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Intersexual conflict in spiders

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Reproductive strategies of males and females usually differ and. as a consequence, may impose asymmetric costs of reproduction on tire two sexes and result in conflict between the sexes. In spiders, males do not provide parental care and females can store sufficient sperm for several clutches. These characteristics define the stage for a conflict between males and females that occurs mainly over the frequency of mating. Factors such as sexual size dimorphism, operational sex ratio, mating system and life-ltistory strategies are likely to influence the degree of conflict and its outcome for different species. Male spiders may suffer large costs of mating due to mate search, assessment of female condition, courtship and cannibalistic tendencies of their mates. Courtship may reduce cannibalism, although in some cases, males benefit from being cannibalised by having an increased fertilisation rate or greater offspring fitness. In some species, limited mating capacities will increase tire value of the current mating relative to future reproduction. Apart from a possible benefit of genetic variability within a clutch, females may not benefit from multiple mating and multiple mating may even be costly. Exceptions occur if additional resources are provided by males or when offspring fitness increases with additional mating. Forced copulation, prey theft, loss of the web and reduction of foraging time can all result in reduced reproductive success for females. We discuss the interacting influences of life-history traits (especially patterns of growth and maturation and sexual size dimorphism) and the reproductive strategies of males and females, using a semelparous spider, *Stegodyphus lineatus* (Eresidae), as an example of a species in which males and females can have strongly conflicting interests.

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Males and females of dioecous species must cooperate to produce viable offspring, but their investment in their common young often differs greatly. Males produce a large number of small sperm whereas the female sex produces few but large eggs. Anisogamy is the basis for a conflict of interests between the sexes (Parker 1984). Owing to the numerous gametes they produce, male fitness can generally be increased by mating with as many females as possible, thereby maximising the number of eggs fertilised. The female's reproductive success will not necessarily depend on the number of mates; rather, it will be to her advantage to select the best possible mate and gain paternal investment that will either improve the quality of the young or enable her to produce more young. Thus, strategies that enhance the reproductive success of one sex may conflict with those of the other and impose a cost on the other sex. Such a cost can affect both mating partners through its effect on the progeny. Both the level of the cost and the threshold of acceptance of such a cost can differ for the sexes and this difference defines the degree of conflict.

The simplest case of intersexual conflict is that of males attempting to mate with every female they encounter and to protect their sperm from rival males, whereas females attempt to mate with the best male only and reject others. For females, additional copulations beyond those necessary to fertilise the available

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eggs can be costly and the greater the cost to the female, the more vigorous will be the rejection of additional males. Females may reduce receptivity after one mating (Elgar 1998 and references therein), they may respond aggressively towards male approaches or evolve structures that enhance their control over mating (e.g. abdominal spines, Amqvist and Rowe 1995). Rejected males risk not gaining any reproductive success. Thus, males may attempt to mate with unreceptive females and selection will favour behaviours that enhance their chances of mating with a female. Forced copulation is one example of a male strategy that is costly to the female.

Conflict can occur also over the relative investment of the sexes in brood care. In cases where the care of both parents is not essential for the survival of all offspring, one sex may benefit from deserting, leaving the other parent the options of caring for the brood alone or deserting as well. Internal fertilisation usually results in the female being the parent that can not easily desert. In systems where the male does not provide any other investment but his sperm to the common offspring, the conflict over brood care appears resolved in favour of male interests. When mates do invest in brood care, paternal investment may include providing nutritive substances together with copulation (e.g. spermatophores and nuptial gifts in many arthropods), defending resources for the females and their young (many mammals), assisting in parental care (many birds) and providing postnatal brood care (sea horses and many fish) (Krebs and Davies 1993). Such male strategies may reduce the relative cost of reproduction for females.

Reproductive systems are likely to represent a compromise between the female and male reproductive interests. When the resolution of intersexual conflict is fixed it is difficult to identify the selection pressures that led to the observed pattern and the system may not be accessible for experimental manipulation. The study of intersexual conflict requires situations where male and female interests over mating frequency or parental care conflict and may be resolved only after a contest. Mating systems where the resolution of the conflict is not fixed are of particular interest because they provide an opportunity to study experimentally the factors that determine the outcome of conflicting reproductive interests of the sexes.

Spiders are suitable for investigations of sexual conflicts for several reasons. First, they have a variety of mating systems combined with differences in factors such as sexual size dimorphism, operational sex ratio, brood care, life-history strategies and mating strategies (Elgar 1998). Thus, diverse solutions to sexual conflicts can be expected in this group. Second, males do not contribute directly to parental care. Males may benefit from multiple mating and females have the ability to store sperm. Thus, sexual conflict is likely to be mainly over mating. Finally, spiders are predators and potentially cannibalistic, so that conflicts are often visible and risky.

The first goal of this paper is to review current knowledge of intersexual conflict in spiders. Research on spider mating systems has been largely descriptive and questions related to the conflict between the sexes have been rarely addressed. A second goal is to provide a framework and ideas for future research on intersexual conflict in spiders. In the following sections, we discuss male and female mating strategies that lead to asymmetric costs for the sexes and strategies that are employed to reduce or circumvent these costs. Finally we examine how life-history and reproductive strategies may be important in determining the degree of conflict

Costs of mating for males

The relative cost of mating for males is determined by a large variety of factors. In spiders, mature males usually leave their webs and search for sedentary females. Mate search is possibly very risky and energetically costly (Vollrath and Parker 1992). Once mate search has been successful, a male usually has to compete with other males for access to females. Males may fight against rivals and risk injury and possibly death (Robinson and Robinson 1980, Whitehouse 1997). Alternatively, males may invest a large amount of energy in courtship or signalling to impress choosy females (Lubin 1986, Kotiaho et al. 1996, Mappes et al. 1996). If females mate multiply, males have to maximise their fertilisation success by promoting their own sperm or excluding sperm of other males. In many species, females are sexually cannibalistic, which imposes another potential cost on the male. Generally, the value of a mating depends on the reproductive prospective that remains after one mating has occurred. This residual reproductive value of a male, i.e. his chance to find and inseminate another female, is a function of the operational sex ratio and the species (or population) specific combination of the above factors.

In our discussion of costs of mating for males, we concentrate on examples that, in our opinion, are promising for the study of intersexual conflict in spiders. In some instances, the costs of mating for males appear to be directly inflicted by the female's behaviour, as in the case of sexual cannibalism. In others such as male courtship and male provisioning of the female, it is not always clear if the behaviour is a direct response to the female's demands, but it is nonetheless a variable cost for the males. Finally, we discuss an intrinsic cost for spider males, namely the possible limitation in the potential for multiple mating.

Sexual cannibalism

In spiders, female aggressiveness inflicts one of the most spiking potential costs to courting males. Sexual cannibalism by females occurs in a variety of spider species (Elgar 1992). For a male that maximises reproductive success by mating with many females, being cannibalised by the female does not seem to be to his advantage. The conflict is most extreme when sexual cannibalism occurs before mating (Newman and Elgar 1991). However, sexual cannibalism cannot be considered conclusive proof that the male has lost the battle of the sexes, because in some cases of post-mating cannibalism the male may indeed benefit. For example, the male Australian red-back spider, *Latrodectus hasselti* (Theridiidae), performs a somersault during mating, which brings him to a position within reach of the female's chelicerae (Forster 1992). Most, but not all, males are consumed by the female during mating. Andrade (1996) showed that males that were cannibalised had longer copulation durations and fertilised a larger proportion of the eggs than males that were not eaten. Such suicidal behaviour can be expected only if further mating opportunities for the males are limited and this, indeed, seems to be the case in the population studied, where the probability of finding and mating with a second female is very low. One would thus expect cannibalism to be common in mating systems where the residual reproductive value of males is low after one mating.

Males of *Agenelopsis aperta* (Agelenidae) usually mate only once (Singer and Riechert 1995), although cannibalism is rare in this species. Thus, limited mating possibilities alone are not always sufficient to provide a selective advantage for males to be cannibalised. Even with low mating success a suicidal male mating strategy will evolve only if his sacrifice increases fertilisation success or female fecundity. In most species, males probably have some chance of mating with more than one female and the benefits of suicidal mating for these males will be much lower than in the above case of *L.* hasselti. In addition, sexual cannibalism may not evolve if males possess other strategies to increase their paternity, for example by applying a sperm plug.

Given a sexual conflict over mating that can lead to cannibalism of the male, males must develop behaviours that enable them to escape the females' cannibalistic tendencies. One such strategy may be to restrict the movement of the female. In the hunting spider, Pisaurina mira (Pisauridae), males wrap receptive females with silk during courtship. Before the palps are inserted for a last time, the male will apply additional silk strands around the female's body. During the final insertion, the formerly motionless female suddenly becomes active and the time it takes her to disentangle herself from the silk is just long enough to allow the male to escape to the nearby vegetation (Bruce and Carico 1988). In this species we may expect a conflict over mating and it would be interesting to know whether an unwrapped female would kill its mate.

Another male strategy to reduce the risk of sexual cannibalism is to approach a female when she is feeding on prey and is perhaps less responsive to the male's approach. For example, males of *Nephila plumipes* (Nephilinae) preferably mate while the female is feeding on a prey item (Elgar and Fahey 1996) and males of Meta *segmentata enter* the female's web only after she has captured a prey item (Prenter et al. 1994a, b). Mating attempts with females that are occupied by feeding occurs in many species (pers. obs.), but does not appear to be the main male mating strategy for most of these. Possible selection pressures of sexual cannibalism on various features such as courtship are discussed in greater detail by Elgar (1992). In those species where the males show a behaviour that appears to prevent cannibalism, experimental studies on the costs and benefits of these behaviours would be very useful.

Male courtship

Courtship in males may be energetically costly, as well as exposing males to risks of cannibalism and predation. Watson and Lighton (1994) showed that the preinsemination copulation of male *Linyphia litigiosa,* a 2-6 h long part of courtship, was energetically costly and correlated positively with male fighting ability in intra-sexual encounters. Kotiaho et al. (1996) showed that female *Hygrolycosa rubrofasciata* preferred males that drummed at a higher rate.

Males of the social theridiid, *Achaearanea w*au, spent 13-53% of their activity time engaged in courtship (Y. Lubin, unpubl.). Courtship, which continued throughout the day, involved cutting silk threads, spinning silk, vibrations of the body and web-plucking (Lubin 1986). The probability of mating following a courtship bout was 0.003. Thus, in this species, the energetic cost of courting is high and the expected rewards are low, and it is not surprising that alternative mating tactics have evolved that circumvent this costly display. Mating with newly moulted females is one alternative tactic. Although mating success is higher (probability of mating =0.024), this tactic poses other risks for the male. Males that mate with moulting females risk becoming stuck during copulation and losing all reproductive investment.

In addition to lowering the costs and risks of courtship, mating with moulting or recently moulted females may ensure maximum fertilisations in species with first-male sperm precedence and may reduce the chances of cannibalism. Other opportunistic mating tactics, such as copulating with females while they feed (see above), may have also evolved as a means of reducing costs of courtship.

Male provisioning

Male provisioning (Elgar 1998) may have evolved in the context of courtship (1) to attract the female, (2) to reduce her aggressiveness, or (3) to gain acceptance as a mate (by influencing female choice); or, it could have evolved as male parental investment and a contribution to reproduction. Similarly, cannibalistic consumption of a mating partner could be a form of parental investment for the male, in addition to potentially increasing his fertilisation rate.

Provisioning of the female with a nuptial gift occurs in males of *Pisaura mirabilis* who bring a wrapped prey item to the female (Austad and Thornhill, 1986). Larger gifts result in longer copulation duration and probably higher paternity. The nuptial gift is valuable to the male because when copulations were interrupted experimentally, 93% of males retrieved their nuptial gift from the females. However, after a complete mating event only 17% of the males retrieved their prey (I. L. Drengsgaard pers. comm.). Interestingly, female P. *mirabilis* remain receptive until the last day before egg laying, suggesting that, for the female, nuptial gifts may be a desirable resource and females may mate multiply to gain nuptial gifts. Unfortunately, we do not know whether sated females are less likely to mate than hungry females.

Apart from the possibility of genetic benefits of multiple mating (e.g. genetic bet-hedging; Watson 1990, 1991a, b, 1998), there may be other direct advantages to mating with more than one male. Laboratory experiments with P. *mirabilis* showed that egg sacs of females mated to two males had a higher hatching success than egg sacs of females that experienced only one mating (I. L. Drengsgaard pers. comm.). Thus, there may be a direct advantage for multiple mating for females: maximising their fertilisation success by receiving more sperm or getting more food. For male P. *mirabilis*, the cost of mating may be high because they can mate only after catching a prey item and females will not mate with a mate that does not bring a gift. According to Austad and Thornhill (1986), females in the field produce only a single egg sac; however, they can lay up to five egg sacs in the laboratory (Nitzsche 1988). Mating with a female that already produced eggs should be costly for males, because if females are usually semelparous, these males will not gain any reproductive success. It would be interesting to know if a male mates with a female that has already reproduced because he has no information about her receptive status, or because some females may lay eggs again and even a small chance of success will select for mating even at a high cost.

A rather curious case of mate provisioning of the female is reported for males of *Baryphyma pratense* (Linyphiidae) (Blest 1987). During mating the males excrete haemolymph from glands on the dorsal pro soma that the females consume. It is not known if the "blood meal" is of any significance for the female's nutrition. Males of other spiders, such as *4rgyrodes antipodiana* (Theridiidae), also possess glands on their cephalothorax that excrete a substance during mating (Whitehouse 1987). The substance may act as a pheromone and increase the female's receptivity (Whitehouse 1987), in which case it may be part of the courtship display rather than a nuptial gift.

Limited mating capacity

Many studies assume that males have no limit on their ability to inseminate as many females as they meet. One obvious limitation of male mating success is a consequence of a risky mate search or sexual selection, as described above. However, there may be intrinsic limits as well and the expected number of possible mates for males will determine the value of each mating event for a male.

In linyphiids, a pseudo-copulation phase that precedes insemination and does not involve sperm transfer may last several hours (van Helsdingen 1965). Watson and Lighton (1994) showed for *Linyphia litigiosa* that the pseudo-copulation is energetically costly for the male. Several functions of pseudo-copulation are suggested. By repeatedly inserting his palps the male may stimulate the female internally and in that way try to induce the female to use his sperm. This would be an example of cryptic female choice as suggested by Watson (1991b), see also Elgar 1998). However, Suter (1990) found that males of *Frontinella pyramitella will* not inseminate non-virgin females, which suggested that the pseudo-copulation is a phase during which the male assesses the female's virginity. If males expend effort to check whether the female is virgin and only then transfer sperm, then constraints such as sperm or energy limitation may force males to be choosy. This observation contradicts the common assumption that males are not limited in their mating capacity, an assumption that may well be unrealistic. Additional support for male choosiness is presented by Bukowski and Christenson (1997) who showed that *Micrathena gracilis* (Araneidae) males discriminate between virgin and non-virgin females and release few or no sperm in copulation with non-virgins.

Another explanation for limited mating capacities that does not require sperm depletion is that copulation may cause physical damage to the pedipalp that the male inserted. Males of Linyphia triangularis use only one palp if they mate with a particular female, and they use the other palp to mate with an additional female (S. Toft pers. comm.). In this species, males mate with mated females but they insert twice the amount of sperm that is usually inserted when mating with a virgin. Here, the male assesses the reproductive status of the female and adapts his sperm transfer accordingly.

If mating frequency is limited for males, they should be selective and test the quality of females before insemination. Limited mating capacities of males may explain the results obtained by Prenter et al. (1994b) who found that males of *Metellina segmentata guard* large, fecund females but abandon small females. However, first male sperm precedence and costs of mateguarding will select for male choosiness as well. An extreme example of a reversal of mating costs is described for *Nephila clavipes* where the sperm of some males appeared depleted after a single mating (Christenson 1989). In this case, we expect the males to be the choosy sex and females should compete for males. However, the operational sex ratio is male-biased and males compete intensely for access to the females, both factors that may override any effect of mating being costlier to males than to females (Clutton-Brock and Parker 1994).

Summary

Males may have large mating costs due to the cannibalistic tendencies of their mates. However, when the expected success of an additional mating is low and suicide increases fertilisation rate, males may benefit by being cannibalised after sperm has been transferred. In many spider species sexual cannibalism appears to be a serious threat to the males and behaviours that reduce female aggressiveness or inhibit the female's predatory behaviour are widely suggested functions of male courtship behaviour. Choosy females may select for costly courtship displays by males whereas males counter sexual selection and circumvent these costs by evolving alternative mating tactics.

Males of some species may have a limited supply of sperm and thus should prefer to mate with virgins, especially where there is first-male sperm priority. Damage to the pedipalps during mating should have similar effects to sperm depletion, i.e. adding a cost of mate assessment and mate selection. When males are limited in their mating chances and hence choosy, intersexual conflict will be greatest when the female benefits from multiple mating. Male mating success can be limited not only by intrinsic causes such as sperm depletion and energy constraints, but also by high costs of searching for mates in terms of energy and predation risks, and by a male-biased sex ratio and male-male competition.

Costs of mating for females

Females do not benefit from multiple mating unless (1) they gain a valuable resource (e.g., food or protection) with mating or (2) multiple mating increases the fitness of the offspring. Direct benefits of multiple mating may be found in species where males provide a nuptial gift or where males are cannibalised. Elgar and Nash (1988) showed that females of *Araneus diadematus, where* males are roughly 25°/, of the females' body mass, increased their body mass after consumption of a male, but other studies did not find an effect of cannibalism on fecundity (Andrade 1998, Fahey and Elgar 1997). The question remains whether sexual cannibalism benefits females. Additionally, females will benefit from multiple mating if one mate is not enough to fertilise all the eggs (see above for *Pisaura mirabilis).*

Indirect benefits may occur when males differ in genetic quality and females can only assess this quality by mating (Eberhard 1985, Coyle and O'Shields 1990). Eberhard (1985, 1996) suggested that female choice is the mechanism favouring the evolution of elaborate male mating structures, such as the pedipalps of spiders, and "cryptic" female choice in the case of internal mechanisms used by the female to influence how the sperm are used in fertilisation (the pattern of sperm priority). A possible example may be *Pholcus phalan*gioides (Pholcidae) which lacks special sperm-storage organs (spermathecae), and the sperm are stored in the female's genital cavity (Uhl 1994). Male pedipalp movements during insemination result in the extrusion of sperm from the genital opening (Uhl et al. 1995). Thus, a female could choose to mate with a second male who will use this mechanism to replace some of the first male's sperm with his own.

Females of *Linyphia* litigiosa mate multiply and the paternity of the second male depends on his size relative to the size of the first male. Females chose the first male, which is the principal sire, by mating with the winner of a contest on her web. They adjust the fertilisation of the second mate according to his quality and thereby may correct for mistakes in their initial choice (Watson 1991 a, b). Watson (1991 b) suggested an internal choice mechanism in this species. Females may practise sequential choice by not allowing the first male to fertilise all her eggs (see also Bukowski and Christenson 1997). However, waiting for another mating entails a risk of incomplete fertilisation if a second male does not appear. Parri et al. (1997) suggested sequential choice as the female strategy for the wolf spider Hygrolycosa *rubrofasciata where* females mate only once and thus risk their entire clutch to be unfertilised. Masumoto (1993) found in Agelena limbata that highquality males apply a more complete mating plug than do low-quality males and that females with incomplete mating plugs (having mated with a low-quality male) are more likely to re-mate, even though a single mating was sufficient to fertilise more than 90% of her eggs.

Another potential advantage of multiple mating for females is higher fitness of clutches with multiple paternity. Watson (1991b) has suggested that multiple matng in linyphiids represents "genetic bet-hedging", and that females are more choosy when mating with a second male. Thus, even with first-male sperm priority, there may be a genetic benefit to multiple mating. Finally, it is conceivable that multiple mating does not have additional costs or benefits to the female, but, it may be costly or risky to reject a male that attempts to mate (Austad 1984, Christenson et al. 1985). Thus, multiple mating may be tolerated by the female for the simple reason that it would be more costly to refuse to mate.

Forced copulation

A conflict between the sexes over mating will arise when multiple mating carries additional costs for the females and when these costs override the benefits. Males then must try to mate against the will of the female, while females will try to protect themselves against mating attempts. In cases where males are larger and stronger than females, males sometimes use violence to win the conflict. For spiders, forced copulation, as described in vertebrate systems, has not been reported (Clutton-Brock and Parker 1994). Among mygalomorph spiders in which the sexes are similar in size or males are larger than females, there are no reports of coercion by males, though sexual cannibalism both by females and by males is known (reviewed in Jackson and Pollard 1990). The complicated structure of spider genitalia may also make forced copulation difficult for males since mating requires a large degree of cooperation by the female. In order to transfer sperm, the male must ensure that the female's genital opening is accessible and that she remains still for the time he needs to insert his palp.

Only during moulting might females be vulnerable and unable to resist a mating attempt. Opportunistic mating with moulting females is reported sporadically (and anecdotally) for several spider species (e.g., *Nephila maculate;* Robinson and Robinson 1973). In the case of a social spider, *Achaearanea wau* (Theridiidae), a male that discovers a moulting female will attempt to mate with her before her exoskeleton has hardened and while she is incapable of reacting (Lubin, 1986). If the female's cuticle hardens while the male is still copulating, he may become stuck and this will result in the death of both members of the pair. Overall, 10% of "raped" females died during copulation. Perhaps because of this risk, females moulted to maturity at times of day and in locations in the communal web where males were less active. Nonetheless, 29% of all moulting females were discovered by males, resulting in a 3% mortality risk for females due to the male mating strategy.

Prey stealing by males

Other direct mating costs for females result from the activity of males on the webs or near the nests of females. Mates searching for females may steal and consume eggs of the female (see below for *Stegodyphus lineatus). Loss* of prey to males is another potential cost. Males of the autumn spider, *Metellina (=Meta) segmentata,* wait at the edge of the female's web until she catches a relatively large prey item. The male enters the web as the female inserts her fangs in the prey. For the male, the timing of his approach functions to reduce the risk of being attacked by a hungry female (Blanke 1974, Prenter et al. 1994c, Elgar and Fahey 1996). The female loses her prey unless she allows the male to copulate. However, even after the copulation, the male will sometimes feed with the female, thus reducing her food (Prenter et al. 1994a).

In some cases, males cohabit with females on or near their webs and may steal prey from the females (kleptoparasitism). In linyphiids, males are large enough to win most fights over prey (Rovner 1968, Watson 1990) and they use this advantage to steal prey from webs of females. This is a substantial cost to females because fecundity is food limited (Wise 1975). Females of *Linyphia litighiosa* adopt the counter-strategy of attracting males by pheromone production during a very short interval just before their final moult. During this time they feed very little and the costs of prey loss due to male kleptoparasitism are likely to be lower than at later stages (Watson 1990).

Male *Holocnemus pluchei* (Pholcidae) cohabit the webs of females both before and after copulation and frequently win fights over prey, particularly if the male is > 10% larger than the female (Blanchong et al. 1995). In pholcids, males and females are similar in body size and feed on similar-size prey. Thus, in H. *pluchei,* a female with a male in the web can lose a substantial amount of food. In other pholcid species, however, males were reported to capture prey and then step aside and allow the female to feed (Eberhard and Briceno 1983), a behaviour which may represent another form of male provisioning.

In species of *Nephila,* large females are guarded by dwarf males from the penultimate stage until they stop being receptive, and males may be present on the web even afterward (Robinson and Robinson 1973, 1976). The largest male sits at the hub and may feed on prey captured by the female, while smaller males on the periphery of the web may steal small prey. The cost to the female in terms of lost prey may be small because of the small size of the male. However, the presence of several kleptoparasitic males on the web could significantly affect her food intake, in a manner analogous to the reduction in food intake caused by other spider species *(Argyrodes spp.)* that live as kleptoparasites on the web of *Nephila* (Robinson and Robinson 1973, Vollrath 1979). Loss of prey may explain why webs are sometimes abandoned when males are present. Juvenile and sub-adult females of a widow spider, *Latrodectus revivensis*, re-located their webs within several days of being found by a mate, in spite of a 40% risk of mortality during moving (Lubin et al. 1993).

Web loss

Web loss can be another immediate cost of male presence. Web reduction or web removal by the male occurs in many Theridiidae and Linyphiidae (Watson 1986, Anava and Lubin 1993). In the Linyphiidae, females attract males by means of a pheromone on the web silk (Suter and Renkes 1982). The first male to find such a receptive female removes part or all of the web, thereby reducing the chances that other males will be attracted to his mate (Watson 1986). Loss of the web may be a considerable cost to the female in terms of protein (Foelix 1996). The female loses not only the web, but she loses also the prey she could have caught with the old web and the time and energy it takes to rebuild, as well as increasing her exposure to predators when forced to rebuild the web. As with the costs of loss of prey, the costs of web loss may be minimised by the tendency of these linyphiids to mate with only a single male. After having mated with one male, the females do not add pheromone to the web silk (Schulz and Toft 1993) and the existing pheromone is dissipated after one week (Watson 1986, Watson, 1990). However, if the female has no interest in attracting a second male, removal of the web may be advantageous to both sexes (Rovner 1968, Nielsen and Toll 1990).

Summary

In many species the behaviour of females towards potential mates strongly suggests that multiple mating is undesirable from the female perspective. However, females of many species do mate more than once and the costs and benefits of multiple mating are poorly understood. Only a few studies show a cost of mating for female spiders. There is some evidence that male mate guarding results in a cost to the female via reduced foraging success. It is too early to decide whether mating costs for females are rare in spiders or whether people simply have not looked for them. In most spider species, females are larger than males so that conflicts may be decided mostly in favour of the females. Why should this be so? What are the reasons for female dominance and when are males likely to dominate? Here it is necessary to examine the mating decisions in the context of the ecology and life history of the different species to determine what factors will favour different mating strategies, when conflict is to be expected and what will determine the outcome of conflicts over mating.

Intersexual conflict, reproductive strategies and spider life history

Life-history parameters, such as the timing of sexual maturation and oviposition, body size at maturity, mortality of juveniles and adults, longevity of males and females and the female's reproductive strategy are likely to influence the degree and outcome of conflict between the sexes. Furthermore, sexually selected factors such as the pattern of sperm precedence and male mating success can act only within the limitations of the life history and ecology of a species. In the following, we use the example of an eresid spider, *Stegodyphus lineatus'* to illustrate the influence of life-history and sexual traits on intersexual conflict.

Mate and female S. *lineatus* sometimes have strongly conflicting mating strategies (Schneider and Lubin 1996, 1997b, Schneider 1997). A male that encounters a female guarding an egg sac will attempt to force her to remate and produce a second clutch by removing her egg sac. Loss of a clutch is very costly for the female because she suffers both lower survival with time and reduced fecundity. Adult females have a constant daily mortality risk throughout the reproductive season and in losing the clutch, a female loses time equivalent to the age of the lost clutch plus the time it takes to replace it. Replacement clutches contain fewer eggs than the original ones, and the longer the females takes to replace the clutch the fewer eggs she lays. The females defend their eggs aggressively against infanticidal males. The opponents fight and the relative size difference between them influences who wins the conflict: large males are likely to succeed against smaller females (Schneider and Lubin 1997a). Several interrelated characteristics of life history, functional morphology and ecology may explain this extraordinary example of sexual conflict.

Life history

Maturation time

Males mature over a period of 2 to 3 months and the first females mature about 2 weeks after the first males (Schneider 1997). As the females produce eggs on average 30 days after their final moult, some males are still present and searching for mates when many females have already laid eggs. In a study population in the Negev desert, Israel, males were still active when 50% of the females had egg sacs. This overlap in maturation time creates the potential for conflict between the mating interests of the male and brood-rearing interests of the female.

Size at maturity

Males of S. lineatus mature one moult earlier than females (Kraus and Kraus, 1990). Although females are significantly larger than males, there is some overlap, and the largest males are larger than the smallest females. In addition, males differ from females in their body proportions (Schneider and Lubin 1996) in having a relatively small abdomen, a large prosoma and long legs. For males, a large prosoma and long legs are important in contests with females because the opponents hook their chelicerae and then both pull and push one another. Such a behaviour is reminiscent of armwrestling and, similarly, may function as a test of strength. In addition, the front legs are used to pluck the web as the spiders approach each other and the displacement of the silk may also provide an indication of the size and the strength of each contestant. Because of the overlap in body size, contests over mating between males and females may be intense and risky for both sexes, and the probability of winning is correlated with the size difference.

Female reproductive strategy

Stegodyphus lineatus females normally produce a single egg sac that usually contains 70 eggs (40 to 140, N= 53, Schneider 1996). Females guard the egg sac and release the altricial hatchlings after 30 d of egg development by biting a slit in the disk-shaped egg sac. After hatching, the young depend completely on the mother who feeds them by regurgitation. The young grow rapidly on this diet, moult several times and after about 10 d they start to feed on the mother until she dies. The mother dies on average 14 d after the young hatch. As a consequence of this life cycle, S. lineatus is semelparous in the strictest sense. Only if the first clutch is lost or if the young die, will the female replace the egg sac.

Two factors may be responsible for the evolution of such an extreme form of brood care. First, spiderlings hatch at a small body size, without any reserves and unable to hunt on their own and do not survive without the care of the female. This seems to be a conservative trait in the Eresidae. Second, females suffer high predation rates and are unlikely to survive to reproduce a second time even if the duration *of* brood care could be reduced (Schneider and Lubin 1997b). The suicidal maternal care of the females means that a male that encounters a female with an egg sac cannot expect any fertilisation success because her sole clutch would be fathered by an earlier male. However, a male that succeeds in removing her egg sac and forcing her to re-mate, may have some reproductive success. The combination of overlap in maturation time, large size variation within each sex, little sexual size dimorphism, and extreme female brood care are life-history preconditions for the extreme sexual conflict described above.

Functional morphology and sperm priority

Since female spiders store sperm, they can produce several clutches without having to re-mate. If females mate more than once, the reproductive morphology of the spermathecae may play a role in determining the sperm precedence pattern (Austad 1984; but see Uhl and Vollrath 1998). Entelegyne spiders have conduit spermathecae: after mating, the sperm enters through one duct and at fertilisation it leaves through a different duct. Thus, the sperm that was deposited in the spermatheca first is likely to be the first to leave it and will have a greater chance *of* fertilising the eggs (Austad 1984, Elgin 1998). If this pattern were the case in S. lineatus (an entelegyne species), a late male that mated with a previously mated female, or with a female with eggs, would not fertilise many eggs.

We tested the sperm priority pattern in S. lineatus using the sterile male technique and found that sperm of several males have equal opportunities of fertilising the eggs (Schneider and Lubin 1996). Such a pattern of sperm mixing means that male fertilisation success does not depend on mating order. Thus, the second male that mates with a female that has already laid eggs can expect a 50% probability of fertilising the eggs in a replacement clutch.

Ecology

The mating success of males depends not only on the sperm priority pattern but also on the sex ratio and population density. Nests of S. lineatus are patchily distributed, and movement between patches in search of females may be risky and costly for the male. Male encounter rates with females may depend on the density of females within a patch, on patch size and on the distance between patches. In a field study we found that the overall sex ratio at maturation was 1:1 and that males visited an average of 1.2 females in their lifetime (Schneider and Lubin 1996). This means that a male that encounters a female and does not mate with her loses most of his expected mating success. Therefore, males should attempt to mate with every female they encounter, regardless of her reproductive status.

Mating with virgin or non-virgin females may yield similar fertilisation success if every female mates at least twice. However, the assumption of multiple mating for each female may not apply and males may prefer to mate with virgin females because of the possibility of fertilising the entire clutch. The mating strategy of a male, to remain with a virgin female and attempt to monopolise her or to search for other females, is likely to depend on his relative body size, the time in the season, population density and the probability of encountering other females. Thus, a male's reproductive success may depend on his mating strategy as well as the ecological conditions described above.

A combination of the above ecological and life-history conditions may be responsible for the evolution and persistence of such an extreme conflict between males and females. It is too early to decide if some factors are more important than others or if all the described factors are necessary for the evolution of the observed mating strategies. For example, the small sexual size dimorphism in S. lineatus may be a result of the strong dependence of male mating success on body size. However, it is also possible that males are large because reproduction is strictly seasonal and males will not gain anything by maturing earlier at a smaller body size.

lntersexual conflict: prospects and goals

The mating systems and sexual conflict have been examined beyond merely anecdotal evidence in only a few spider species. We need more data on spider mating systems to allow an analysis of the relative costs of reproduction for females and males. In order to identify the different selection pressures that can act on females and males, field studies of mating strategies, the costs of mating and the mating chances of individuals of both sexes are required. The ecological context must be taken into account to understand these selection pressures. Neither the benefits nor the costs of multiple mating are well studied in female spiders although many spider species could be used for these investigations. Spiders would be ideal animals to study the evolution of female dominance and sexual size dimorphism, questions of considerable general interest.

Characteristics that make spiders promising study animals in the context of the evolution of mating systems are a low male mating success in some species, which is perhaps related to low variation in male mating success, adaptations and constraints in male and female reproductive morphology and the variation in female reproductive strategies. Additionally, female spiders can produce few large or many small clutches and they may provide post-hatching care in some species. Comparative studies of related species that differ in some of these aspects should be very informative.

The degree and the expression of the conflict between the sexes are important factors with high potential of interacting with the life history *of* both sexes. The degree of sexual conflict should be a result *of* the life history but may also shape it to some degree. In addition, sexual conflict should be considered in studies *of* sexual size dimorphism. If sexual conflict is resolved by relative body size as in S. lineatus, any increase in body size of one sex will act as a selection pressure on an increase in size of the other sex. However, small sexual size dimorphism is not necessarily evidence for size-dependent intersexual conflict, because parallel changes can take place also as a result of pleiotropy rather than direct selection. Nevertheless, if the conflict is resolved in favour of one sex and *if* the resolution is stable, selection can act differently on life-history traits in the two sexes, for example resulting in different maturation time and size at maturity for males and females.

We conclude by emphasising the interaction of life history traits shaped by the ecology of a species and sexual selection in the expression of sexual conflict. We believe that it is essential to investigate the connections between the life history and ecology of an organism and sexually selected traits in order to understand its mating system. Mating systems of spiders provide abundant material for such investigations.

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References

Annex, A. and Lubin, Y. 1993. Presence of gender cues in the web of a widow spider, *Latrodectus revivensis, and* a description of courtship behaviour. - Bull. Br. Arachnol. Soc. 9: 119-122.

Andrade, M. C. B. 1996. Sexual selection for male sacrifice in the Australian redback spider. - Science 271: 70-72.

Andrade, M. *C.* B. 1998. Female hunger can explain variation in cannibalistic behavior despite male sacrifice in redback spiders. - Behav. Ecol. 9: 33-42.

Arnqvist, G. and Rowe, L. 1995. Sexual conflict and arms races between the sexes: a morphological adaptation for control of mating in a female insect. - Proc. R. Soc, Lond. B 261: 123-127.

Austad S. N. 1984. Evolution of sperm priority patterns in spiders. - In: Smith, R. L. (ed.), Sperm competition and the evolution of animal mating systems. Academic Press, London, pp. 223-249.

Austad, S. N. and Thornhill, R. 1986. Female reproductive variation in a nuptial-feeding spider, Pisaura *mirabilis.* Bull. Br. Arachnol. Soc. 7: 48-52.

Blanchong, J. A., Summerfield, M. A., Parson, M. A. and Jakob, E. M. 1995. Chivalry in pholcids revisited. - J. Arachnol. 23: 165-170.

Blanke, R. 1974. Rolle der Beare beim Kopulationsverhalten von Meta segmentata (C.L.K.) (Araneae, Araneidae). Forma et Functio 7: 83-94.

Blest, A. D. 1987. The copulation of a linyphiid spider, *Baryphyma pratense:* does a female receive a blood meal from her mate? - J. Zool. 213: 189-192.

Bruce, J. A. and Carico, J. E. 1988. Silk use during mating in Pisaurina mira Walckenaer (Araneae: Pisauridae). - J. Arachnol. 16: l-4.

Bukowski, T. C. and Christenson, T. E. 1997. Determinants of sperm release and storage in a spiny orbweaving spider.

Anim. Behav. 53: 381-395.

Christenson, T. E. 1989. Sperm depletion in the orb-weaving spider *Nephila clavipes*. - J. Arachnol. 17: 115-118.

Christenson, T. E., Brown, S. G., Wenzl, P. A., Hill, E. M. and Geist, K. C. 1985. Mating behaviour of the golden orb-weaving spider, *Nephila clavipes:* 1. Female receptivity and male courtship. - J. Comp. Psychol. 99: 160-166.

Clutton-Brock, T. H. and Parker, G. A. 1994. Sexual coercion in animal societies. - Anim. Behav. 49: 1345-1365.

Coyle F. A. and O'Shields, T. C. 1990. Courtship and mating behavior of *Thelechoris karschi* (Araneae, Dipluridae), an African funnelweb spider. - ,1. Arachnol. 18: 286-296

Eberhard, W. G. 1985. Sexual selection and animal genitalia. - Harvard Univ. Press, Cambridge. MA.

Eberhard, W. G. 1996. Female control: sexual selection by cryptic female choice. - Princeton Univ. Press, Princeton, NJ.

Eberhard, W. G. and Briceno, L. 1983. Chivalry in pholcid spiders. -Betas, Ecol. Sociobiol. 13: 189-195.

Elgar, M. A. 1992. Sexual cannibalism in spiders and other invertebrates. -In: Elgar, M. A. and Crespi, B. J. (eds). Cannibalism. Oxford Univ. Press, New York, pp. 128-155.

Elgar M. A. 1998. Sperm competition and sexual selection in spiders and other arachnids. - In: Birkhead, T. R. and Moller, A. P. (eds), Sperm competition and sexual selec lion. Academic Press, London, pp. 307-337.

Elgar, M. A. and Fahey, D. F. 1996. Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae: Araneoidea). Behav. Ecol. 7: 195-198.

Elgar, M. A. and Nash, D. R. 1988. Sexual cannibalism in the garden spider *Araneus diadematus* - *A*nim. Behav. 36: 1511-1517.

Fahey, B. and Elgar. M. 1997. Sexual cohabitation as mate guarding in the leaf-curling spider *Phonognatha graeffei* Keyserling (Araneoidea Araneae). - Behav. Each Sociobiol. 40: 127-133.

Foelix, R. F. 1996. Biology of spiders. 2nd ed. - Oxford Univ. Press and Georg Thieme Verlag, New York.

Forster, L. M. 1992. The stereotyped behaviour of sexual cannibalism in *Latrodectus hasselti* (Araneae, Thertidiidae), the Australian redback spider. - Aust. J. Zool. 40: 1-11.

van Helsdingen, P. J. 1965. Sexual behaviour of *Lepthyphantes leprosus* (Ohlert) (Araneae, Linyphiidae), with notes on the function of the genital organs. - Zeal. Meded Leiden 41: 15-42.

Jackson, R. R. and Pollard, S. D. 1990. Intraspecific interactions and the function of courtship in mygalomorph spiders: a study of *Porrhothele antipodiana* (Araneae: Hexathelidae) and a literature review. - N- Z. J. Zool. 17: 499-526.

Kotiaho, J-, Alatalo, R. V., Mappes, J. and Parri, S. 1996. Sexual selection in a wolf spider: male drumming activity, body size and viability. - Evolution 50: 1977-1981.

Kraus, O- and Kraus, M. 1990. The genus *Stegodyphus:* systematics, biogeography and sociality (Araneida, Eresidae). - Acta. Zool. Fenn. 190: 223-228.

Krebs J. R. and Davies, N. B. 1993. An introduction to behavioural ecology. 3rd ed. - Blackwell Scientific. London.

Lubin, Y. D. 1986. Courtship and alternative mating tactics in a social spider. - J. Arachnol. 14: 239-257.

Lubin, Y., Ellner, S. and Kotzman. M. 1993. Web relocation and habitat selection in a desert widow spider. - Ecology 74: 1915-1928.

Mappes, J., Alatalo, R. V., Kotiaho, J. and Parri, S. 1996. Viability costs of condition-dependent sexual male display in a drumming wolf spider. - Proc. R. Soc. Load. B 263: 785-789.

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

Newman, J. A. and Elgar, M. A. 1991. Sexual cannibalism in orb-weaving spiders: an economic model. - Am. Nat. 138: 1372-1395.

Nielsen, N. and Top, S. 1990. Alternative male mating strategies in *Linyphia* triangularis (Araneae, Linyphiidae). Acta. Zeal. Fenn. 190: 293-298.

Nitzsche, R. O. M. 1988. Brautgeschenk' and Umspinnen der Beute bei Pisaura mirabilis, *Dolomedes fimbriatus and Thaurnasia uncata* (Arachnids, Araneida, Pisauridae). Verb. Nor. Ver. Hamb. 30: 353-393.

Parker, G- A. 1984. Sperm competition and the evolution of animal mating strategies. - In: Smith, R.L. (ed.), Sperm competition and the evolution of animal mating systems. Academic Press. Orlando, FL, pp. 1-60.

Parri, S., Alatalo, R. V., Kotiaho, J. and Mappes. J. 1997Female preferences for male drumming in the wolf spider *Hygolysosa rubofasciata. - A*nimn Behav. 53: 305-312.

Prenter, J., Elwood, R. W. and Montgomery, W. I. 1994x. Male exploitation of female predatory behaviour reduces sexual cannibalism in male autumn spiders- - Anim. Behav. 47: 235-236.

Premier, J., Elwood, R. W. and Montgomery, W. 1. 19946. Assessment and decisions in *Metellina segmentata* (Araneae: Metidae): evidence of a pheromone involved in mate guarding. - Behav. Ecol. Sociobiol. 35: 39-43.

Prenter, J., Elwood, R. W. and Colgan, S. 1994c. The influence of prey and female reproductive strategy on the courtship of the autumn spider *Metellina segmentata.* Anim. Behav. 47: 449-456.

Robinson, M. H. and Robinson, B. 1973. Ecology and behavior of tire giant wood spider *Nephila maculata* (Fabricius) in New Guinea. -Smithsonian Contrib. Zoo]. 149: 1-76.

Robinson, M- H. and Robinson, B. 1976. Ecology and behavior of the giant wood spider *Nephila maculates* (Fabricius): a supplement. -Smithsonian Contrib. Zeal. 218: 1-22.

Robinson, M. H. and Robinson, B. 1980. Comparative studies of the courtship and mating behavior of tropical araneid spiders. - Pacific Insects 36: 1-218.

Rovner, y. S. 1968. Territoriality in the sheet web spider *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). - Z. Tierpsychol. 25: 232-242.

Schneider, 1. M- 1996. Differential mortality and relative maternal investment in different life stages in *Stegodyphus* lineatus (Araneae: Eresidae). - J. Arachnol. 24: 148-154.

Schneider, J. M. 1997. Timing of maturation and the mating system of the spider, *Stegodyphus lineatus: how* important is body size? - Biol. J. Linn. Soc. 60: 517-525.

Schneider, J. M. and Lubin, Y. 1996. Infanticidal male spiders. - Nature 381: 655-656.

Schneider, J. M. and Lubin, Y. 1997x. Infanticide by males in a spider with suicidal maternal care *Stegodyphus lineatus* (Eresidae), - Anim. Behav. 54: 305-312.

Schneider, J. M- and Lubin, Y. 19976. Does high adult mortality explain semelparity in the spider *Stegodyphus lineatus? - Oikos* 79: 92-100.

Schutz. S. and Taft, S. 1993. Identification of a sex pheromone from a spider. - Science 260: 1635-1636.

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

Suter, R. B. 1990. Courtship and the assessment of virginity by male bowl and doily spiders. - Amon Beaus. 39: 307-314.

Suter R. B. and Renkes, G. 1982. Linyphiid spider courtship: releaser and attractant functions of a contact sex pheromone. - Anim. Behav. 30: 714-718.

Uhl, G. 1994. Genital morphology and sperm storage in *Pholcus phalangioides* (Fuesslin, 1775) (Pholcidae, Araneae). - Acta Zeal. (Stockholm) 75: 1-12.

Uhl, G. and Vollrath, F. 1998. Genital morphology of *Nephila edults:* implications for sperm competition in spiders. Can. J. Zool. 76: 39-47.

Uhl, G., Huber, B. A. and Rose, W. 1995. Male pedipalp morphology and copulatory mechanism in *Pholcus* phalan*gioides* (Fuesslin, 1775) (Araneae, Pholcidae). - Bull. Br. Arachnol. Soc. l0:1-9.

Vollrath, F. 1979. Behaviour of the kleptoparasitic spider, *Argyrodes elevates. - A*nim. Behav. 27: 515-521.

Vollrath. F. and Parker. G- A. 1992. Sexual dimorphism and distorted sex ratios in spiders. - Nature 360: 156-159.

Watson, P. J. 1986. Transmission of a female sex pheromone thwarted by males in the spider *Linyphia litigiosa* (Linyphiidae). - Science 233: 219-221.

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

Watson, P. J. 1991a. Multiple paternity and first mate sperm precedence in the Sierra Dome Spider *Linyphia* litigiosa Keyserling (Linyphiidae). - Anim. Behav. 41: 135-149.

Watson, P. J. 1991b. Multiple paternity as genetic bet hedging in female Sierra dome spiders, *Linyphia l*itigiosa (Linyphiidae). - Anim. Behav. 41: 343-360.

Watson, P. J. 1998. Multi-male mating and female choice increase offspring growth in the spider Nereine litigiosa (Linyphiidae). -Anim. Behav. 55: 387-403.

Watson, P. 1. and Lighton, J. R. B. 1994. Sexual selection and the energetics of copulatory courtship in the Sierra dome spider, *Linyphia l*itigiosa. - Anim. Behav. 48: 615-626.

Whitehouse, M. E. A. 1987. The external structural detail of the protrusions on the cephalothorax of male Argyrodes antipodiana (Theridiidae). - Bull. Br. Arachnol. Soc. 7: 142-144.

Whitehouse, M. E. A. 1997. Experience influences male-male contests in the spider Argyrodes anlipodiana (Theridiidae: Araneae). - Anim. Behav. 53: 913-923.

Wise, D. H. 1975. Food limitation of the spider *Linyphia* marginata: experimental field studies. - Ecology 56: 637646.