

Jutta M. Schneider · Melissa L. Thomas  
Mark A. Elgar

## Ectomised conductors in the golden orb-web spider, *Nephila plumipes* (Araneoidea): a male adaptation to sexual conflict?

Received: 6 April 2000 / Revised: 22 June 2000 / Accepted: 5 November 2000 / Published online: 2 February 2001  
© Springer-Verlag 2001

**Abstract** Male genitalia may facilitate sperm protection by acting as a plug that prevents or hinders future matings. The pedipalps (intromittant organs) of males of the orb-web spider, *Nephila plumipes*, have a conductor with a peculiarly curved ending and a triangular process near the terminal end. The tip of the conductor, including the process, breaks during most matings and remains inside the female genital tract. We explored the possible function of the conductor as a mating plug using the double-mating sterile-male technique. Our data are not consistent with a plug function because males use only one pedipalp in each mating, thus leaving an unobstructed insemination duct available for future matings; conductors of males mating with virgin females are not more likely to break than those of males mating with mated females, and second males show no preference for used or unused spermathecae. In addition, males that inserted their palp in the insemination duct that contained a tip of the conductor from a previous male obtained a share in the paternity of the female's clutch of eggs. Interestingly, the conductor is more likely to break if it is inserted in an unused spermatheca. We argue that several lines of evidence suggest that the conductor breaks as a result of intersexual conflict over the duration of copulation.

**Keywords** Genital morphology · Sperm competition · Intersexual conflict · Spider · *Nephila*

### Introduction

Sexual selection, operating through female choice (Eberhard 1996), sexual conflict (e.g. Arnquist 1989; Sakaluk et al. 1995), sperm competition (Simmons and Siva-Jothy 1998) or a combination of all three processes, is likely to be an important force behind the evolution of the diversity of animal genitalia (see also Eberhard 1985). In insects, male genitalia are most elaborate in species with promiscuous mating systems that have a high potential for sperm competition (Arnquist 1998). Males may maximise their share of paternity by either preventing other males from mating with the female, or by 'stacking' the odds of fertilisation success when several males can inseminate the female. The latter may be achieved by delivering more sperm, removing the sperm of rival males and/or by influencing female choice (see Birkhead and Møller 1998). In some species, the male intromittant organ may not only transfer sperm but also facilitates the removal of sperm delivered by rival males (e.g. Waage 1979). In other species, the male genital apparatus appears to become permanently or semi-permanently locked to the female during copulation, thereby preventing the female from mating with other males (e.g. Hölldobler 1976; Downes 1978; Monnin and Peeters 1998; see also Thornhill and Alcock 1983).

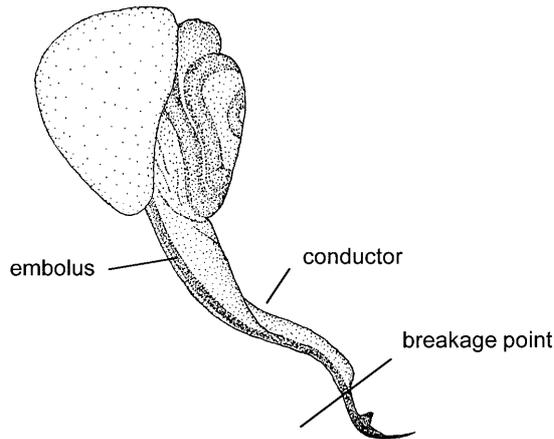
In spiders, males use secondary genital structures for mating; these modified appendices (pedipalps) must be filled with sperm and then inserted into the female genital opening. In the orb-weaving spider, *Nephila*, the pedipalp consists of a sclerotised conductor, which acts as a guide for the flexible embolus. The embolus resides in a fold of the conductor and expands during copulation, extending into the spermatheca where the sperm are deposited. The conductor does not enter the insemination duct but helps to attach the male pedipalp to the female genital opening, situated inside the epigastral furrow.

The conductor of the Australian orb-web spider, *Nephila plumipes*, has a peculiarly curved ending with a triangular process not far from the terminal end (see Fig. 1). This contrasts with the closely related

Communicated by L. Simmons

J.M. Schneider (✉)  
Department of Population Biology, Zoological Institute,  
University Mainz, 5099 Mainz, Germany  
e-mail: jutta@oekologie.biologie.uni-mainz.de  
Tel.: +49-61-38980560, Fax: +49-61-313923731

M.L. Thomas · M.A. Elgar  
Department of Zoology, University of Melbourne, Parkville,  
Victoria 3052, Australia



**Fig. 1** The male pedipalp of *Nephila plumipes*

*N. edulis*, which has a straight, pointed conductor (Uhl and Vollrath 1998a). Both species mate multiply but *N. plumipes* females show a high degree of sexual cannibalism (Elgar and Fahey 1996; Schneider and Elgar, in press) whereas *N. edulis* females rarely cannibalise males (Uhl and Vollrath 1998b; Schneider et al. 2000). The curved tip of the conductor, including the process, can break off during copulation and will remain stuck in the female genital opening after the male withdraws. It is not known whether the embolus also breaks with the conductor, and thus if the pedipalp of the male is dysfunctional after he loses the tip of the conductor. The tip of the embolus breaks during copulation and remains in the insemination duct in several species, including *Nephila* (Wiehle 1960, 1967; Foelix 1996). Why the embolus breaks in this way is not clear, although there are reports of several emboli tips found in single spermathecae (Foelix 1996). We are not aware of previous reports of the conductor breaking during copulation in any species of spider.

A morphological structure that breaks and remains inside the female may function as a male adaptation for sperm protection. Structures associated with the conductor are probably not useful for sperm removal or displacement since the conductor does not enter very far into the insemination duct of the female (G. Uhl, personal communication). If the conductor of *N. plumipes* evolved under sperm competition, it most likely acts as a plug (see Masumoto 1993). However, the embolus can reach the spermatheca and may manipulate sperm of previous males.

Several predictions arise if the conductor breaks off in order to reduce sperm competition with rival males. Most spiders possess paired spermathecae and entelgyne spiders (including orb-weavers) have two independent insemination ducts. Therefore, a sperm protection device that is applied to only one side will not necessarily prevent rival males from achieving paternity, since rival males could deliver sperm to the other spermatheca. Therefore, if the conductor acts as an efficient mating plug we predict that (1) the first male to mate with a fe-

male should use both pedipalps, (2) males that are the female's second mate should avoid the previously used insemination duct and (3) first males that ectomise their conductor should have an increased paternity. We used the double-mating, sterile-male technique (see Parker 1970; Simmons and Siva-Jothy 1998) to explore the possible function of the conductor of *N. plumipes*, focussing on its potential as a sperm protection device.

## 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 Towra Point mangroves in Botany Bay, Sydney, Australia. Most of the females were housed in separate Perspex frames (100×75×20 cm), where they built typical orb-webs; the remaining females were kept in plastic cups (750 ml). The females were watered and fed about ten bushflies, *Lucilia cuprina*, three 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 total body length and the width of the cephalothorax across the dorsal eyes. The female was immobilised by covering her with plastic film (Glad-wrap). Males were collected as adults from webs of females or as sub-adults from their own webs, which were mostly found near the trunks of mangrove trees. In the laboratory, males were maintained in individual cups (250 ml) on a diet of *Drosophila*. They were weighed and their body length was measured to the nearest 0.5 mm. Each male was inspected for the condition of his conductors.

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  $\gamma$ -emitter. The proportion of developed eggs was then used to calculate  $P_2$ , the proportion of eggs fertilised by the second male. Females were randomly assigned to one of four categories that varied in the order and composition of the two kinds of male mating partners. Thus, each female was provided with either (1) a normal male first and then an irradiated male (NI), (2) an irradiated male first and then a normal male (IN), (3) two irradiated males (II), which controls for sterilisation success, or (4) 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 after the first mating. However, not every female remated on the following day, and it was sometimes necessary to exchange the male or to repeatedly introduce him to the web for a few days.

We staged copulations 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 to the female. We noted when the male reached the edge of the web and the hub. Males rarely move from this location unless the female captures a prey item (Elgar and Fahey 1996), so we threw several bushflies into the web. Shortly after the female had captured a fly, and sometimes while she was returning to the hub, the male would jump onto her body, run over her a few times and then commence inserting his pedipalp. At that point, we started to time the duration of copulation, and noted which pedipalp was inserted. Entelgyne spiders always insert their pedipalps contralaterally, that is, the right-hand palp is inserted into the left-hand insemination duct, and vice versa. The male changed his position by 180° in the same plane during copulation, ending with his opisthosoma (abdomen) in the direction of the female's chelicerae.

We recorded the time when either the male removed his pedipalp and jumped off the female, or when the female caught and wrapped him. A few males inserted repeatedly either the same or the other pedipalp, and we stopped and restarted timing the dura-

tion of copulation accordingly. We always checked immediately at the end of copulation whether the male had lost the tip of his conductor. Males that were attacked by the female were quickly removed from her chelicerae and the pedipalps were inspected. However, we were not always successful in removing the male before the female had commenced digesting him, and hence some of these data are missing.

Mated females were transferred to separate cups where they were watered and fed about ten bushflies three 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 shortly before hatching. The vials containing the egg sacs were placed in a large open basin of water in a controlled-temperature room (25°C). Eggs usually hatched after 1 month, and so the contents of the vial were preserved in alcohol and the hatchlings and undeveloped eggs were counted under the microscope.

## Results

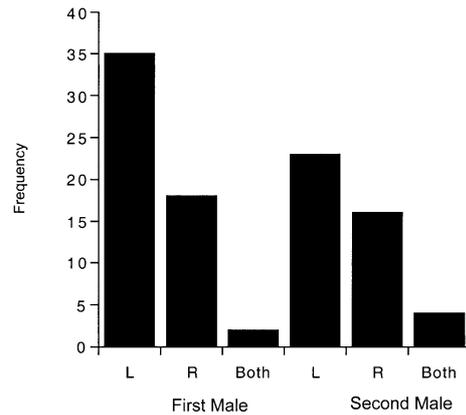
There was no association between the mating status of the female and damage to the tip of the conductor, which broke off in 70% of first matings (49 of 70 cases) and 80% of second matings (43 of 54 cases) ( $\chi^2=1.07$ ,  $P>0.29$ ; see Fig. 1).

### Selection of insemination duct

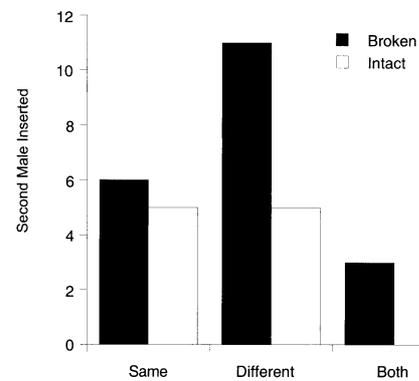
Most *N. plumipes* males insert only one of their pedipalps into only one duct of the female (Fig. 2). Only 6 of 96 males were observed inserting both pedipalps sequentially. As expected for entelegyne spiders, males never inserted both pedipalps simultaneously. Interestingly, first males showed a significant preference for the use of their left pedipalpus ( $\chi^2=5.45$ ,  $P<0.02$ ), although there was no significant tendency among second males ( $\chi^2=1.26$ ,  $P>0.26$ ).

There was no statistical evidence for side selectivity in either direction by second males (Fig. 3) perhaps due to low sample sizes. In 11 of 27 cases ( $\chi^2=0.93$ ,  $P>0.34$ ), the second male inserted his pedipalp into the same insemination duct as the previous male. Second males may select the insemination duct independently of whether it contains the broken tip of the conductor of the first male, although one may see a tendency towards usage of the other duct. When the conductor of the first male had broken, 6 males inserted in the same duct and 11 males inserted in the other duct. Similarly, if the conductor of the first male had not broken, 5 males inserted in the same and 5 in the other insemination duct ( $\chi^2=0.57$ ,  $P>0.45$ ; Fig. 3). However, the low power of this test does not allow a confident rejection of the null hypothesis.

Paternity could be assigned in four cases in which males inserted their palp into a insemination duct that contained the tip of the conductor of a previous male. In these cases,  $P_2$  was 14.6, 42.5, 69.9, and 100%, and thus covered the entire range of variation.  $P_2$  of second males that mated into a different insemination duct show similar variation (min=19%, max=100%, mean $\pm$ SE=60 $\pm$ 8%).



**Fig. 2** Frequencies of males using their left, right or both conductors when mating as the first or second male



**Fig. 3** Frequencies of the second male inserting into the same or the other spermatheca as the previous male (black bars) cases where the first male broke the tip of his conductor, white bars the conductor of the first male remained intact

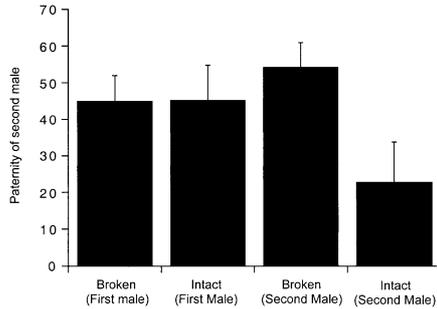
However, the tip of the conductor of the second male was more likely to break in the insemination duct that did not contain the tip of the conductor of the previous male (13 of 16 cases;  $\chi^2=6.25$ ,  $P<0.02$ ). Furthermore, the tip of the conductor of the second male was more likely to break if it had been inserted in an unused insemination duct, independently of whether the conductor of the first male had broken. The conductor of the second male broke 14 times in the unused and 5 times in the previously used insemination duct (Fisher exact  $P=0.017$ ).

### Conductor breakage 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 fertilised by the second male.  $P_2$  ranged from 0 to 1, with a median of 0.42 and a mean of 0.46 $\pm$ 0.05, which was not significantly different from 0.5 ( $t=-0.81$ ,  $P>0.4$ ,  $n=33$ ). The distribution was not significantly different from normal (Shapiro-Wilk test,  $W=0.94$ ,  $P=0.08$ ).

**Table 1** The combined effects of cannibalism and breakage of the conductor in matings of first and second males. Means with SEs are given with sample sizes in *parentheses* (there are missing values for variables in some categories)

	Male not cannibalised		Male cannibalised	
	Conductor intact	Conductor broken	Conductor intact	Conductor broken
<b>First male</b>				
Frequency	4	28	15	21
Copulation duration	46.0±14.0 (2)	33.2±4.0 (16)	97.9±18.7 (13)	63.7±15.2 (14)
$P_2$	–	38.5±9.9 (12)	45.2±9.6 (9)	51.8±10.0 (11)
<b>Second male</b>				
Frequency	12	14	8	20
Copulation duration	26.1±8.7 (11)	41.0±4.1 (10)	70.7±24.6 (6)	116.3±25.9 (14)
$P_2$	14.8±7.0 (7)	46.5±16.4 (6)	50.8±47.9 (2)	57.8±6.5 (13)



**Fig. 4** Mean (+SE) paternity ( $P_2$ ) when the tip of the conductor broke or remained intact, separated for matings of first and second males. Second males have a higher paternity when they break off the conductor. First males do not increase their relative paternity by ectomising the conductor

The median  $P_2$  of 16 IN females was 0.37 (mean±SE=0.37±0.08), which was not significantly different from that for 17 NI females (median=0.43; mean±SE=0.54±0.07;  $t_{31}=1.55$ ,  $P>0.13$ ). We corrected  $P_2$  values 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). The higher  $P_2$  in the NI treatment may result from 8 cases where the entire pedipalp of the male remained stuck in the female genital opening; exclusion of these values yields a median of 0.37 (mean±SE=50.9±0.11), which is closer to the IN treatment. The paternity of those 8 males varied around a median of 0.5 (mean±SE=0.52±0.09).

Analysis of variance revealed that the variation in  $P_2$  was not influenced by whether the tip of the first male's conductor was broken ( $F_{2,27}=0.03$ ,  $P>0.8$ ), but  $P_2$  was significantly higher when the tip of the conductor of the second male was broken ( $F_{2,27}=4.55$ ,  $P<0.05$ ). The interaction term was not significant ( $F_{2,27}=0.02$ ,  $P>0.8$ ; Fig. 4).

Cannibalism during or after copulation is frequent in this species (around 60%), and does not differ between first and second males (Schneider and Elgar, in press). The frequency of cannibalism was not independent of the loss of the tip of the conductor for matings of first males ( $\chi^2=7.16$ ,  $P<0.01$ ; Table 1). This arises because first males that survived with an intact conductor were extremely rare (4 of 68), whereas all other combinations

occurred with similar frequency. This complicates the analysis and results in low statistical power of all further tests involving first males, their paternity and conductor breakage.

Therefore, it is not possible to interpret the influence of losing the tip of the conductor independently of the effect of cannibalism for first males. However, there was no evidence of an association between cannibalism and the loss of the tip of the conductor for second males ( $\chi^2=1.79$ ,  $P>0.18$ ; Table 1). Breakage of the conductor and cannibalism seem to enhance each other in their positive effect on paternity for second males (Table 1). Analysis of variance reveals that the variation in  $P_2$  was not significantly explained by either the loss of the conductor ( $F_{3,27}=1.97$ ,  $P>0.17$ ) or whether the second male was cannibalised ( $F_{2,27}=2.91$ ,  $P>0.1$ ). The interaction term was not significant ( $P>0.3$ ).

#### Duration of copulation

The frequency distribution of the duration of copulation was not normally distributed. Therefore, we used non-parametric statistics or Box-Cox-transformed data. The duration of copulation of second males was longer if the tip of the conductor broke (median=42.9, mean±SE=84.9±16.9 s,  $n=24$ ) than if it did not (median=18, mean±SE=41.8±11.2 s,  $n=17$ ; Kruskal-Wallis test:  $Z=-2.36$ ,  $P<0.02$ ). This suggests that these males obtained a higher paternity by copulating for longer. Analysis of variance reveals that variation in the duration of copulation is explained by both cannibalism ( $F_{3,40}=9.04$ ,  $P<0.005$ ) and conductor ectomism ( $F_{3,40}=4.55$ ,  $P<0.04$ ; interaction  $P>0.72$ ), but the longest copulations were achieved by males that both broke the conductor and were cannibalised (Table 1). The duration of copulation of a second male was independent of whether he used the same (mean±SE=105±25.4 s,  $n=13$ ) or a different (mean±SE=88.5±18.4 s,  $n=20$ ) insemination duct than used by the previous male (Kruskal-Wallis test,  $Z=0.24$ ,  $P>0.8$ ).

The relationships between paternity, copulation duration and conductor ectomisation are less straightforward for first males, as may be expected from the earlier results. The duration of copulation for these males was shorter if the tip of their conductor broke (median=35,

mean±SE=47.4±7.8 s,  $n=30$ ) than if it did not (median=61, mean±SE=90.9±16.9 s,  $n=15$ ; Kruskal-Wallis test:  $Z=3.76$ ,  $P<0.001$ ). Again, the explanation for this unexpected relationship may be found in the occurrence of sexual cannibalism (Table 1). Analysis of variance reveals that the duration of copulation of first males was influenced by breakage of the conductor tip ( $F_{3,44}=4.39$ ,  $P<0.05$ ) but cannibalism had a stronger effect ( $F_{3,44}=7.24$ ,  $P<0.02$ ); the interaction was not significant ( $P>0.8$ ).

$P_2$  was not significantly correlated with the duration of copulation of the first male ( $r_s=0.1$ ,  $n=26$ ,  $P>0.6$ ), but there was a significant positive correlation for the second male ( $r_s=0.55$ ,  $n=21$ ,  $P<0.01$ ) (Schneider and Elgar, in press).

## Discussion

During mating, the tip of one of the conductors of the male of *N. plumipes* may break off and remain lodged in the female's reproductive tract. Explanations for this kind of phenomenon, in which males leave parts of their genital apparatus attached to the female, usually relate to the risk of sperm competition with other males (e.g. Thornhill and Alcock 1983; Elgar 1992), but none are convincingly supported by our data. Instead, ectomising the conductor may have evolved for reasons that are associated with sexual conflict over the duration of copulation.

While we cannot entirely exclude the possibility that the conductor functions as a mating plug, thereby making insemination by subsequent rival males impossible or at least difficult, there are several reasons why this is unlikely. First, there is little evidence that the tip of the conductor prevents rival males from mating successfully. In contrast with many other orb-weaving spiders (Elgar 1995), *N. plumipes* males generally insert only one of their palps. Thus, a male who mates with a virgin female and leaves the tip of his conductor in one insemination duct fails to leave an obstruction in the other duct, thereby allowing subsequent males to insert their pedipalp into an effectively 'virgin' duct. Second, males showed no clear preference for either insemination duct, indicating that a broken tip does not obstruct the entrance to the spermatheca. Third, first males do not improve their share of paternity if the tip of their conductor breaks, although these data must be interpreted cautiously because there were few cases in which males that mated with virgin females also escaped with an intact conductor. Even if the broken conductor functions as a plug, it does not provide a complete obstruction. The paternity of second males that copulated into an insemination duct that contained a broken conductor was highly variable, indicating that the sperm of a second male competes with that of the first male. However, we do not know how long the tip of the conductor remains attached to the female and the tip may not have been ejected in some of these trials. Of course, it is possible that mating trials with more than two males may reveal different patterns of paternity (see

Zeh and Zeh 1994), and that breaking the tip of the conductor only becomes an effective sperm protection mechanism when the female mates with more than two males. However, even in this case, males mating with previously mated females should prefer to use an 'unused' insemination duct.

The conductor is possibly used for internal courtship and optimal stimulation of the female may result in increased paternity (see Eberhard 1996, 1998). The conductor itself is an unlikely source of stimulation because it does not move after it is attached to the female. The shape and movement of the embolus may allow females to exert cryptic choice, although we cannot comment further without knowing more about male reproductive morphology and its relationship with male quality. Nevertheless, internal courtship seems unlikely because breaking this structure limits, rather than enhances, male mating success. This raises the more general question as to why selection should favour the loss of functional mating organs following copulation. Perhaps this potential loss of future mating opportunities is nullified by the high risk of sexual cannibalism that is characteristic of this species.

An alternative explanation for ectomising the tip of the conductor is related to a conflict of interest between the sexes over the duration of copulation. In many insects, both sexes have evolved anatomical features that apparently enhance their interests against those of the other sex (Arnquist and Rowe 1995). For example, males of some insects possess special claspers that firmly attach their genitals to those of the female (Downes 1978; Thornhill and Alcock 1983; Arnquist 1989; Sakaluk et al. 1995), while females of other species have abdominal spines that can prevent males from mating (Arnquist and Rowe 1995). Females of *N. plumipes* may use sexual cannibalism as a means to control the duration of copulation. For example, multiple-mating females of *Argiope keyserlingi* influence the paternity of their offspring by adjusting the timing of sexual cannibalism and hence the duration of copulation (see Elgar et al., 2000). Perhaps males of *N. plumipes* have evolved means of preventing the female from dislodging him during sexual cannibalism, thereby prolonging the duration of copulation. Manipulating the duration of copulation may allow males to either interfere with the sperm of rival males or to maximise sperm uptake or storage by the female. The former is unlikely because breakage of the conductor was more common when second males used the virgin insemination duct. Males may prolong copulation beyond the interests of the female by making it harder for the female to dislodge them. The conspicuous process located near the tip of the conductor may have evolved to facilitate this process, and several aspects of the behaviour of males before and during mating support this interpretation. Courting males only approach females that have captured a prey item (Elgar and Fahey 1996). The male then jumps onto the body of the female, and inserts one of his pedipalps. Immediately, he twists his body 180°, as if to screw in the conductor. The fe-

male often responds by moving a pair of her legs over her ventral body, giving the impression that she is attempting to brush off the male.

The tip of the conductor, with its curved form and conspicuous process, may act like a corkscrew; making it difficult for the female to dislodge the male and allowing him to remain attached to her and continue insemination. The male may eventually ectomise the tip of his conductor to facilitate his escape or it may simply break as a result of the actions of the female. We observed numerous matings in which the female attempted to pull the male away from her genital opening, stretching the pedipalp until the tip of the conductor snapped. In 15 cases (9 first males and 6 second males), the tip of the conductor did not snap at its usual location, and the entire pedipalp remained stuck in the genital opening of the female.

One corollary of this interpretation is that males are expected to prefer to copulate in the unused insemination duct, where the conductor may be more likely to attach firmly, as suggested by the higher probability of breakage in the unused side. Although male *N. plumipes* exhibit little preference for a particular side, the tip of the conductor was more likely to break in the genital opening that did not contain the tip of the conductor of a previous male. Furthermore, the tip of the conductor of the second male was more likely to break if it had been inserted in an unused duct, independently of whether the conductor of the first male had broken. Perhaps a structure in the female reproductive duct facilitates breaking of the tip of the male conductor, and this structure is changed or damaged during a mating so that a second male cannot firmly attach his conductor. The spermatheca of *N. clavipes* changes shape after mating but the ducts do not (Higgins 1989). Further morphological studies may shed light on this question.

**Acknowledgements** We thank Yael Lubin, Mariella Herberstein, Leigh Simmons, Gabriele Uhl and two anonymous referees for discussions and comments on the manuscript, Janet Yen and John Mackenzie for kindly providing *Lucilia*, and the Australian Academy of Science and the Australian Research Council (A19802502) for financial support.

## References

- Arnquist G (1989) Sexual selection in a water strider: the function, nature of selection and heritability of a male grasping apparatus. *Oikos* 56:344–350
- Arnquist G (1998) Comparative evidence for the evolution of genitalia by sexual selection. *Nature* 393:784–786
- Arnquist G, Rowe L (1995) Sexual conflict and arms race between the sexes: a morphological adaptation for control of mating in a female insect. *Proc R Soc Lond B* 261:123–127
- Birkhead TR, Møller AP (1998) Sperm competition and sexual selection. Academic Press, London
- Boorman E, Parker GA (1976) Sperm (ejaculate) competition in *Drosophila melanogaster*, and the reproductive value of females to males in relation to female age and mating status. *Ecol Entomol* 1:145–155
- Downes JA (1978) Feeding and mating in the insectivorous Ceratopogoninae (Diptera). *Mem Entomol Soc Can* 104:1–62
- Eberhard WG (1985) Sexual selection and animal genitalia. Harvard University Press, Cambridge, Mass
- Eberhard WG (1996) Female control: sexual selection by cryptic female choice. Princeton University Press, Princeton, NJ
- Eberhard WG (1998) Female roles in sperm competition. In: Birkhead TR, Møller AP (eds) Sperm competition and sexual selection. Academic Press, London, pp 307–337
- 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, New York, pp 128–155
- Elgar MA (1995) Duration of copulation in spiders: comparative patterns. *Rec Wash Mus (Suppl)* 51:1–11
- Elgar MA, Fahey DF (1996) Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae:Araneoidea). *Behav Ecol* 7:195–198
- Elgar MA, Schneider JM, Herberstein ME (2000) Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. *Proc R Soc Lond B* 267:2439–2443
- Foelix RF (1996) Biology of spiders, 2nd edn. Oxford University Press, New York
- Higgins LE (1989) Effect of insemination on the morphology of the internal female genitalia of the spider *Nephila clavipes* (Araneae: Araneidae). *Ann Entomol Soc Am* 82:748–753
- Hölldobler B (1976) The behavioral ecology of mating in harvester ants (Hymenoptera: Formicidae, Pogonomyrmex). *Behav Ecol Sociobiol* 1:405–423
- Masumoto T (1993) The effect of the copulatory plug in the funnel-web spider, *Agelena limbata* (Araneae: Agelenidae). *J Arachnol* 21:55–59
- Monnin T, Peeters C (1998) Monogyny and regulation of worker mating in the queenless ant *Dinoponera quadricaps*. *Anim Behav* 55:299–306
- Parker GA (1970) Sperm competition and its evolutionary consequences in the insects. *Biol Rev* 45:525–567
- Sakaluk SL, Bangert PJ, Eggert AK, Gack C, Swanson LV (1995) The gin trap as a device facilitating coercive mating in sagebrush crickets. *Proc R Soc Lond B* 261:65–72
- Schneider JM, Elgar MA (in press) Sexual cannibalism and sperm competition in the golden orb-web spider *Nephila plumipes* (Araneoidea): female and male perspectives. *Behav Ecol*
- Schneider JM, Herberstein ME, Crespi FC de, Ramamurthy S, Elgar MA (2000) Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. *J Evol Ecol* 13:939–946
- Simmons L, Siva-Jothy M (1998) Sperm competition in insects. In: Birkhead TR, Møller AP (eds) Sperm competition and sexual selection. Academic Press, London, pp 55–90
- Thornhill R, Alcock J (1983) The evolution of insect mating systems. Harvard University Press, Cambridge, Mass
- Uhl G, Vollrath, F (1998a) Genital morphology of *Nephila edulis*: implications for sperm competition in spiders. *Can J Zool* 76:39–47
- Uhl G, Vollrath, F (1998b) Little evidence of size-selective sexual cannibalism in two species of *Nephila* (Araneae). *Zoology* 101:101–106
- Waage J (1979) Dual function of the damselfly penis: sperm removal and transfer. *Science* 203:916–918
- Wiehle H (1960) Der Embolus des männlichen Spinnentasters. *Verh Dtsch Zool Ges*:457–480
- Wiehle H (1967) Steckengebliebene Emboli in den Vulven von Spinnen (Arach., Araneae). *Senck Biol* 48:197–202
- Zeh JA, Zeh DW (1994) Last-male sperm precedence breaks down when females mate with three males. *Proc R Soc Lond B* 257:287–292