than males competing over adult virgin females (Table 2). Cohabiting males pulled on the webs significantly more frequently (mean = 1.40 ± 0.37 per min) than intruding males (mean = 0.70 ± 0.17 per min; $t_{\text{paired}} = 2.91$, $df = 29$, $P < 0.01$). There was no significant difference in the frequency of abdominal flexions between cohabiting (mean = 0.97 ± 0.36 per min) and intruding males (mean = 0.71 ± 0.22 per min; $t_{\text{paired}} = 1.35$, $df = 29$, $P > 0.18$).

The contests between defending and intruding males resulted in one individual being ejected from the web, either by being chased off the edge of the web or, following physical contact, by dropping off the web. The outcome of these contests was not influenced by female status: 53% ($n = 15$) of males cohabiting with immature females ejected the intruder, compared with 40% ($n = 15$) of males cohabiting with a mature virgin female (Yate's corrected $\chi^2 = 0.134$, $P > 0.7$). In contrast, the

Table 1 Courtship duration of males introduced to female *Phonognatha graeffei* at different developmental stages. Values are means with standard errors in *parentheses*. All values were log-transformed before applying the one-way analysis of variance

	Immature	Adult		F
		Virgin	Mated	
Number of trials	10	43	18	
Mean time to reach the leaf retreat (min)	2.21 (0.42)	5.58 (0.82)	14.67 (0.54)	3.130*
Mean time spent outside the leaf retreat (min)	4.21 (1.91)	3.34 (0.82)	1.74 (0.54)	0.433
Mean frequency of female web tugs (per min)	0.74 (0.38)	0.66 (0.13)	0.62 (0.18)	0.026

*$P < 0.05$

Table 2 Behaviour of intruding males and males defending immature or adult, virgin females in *P. graeffei*. Values are means with standard errors in *parentheses*

	Female reproductive status		Mann-Whitney U
	Immature	Adult	
Number of trials	15	15	
Defending male			
Mean frequency of abdominal flexions (per min)	1.25 (0.46)	0.70 (0.18)	152^{*}
Mean frequency of web-tugs (per min)	1.89 (0.57)	0.92 (0.45)	159^{*}
Intruding male			
Mean frequency of addominal flexions (per min)	1.06 (0.30)	0.32 (0.32)	160^{*}
Mean frequency of web-tugs (per min)	1.01 (0.28)	0.39 (0.18)	175^{**}

$^{*}P < 0.05$, $^{**}P < 0.01$

larger male won 90% ($n = 30$) of these interactions (Yate's corrected $\chi^2 = 19.2$, $P < 0.001$), suggesting that body size is a more important determinant of competitive ability than tenure on the web. In these contests, the mean weight difference between large and small males was 14.7 ± 1.7 mg.

Both males and females chased intruding spiders that ventured onto the orb-web, but the sex of the defending spider depended on the sex of the intruder. The cohabiting male reacted in all of the 30 trials involving an intruding male. In contrast, only females reacted in the five trials involving an intruding female (Fisher's exact probability < 0.001).

Cohabitation and female fertility

P. graeffei copulated numerous times over several days, and the fertility of females was influenced by the duration of male cohabitation and hence the frequency and/or total duration of copulation. Females that cohabited with males for less than an hour had a lower fertility (the proportion of eggs in the clutch from which spiderlings emerged) than females that cohabited over longer periods and thus could copulate more frequently (Fig. 1). An analysis of covariance with duration of male cohabitation as the main factor and female fecundity as a covariate revealed that female fertility was influenced significantly by the length of cohabitation ($F_{3,40} = 4.56$, $P < 0.008$), but not by female fecundity ($F_{1,40} = 3.39$, $P > 0.07$) or an interaction between these variables ($F_{3,37} = 2.44$, $P > 0.08$).

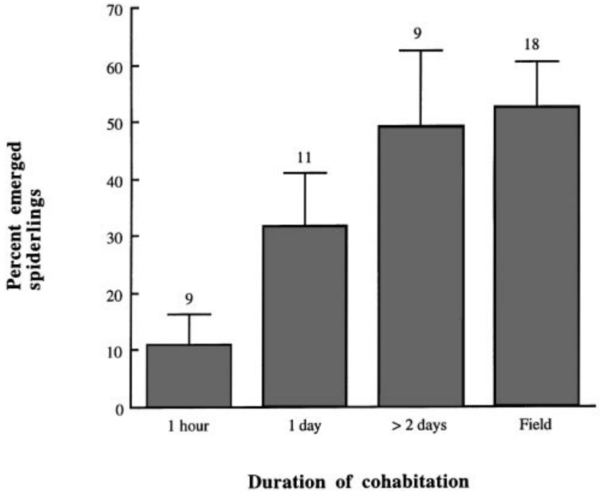

Fig. 1 The number of fertile eggs produced by female *Phonognatha graeffei* following different durations of cohabitation with males. Values are means with standard error *bars* and sample sizes *above*

Sexual cannibalism

Females sometimes cannibalised their mate after mating, but the frequency of cannibalism was not influenced by the availability of food: 26% ($n = 34$) of the females provided with food every day cannibalised their mate compared with 27% ($n = 11$) of females that were deprived of food.

The fecundity of females was not increased by cannibalising a single male (Fig. 2). An analysis of covariance with two levels of feeding regime and 3 levels of cannibalism (no cannibalism, cannibalism immediately after mating and cannibalism 3 weeks after mating) as factors, and the initial weight of the female and the time from mating until oviposition as covariates revealed that female fecundity was significantly influenced by the feeding regime ($F_{1,50} = 125.43$, $P < 0.001$) and initial female weight ($F_{1,50} = 5.90$, $P < 0.02$), but not by the

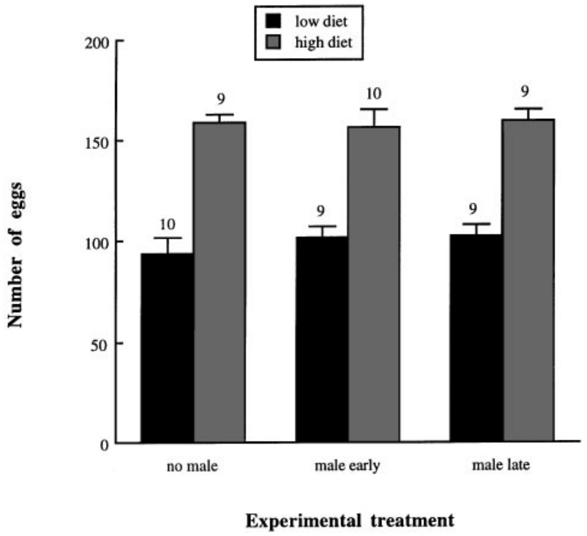

Fig. 2 The mean number of eggs produced by female *P. graeffei* fed either one fly each day or one fly every 3 days and either no males, one male immediately after mating (*male early*) or one male 3 weeks after mating (*male late*). Values are means with standard error *bars* and sample sizes *above*

occurrence of cannibalism ($F_{2,50} = 0.47$, $P > 0.6$), time until oviposition ($F_{1,50} = 1.49$, $P > 0.2$), or the interactions among these variables ($P > 0.45$ in all cases). The fecundities of experimental females (on both dietary regimes) fell within the range of females collected from the field population (range 77–238, mean = 149.8 ± 41.2, $n = 31$), suggesting that the experimental dietary regimes were similar to those experienced by females in natural populations. There was also a positive correlation between female fecundity and female weight immediately prior to oviposition for females collected from the field ($r = 66$, $n = 31$, $P < 0.001$).

Discussion

Males of *P. graeffei* cohabit in the leaf retreat of both immature and mature females. In our experiments, all males cohabited with immature females, typically mating with them after they had completed their final moult, and leaving after a relatively brief period of post-copulation cohabitation. This pattern of pre-copulation cohabitation between sexually mature males and sexually immature females is widespread in spiders (Jackson 1986; Miller and Ramey Miller 1986; Dodson and Beck 1993), including orb-weaving spiders (Robinson and Robinson 1980; Prenter et al. 1994; Elgar and Fahey 1996).

The active defence of females by cohabiting males suggests that pre-copulation mate-guarding is the primary function of cohabitation (see also Austad 1983; Prenter et al. 1994). *P. graeffei* is an entelegyne spider, currently placed within the Nephilinae (Hormiga et al. 1995). The spermatheca of entelegyne spiders consists of two ducts; the insemination duct that opens near the vaginal opening and into which the male intromittent organ dispenses seminal fluid, and the fertilisation duct from which sperms issue when the eggs are fertilised (Austad 1984). The first sperms to enter females with this so-called "conduit" spermathecal tract are likely to be nearest the fertilisation duct and hence may be the first to be used in fertilisations (Austad 1984; Watson 1991; Eberhard et al. 1993; Christensen and Cohn 1988; but see Masumoto 1993). Thus, males that cohabit with an immature female, defending her from rival males and mating with her when she attains sexual maturity may have a higher reproductive success than males that leave immature females in search of receptive, sexually mature females.

It is not clear why males defend immature females more vigorously than mature virgin females, since both are equally valuable to the male in terms of the proportion of eggs he is likely to fertilise. One explanation is that if females mate with several males, then the fertilisation success of males mating with females they encounter as adults will be lower, on average, than that when mating with females they encounter as immatures. If males cannot discriminate accurately between adult, virgin females and mated females, then adult, virgin females will be less "valuable" to males than immature females, and accordingly should be defended less vigorously (e.g. Austad 1983; Enquist and Leimar 1990). Although courting males in this study reacted differently to virgin and mated adult females, suggesting that they can distinguish between female reproductive condition, this may reflect differences in the behaviour of females (e.g. Watson 1993; Singer and Riechert 1995) rather than active discrimination by the males.

The duration of pre-copulation cohabitation may be a function of the risk of mortality associated with cohabitation and the probability of locating another unguarded female closer to sexual receptivity. The latter appears to be low for some orb-weaving spiders (Christenson and Goist 1979; Robinson and Robinson 1980; Miyashita 1993; Elgar and Fahey 1996; Elgar and Bathgate 1996). The leaf retreat may reduce the risk of mortality by either sexual cannibalism or predation during pre-copulation cohabitation. Cohabiting males may be less conspicuous to predators because they are concealed within the leaf retreat, a feature that is not common to other orb-weaving spiders. Additionally, the leaf retreat appears to provide males with at least some protection from pre-copulation sexual cannibalism, which occurs at a lower rate in *P. graeffei* than in other orb-weaving spiders (Elgar and Nash 1988; Elgar and Fahey 1996). The female leaf-curling spider resides in the lower half of the retreat with her front legs resting on the orb-web, and the male enters the retreat from the top of the leaf where he remains. The size of the retreat makes it virtually impossible for the female to turn around swiftly and cannibalise her prospective mate. Not surprisingly, male *P. graeffei* may remain with immature females for a long time; in our laboratory population, one male cohabited with an immature female for 39 days, and the female of another cohabiting male moulted twice before reaching sexual maturity (see also Christenson and Goist 1979; Jackson 1986; Toft 1989). Selection may favour males that guard any encountered immature female if the encounter rate with virgin females and the risk of pre-copulation sexual cannibalism are low (see also Ridley 1983). Pre-copulation mate-guarding may still be favoured even if females remain sexually receptive after mating, if the male that mates first fertilises more eggs than subsequent males.

The duration of copulation in *P. graeffei* is considerably longer than that of most other araneid spiders (Elgar 1995). Copulation in araneids typically lasts a few minutes, and consists of one pedipalp insertion followed by a bout of male courtship and then a second pedipalp insertion. There may be little selection for shorter copulation durations in *P. graeffei* compared with other araneids, if the leaf retreat provides protection from both predation and sexual cannibalism (see Elgar 1995). Male *P. graeffei* copulate for significantly longer with mated females than with virgin females. Similar patterns have been recorded in several other spiders (Elgar 1995). The longer duration of copulation for mated females can be interpreted within the context of sperm competition. For example, males may copulate for longer with mated females in order to increase the amount of sperm transferred, thereby decreasing the value of the sperm of the rival male (Andrade 1996).

Why do male *P. graeffei* remain with females after mating, despite the possibility of finding other receptive females and the potential risk of sexual cannibalism? First, the duration of post-mating cohabitation, and hence the frequency and/or duration of copulations, influences female fertility. Males that remain with sexually mature females for 24 h fertilise fewer eggs than those that remain with the female for longer periods. In fact, the fertility of captive females that spend more than 2 days in post-copulation cohabitation is similar to that of females collected from the field, suggesting that the typical duration of post-copulation cohabitation in the field is greater than 2 days. Like other orb-weaving spiders, female *P. graeffei* will mate with several males (Austad 1984; Elgar 1995; but see Elgar and Bathgate 1996), and post-copulation cohabitation could represent a further period of mate-guarding (Christenson and Goist 1979, Robinson and Robinson 1980) if the pattern of sperm priority depends upon inter-copulation time. For example, the sperm may take some time to reach the seminal receptacles and are more easily displaced while in the sperm ducts. Additionally, females may tolerate cohabiting males after the initial copulation because their fertility might otherwise be reduced.

One cost of post-mating cohabitation is the risk of sexual cannibalism. Buskirk et al. (1984) predicted that post-copulation sexual cannibalism with male complicity will evolve when the number of expected matings during the lifetime of a male (in the absence of sexual cannibalism) is low, and that the increase in reproductive output through sexual cannibalism is high. There was no evidence that the consumption of an additional male by a female increased her reproductive output (see Elgar and Nash 1988; Andrade 1996). Thus, while a female may benefit by cannibalising a male (as she would by consuming any single prey item), post-mating sexual cannibalism cannot benefit males, and hence this form of sexual cannibalism with male complicity is unlikely to evolve in this species.

Acknowledgements We thank Rachael Bathgate, Anthony Boxshall, Danielle Clode, Bill Eberhard, Theodore Evans, Johannah Fahey, Simon Goldsworthy, Mark Harvey, Robert Jackson, Michael Magrath and Sally Troy for their technical support, helpful suggestions and comments on the manuscript; John Mackenzie and Janet Yen for supplying the flies; and the W. V. Scott Fund, the University of Melbourne and the Australian Research Council (grant A19130739) for financial support.

References

Alcock J (1994) Post-insemination associations between males and females in insects: the mate guarding hypothesis. Ann Rev Entomol 39:1–21

Andersson M (1994) Sexual selection. Princeton University Press, Princeton.

Andrade MCB (1996) Sexual selection for male sacrifice in the Australian redback spider. Science 271:70–72

Austad SN (1983) A game-theoretical interpretation of male combat in the bowl and doily spider (*Frontinella pyramitela*). Anim Behav 31:59–73

Austad SN (1984) Evolution of sperm priority patterns in spiders. In: Smith RL (ed) Sperm competition and the evolution of animal mating systems. Academic Press, New York, pp 233–249

Birkhead TR, Møller AP (1992) Sperm competition in birds: evolutionary causes and consequences. Academic Press, London

Buskirk RE, Frohlich C, Ross KG (1984) The natural selection of sexual cannibalism. Am Nat 123:612–625

Christenson TE, Cohn J (1988) Male advantages for egg fertilisation in the golden orb-weaving spider (*Nephila clavipes*). J Comp Psychol 102:312–318

Christenson TE, Goist KC Jr (1979) Costs and benefits of male-male competition in the orb-weaving spider *Nephila clavipes*. Behav Ecol Sociobiol 5:87–92

Dodson GN, Beck MW (1993) Pre-copulatory guarding of penultimate females by male crab spiders *Misumenoides formosipes*. Anim Behav 46:951–959

Eberhard WG, Guzmàn-Gòmez S, Catley KM (1993) Correlation between spermathecal morphology and mating systems in spiders. Biol J Linn Soc 50:197–209

Elgar MA (1992) Sexual cannibalism in spiders and other invertebrates. In: Elgar MA, Crespi BJ (eds) Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, Oxford, pp 128–155

Elgar MA (1995) Copulation duration in spiders: comparative patterns. Rec West Aust Mus Suppl 51:1–11

Elgar MA, Bathgate R (1996) Female receptivity and male mate-guarding in the jewel spider *Gasteracantha minax*. Thorell (Araneidae). J Insect Behav 9:729–738

Elgar MA, Fahey BF (1996) Sexual cannibalism male-male competition and sexual size dimorphism in the orb-weaving spider *Nephila plumipes*. Behav Ecol 7:195–198

Elgar MA, Nash DR (1988) Sexual cannibalism in the garden spider *Araneus diadematus*. Anim Behav 36:1511–1517

Enquist M, Leimar O (1990) The evolution of fatal fighting. Anim Behav 39:1–9

Hormiga G, Eberhard WG, Coddington JA (1995) Web-construction behaviour in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae: Tetragnathidae). Aust J Zool 43:313–364

Jackson RR (1986) Cohabitation of males and juvenile females: a prevalent mating tactic of spiders. J Nat Hist 20:1193–1210

Main BY (1976) Spiders. Collins, Sydney

Masumoto T (1993) The effect of the copulatory plug in the funnel-web spider *Agelena limbata* (Araneae: Agelenidae). J Arachnol 21:55–59

Miller GJ, Ramey Miller P (1986) Pre-courtship cohabitation of mature male and penultimate female *Geolycosa turricola*. J Arachnol 14:133–4

Miyashita T (1993) Male-male competition and mating success in the orb-web spider *Nephila clavata*, with reference to temporal factors. Ecol Res 8:93–102

Parker GA (1974) Courtship persistence and female-guarding as male time investment strategies. Behaviour 48:157–184

Prenter J, Elwood RW, Montgomery WI (1994) Assessments and decisions in *Metellina segmentata* (Araneae: Metidae): evidence of a pheromone involved in mate-guarding. Behav Ecol Sociobiol 35:39–43

Ridley M (1983) The explanation of organic diversity: the comparative method and adaptations for mating. Clarendon Press, Oxford

Robinson MH, Robinson B (1980) Comparative studies on the courtship and mating behavior of tropical araneid spiders. Pac Insects Monog 36:1–218

Singer F, Riechert S (1995) Mating system and mating success of the desert spider *Agelenopsis aperta*. Behav Ecol Sociobiol 36:313–322

Thirunavukarasu P, Nicolson M, Elgar MA (1996) Leaf selection by the leaf-curling spider *Phonognatha graeffei* (Keyserling) (Araneoidea: Araneae). Bull Br Arachnol Soc 10:187–189

Thornhill R, Alcock J (1983) The evolution of insect mating systems. Harvard University Press, Cambridge

Toft S (1989) Mate guarding in two *Linyphia* species (Araneae: Linyphiidae). Bull Br Arachnol Soc 8:33–37

Watson PJ (1990) Female-enhanced male competition determines the first mate and principle sire in the spider *Linyphia litigiosa* (Linyphiidae). Behav Ecol Sociobiol 26:77–90

Watson PJ (1991) Multiple paternity and first mate sperm precedence in the sierra dome spider *Linyphia litigiosa* Keyserling (Linyphiidae). Anim Behav 41:135–48

Watson PJ (1993) Foraging advantage of polyandry for female sierra dome spiders (*Linyphia litigiosa*: Linyphiidae) and assessment of alternative direct benefit hypotheses. Am Nat 141:440–465

Wilkinson L (1992) SYSTAT: statistics, version 5.2 edn. SYSTAT, Evanston

Communicated by D.T Gwynne