

Male mate choice and patterns of paternity in the polyandrous, sexually cannibalistic orb-web spider *Nephila plumipes*

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Abstract

Studies that investigate patterns of paternity in polyandrous species typically employ double-mating trials, in which the paternity share of each male is established by either the sterile male technique or using genetic markers. However, polyandrous females may mate with more than two males and, in some species, triple-mating trials produce different patterns of paternity from double-mating trials. We investigated patterns of paternity share in triple-mating trials of the sexually cannibalistic orb-web spider *Nephila plumipes*. These experiments reveal little quantitative changes to paternity share when more than two males mate with the female; the third male apparently diluted the fertilisation success of the second male but not of the first male. Sexual cannibalism had little impact on the fertilisation success of the first male, but greatly increased the fertilisation success of the third male. When offered a choice, males did not prefer to mate with virgin over mated females, but males that chose virgin females were significantly heavier than those that chose mated females.

Introduction

For species in which females typically copulate with more than one male during their reproductive cycle, mate acquisition is only one stage in a process of sexual selection that may persist after insemination has occurred. In these species, the sperm from different males may coexist within the reproductive tract of the female, and consequently compete for fertilisation success. The resulting sperm competition has been a potent selective pressure, favouring numerous adaptations that enhance male fertilisation success (see Birkhead and Møller 1998; Simmons 2001). Where mating has costs for males, the risk and intensity of sperm competition have implications for male mating decisions (Parker 1998; Bonduriansky 2001; Simmons 2001).

Among terrestrial invertebrates, the most common factors that influence the patterns of paternity share include the order of mating, which may depend on male mate-searching strategies, and the relative quantity of sperm in the ejaculate (Elgar 1998; Simmons 2001). For example, the last male to mate fertilises most of the eggs in many insect species (Parker 1970; Simmons 2001), while in some linyphiid spiders the first male to mate has the greatest share of paternity (Austad 1984; Elgar 1998). When sperm are in

competition, the fertilisation success of each male may be a function of the relative quantity of his sperm in the female sperm-storage organ at the time of fertilisation (Parker 1998). Thus, males may increase their share of paternity by delivering relatively larger ejaculates and/or mating repeatedly with the same female (e.g. Simmons 2001; Elgar *et al.* 2003).

Most studies that have investigated the sources of variation in paternity have employed mating trials involving two males mating with the same female (e.g. Birkhead and Møller 1998; Simmons 2001). However, it is evident that females of many species mate with more than two males and, more importantly, the patterns of paternity share may not be the same when more than two males mate with the female (Simmons 2001). For example, in two-male mating trials, the second male of the harlequin beetle-riding pseudoscorpion, *Cordylocheres scorpoides*, fertilises almost all of the eggs. However, this mating-order pattern disappears when females mate with three males, with each male fertilising a similar number of eggs (Zeh and Zeh 1994). In contrast, the number of mating partners does not change the pattern of first-male sperm precedence in the sierra dome spider, *Neriene litigiosa* (Watson 1991), or last-male sperm precedence in the beetles *Tribolium castaneum* (Arnaud *et al.* 2001) and *Callosobruchus maculatus* (Lady and Tubman 1996). Nevertheless, the study by Zeh and Zeh (1994) suggests that it is unwise to infer patterns of sperm usage in matings involving more than two males from conventional double-mating experiments (Elgar 1998).

The pattern of male mate choice is likely to be determined by the potential fertilisation success of different kinds of females (Bonduriansky 2001). For example, males may choose between females according to body size or condition, when these indicate female fecundity (Bonduriansky 2001). Males may also discriminate between females according to their expected fertilisation success, which may depend upon the intensity and risk of sperm competition and the patterns of sperm utilisation (Simmons 2001). There is evidence of male preference for virgin over mated females in insects and spiders, presumably to avoid engaging in sperm competition (e.g. Suter 1990; Simmons 2001; Herberstein *et al.* 2002). Nevertheless, a preference for virgins is not inevitable, particularly if most females mate multiply and the last male to mate sires most of the offspring.

The golden orb-web spider, *Nephila plumipes*, is common along the east coast of Australia. It is typically abundant where it occurs, forming large aggregations, with as many as 10 webs that either share structural threads or are found within 20 cm of another web (Elgar 1989). The webs of an adult or sub-adult female may also contain several mature males (Robinson and Robinson 1980; Elgar 1989; Elgar and Fahey 1996) and, like other species in this genus, some males may weigh less than 1% of the body weight of mature, fecund females (Schneider *et al.* 2001). Females frequently cannibalise males both before and during copulation and males that avoid sexual cannibalism may still lose one or two legs (Elgar and Fahey 1996; Schneider *et al.* 2001; Schneider and Elgar 2001, 2002). Thus, there is a potentially high cost of mating for males of *N. plumipes*. Double-mating experiments have shown that the fertilisation success of the second male is greater if he is a victim of sexual cannibalism (Schneider and Elgar 2001) or his reproductive organ is damaged (Schneider *et al.* 2001), but mating order does not influence paternity (Schneider *et al.* 2001).

Here, we investigate the patterns and sources of variation in paternity in females of *N. plumipes* that mate with three males. We use the sterile male technique, in which either the first or last male to mate is sterilised. We also examine whether virgin males prefer the webs built by either virgin or mated females.

Methods

Sub-adult female and both sub-adult and adult male *N. plumipes* were collected during January 1999 and 2000, from several suburban populations in metropolitan Sydney, Australia. Most of the females were housed in separate perspex frames (58 × 58 × 15 cm), where they built typical orb-webs; the remaining females were kept in up-turned plastic cups (500 mL). The females were watered and fed ~10 bushflies, *Lucilia cuprina*, on each of 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 the total body length and the width of the cephalothorax across the dorsal eyes. The female was immobilised by covering her with plastic film. Males were collected as adults from the webs of females or as sub-adults from their own webs. In the laboratory, males were maintained in individual cups (250 mL) on a diet of *Drosophila*. Under a dissecting microscope, males were carefully inspected for species-specific traits and the status of their conductor. The body length of each male was measured to the nearest 0.5 mm and their body mass was determined shortly before the mating trials.

Patterns of paternity were determined using standard double-mating trials (Parker 1970). Mature males were randomly assigned to either normal (N) or irradiated (I) treatments; males in the latter were irradiated with a dosage of 10 krad from a cobalt- γ -emitter. Paternity can then be estimated as the proportion of developed eggs for control males or undeveloped eggs for irradiated males. Each female was provided with either a normal male followed by two irradiated males (NII) or two irradiated males followed by a normal male (IIN). This procedure allowed us to estimate the paternity of the first and last male to mate with a female that mated with three males. Although subsequent males were typically introduced to the female on the day after her first and second mating, female receptivity was apparently unpredictable and they often did not re-mate at that time. Thus, it was sometimes necessary to exchange the male or to repeatedly introduce him to her web over a period of several days. The modest sample sizes in our study reflect the difficulty of arranging three matings for each female.

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 this location unless the female captured a prey item (Elgar and Fahey 1996; Schneider and Elgar 2001, 2002), and so we threw several bushflies into the web to induce mating behaviour. 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. At that point we started to time the duration of copulation, and checked which pedipalp was inserted into which opening of the female. We recorded the time when either the male removed his pedipalp and jumped off the female, or when the female caught and wrapped him. Some males inserted repeatedly either the same or the other pedipalp and we stopped and restarted timing the duration of copulation accordingly (see also Schneider and Elgar 2001). We always checked immediately at the end of copulation whether the male had lost the tip of his conductor (see Schneider *et al.* 2001), so males that were attacked by the female were quickly removed from her chelicerae.

Mated females were transferred to separate cups, where they were watered and fed ~10 bushflies on each of three days per week. The mated female laid an egg sac ~35 days after mating, and this was removed and placed in a separate sterile plastic container that was closed with cotton wool. The vials containing the egg sacs were placed in a humid, controlled-temperature (25°C) incubator. Eggs hatched one month later and were preserved in alcohol. The hatchlings and undeveloped eggs were subsequently counted under the microscope. A number of females died either before they had produced eggs or shortly after they had made their first egg sac (containing eggs). The causes of death are unknown.

Mate choice bioassay

We collected penultimate males and females from West Pymble Park (Sydney) in January 2002 and reared them to maturity in the laboratory in separate perspex frames (50 × 50 × 10 cm). After their final moult half of the females were mated with a virgin male, the other half remained unmated. We waited at least 48 h after the mating before using the females in the mate-choice bioassays, which follow Herberstein *et al.* (2002). The evening before the trial, the web of the female was cut down to encourage her to build a new web. The female was then removed from her recently constructed web to eliminate the influence of female behaviour on male choice. A single strand of support silk was drawn from a virgin and mated female to the tip of a 20-cm wooden skewer, which was placed centrally between the two webs. The skewer was fixed at an inclination (30°) to encourage the male to walk up. The virgin males were released on the lower end of the

skewer and typically walked along it until they reached the point where the silks of both webs came together. We included data only from those males that touched (and thus sampled) both strands of silk. A choice was recorded if the male walked along one of the silk lines into the web and proceeded towards the hub. Males and females were weighed after the trial.

Data analysis

Data were visually and statistically inspected for normality and transformed where appropriate. We used non-parametric tests for those data for which we could not obtain normal distributions. The data were analysed using JMP 3.2.2 (SAS Institute). Means are given \pm standard error, unless specified otherwise. Sample sizes can be different because not all measurements were taken from all spiders.

Results

The size of the males did not differ with mating order (Table 1). There were also no significant differences between the three males in the time taken by the male to reach the female and initiate copulation, the frequency of cannibalism, or the duration of copulation (Table 1). Finally, males that were cannibalised did not differ in size from those that survived copulation (Table 2). A Nested Anova showed that variation in male body mass was not explained by female mating order ($F_{2,113} = 0.155$, $P > 0.8$) or cannibalism (nested within mating order: $F_{6,113} = 0.284$, $P > 0.9$). A similar result emerged for male leg length (mating order: $F_{2,113} = 0.477$, $P > 0.6$; cannibalism: $F_{6,113} = 0.404$, $P > 0.8$).

Paternity of first and last males

Paternity values were corrected for the 72.8% hatching success in NN controls and 1.17% success in II controls (see Schneider and Elgar 2001), using the formula suggested by Boorman and Parker (1976). Thus, the corrected values, which are those given unless otherwise stated, are not on a 0–1 scale. Although the average paternity of first males was twice that of last males, the difference was not strongly significant ($t_{41} = 1.72$, $P = 0.093$) (Table 3). When the transformed paternity values were rescaled to a scale of 0–100%, first males obtained 45% paternity and third males obtained 23%, which leaves the intermediate value of 32% for second males. The paternity of the last male was less variable than that of the first male; the last males rarely obtained values above 0.5 and they never obtained the maximum paternity of first males.

Paternity, cannibalism and copulation duration

Cannibalism by virgin females had no effect on paternity; males that were cannibalised had a mean corrected paternity of 1.13 ± 0.23 ($n = 9$) compared with 0.86 ± 0.25 ($n = 12$) for males that survived mating (Mann–Whitney U-test, $Z = 0.89$, $P > 0.37$). The mean duration of copulation of first males that were cannibalised (35.8 ± 6.0 s, $n = 8$) was not significantly different from those first males that survived (35.1 ± 3.7 s, $n = 12$; Mann–Whitney U-test, $Z = 0.46$, $P > 0.6$). Two outliers were excluded from the analysis; these two spiders had extremely long copulation durations (>200 s). The paternity of first males was not correlated with the duration of copulation ($r^2 = 0.0003$, $F_{1,18} = 0.005$, $P > 0.94$).

Last males that were cannibalised (0.75 ± 0.19 , $n = 13$) could expect more than twice the share in paternity than last males that survived (0.32 ± 0.2 , $n = 8$; $Z = -1.98$, $P < 0.05$). The duration of copulation of last males that were cannibalised (39.46 ± 9.2 s, $n = 11$) was significantly longer than that of the last males that survived (17.0 ± 7.0 s, $n = 8$; $Z = -1.99$, $P < 0.05$). However, there was no significant correlation between paternity and the duration of copulation of the last male ($r^2 = 0.07$, $F_{1,17} = 1.26$, $P > 0.27$). There was no significant

Table 1. The frequency of cannibalism, the duration of copulation and the time to copulation of first, second and third males
Values are means \pm s.e., unless otherwise stated

	First male	Second male	Third male	Test statistic
Male leg length (mm)	4.91 \pm 0.10	4.90 \pm 0.13	5.07 \pm 0.13	$F_{2,120} = 0.59, P > 0.55$
Male body weight (g)	0.0197 \pm 0.0011	0.0206 \pm 0.0020	0.0216 \pm 0.0013	$F_{2,123} = 0.80, P > 0.80$
Percentage cannibalised	54.5	63.6	48.8	$\chi^2 = 1.98, P > 0.30$
Copulation duration (s)				
Mean \pm s.e.	31.5 \pm 2.2 ^A	38.16 \pm 4.80	32.76 \pm 5.20	$F_{2,120} = 0.72, P > 0.48$
Median (interquartiles)	31 (19.8–40)	22 (10–48)	22 (9.8–45.8)	
Time to copulation (min)				
Mean \pm s.e.	72.55 \pm 11.21	61.57 \pm 9.81	73.09 \pm 10.21	$F_{2,128} = 0.39, P > 0.67$
Median (interquartiles)	46 (9.8–107.5)	43.5 (19–87)	49 (20–100)	

Table 2. Measures of the body size of males that either survived or were eaten by females during copulationValues are means \pm s.e.

Female mating order	Male leg length (mm)		Male body mass (g)	
	Survived	Eaten	Survived	Eaten
First	4.80 \pm 0.12 <i>n</i> = 22	5.03 \pm 0.15 <i>n</i> = 19	0.0198 \pm 0.0016 <i>n</i> = 24	0.0195 \pm 0.0015 <i>n</i> = 18
Second	4.78 \pm 0.17 <i>n</i> = 26	5.10 \pm 0.21 <i>n</i> = 15	0.0192 \pm 0.0016 <i>n</i> = 27	0.0231 \pm 0.0047 <i>n</i> = 15
Third	5.08 \pm 0.17 <i>n</i> = 20	5.05 \pm 0.21 <i>n</i> = 20	0.0206 \pm 0.0020 <i>n</i> = 21	0.0212 \pm 0.0017 <i>n</i> = 20

Table 3. Average paternity achieved by first versus last males in triple-mating trials

Mean \pm s.e. as well as median and quantiles are provided. The values are corrected for the proportions of eggs hatched in SS controls and the proportion of unfertilised eggs in NN controls. Therefore, values are not on a 0–1 scale. Values in parentheses are rescaled to a proportional axis

Paternity	Mean	s.e.	Median	Interquartiles
First male	0.60 (0.45)	0.11	0.44	0.14–1.09
Last male	0.32 (0.23)	0.08	0.18	0.00–0.55

Table 4. Number of first, second and third males that ended copulation with either a broken or an intact conductor

Conductor	Intact	Broken	% Broken
1st male	9	23	71.9
2nd male	19	11	36.7
3rd male	14	12	46.2

correlation between the difference in copulation duration and the difference in paternity of first ($r^2 = 0.11$, $F_{1,15} = 1.75$, $P > 0.21$, two outliers removed) and last males ($r^2 = 0.02$, $F_{1,17} = 0.34$, $P > 0.57$).

Breakage of the male conductor

The likelihood of the conductor breaking during mating was significantly associated with the order of mating (Table 4). The male's conductor was more likely to break if he was the first male to mate than if he were the second or third male ($\chi^2_2 = 8.47$, $n = 88$, $P = 0.015$). Breakage of the conductor was not associated with whether the male was cannibalised or not (1st male: $\chi^2_2 = 2.42$, $n = 32$, $P > 0.12$; 2nd male: $\chi^2_2 = 1.21$, $n = 30$, $P > 0.27$; 3rd male: $\chi^2_2 = 2.10$, $n = 27$, $P > 0.35$).

First males used their left or right pedipalp with a similar frequency (left: 15, right: 20; exact binomial $P = 0.095$). However, second males tended to use their right pedipalp more frequently (left: 9, right: 20; exact binomial $P = 0.019$) and the third male to mate used his left pedipalp more frequently (left: 17, right: 7; exact binomial $P = 0.021$).

Mate selection by males

We offered 21 virgin males a choice between a virgin and a mated female. All males made a choice and proceeded into the web of a female, but there was no preference for either mated or virgin females: 9 males chose mated females and 12 chose virgin females (binomial $P = 0.140$). There was no difference in the weight of virgin (0.39 ± 0.03 g) and mated (0.42 ± 0.03 g) females (paired t -test: $t_{20} = 0.84$, $P = 0.41$). However, those males that chose virgin females were significantly heavier (0.15 ± 0.002 g) than those that chose mated females (0.09 ± 0.001 g) (t -test: $t_{16,4} = 2.54$, $P = 0.02$).

Discussion

The paternity of a male that mates with a virgin female does not appear to be substantially influenced by the number of times she mates. The adjusted proportion of eggs fertilised by the first male of *N. plumipes* to mate in trials with copulations by three males was 0.60 ± 0.11 , which is comparable to that (0.54 ± 0.05 , $n = 33$) obtained in experiments involving only two males (Schneider and Elgar 2001). The similarity of the data from double- and triple-mating trials is consistent with other studies of spiders (e.g. Watson 1991) and insects (Lady and Tubman 1996; Arnaud *et al.* 2001). More generally, these data suggest that the paternity of the first male to mate is not influenced by the intensity of sperm competition (*sensu* Parker 1998), but that the paternity of subsequently mating males is reduced with increasing intensity of sperm competition (see also Watson 1991). However, the pattern of paternity share with three copulations differs from that observed in the sister species *N. edulis*. In this species, paternity declines with the intensity of sperm competition, irrespective of mating order. In trials involving three copulations by two males, the paternity obtained by a male *N. edulis* that copulated once with a virgin female (while his rival copulated twice) was 0.33 ± 0.07 ($n = 46$) (Schneider *et al.* 2001), which is almost half that obtained by males of *N. plumipes*. The reason for this difference between these two species is not clear, but may relate to the physiology of sperm induction and storage; for example, the duration of copulation in *N. plumipes* is very considerably shorter than that in *N. edulis* (Schneider *et al.* 2000; Elgar *et al.* 2003).

The effects of sexual cannibalism and conductor breakage on the outcome of paternity in this study are broadly similar to those obtained from double-mating experiments (Schneider and Elgar 2001). Cannibalism had no effect on the paternity of the first male to mate, but the paternity of the last male to mate was significantly increased if he was cannibalised. This study was unable to determine the degree to which these two factors affect the paternity of the second male, when the female mates with three males. Thus, it remains to be seen whether the advantage of cannibalism for the second male over the first male is maintained when another male mates, or if both males similarly lose their share of paternity to the third male.

The patterns of male palp usage, depending on the mating history of non-virgin females, are intriguing and may reflect male attempts to avoid sperm competition. Entelegyne spiders, such as *Nephila*, always insert their pedipalps contralaterally; that is, the right-hand palp is inserted into the left-hand insemination duct, and *vice versa*. Schneider and Elgar (2001) found that the two spermathecae of female *N. plumipes* are filled separately by each male. Thus, males mating with an already mated female may be able to avoid sperm competition by utilising the 'virgin' insemination duct (see also Bukowski *et al.* 2001). However, this explanation does not predict a general preference for the left or right insemination duct by males mating with mated females.

According to the paternity data obtained in our experiments, males should prefer virgin over mated females, primarily because, on average, they will obtain a higher fertilisation success. Males that mate with virgins can expect either exclusive paternity or shared paternity, while males that mate with mated females can only expect shared paternity. Surprisingly, males of *N. plumipes* apparently do not prefer virgin females over mated females, in contrast with another orb-web spider *Argiope keyserlingi* (Herberstein *et al.* 2002). Perhaps the frequency of multiple mating is sufficiently high in *N. plumipes* that few females remain monogamous and thus there is little to be gained by preferring a virgin over a mated female.

The result that males that preferred virgin females were generally heavier than those that preferred mated females was unexpected. Perhaps larger males are more capable of preventing rival males from gaining access to the female (see Elgar and Fahey 1996), and thus these males are more likely to benefit from preferring to mate with a virgin female. For these larger males, the timing of mating with respect to female oviposition may be critical because there is a relatively high risk of cannibalism, which clearly prevents any further mate guarding.

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References

- Arnaud, L., Gage, M. J. G., and Haubruge, E. (2001). The dynamics of second- and third-male fertilisation success in *Tribolium castaneum*. *Entomologia Experimentalis et Applicata* **99**, 55–64.
- Austad, S. N. (1984). Evolution of sperm priority patterns in spiders. In 'Sperm Competition and the Evolution of Animal Mating Systems'. (Ed. R. L. Smith.) pp. 233–249. (Academic Press: London.)
- Birkhead, T. R., and Møller, A. P. (1998). 'Sperm Competition and Sexual Selection.' (Academic Press: London.)
- Bonduriansky, R. (2001). The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biological Reviews* **76**, 305–339.
- Boorman, E., and Parker, G. A. (1976). Sperm (ejaculate) competition in *Drosophila melanogaster*, and the reproductive value of females to males in relation to female age and mating status. *Ecological Entomology* **1**, 145–155.
- Bukowski, T. C., Linn, C. D., and Christenson, T. E. (2001). Copulation and sperm release in *Gasteracantha cancriformis* (Araneae: Araneidae): differential male behaviour based on female mating history. *Animal Behaviour* **62**, 887–895.
- Elgar, M. A. (1989). Kleptoparasitism: a cost of aggregating for the orb-weaving spider *Nephila edulis*. *Animal Behaviour* **37**, 1052–1055.
- Elgar, M. A. (1992). Sexual cannibalism in spiders and other invertebrates. In 'Cannibalism: Ecology and Evolution among Diverse Taxa'. (Eds M. A. Elgar and B. J. Crespi.) pp. 129–156. (Oxford University Press: Oxford.)
- Elgar, M. A. (1998). Sexual selection and sperm competition in arachnids. In 'Sperm Competition and Sexual Selection'. (Eds T. R. Birkhead and A. P. Møller.) pp. 307–337. (Academic Press: London.)
- Elgar, M. A., and Fahey, B. F. (1996). Sexual cannibalism, male–male competition and sexual size dimorphism in the orb-weaving spider *Nephila plumipes*. *Behavioral Ecology* **7**, 195–198.
- Elgar, M. A., Schneider, J. M., and Herberstein, M. E. (2000). Females control paternity in a sexually cannibalistic spider. *Proceedings of the Royal Society, London* **267**, 2439–2443.
- Elgar, M. A., Champion de Crespigny, F., and Ramamurthy, S. (2003). Male copulation behaviour and the risk of sperm competition. *Animal Behaviour* **66**, 211–216.

- Herberstein, M. E., Schneider, J. M., and Elgar, M. A. (2002). Costs of courtship and mating in a sexually cannibalistic orb-web spider: female and male strategies. *Behavioral Ecology and Sociobiology* **51**, 440–446.
- Lady, P., and Tubman, S. (1996). Last-male sperm precedence does not break down when females mate with three males. *Ecological Entomology* **21**, 303–304.
- Parker, G. A. (1998). Sperm competition and the evolution of ejaculates: towards a theory base. In 'Sperm Competition and Sexual Selection'. (Eds T. R. Birkhead and A. P. Møller.) pp. 3–54. (Academic Press: London.)
- Schneider, J. M., and Elgar, M. A. (2001). Sexual cannibalism and sperm competition in the golden orb-web spider *Nephila plumipes* (Araneioidea): female and male perspectives. *Behavioral Ecology* **12**, 547–552.
- Schneider, J. M., and Elgar, M. A. (2002). Sexual cannibalism in *Nephila plumipes* as a consequence of female life history strategies. *Journal of Evolutionary Biology* **15**, 84–91.
- Schneider, J. M., Herberstein, M. E., Champion de Crespigny, F., Ramamurthy, S., and Elgar, M. A. (2000). Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. *Journal of Evolutionary Biology* **13**, 939–946.
- Schneider, J. M., Thomas, M. L., and Elgar, M. A. (2001). Ectomised conductors in the golden orb-web spider *Nephila plumipes* (Araneioidea): a male adaptation to sexual conflict. *Behavioral Ecology and Sociobiology* **49**, 410–415.
- Simmons, L. W. (2001). 'Sperm Competition and its Evolutionary Consequences in the Insects.' (Princeton University Press: Princeton.)
- Watson, P. A. (1991). Multiple paternity and first male sperm precedence in the sierra dome spider *Linyphia litigiosa* (Linyphiidae). *Animal Behaviour* **41**, 135–149.
- Zeh, J. A., and Zeh, D. W. (1994). Last-male sperm precedence breaks down when females mate with three males. *Proceedings of the Royal Society, London, Series B* **257**, 287–292.

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