



Male copulation behaviour and the risk of sperm competition

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When females mate with more than one male during their reproductive cycle, males may increase their share of paternity by copulating repeatedly with the same female. Accordingly, males should mate repeatedly with the same female more frequently when the risk of sperm competition is greater. We examined this idea experimentally in the orb-web spider *Nephila edulis*, which is characterized by both extreme sexual size dimorphism and extreme male size variation. Comparison of the mating behaviour of solitary and pairs of males on the webs of virgin and mated females revealed that males adjust the frequency and duration of copulation according to the mating history of the female and the presence of rival males. Males copulated more frequently and for longer with virgin than mated females. The copulation behaviour of males in the presence of rivals depended upon their relative size. Typically, larger males prevented smaller rivals from gaining access to the female and therefore were able to copulate more frequently. Smaller males copulated less frequently, but for longer periods, which may have increased their share of paternity. The size of male *N. edulis* can vary by an order of magnitude, and our results suggest that this variation may be maintained by the alternative size-dependent strategies of preventing or winning sperm competition.

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Polyandry, together with the simultaneous storage of sperm from different males, creates the opportunity for sperm competition and an extraordinary variety of male traits have evolved apparently in response to sexual selection through sperm competition (Birkhead & Møller 1998; Simmons 2001). Simmons (2001) identified two broad categories of mechanisms by which a male increases the probability that his sperm fertilizes the eggs of his mating partner. The first includes mechanisms by which males prevent sperm competition from taking place, for example by mate guarding, inducing a refractory (nonreceptive) period, or manipulating the ejaculates already deposited by rival males. The second includes attributes of the male's ejaculate that may increase his fertilization success at the expense of his rivals, for example by depositing more sperm or by producing sperm of greater competitive ability.

The outcome of sperm competition may resemble a lottery, in which the fertilization success of each male is a function of the relative quantity of his sperm in the female's sperm storage organ at the time of fertilization (Parker 1998; Simmons 2001). Thus, males may increase their share of paternity by delivering relatively larger ejaculates or mating repeatedly with the same female.

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There is some evidence that extended copula duration allows males to increase their relative fertilization success (Simmons 2001), presumably as a result of delivering larger quantities of sperm, and thus longer copulations are expected when there is a greater risk of sperm competition (Parker et al. 1997). However, the relation between copula duration and sperm competition is not straightforward (Simmons 2001), and empirical evidence often appears conflicting. For example, water striders (Gerridae) copulate for longer when the operational sex ratio is male biased (Arnqvist 1997), but the risk of sperm competition has little effect on copula duration in the damselfly *Mnais pruinosa pruinosa* (Siva-Jothy & Tsubaki 1989).

Males may increase their share of paternity by repeatedly mating with the same female, a behaviour that is common among birds (Birkhead 1998) and mammals (Gomendio et al. 1998). However, this behaviour can be difficult to interpret because, in some species, it is the female that solicits repeated copulations, perhaps thereby ensuring the male provides greater care to her offspring. Repeated mating with the same female is apparently less common among invertebrates, probably because the typically greater mobility of females makes it difficult for the male to remain with his mate. Nevertheless, repeated mating with the same female has been reported in several insects (Smith 1979; Sivinski 1983; Lissemore 1997) and, in some species, attracts some resistance by the female (Archer & Elgar 1999). However, few studies

have examined whether repeated mating is more likely under conditions of increased risk of sperm competition (Choe 1997).

The mating system of many orb-web spiders is promiscuous and both males and females are capable of mating with more than one partner (Elgar 1998). The female reproductive tract is bilateral with two genital pores covered by a sclerotized plate called the epigynum, two sperm ducts and two receptacula seminis where the seminal fluid is stored. Males copulate using pedipalps (secondary genital structures), which must be filled with sperm and then inserted into the female's genital opening. A single copulation is sufficient to fertilize a clutch of eggs, but experimental studies of double-mating females show that paternity share in orb-web spiders is positively correlated with copula duration and frequency (e.g. Christenson & Cohn 1988; Cohn 1990; Elgar et al. 2000; Schneider et al. 2000). The order of mating does not strongly influence a male's share of paternity (Elgar 1998), although males typically prefer to court virgin than mated females (Herberstein et al. 2002).

The Australian female golden orb-weaver spider *Nephila edulis* builds semipermanent webs in the drier woodlands of eastern Australia, from Victoria to Queensland. The spiders are relatively common where they occur, but are not found in the larger aggregations that are typical of the closely related *N. plumipes* (Elgar 1989). Mature males weigh between 0.002 and 0.200 g, that is, between 1 and 80% of the typical weight of a mature virgin female. Numerous males may cohabit on the webs of both penultimate and mature females, and these males may interact aggressively with other males (personal observations). Mating takes place at the central hub of the orb-web, and larger males tend to exclude smaller males from the web. These smaller males are typically found at the edge of the web or on the support strands leading to the frame. Double-mating experiments have shown that smaller males obtain a greater share of paternity through increased duration of copulation (Schneider et al. 2000). Female *N. edulis* are typically not sexually cannibalistic during copulation (Uhl & Vollrath 1998; Schneider et al. 2000), unlike the congener, *N. plumipes* (Schneider & Elgar 2001, 2002; Schneider et al. 2001).

In this study, we investigated how the risk of sperm competition (sensu Parker 1998) may influence male mating behaviour. In particular, we examined whether female reproductive state and the presence of rivals influence the frequency and duration of copulation. We also investigated whether the patterns of male mating behaviour are influenced by male body size.

METHODS

We collected subadult female *N. edulis* during February and March 2000 from several populations around Euroa in northern Victoria, Australia. The females were maintained in individual cups (600 ml) until they were about two moults from sexual maturity, after which they were transferred to separate Perspex frames (100 × 75 × 20 cm), in which they built typical orb-webs. Courtship and mating trials were conducted in these frames. The females

were watered and fed about eight blowflies *Lucilia cuprina* (Diptera) at least 3 days per week. Males were collected as adults or subadults from the webs of females, and were maintained in the laboratory in individual cups (250 ml) on a diet of *Drosophila* (Diptera). We weighed males several hours before their mating trial.

We examined the effects of female mating status and the risk of sperm competition on male mating behaviour in a simple experiment involving four treatments: we placed either one or two males in the frame containing the orb-web of either a virgin or mated female. The latter had mated at least several days before the experiment. We observed females for 5 h after the males had been introduced, or until both males had been cannibalized. Females allocated to treatments with two males had a large and small male and, in these trials ($N=30$), the mean mass of the small males ($\bar{X} \pm \text{SE} = 0.0013 \pm 0.0002$ g) was significantly less than that of large males (0.0276 ± 0.0037 g; $t_{58} = 18.48$, $P < 0.001$). The mean mass of the males in the single-male treatment (0.010 ± 0.003 g, $N=28$) was not significantly different from that of the males in the two-male treatments (0.016 ± 0.002 g, $N=60$; $t_{186} = 1.57$, $P > 0.12$). We recorded, in each trial, the timing and duration of copulations performed by each male, and the timing and outcome of aggressive encounters between rival males and between the female and males. We also noted the location of males on the web throughout the experiment.

Field Census

During a census in late February and another in early April, we recorded the number and size of males on each web of female *N. edulis* from a single, unmanipulated population near Euroa. We attempted to survey all of the female webs in the population, although we excluded some because they were too high in the trees and the males were not clearly visible. Males were arbitrarily categorized as small (<10 mm long) or large (>10 mm long). These categories roughly correspond to the size categories used in the experiments.

Data Analysis

All data were inspected for normal distributions and, accordingly, copulation duration was log transformed for the statistical analyses. Values given are means \pm SE of untransformed data unless stated otherwise. We used two-tailed tests.

RESULTS

Male Web Attendance in Natural Populations

We observed up to nine males on the webs of females during the 2 days of sampling (Fig. 1). We have observed as many as 15 males on a web in other surveys. The mean number of males per web (excluding those webs without males) was 2.1 ± 0.2 ($N=101$ webs), with small males being typically more numerous (1.3 ± 0.1) than large males (0.7 ± 0.1 ; paired t test: $t_{100} = 3.45$, $P < 0.001$).

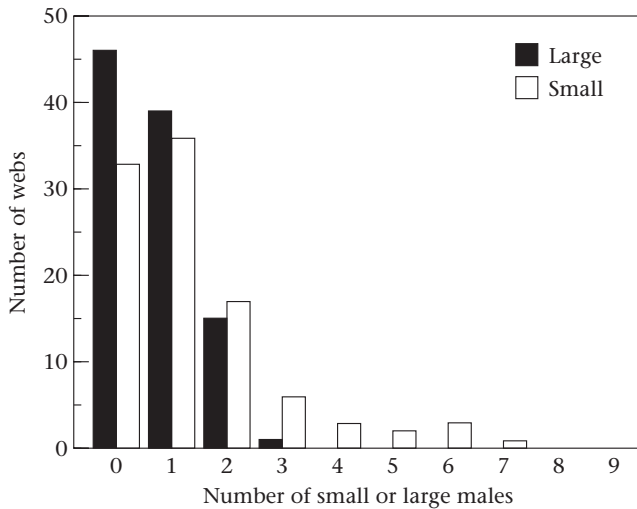


Figure 1. Number of small or large males found on webs ($N=101$) of female *N. edulis*. The data are taken from webs in which there was at least one male present. The zero category represents webs in which there were no males of one size, but a variable number of the other size. The largest number of males on a web was nine: seven small and two large.

Female Cannibalism of Courting Males

Sexual cannibalism occurred during 7% of copulations ($N=59$ with 24 females) in trials in which a single male was on the web and 6% of copulations ($N=116$ with 25 females) in trials in which two males were initially on the web. Females also captured and cannibalized males that were on the web but not copulating, and 21% ($N=28$) of the solitary males perished in this manner compared with 26% ($N=60$) of the males that had a rival on the web (Fisher's exact test: $P=0.79$). Female mating status did not influence cannibalism when either a solitary male (virgin: two of 10; previously mated: four of 18; Fisher's exact test: $P=0.99$) or two males were on the web (virgin: seven of 18; previously mated: nine of 42; Fisher's exact test: $P=0.21$). Males cannibalized while on the web tended to weigh less (0.009 ± 0.002 g, $N=22$) than males that were not cannibalized (0.016 ± 0.002 g, $N=44$; Wilcoxon test: $Z=1.88$, $P=0.06$).

Male Mating Behaviour

The copulation rate of females with one male on the web (0.61 ± 0.10 copulations/h, $N=28$) was not significantly different from that when two males were on the web (0.78 ± 0.16 copulations/h, $N=30$; $t_{56}=0.89$, $P>0.3$). This arises because of an asymmetry in male copulation rate when two males were on the web. The mean male copulation rate while two males were on the web was 0.57 copulations/h ($N=60$) and the variance was 1.24, which was significantly greater than that when only one male was on the web (0.28; F_{\max} test: $F_{59,27}=4.47$, $P<0.001$). The most frequently copulating male of each pair obtained 0.91 ± 0.27 copulations/h (maximum 6.98), compared with 0.23 ± 0.07 copulations/h (maximum 1.20) for the less frequently copulating male. The more

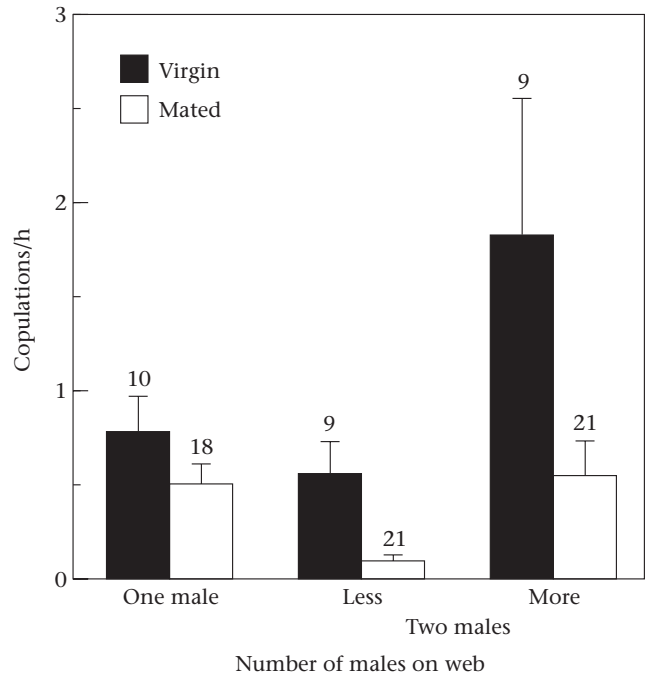


Figure 2. Copulations/h of male *N. edulis* with or without a rival and paired with either a virgin or previously mated female. The rates when two males were on the web are partitioned into the more or less frequently copulating male of the pair. Values are means \pm SE, with sample sizes above the bars.

frequently copulating male was significantly heavier (0.025 ± 0.004 g) than the less frequently copulating male (0.008 ± 0.001 g; paired t test: $t_{29}=3.621$, $P=0.001$). The difference between males in their copulation rates tended to increase with the difference in their size (Kendall rank correlation: $\tau_{23}=0.25$, $N=24$, $P=0.08$, excluding trials in which mating did not occur).

The influence of female reproductive history and presence of rivals on copulation can be examined by comparing separately the behaviour of solitary males with either the most or the least frequently copulating individual in the trials with pairs of males (Fig. 2). A two-way ANOVA that included the most frequently copulating males in the trials with two males revealed a tendency for male copulation rate to be influenced by an interaction between the female's reproductive history and the number of males on the web ($F_{1,54}=3.038$, $P=0.09$; female reproductive history: $F_{1,54}=7.11$, $P=0.01$; number of males on the web: $F_{1,54}=3.21$, $P=0.08$). The same analysis, but now including the less frequently copulating males, revealed an influence of the female's reproductive history ($F_{1,54}=9.65$, $P=0.01$) and the number of males on the web ($F_{1,54}=7.47$, $P=0.008$; Fig 2) but the interaction term was not significant ($F_{1,54}=0.65$, $P>0.4$).

The duration of copulation varied across all treatments from 0.3 to 26.5 min. Single males on the web copulated for significantly longer with virgin (534.6 ± 152.0 s, $N=9$) than mated (138.8 ± 31.7 s, $N=15$) females ($t_{22}=3.96$, $P<0.01$). When two males were on the web and both obtained at least one copulation, the smaller male

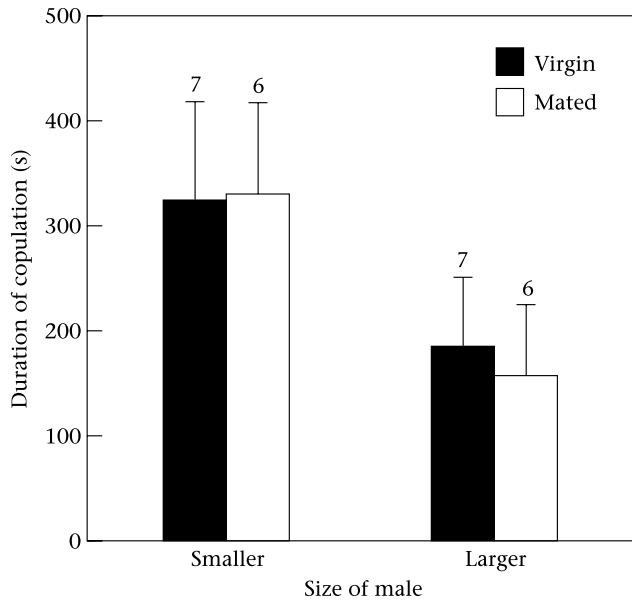


Figure 3. The duration of copulation of virgin and mated females mating with either the smaller or the larger male when two males were on the female's web. Values are means \pm SE, with sample sizes above the bars.

copulated for significantly longer (325.8 ± 61.1 s) than the larger male (169.1 ± 46.9 s; paired t test: $t_{12}=3.50$, $P<0.01$). However, the duration of copulation for these males did not differ between virgin or previously mated females for either the larger ($t_{11}=0.625$, $P>0.5$) or smaller males ($t_{11}=0.142$, $P>0.8$; Fig. 3).

Male Antagonistic Behaviour

Males typically behaved aggressively towards each other, and these aggressive interactions escalated from simple tugging on the web to physical conflicts in which males sometimes lost a leg. The interactions were resolved when one male retreated to the edge of, or even off, the web. The larger male typically initiated the aggressive interactions between males ($\chi^2_2=10.5$, $P=0.007$), and these larger males were able to exclude the smaller male from the hub or even the orb-web ($\chi^2_2=24.0$, $P=0.001$; Fig. 4).

DISCUSSION

Our results show that males of the golden orb-web spider *N. edulis* adjust the frequency and duration of copulation according to the mating history of the female and the presence of rival males. Males copulated more frequently and for longer with virgin than mated females. The copulation behaviour of males in the presence of rivals depended upon their relative size. The larger male of the pair copulated more frequently than his rival, and also more frequently than a solitary male. The smaller male copulated less frequently but typically for longer than his larger rival. The larger male copulated more frequently because he was able to prevent his smaller rival from gaining access to the female.

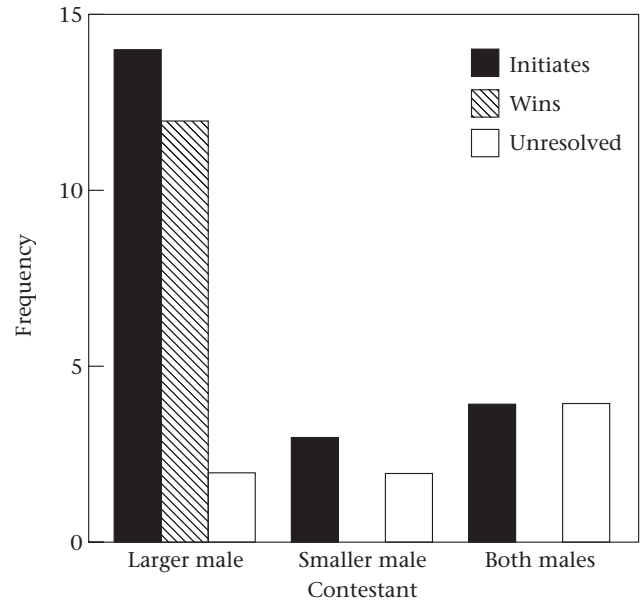


Figure 4. Number of contests initiated, won or unresolved in relation to size of male. We observed four cases in which it was not clear which male initiated the conflict, which was not resolved by one male retreating.

Repeated mating occurs in a variety of insects and spiders (Smith 1979; Sivinski 1983; Christenson & Cohn 1988; Choe 1997; Lissemore 1997; Archer & Elgar 1999). However, it is not clear whether repeated mating increases the male's fertilization success by preventing sperm competition through mate guarding, by increasing the relative quantity of his ejaculate in the female's sperm storage organ, or by both processes (Simmons 2001). Studies investigating how male insects adjust their reproductive investment in response to changes in the risk of sperm competition mostly focus on the quantity of ejaculate in a single copulation (Parker 1998; Simmons 2001). Male *N. edulis* increase the frequency of remating and the duration of copulation when there is a greater risk of sperm competition. Both behaviours may allow males to increase their fertilization success. Paternity share is positively correlated with the duration of copulation, and males that copulate twice sire over 70% of the clutch compared with their single-mating rivals, which sire less than 30%, regardless of the order of mating or male body size (Schneider et al. 2000). However, remating will be beneficial only if the male mates relatively more frequently than his rival. In this study, the larger male typically mated more frequently and also prevented his rival from copulating with the female, thereby creating a significant difference in the copulation rates between the two males.

Increasing fertilization success through repeated mating might be an option only in species in which males can maintain contact with their partner. Among terrestrial invertebrates, these might include species that form pair bonds (e.g. *Ips pini*: Lissemore 1997; *Necrophorus vespilloides*: Müller & Eggert 1989), long mating associations (e.g. *Abedus herberti*: Smith 1979), or where

the female is relatively sedentary (e.g. *Nephila clavipes*: Christenson & Cohn 1988). Females of web-building spiders have limited mobility because they forage and mate on their webs, so males can easily remain with their mates for as long as the web remains intact. Repeated mating may be a widespread strategy among male web-building spiders that is used to improve their fertilization success.

The female's mating history also influenced the frequency and duration of copulation; copulations involving initially virgin females were more frequent and lasted longer than those involving initially mated females. This pattern is surprising because theory predicts greater investment in mating effort when the intensity of sperm competition increases and, in particular, when males mate with mated rather than virgin females (Parker 1998). These data also contrast with previous studies of spiders that reported longer copulations with mated than virgin females (Elgar 1998). The influence of female status on the duration of copulation ceased when more than one male was on the web. This was probably caused by male interference; rival males often walked on to the female and attempted to dislodge the copulating male, or created disturbances during copulation by tugging at the web (personal observations). The greater copulation frequency of males with initially virgin females in *N. edulis* contrasts with that of the congener *N. clavipes*, in which males copulate more frequently with mated than virgin females (Christenson & Cohn 1988). There is no obvious reason for this difference.

The difference in the frequency and duration of copulations involving initially virgin and mated females is more likely to be caused by the behaviour of males than by that of females. Males of the orb-weaver *Argiope keyserlingi* distinguish between virgin and mated females, preferring to approach the webs of virgins even in the absence of the female (Herberstein et al. 2002). The cue is chemical and apparently present on the silk produced by virgin but not mated females (see also Suter 1990). There is some evidence that males of *N. edulis* can similarly distinguish between the webs of virgin and mated females, preferring the former (A. Gaskett, unpublished data). It is not clear whether males or females of *N. edulis* control the duration of copulation. Copulations in *N. edulis* are typically longer than in the congener *N. plumipes*, in which copulations are usually terminated by sexual cannibalism (Schneider & Elgar 2001; Schneider et al. 2001). This form of sexual cannibalism is comparatively rare in *N. edulis*, suggesting that male *N. edulis* either determine the duration of copulation or are better at escaping female attacks during or directly after copulations.

Although large males may prevent rival small males from copulating with their mates, small males that do copulate could still sire a significant proportion of the clutch by copulating for relatively longer. A male's share of paternity when in competition with another male is positively correlated with the duration of copulation in this (Schneider et al. 2000) and other species of orb-web spiders (e.g. Elgar et al. 2000). Smaller males copulated for almost twice as long as larger males and this may partly

offset, in terms of fertilization success, their relatively lower copulation rate. However, the success of smaller males may also depend upon the relative size of their rivals, since the greater the size difference, the less likely the smaller male will be able to secure a mating.

The mating success of smaller males may also depend upon the number of rivals on the web. In our experiments, there were only two males on the web, but under natural conditions many more males may be found on a female's web. Male fertilization success declines with the copulation frequency of each rival, and presumably this effect is more acute when more males are present on the web. Indeed, it is not clear why so many males may be found on the web of a female, nor whether the presence of these rivals influences the time males may remain on the web.

Although the relation between male body size and competition for mating opportunities has been extensively documented, few studies have examined whether sperm competition can also act as a selective pressure on male body size. Selection through male-male competition for mating opportunities favours large body size in *N. edulis*, as with many other species, including other spiders (e.g. Andersson 1994; Choe & Crespi 1997; Elgar 1998; Blankenhorn 2000). Large male size may also be an advantage in terms of preventing sperm competition, if the larger male can prevent his smaller rivals from copulating with his mate (e.g. Arnqvist 1997). Large size in this species may also provide some protection against sexual cannibalism, in contrast with *N. plumipes* (Elgar & Fahey 1996). The relation between body size and paternity in mixed-parentage matings varies among terrestrial invertebrates, with either positive (Parker 1970; McLain 1985; Lewis & Austad 1990; Watson 1991; Simmons & Parker 1992; Otronen 1994) negative (Elgar et al. 2000; Schneider et al. 2000) or no correlation (Archer & Elgar 1999). In *N. edulis*, small males may obtain a greater share of paternity by copulating for longer (Schneider et al. 2000). Perhaps the remarkably large variation in male body size in this species is maintained by the alternative size-dependent strategies of preventing or winning sperm competition.

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References

- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Archer, M. S. & Elgar, M. A. 1999. Female preference for multiple partners: sperm competition in the hide beetle, *Dermestes maculatus*. *Animal Behaviour*, **58**, 669–675.
- Arnqvist, G. 1997. The evolution of water strider mating systems: causes and consequences of sexual conflict. In: *The Evolution of*

- Mating Systems in Insects and Arachnids* (Ed. by J. C. Choe & B. J. Crespi), pp. 146–163. Cambridge: Cambridge University Press.
- Birkhead, T. R.** 1998. Sperm competition in birds: mechanisms and function. In: *Sperm Competition and Sexual Selection* (Ed. by T. R. Birkhead & A. P. Møller), pp. 579–622. London: Academic Press.
- Birkhead, T. R. & Møller, A. P.** 1998. *Sperm Competition and Sexual Selection*. London: Academic Press.
- Blankenhorn, W. U.** 2000. The evolution of body size: what keeps organisms small? *Quarterly Review of Biology*, **75**, 1–23.
- Choe, J. C.** 1997. The evolution of mating systems in the Zoraptera: mating variations and sexual conflicts. In: *The Evolution of Mating Systems in Insects and Arachnids* (Ed. by J. C. Choe & B. J. Crespi), pp. 130–145. Cambridge: Cambridge University Press.
- Choe, J. C. & Crespi, B. J. (Eds)** 1997. *The Evolution of Mating Systems in Insects and Arachnids*. Cambridge: Cambridge University Press.
- Christenson, T. E. & Cohn, J.** 1988. Male advantages for egg fertilisation in the golden orb-weaving spider (*Nephila clavipes*). *Journal of Comparative Psychology*, **102**, 312–318.
- Cohn, J.** 1990. Is it the size that counts? Palp morphology, sperm storage, and egg hatching frequency in *Nephila clavipes* (Araneae, Araneidae). *Journal of Arachnology*, **18**, 59–71.
- Elgar, M. A.** 1989. Kleptoparasitism: a cost of aggregating for the orb-weaving spider *Nephila edulis*. *Animal Behaviour*, **37**, 1052–1055.
- Elgar, M. A.** 1998. Sexual selection and sperm competition in arachnids. In: *Sperm Competition and Sexual Selection* (Ed. by T. R. Birkhead & A. P. Møller), pp. 307–337. London: Academic Press.
- Elgar, M. A. & 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. & Herberstein, M. E.** 2000. Females control paternity in a sexually cannibalistic spider. *Proceedings of the Royal Society of London, Series B*, **267**, 2439–2443.
- Gomendio, M., Harcourt, A. H. & Roldán, E. R. S.** 1998. Sperm competition in mammals. In: *Sperm Competition and Sexual Selection* (Ed. by T. R. Birkhead & A. P. Møller), pp. 667–755. London: Academic Press.
- Herberstein, M. E., Schneider, J. M. & 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.
- Lewis, S. M. & Austad, S. N.** 1990. Sources of intraspecific variation in sperm precedence in red flour beetles. *American Naturalist*, **135**, 351–359.
- Lissemore, F. M.** 1997. Frass clearing by male pine engraver beetles (*Ips pini*; Scolytidae): paternal care or paternity assurance? *Behavioral Ecology*, **8**, 318–325.
- McLain, D. K.** 1985. Male size, sperm competition, and the intensity of sexual selection in the southern green stink bug, *Nezara viridula* (Hemiptera: Pentatomidae). *Annals of the Entomological Society of America*, **78**, 86–89.
- Müller, U. G. & Eggert, A.-K.** 1989. Paternity assurance by 'helpful' males: adaptations to sperm competition in burying beetles. *Behavioral Ecology and Sociobiology*, **24**, 245–249.
- Otronen, M.** 1994. Fertilisation success in the fly *Dryomyza anilis* (Dryomyzidae): effects of male size and the mating situation. *Behavioral Ecology and Sociobiology*, **35**, 33–38.
- Parker, G. A.** 1970. Sperm competition and its evolutionary consequences in the insects. *Biological Reviews*, **45**, 525–567.
- Parker, G. A.** 1998. Sperm competition and the evolution of ejaculates: towards a theory base. In: *Sperm Competition and Sexual Selection* (Ed. by T. R. Birkhead & A. P. Møller), pp. 3–54. London: Academic Press.
- Parker, G. A., Ball, M. A., Stockley, P. & Gage, M. J. G.** 1997. Sperm competition games: a prospective analysis of risk assessment. *Proceedings of the Royal Society of London, Series B*, **264**, 1793–1802.
- Schneider, J. M. & 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. & 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. E., Ramamurthy, S. & 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. & 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, New Jersey: Princeton University Press.
- Simmons, L. W. & Parker, G. A.** 1992. Individual variation in sperm competition success of yellow dung flies, *Scatophaga stercoraria*. *Evolution*, **46**, 366–375.
- Siva-Jothy, M. T. & Tsubaki, Y.** 1989. Variation in copulation duration in *Mnais pruinosa pruinosa* Selys (Odonata: Calopterygidae). 2. Causal factors. *Behavioral Ecology and Sociobiology*, **25**, 261–267.
- Sivinski, J.** 1983. Predation and sperm competition in the evolution of coupling durations, particularly in the stick insect *Diaperomera veliei*. In: *Orthopteran Mating Systems; Sexual Competition in a Diverse Group of Insects* (Ed. by D. T. Gwynne & G. K. Morris), pp. 147–162. Boulder, Colorado: Westview Press.
- Smith, R. L.** 1979. Repeated copulation and sperm precedence: paternity assurance for a male brooding water bug. *Science*, **205**, 1029–1031.
- Suter, R. B.** 1990. Courtship and assessment of virginity by male bowl and doily spiders. *Animal Behaviour*, **39**, 307–313.
- Uhl, G. & Vollrath, F.** 1998. Little evidence for size dependant sexual cannibalism in two *Nephila* species. *Zoology*, **101**, 101–106.
- Watson, P. J.** 1991. Multiple paternity and first mate sperm precedence in the Sierra Dome spider *Linyphia litigiosa* Keyserling (Linyphiidae). *Animal Behaviour*, **41**, 135–149.