Records of the Western Australian Museum Supplement No. 52: 1–11 (1995).

The duration of copulation in spiders: comparative patterns

Mark A. Elgar

Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia

Abstract – The duration of copulation in spiders varies both within and between species, and in the latter by several orders of magnitude. The sources of this variation are explored in comparative analyses of the duration of copulation and other life-history variables of 135 species of spiders from 26 families. The duration of copulation is correlated with body size within several species, but the pattern is not consistent and more generally there is no inter-specific covariation between these variables. The duration of copulation within orb-weaving spiders is associated with both the location of mating and the frequency of sexual cannibalism, suggesting that the length of copulation is limited by the risk of predation. Finally, entelegyne spiders copulate for longer than haplogyne spiders, a pattern that can be interpreted in terms of male mating strategies or the complexity of their copulatory apparatus.

INTRODUCTION

It is widely recognised that there are conflicts of interest between males and females in the choice of mating partner and the frequency of mating (e.g. Elgar 1992). Thus, while the principal function of copulation is to transfer gametes, the act of mating may have several additional functions, such as mate assessment or ensuring sperm priority, and activities other than sperm transfer can take place during copulation. These additional activities may be time-consuming, and thus the time spent copulating may not simply reflect the amount of time required to transfer gametes. Despite the potential benefits of these activities, the additional time spent copulating may also incur costs, such as reducing the amount of time available to find other mates (e.g. Parker 1970a). Therefore, the considerable variation in the duration of copulation that occurs both within and between species may be at least partly attributable to the different costs and benefits of various durations.

There are several reasons why copulation may be longer than is necessary to transfer sperm. Eberhard (1985) argues that copulation for some species may represent an additional component of courtship, allowing the female to exercise some degree of mate choice. Supporting evidence for this view is provided by species in which copulation takes place without insemination, such as the linyphiid spider *Lepthyphantes leprosus*, in which the male courts and then copulates with the female, even though the male is unable to transfer sperm (van Helsdingen 1965). It may also explain why insemination does not always occur immediately after the copulatory organ has been inserted. In species in which females mate with several males, copulation may provide the male with the opportunity to manipulate the sperm of other males that previously mated with that female. For example, copulating male damselflies not only transfer their own sperm, but also remove the sperm of rival males (e.g. Waage 1979; Siva-Jothy and Tsubaki 1989). Finally, copulating males may also deposit a sperm plug that prevents the sperm of rival males from fertilising the eggs of the female (e.g. Lorch *et al.* 1993; Masumoto 1993).

While longer copulations may provide opportunities to increase mating success, there are several costs of mating that may favour shorter durations (see Daly 1978; Lewis 1987). For some species, the additional time spent copulating may reduce the time available to males for seeking and courting other females (e.g. Parker 1970a), and the time available to females for foraging. Copulating pairs may also be more vulnerable to predators because they are more obvious or less able to escape. Finally, the proximity necessary for mating may increase the likelihood that parasites and infectious diseases are transmitted between the mating partners.

Studies of the factors responsible for the variation in the duration of copulation have focussed primarily on single species, and particularly the relationship between the duration of copulation and sperm competition (e.g. Parker 1970a; Jackson 1980; Siva-Jothy and Tsubaki 1989; Lorch *et al.* 1993). In contrast, few studies have examined the patterns of inter-specific variation in the duration of copulation (but see Parker 1970b). The aim of this study is to both describe the variation in the duration of copulation in spiders, and explore some of the factors that may explain this variation.

Male spiders lack primary copulatory organs, and instead transfer sperm using modified pedipalps. As a consequence, the transfer of gametes in spiders involves two phases. The initial phase, called sperm induction, involves the transfer of sperm from the male gonopore to his palps. First the male constructs a sperm web, usually a small, horizontally-suspended, triangular structure. He then presses his abdomen against the surface of this web, moving his abdomen up and down, until a drop of sperm emerges from his genital opening and is deposited on the sperm web. The male dips his pedipalps into the sperm, which is taken up into the palps. Females can only mate after they have completed their final moult, and following a successful courtship, the male copulates with the mature female by inserting his palpal organ into her genital opening. There are differences between species in the frequency of palpal insertions, and whether the palps are inserted simultaneously or consecutively. Further details of the copulatory behaviour of spiders are provided by Foelix (1982).

METHODS AND DATA

Data on the duration of copulation, assembled from the literature and unpublished data, were obtained for 135 species of spiders in 27 families. The number of observations of copulations used to yield a species value varied from study to study, and in some cases may represent a single observation. It is unlikely that this is an exhaustive summary of the available data. Furthermore, the values for particular species may change with the accumulation of more observations. Additional information on male and female body length, and several behavioural characters, were also obtained for most of these species. These data, together with the sources, are given in the Appendix. The taxonomy of spiders are still poorly understood, despite considerable progress over the last twenty years (see Coddington and Levi 1991), and hence the species names given in the Appendix may differ from the original sources. It also seems inevitable that some of the generic names listed in the Appendix will change.

Analysis

In general, species within lower taxonomic categories have similar characteristics as a result of their most recent shared ancestry. Hence, species can rarely be assumed to represent independent data points for the purposes of statistical analyses (Ridley 1989). Nevertheless, character differences between species within lower taxonomic categories can, and do, arise through evolutionary processes. Consequently, comparative studies are frequently plagued with the problem of distinguishing patterns that arise through convergent and/or parallel evolution from those that arise from shared ancestry (Harvey and Pagel 1991).

This problem has stimulated the development of increasingly sophisticated statistical methods for comparative analyses (Harvey and Pagel 1991), all of which require an accurate phylogenetic arrangement of the data. Unfortunately, the phylogenetic relationships of spiders are still unclear, and in many taxa the systematics are incomplete (Coddington 1990; Coddington and Levi 1991). Hence, these statistical techniques are unlikely to be appropriate for the present study and have not been used. Instead, a simple approach has been used in which values for higher taxonomic levels are the units of analysis (e.g. Elgar *et al.* 1990). In most cases, this is the family, and the value calculated is the average of the constituent values for the genera. The generic values are the averages of their constituent species values. This is not an ideal procedure, and hence the patterns revealed by this analysis should be interpreted cautiously, since it is possible that the patterns may reflect phylogenetic affinities, rather than convergent or parallel evolution.

The duration of copulation and body length values were logarithmically transformed in order to normalise their distributions. Statistical analyses were performed using procedures in the Systat 5.2 computer package (Wilkinson 1991).

RESULTS AND DISCUSSION

The duration of copulation in the present sample of spider species varied by several orders of magnitude. In some species, especially web-building spiders, copulation is completed in less than half a minute (e.g. Bristowe 1958; Robinson and Robinson 1980; Elgar and Nash 1988). In contrast, copulation in the salticid spider *Pseudicius* can last up to 15 hours (Jackson 1986a). The distribution of the data favoured short copulations; almost three-quarters of the families surveyed copulated for less than an hour, and representatives of only three families copulated for longer than two hours (see Fig. 1).

Body size

The duration of copulation may be influenced by body size in several ways, if the number of sperm transferred is positively correlated with the duration of copulation (e.g. Austad 1982; Fahey 1992; but see Jackson 1980; Watson 1991). For example, larger females may produce more eggs

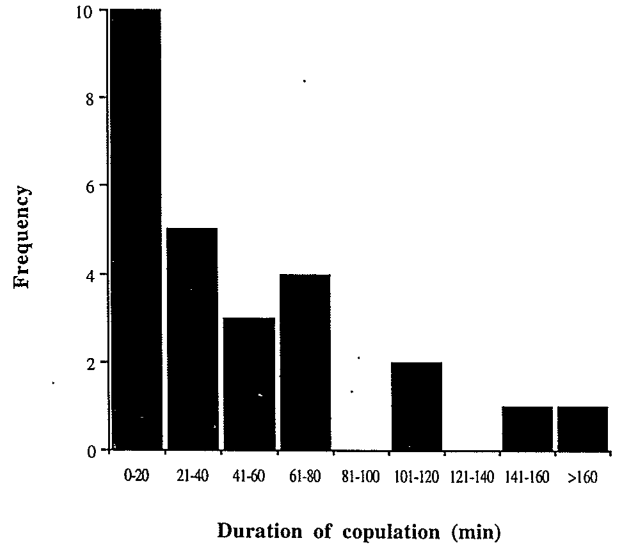

Figure 1 Frequency distribution of the duration of copulation across 26 families of spiders.

than smaller females, and thus longer durations of copulation may be required to transfer more sperm. The patterns obtained from studies of several species are not consistent. The duration of copulation is positively correlated with female size in the golden orb-weaver *Nephila plumipes* (Elgar, unpublished) and autumn spider *Metellina segmentata* (Prenter *et al.* 1994), but with male body size in the orb-weaver *Araneus diadematus* (Elgar and Nash 1988). However, there were no significant correlations between the duration of copulation and either male or female body size in the orb-weavers *Gasteracantha minax* or *Argiope appensa* (Elgar, unpublished). Interestingly, these intra-specific correlations are not apparent in comparisons across taxa. There is no correlation across taxa between the duration of copulation and either male body length ($r = 0.22$, ns, $n = 26$) or female body length ($r = 0.09$, ns, $n = 26$).

It is possible that the duration of copulation is influenced by size dimorphism. Perhaps copulation takes longer in strongly dimorphic species because the relatively smaller males will take longer to transfer larger quantities of sperm. The residuals from the regression equation of male size on female size are one measure of size dimorphism: families with males that are much smaller than females have negative residuals, while positive residuals indicates little size dimorphism (see Elgar *et al.* 1990). There is a significant positive correlation between male and female body size ($r = 0.91$, $p < 0.001$, $n = 26$), but there is no evidence that size dimorphism (measured as residuals) and the duration of copulation are correlated ($r = 0.34$, ns, $n = 26$).

Risk of predation

Animals *in copula* may be at a higher risk of predation because they are more easily detected or have slower flight responses. Many spiders build silk nests, which may allow them to remain concealed and hence avoid predators (see Jackson 1986b). If the risk of predation is higher for spiders *in copula*, then spiders mating in the open should copulate for shorter periods than those that mate inside the nest. The results of studies of several cursorial spiders are consistent with this view. The duration of copulation is longer for spiders mating inside the nest than outside in the dysderid *Dysdera crocata* (Jackson and Pollard 1982), and in three salticids *Holoplatys* sp. (Jackson and Hardin 1982), *Plexippus paykulli* (Jackson and McNab 1989) and *Phidippus johnsoni* (Jackson 1980).

The location of copulation may similarly influence inter-specific variation in the duration of copulation. For example, *Portia* is a web-building salticid that never mates inside a nest, and also has a relatively short copulation time for a salticid (Jackson and Hallas 1986). Unfortunately, there are insufficient data to examine this possibility for cursorial spiders; although there are records of spiders living in nests, it is not always clear whether mating takes place within these nests. Nevertheless, a similar argument may apply to orb-weaving spiders, which mate in different locations on the web. In general, orb-weaving spiders copulate at either the central hub of the web, or while suspended from a specially constructed thread that is attached to either the orb-web or the supporting threads. Spiders copulating while suspended from a mating thread may be at a higher risk of predation than those copulating at the hub, because pairs on a mating thread can be attacked from any direction and may be less able to take evasive action, while pairs at the hub are protected at least from one side by the orb-web. The comparative data on the duration of copulation among orb-weaving spiders provide support for this view: genera that mate on the hub (*Argiope, Gasteracantha, Herennia, Isoxya, Mecynogea, Nephila, Nephilengys* and *Phonognatha*) remain *in copula* for significantly longer than genera that mate on a thread (*Araneus, Cyclosa, Cyrtophora, Eriophora, Gea, Metellina, Micrathena, Uloborus* and *Zilla*) (Table 1).

Sexual cannibalism

Sexual cannibalism may influence at least some components of the courtship behaviour of species in which it occurs (e.g. Elgar 1991, 1992; Prenter *et al.* 1994). Like predation, it may also influence the duration of copulation. For example, the risk of sexual cannibalism may increase with the duration of copulation: larger male orb-weavers *Araneus diadematus* are less likely to be cannibalised by females than smaller males, and larger males also copulate for longer periods than smaller males

(Elgar and Nash 1988). Alternatively, a female may control the duration of copulation more effectively by killing her mate. Both conditions predict that durations of copulation will be shorter among sexually cannibalistic species than non-cannibalistic species.

Sexual cannibalism occurs relatively frequently in three (Araneidae, Metidae and Pisauridae) of the 28 families sampled (see Elgar 1992). Although the duration of copulation appears to be shorter in sexually cannibalistic families (Table 1), the variation is sufficiently large that the difference is not significant. Comparisons of the duration of copulation among orb-weaving spiders and among salticids reveals that sexually cannibalistic genera copulate for shorter times than those genera that are not usually sexually cannibalistic (Table 1).

Female mating frequency

Multiple mating by females is a powerful selection pressure favouring a variety of male behaviours that ensure the eggs of the female he has mated with are not fertilised by the sperm of a rival male. The mechanisms of sperm competition, the competition between the ejaculates of different males over fertilization of a given set of eggs (Parker 1970b), can be quite varied. For example, males may either displace or remove sperm of previously-mating males (e.g. Siva-Jothy and Tsubaki 1989), or produce large quantities of sperm if the fertilization success of a male depends upon the proportionate representation of his sperm in the female's reproductive tract (e.g. Parker 1990; Stockley and Purvis 1993). Similar strategies occur in spiders: a male *Linyphia litigosa* may guard a female from rival males by destroying her web so that other males cannot detect her sex pheromones (Watson 1986); and males of many species place a sperm plug in the female's reproductive tract which prevents the sperm of other males from fertilising the eggs (e.g. Masumoto 1993). These behaviours all function to reduce the probability that the sperm of a rival male fertilises the female's eggs, and they can lead to variation in both the duration of copulation and patterns of sperm precedence (e.g. Lorch *et al.* 1993).

Reproductive morphology

Spermathecal morphology of spiders has interesting implications for sperm precedence patterns, assuming that little, or no, mixing of the sperms occurs when females mate with several males (see Austad 1984; Eberhard *et al.* 1993). In general, spiders can be conveniently assigned to one of two groups according to their spermathecal morphology. The spermatheca of one group, the entelegynes, consists of two ducts; the insemination duct that opens near the vaginal opening and into which the male intromittent organ dispenses seminal fluid, and the fertilisation duct from which sperms issue when the eggs are fertilised. In contrast, the spermathecae of haplogyne spiders are more simple, consisting of a single duct that joins the lumen of the spermatheca to the vagina. Sperms pass through this duct on their way to the storage organ, and must then return by the same route when the eggs are fertilised (see Foelix 1982).

For entelegyne spiders with a 'conduit'

Table 1 Sources of variation in the duration of copulation in spiders.

Sources of variation	Mean duration (min)	SE	n	t^1
Location of mating (among orb-weavers)				
Mating thread	3.7	1.9	9	2.98**
Hub	37.6	14.3	8	
Sexual cannibalism (all families)				
Sexually cannibalistic	15.3	7.2	3	1.03
Not sexually cannibalistic	54.8	12.9	24	
Sexual cannibalism (among orb-weavers)				
Sexually cannibalistic	2.8	3.5	7	2.84**
Not sexually cannibalistic	31.5	12.0	10	
Sexual cannibalism (among salticids)				
Sexually cannibalistic	6.5	3.5	3	1.92†
Not sexually cannibalistic	61.7	36.5	12	
Spermathecal morphology (all families)				
Haplogyne	21.9	5.7	9	2.06*
Entelegyne	64.6	16.5	18	

[1]. t-values are derived from tests with log-transformed data.
†. p = 0.08; * p = 0.05; ** p = 0.01

spermathecal tract, the last sperm to enter the female is likely to be furthest from the fertilisation duct and hence the last to be used in fertilisations. Thus, the sperm of the male that is first to mate with a female is thought to fertilise most or all of her eggs. In contrast, the 'cul-de-sac' spermathecal tract of haplogyne spiders favours last male sperm priority because the last sperm to enter is closest to the fertilisation duct, and hence the first to fertilise the eggs (see Austad 1984). This view was, until recently, generally supported by the available evidence for entelegyne spiders. First-male sperm precedence occurs in three families (but see Austad 1984), including salticids (Jackson 1980), araneids (Vollrath 1980; Christenson and Cohn 1988), and linyphiids (Austad 1982; Martyniuk and Jaenike 1982; Watson 1982), but not in an agelenid (Masumoto 1993). However, there appears to be highly variable sperm precedence arrangement in the haplogyne *Physocyclus globosus* that has a cul-de-sac tract (Eberhard *et al.* 1993).

Different sperm precedence patterns are likely to influence the mating systems of a wide range of organisms, including spiders (Austad 1984, see also Ridley 1989). Males of entelegyne spiders (with conduit-type spermathecae) should preferentially associate with virgin rather than mated females, while males of haplogyne spiders (with cul-de-sac spermathecae) should either show no preference or attempt to ensure that they are last to mate. Several lines of evidence support this prediction: in a broad survey of largely anecdotal data, Jackson (1986b) catalogued 156 entelegyne species and five haplogyne species that cohabit with immature females. Watson (1990) demonstrated that males of the entelegyne *Linyphia litigiosa* prefer to cohabit with immature rather than mature females when both are available, and Eberhard *et al.* (1993) showed that males of two of three entelegyne species show a strong preference for immature females, while males of all three haplogyne species studied did not show any preference.

The differences in spermathecal morphology, together with the associated trends in male mate preferences, may also explain differences in the duration of copulation. If male entelegyne spiders that mate with virgin females fertilise most of the female's clutch, then males could maximise their reproductive success by ejaculating larger quantities of sperm. In contrast, it appears that male haplogyne spiders can obtain high levels of paternity only by preventing (e.g. with mating plugs) rival males from subsequently mating with the female. In the absence of such mechanisms, males of these spiders may maximise their reproductive success by ejaculating smaller quantities of sperm, but mating with many females (see also Parker 1990). Under these conditions, and assuming that the number of spermatozoa transferred is positively correlated with the duration of copulation (e.g. Austad 1982; Fahey 1992), selection may favour longer durations of copulation in entelegyne spiders than in haplogyne spiders. A comparison of the durations of copulation at the family level for these two groups of spiders is consistent with this view: the duration of copulation of entelegyne spiders is significantly longer than that of haplogyne spiders (Table 1).

While the covariation between the duration of copulation and spermathecal morphology may have arisen through male mating strategies, other interpretations are possible. For example, the longer copulation duration of entelegyne spiders may arise if these species more commonly place and remove sperm plugs. Alternatively, the duration of copulation may be positively correlated with the complexity of the copulatory apparatus. The copulatory apparatus in both male and female haplogyne spiders is relatively simple compared with entelegyne spiders (see Foelix 1982). Not only is the male palp of entelegyne spiders more complex, but the embolus (which is used to transfer sperm) must pass through a complex female genital opening into the insemination duct. Thus the longer duration of copulation of entelegyne spiders may simply reflect the longer time required to couple successfully if there are no differences between the two groups in the frequency of palpal insertions during copulation. This latter explanation is unlikely, however, to account for very long copulations.

Mating status of the female

The mating status of the female may also influence the duration of copulation. For example, males may copulate longer with mated females than virgin females because they either transfer more sperm or even displace the sperm of the previous male. Alternatively, males of entelegyne species may terminate copulation with mated females earlier because they are unlikely to fertilise any of the eggs (e.g. Suter 1990).

There are no consistent patterns among the few studies that compare the duration of copulation of virgin and mated females. Copulation among entelegyne spiders was longer for mated females than virgin females in *Phonognatha graeffei* (Tetragnathidae) (Fahey 1992); *Phidippus johnsoni* (Salticidae) (Jackson 1980); *Argyrodes antipodiana* (Theridiidae) (Whitehouse 1991); *Achaearanea wau* (Theridiidae) (Lubin 1986); and *Misumenoides formosipes* (Thomisidae) (Dodson and Beck 1993). Males of the linyphiid *Frontinella pyramitela* (Austad 1982) that copulated with non-virgin females terminated copulation early and failed to transfer sperm. However, there was no difference in the copulation duration of mated and virgin females in three araneids *Gasteracantha minax*, *Nephila plumipes* and *Argiope appensa* (Elgar, unpublished). There are no data available for haplogyne spiders.

It is not clear why males of only some species apparently detect the mating status of the female and adjust the duration of copulation accordingly. From the perspective of the male, the duration of copulation will depend on both the relationship between the duration of copulation and the amount of sperm transferred, and on the pattern of sperm precedence among these spiders. The data from these spiders suggest that there may be exceptions to the sperm precedence patterns predicted by spermathecal morphology. Further studies, using labelled sperm or DNA fingerprinting techniques are likely to resolve this issue.

CONCLUDING REMARKS

The comparative analyses presented here indicate that several factors, including body size, the risk of predation, sexual cannibalism, spermathecal morphology and female mating status, may be responsible for the variation in the duration of copulation in spiders. Several other life-history factors may also influence the duration of copulation, such as the time from copulation to oviposition. If females store sperm for lengthy periods, some sperm mortality may occur, and males may copulate for longer in order to transfer more sperm. Additionally, a longer period may provide additional opportunities for females to mate with other males, and hence selection will favour mechanisms that reduce the probability that the sperm of a rival male fertilises the eggs of the female. These explanations of the variation in copulation duration depend importantly on the ability of each sex to terminate copulation. For example, some of the above explanations could not apply if the duration of copulation was controlled entirely by the female. Few studies were able to state unambiguously which sex terminated copulation, and it may be generally difficult to determine experimentally. Finally, this study has not considered the number of palpal insertions made during copulation, even though there is considerable variation both within and between species. Males of some species may make numerous palpal insertions during each copulation, while in others the male may only insert his palp once. It would be interesting to investigate the factors responsible for this variation.

ACKNOWLEDGEMENTS

I thank Rachael Bathgate, Babette Fahey and Tristram Wyatt for their help in compiling the data set; Rachael Bathgate, Theo Evans, Babette Fahey, Mike Gray, Mark Harvey, Robert Jackson, Michael Magrath, Angus Martin, and Laila Sadler for advice, discussions and comments on the manuscript; and the University of Melbourne, the Australian Research Council (A19130739), and the WV Scott Fund for their financial support. Finally, I wish to express my appreciation of Barbara York Main, whose book and discussions have been responsible for stimulating and maintaining my interest in spiders.

REFERENCES

Arnqvist, G. (1992). Courtship behavior and sexual cannibalism in the semi-aquatic fishing spider, *Dolomedes fimbriatus* (Clerk) (Araneae: Pisauridae). *Journal of Arachnology* **20:** 222–226.

Austad, S.N. (1982). First male sperm priority in the bowl and doily spider, *Frontinella pyramitela* (Walckenaer). *Evolution* **36:** 777–785.

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*: 223–249. Academic Press, New York.

Berry, J.W. (1987). Notes on the life history and behavior of the communal spider *Cyrtophora moluccensis* (Doleschall) (Araneae, Araneidae) in Yap, Caroline Islands. *Journal of Arachnology* **15:** 309–319.

Bristowe, W.S. (1958). *The World of Spiders*. Collins, London.

Catley, K.M. (1993). Courtship, mating and post-oviposition behaviour of *Hypochilus pococki* Platnick (Araneae, Hypochilidae). *Memoirs of the Queensland Museum* **33:** 469–474.

Christenson, T.E. and Cohn, J. (1988). Male advantage for egg fertilization in the golden orb-weaving spider (*Nephila clavipes*). *Journal of Comparative Psychology* **102:** 313–318.

Christenson, T.E., Brown, S.G., Wenzl, P.A., Hill, E.M. and Goist, K.C. (1985). Mating behavior of the golden-orb-weaving spider, *Nephila clavipes*: I. Female receptivity and male courtship. *Journal of Comparative Psychology* **99:** 160–166.

Clausen, I.H.S. (1987). On the biology and behaviour of *Nephila senegalensis senegalensis* (Walckenaer, 1837). *Bulletin of the British Arachnology Society* **7:** 147–150.

Coddington, J.A. (1990). Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). *Smithsonian Contributions to Zoology* **496:** 1–52.

Coddington, J.A. and Levi, H.W. (1991). Systematics and evolution of spiders. *Annual Review of Ecology and Systematics* **22:** 565–592.

Costa, F.G. and Sotelo, J.R., Jr. (1984). Influence of temperature on the copulation duration of *Lycosa malitiosa* Tullgren (Araneae, Lycosidae). *Journal of Arachnology* **12:** 273–277.

Coyle, F.A. (1985). Observations on the mating behaviour of the tiny mygalamorph spider, *Microhexura montivaga* Crosby and Bishop (Araneae, Dipluridae). *Bulletin of the British Arachnology Society* **6**: 328–330.

Coyle, F.A. and O'Shields, T.C. (1990). Courtship and mating-behaviour of *Thelechoris karschi* (Araneae, Dipluridae), an African funnelweb spider. *Journal of Arachnology* **18**: 281–296.

Daly, M. (1978) The cost of mating. *American Naturalist* **112**: 771–774.

Dodson, G.N. and Beck, M.W. (1993). Pre-copulatory guarding of penultimate females by male crab spiders, *Misumenoides formosipes*. *Animal Behavior* **46**: 951–959.

Eberhard, W.G. (1985). *Sexual Selection and Animal Genitalia*. Harvard University Press, Cambridge.

Eberhard, W.G., Guzmàn-Gòmez, S. and Catley, K.M. (1993). Correlation between spermathecal morphology and mating systems in spiders. *Biological Journal of the Linnean Society* **50**: 197–209.

Elgar, M.A. (1991). Sexual cannibalism, size dimorphism and courtship behavior in orb-weaving spiders (Araneae). *Evolution* **45**: 444–448.

Elgar, M.A. (1992). Sexual cannibalism in spiders and other invertebrates. *In* Elgar, M.A. and Crespi, B.J. (eds), *Cannibalism: Ecology and Evolution among Diverse Taxa*: 129–156. Oxford University Press, Oxford.

Elgar, M.A. and Nash, D.R. (1988). Sexual cannibalism in the garden spider, *Araneus diadematus* (Araneae: Araneidae). *Animal Behavior* **36**: 1511–1517.

Elgar, M.A., Ghaffer, N. and Read, A. (1990). Sexual dimorphism in leg length among orb-weaving spiders: a possible role for sexual cannibalism. *Journal of Zoology, London* **222**: 455–470.

Fahey, B. (1992). Reproductive strategies of the male leaf-curling spider *Phonognatha graeffei*. Unpublished BSc Honours Thesis, Department of Zoology, University of Melbourne.

Foelix, R.F. (1982). *Biology of Spiders*. Harvard University Press, Cambridge.

Forster, L.M. (1992). The stereotyped behaviour of sexual cannibalism in *Latrodectus hasselti* Thorell (Araneae: Theridiidae): the Australian redback spider. *Australian Journal of Zoology* **40**: 1–11.

Fraser, J.B. (1987). Courtship and copulatory behaviour of the funnel-web spider, *Hololena adnexa* (Araneae, Agelenidae). *Journal of Arachnology* **15**: 257–262.

Harvey, P.H. and Pagel, M.D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.

Jackson, R.R. (1979). Comparative studies of *Dictyna* and *Mallos* (Araneae, Dictynidae). II. The relationship between courtship, mating, agression and cannibalism in species with differing types of social organization. *Revue Arachnologique* **2**: 103–132.

Jackson, R.R. (1980). The mating strategy of *Phidippus johnsoni* (Araneae: Salticidae): II. Sperm competition and the function of copulation. *Journal of Arachnology* **8**: 217–240.

Jackson, R.R. (1982a). The biology of ant-like jumping spiders: intraspecific interactions of *Myrmarachne lupata* (Araneae, Salticidae). *Zoological Journal of the Linnean Society* **76**: 293–319.

Jackson, R.R. (1982b). The biology of *Portia fimbriata*, a web-building jumping spider (Araneae, Salticidae) from Queensland: intraspecific interactions. *Journal of Zoology, London* **196**: 295–305.

Jackson, R.R. (1982c). The courtship behavior of *Phiddipus femoratus* (Araneae, Salticidae). *Southwestern Naturalist* **27**: 187–195.

Jackson, R.R. (1983). The biology of *Mopsus mormon*, a jumping spider (Araneae, Salticidae) from Queensland: intraspecific interactions. *Australian Journal of Zoology* **31**: 39–53.

Jackson, R.R. (1985). The biology of *Simaetha paetula* and *S. thoracica*, web-building jumping spiders (Araneae, Salticidae) from Queensland: co-habitation with social spiders, utilization of silk, predatory behaviour and intraspecific interactions. *Journal of Zoology, London* (B) **1**: 175–210.

Jackson, R.R. (1986a). Communal jumping spiders (Araneae, Salticidae) from Kenya: interspecific nest complexes, cohabitation with web-building spiders, and intraspecific interaction. *New Zealand Journal of Zoology* **13**: 13–26.

Jackson, R.R. (1986b). Cohabitation of males and juvenile females: a prevalent mating tactic of spiders. *Journal of Natural History* **20**: 1193–1210.

Jackson, R.R. (1988) The biology of *Jacksonoides queenslandica*, a jumping spider (Araneae, Salticidae) from Queensland: intraspecific interaction, web-invasion, predators, and prey. *New Zealand Journal of Zoology* **15**: 1–37.

Jackson, R.R. (1989). The biology of *Cobanus mandibularis*, a jumping spider (Araneae, Salticidae) from Costa Rica: intraspecific interactions, predatory behaviour, and silk utilisation. *New Zealand Journal of Zoology* **16**: 383–392.

Jackson, R.R. and Hallas, S.E.A. (1986). Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata*, and *P. shultzi*, araneophagic, web-building jumping spiders (Araneae, Salticidae): utilisation of webs, predatory versatility, and intraspecific interactions. *New Zealand Journal of Zoology* **13**: 423–489.

Jackson, R.R. and Harding, D.P. (1982). Intraspecific interactions of *Holoplatys* sp. indet., a New Zealand jumping spider (Araneae, Salticidae). *New Zealand Journal of Zoology* **9**: 487–510.

Jackson, R.R. and Macnab, A.M. (1989). Display, mating, and predatory behaviour of the jumping spider *Plexippus paykulli* (Araneae, Salticidae). *New Zealand Journal of Zoology* **16**: 151–168.

Jackson, R.R. and Macnab, A.M. (1991). Comparative study of the display and mating behaviour of lyssomanine jumping spiders (Araneae: Salticidae), especially *Asemonea tenuipes*, *Goleba puella*, and *Lyssomanes viridis*. *New Zealand Journal of Zoology* **18**: 1–23.

Jackson, R.R. and Pollard, S.D. (1982). The biology of *Dysdera crocata* (Araneae, Dysderidae): Intraspecific interactions. *Journal of Zoology, London* **198**: 197–214.

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. *New Zealand Journal of Zoology* **17:** 499–526.

Jackson, R.R. and Whitehouse, M.A. (1989). Display and mating behaviour of *Thorellia ensifera*, a jumping spider (Araneae: Salticidae) from Singapore. *New Zealand Journal of Zoology* **16:** 1–16.

Lewis, W.M., Jr. (1987). The cost of sex. *In* Stearns, S.C. (ed.), *The Evolution of Sex and its Consequences*: 33–57. Birkhuser Verlag, Basel.

Lorch, P.D., Wilkinson, G.S. and Reillo, P.R. (1993). Copulation duration and sperm precedence in the stalk-eyed fly *Cyrtodiopsis whitei* (Diptera: Diopsidae). *Behavioral Ecology and Sociobiology* **32:** 309–311.

Lubin, Y.D. (1986). Courtship and alternative mating tactics in a social spider. *Journal of Arachnology* **14:** 239–257.

Martynuik, J. and Jaenike, J. (1982). Multiple mating and sperm usage patterns in natural populations of *Prolinyphia marginata* (Araneae, Linyphiidae): *Annals of the Entomological Society of America* **75:** 516–518.

Masumoto, T. (1991). Male's visits to females' webs and female mating receptivity in the spider, *Agelena limbata* (Araneae: Agelenidae). *Journal of Ethology* **9:** 1–7.

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

Parker, G.A. (1970a). Sperm competition and its evolutionary effect on copula duration in the fly *Scatophaga stercoraria. Journal of Insect Physiology* **16:** 1301–1328.

Parker, G.A. (1970b). Sperm competition and its evolutionary consequences in insects. *Biological Review* **45:** 525–567.

Parker, G.A. (1990). Sperm competition: raffles and roles. *Proceedings of the Royal Society, London* B **242:** 120–126.

Pollard, S.D. and Jackson, R.R. (1982). The biology of *Clubiona cambridgei* (Aranea, Clubionidea): intraspecific interactions. *New Zealand Journal of Ecology* **5:** 44–50.

Prenter, J., Elwood, R. and Colgan, S. (1994). The influence of prey size and female reproductive state on the courtship of the autumn spider *Metellina segmentata*: a field experiment. *Animal Behavior* **47:** 449–456.

Ridley, M. (1989a). Why not to use species in comparative tests. *Journal of Theoretical Biology* **136:** 361–364.

Ridley, M. (1989b). The incidence of sperm displacement in insects: four conjectures, one corroboration. *Biological Journal of the Linnean Society* **38:** 349–367.

Robinson, M.H. and Robinson, B. (1980). Comparative studies on the courtship and mating behavior of tropical araneid spiders. *Pacific Insects Monographs* **36:** 1–218.

Ross, J., Richman, D.B., Mansour, F., Trambarulo, A. and Whitcomb, W.H. (1982). The life cycle of *Heteropoda venatoria* (Linnaeus) (Araneae: Heteropodidae). *Psyche* **89:** 297–306.

Rovner, J.S. (1972). Copulation in the lycosid spider (*Lycosa rabida* Walckenaer): a quantitative study. *Animal Behavior* **20:** 133–138.

Rovner, J.S. (1974). Copulation in the lycosid spider *Schizocosa saltatrix* (Hentz): an analysis of palpal insertion patterns. *Animal Behavior* **22:** 94–99.

Siva-Jothy, M.T. and Tsubaki, Y. (1989). Variation in copulation duration in *Mnais pruinosa pruinosa* Selys (Odonata: Calopterygidae). 1. Alternative mate-securing tactics and sperm precedence. *Behavioral Ecology and Sociobiology* **24:** 39–45.

Snazell, R. and Jones, D. (1993). The theridiid spider *Steatoda nobilis* (Thorell, 1875) in Britain. *Bulletin of the British Arachnology Society* **9:** 164–167.

Starr, C.K. (1988). Sexual behaviour in *Dictyna volucripes* (Araneae, Dictynidae). *Journal of Arachnology* **16:** 321–330.

Stockley, P. and Purvis, A. (1993). Sperm competition in mammals: a comparative study of male roles and relative investment in sperm production. *Functional Ecology* **7:** 560–570.

Suter, R.B. (1990). Courtship and the assessment of virginity by male bowl and doily spiders. *Animal Behavior* **39:** 307–313.

Uhl, G. (1993). Mating behaviour and female sperm storage in *Pholcus phalangioides*. *Memoirs of the Queensland Museum* **33:** 667–674.

Van Helsdingen, P.J. (1965) Sexual behaviour of *Lepthyphantes leprosus* (Ohlert) (Araneida, Linyphiidae), with notes on the function of the genital organs. *Zoölogische Mededeelingen* **41:** 15–42.

Vollrath, F. (1980). Male body size and fitness in the web-building spider *Nephila clavipes. Zeitschrift für Tierpsychologie* **53:** 61–78.

Waage, J. (1979). Dual function of the damselfly penis: sperm removal and sperm transfer. *Science* **203:** 916–918.

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

Watson, P.J. (1991). Multiple paternity and first mate sperm precedence in the sierra dome spider, *Linyphia litigiosa* Keyserling (Linyphiidae). *Animal Behavior* **41:** 135–48.

Whitehouse, M.E.A. (1991). To mate or fight – male male competition and alternative mating strategies in *Argyrodes antipodiana* (Theridiidae, Araneae). *Behavioral Proceedings* **23:** 163–172.

Wilkinson, L. (1992). *SYSTAT: Statistics, Version 5.2.* ed. SYSTAT, Inc., Evanston.

Manuscript received 5 April 1994; accepted 21 July 1994.

APPENDIX

The duration of copulation of 135 spider species from 26 families.

Taxa	Body length (mm)		Copulation duration (min)	Sexual cannibal	Source
	Male	Female			
HAPLOGYNES					
Dipluridae					
Microhexura montivaga	2.5	2.4	0.5	No	Coyle (1985)
Thelechoris karschi	16.0	14.0	40.4	No	Coyle and O'Shields (1990)
Dysderidae					
Dysdera crocata	12.0	10.0	17.0	Rare	Jackson and Pollard (1982)
Harpactea hombergi	7.0	6.0	4.0	No	Bristowe (1958)
Hexathelidae					
Porrhothele antipodiana			27.0		Jackson and Pollard (1990)
Hypochilidae					
Hypochilus pococki	16.0	11.0	1.4	No	Catley (1993)
Oonopidae					
Oonops pulcher	2.0	1.5	1.5	No	Bristowe (1958)
Pholcidae					
Pholcus phalangioides	7.5	7.5	65.5	No	Uhl (1993)
Psilochorus simoni	2.5	2.5	22.0	No	Bristowe (1958)
Scytodidae					
Scytodes thoracica	5.0	4.0	44.0	No	Bristowe (1958)
Segestriidae					
Segestria florentina	22.0	15.0	10.0		Bristowe (1958)
Tetragnathidae					
Pachygnatha clercki	8.9	5.3	100.0		Bristowe (1958)
Pachygnatha degeeri			25.0		Bristowe (1958)
Tetragnatha extensa	8.5	6.5	15.0	No	Bristowe (1958)
ENTELEGYNES					
Agelenidae					
Agelena limbata			193.0		Masumoto (1991)
Coelotes atropos			150.0		Bristowe (1958)
Hololena adnexa			81.8		Fraser (1987)
Textrix denticulata	7.0	6.5	30.0	No	Bristowe (1958)
Araneidae					
Araneus diadematus	12.0	8.0	0.3	Yes	Elgar and Nash (1988)
Argiope aemula	22.0	4.5	1.5	Yes	Robinson and Robinson (1980)
Argiope aetheria	14.0	5.0	0.9	Yes	Robinson and Robinson (1980)
Argiope appensa	22.0	6.0	1.5	Yes	Present study
Argiope argentata	16.0	4.0	0.9	Yes	Robinson and Robinson (1980)
Argiope aurocincta			0.9	Yes	Robinson and Robinson (1980)
Argiope bruennichi	15.0	4.5	0.3	Yes	Bristowe (1958)
Argiope cuspidata			0.9	Yes	Robinson and Robinson (1980)
Argiope flavipalpis	14.0	5.5	0.9	No	Robinson and Robinson (1980)
Argiope florida	16.0	4.5	0.9	Yes	Robinson and Robinson (1980)
Argiope ocyaloides	9.0	4.0	0.5	Yes	Robinson and Robinson (1980)
Argiope picta	19.0	5.5	0.9	Yes	Robinson and Robinson (1980)
Argiope radon	18.0	6.0	0.9	Yes	Robinson and Robinson (1980)
Argiope reinwardti	18.0	4.5	0.9	Yes	Robinson and Robinson (1980)
Argiope savignyi	14.0	3.5	0.9	No	Robinson and Robinson (1980)
Cyclosa caroli	6.0	3.0	0.4	No	Robinson and Robinson (1980)
Cyclosa insulana	6.5	3.5	0.4	No	Robinson and Robinson (1980)
Cyclosa sp. alpine # 1			0.4	No	Robinson and Robinson (1980)
Cyclosa sp. Mt Kaindi # 1			0.4	No	Robinson and Robinson (1980)
Cyclosa sp. Wau # 5			1.2	No	Robinson and Robinson (1980)
Cyrtophora moluccensis	19.0	3.5	33.0	Yes	Berry (1987)
Cyrtophora nympha			0.9	No	Robinson and Robinson (1980)
Eriophora fuliginea	30.0	27.0	0.4	Yes	Robinson and Robinson (1980)
Gasteracantha brevispina	9.0	2.5	73.0	No	Robinson and Robinson (1980)
Gasteracantha cancriformis	7.2	2.2	69.0	No	Robinson and Robinson (1980)

Taxa	Body length (mm)		Copulation duration (min)	Sexual cannibal	Source
	Male	Female			
Gasteracantha curvispina			40.0	No	Robinson and Robinson (1980)
Gasteracantha falcicornis			49.0	No	Robinson and Robinson (1980)
Gasteracantha minax	8.5	3.0	100.0	No	Present study
Gasteracantha signifera			54.0	No	Robinson and Robinson (1980)
Gasteracantha sp.			13.0	No	Robinson and Robinson (1980)
Gasteracantha taeniata			53.0	No	Robinson and Robinson (1980)
Gasteracantha theisi			65.0	No	Robinson and Robinson (1980)
Gasteracantha versicolor			74.0	No	Robinson and Robinson (1980)
Gea eff	6.6	3.0	0.9	Yes	Robinson and Robinson (1980)
Isoxya tabulata			75.0	No	Robinson and Robinson (1980)
Mecynogea lemniscata			33.0	No	Robinson and Robinson (1980)
Micrathena sagittata	8.5	4.5	0.9	No	Robinson and Robinson (1980)
Micrathena schreibersi	14.3	5.4	2.0	No	Robinson and Robinson (1980)
Micrathena sexpinosa	16.2	5.6	1.2	No	Robinson and Robinson (1980)
Zilla Wau # 1			0.4	Yes	Robinson and Robinson (1980)
Zilla Wau # 2			0.4	Yes	Robinson and Robinson (1980)
Clubionidae					
Clubiona cambridgei	8.0	7.0	44.0	Rare	Pollard and Jackson (1982)
Clubiona reclusa	7.0	6.0	60.0	No	Bristowe (1958)
Clubiona terrestris	6.0	5.0	80.0	No	Bristowe (1958)
Dictynidae					
Dictyna calcarata	5.0	4.0	60.5	Yes	Jackson (1979)
Dictyna civica			14.0		Jackson (1979)
Dictyna latens			15.0		Jackson (1979)
Dictyna uncitata			40.0		Jackson (1979)
Dictyna volucripes	3.3	2.7	87.0	No	Starr (1988)
Dictyna volupis	3.8	3.1	80.0	No	Jackson (1979)
Ixeuticus longiquus			80.0		Jackson (1979)
Mallos gregalis	5.0	4.0	100.0	No	Jackson (1979)
Mallos trivittatus	7.0	5.0	39.0	No	Jackson (1979)
Gnaphosidae					
Drassodes lapidosus	14.0	11.5	31.0	No	Bristowe (1958)
Herpyllus blackwalli	10.0	8.0	24.0	Rare	Bristowe (1958)
Heteropodidae					
Heteropoda venatoria	23.0	20.0	160.0	Rare	Ross *et al.* (1982)
Micrommata virescens	13.5	9.0	280.0	No	Bristowe (1958)
Linyphiidae					
Frontinella pyramitela	3.5	3.2	30.7	Rare	Austad (1982)
Lepthyphantes leprosus	3.0	2.5	49.0	No	van Helsdingen (1965)
Linyphia litigiosa	4.5	3.5	240.0	No	Watson (1991)
Lycosidae					
Alopecosa accentuata	12.0	9.0	0.5	No	Bristowe (1958)
Lycosa malitiosa			98.0	No	Costa and Sotelo (1984)
Lycosa rabida	18.5	11.5	59.0	No	Rovner (1972)
Schizocosa saltatrix			166.0	No	Rovner (1974)
Xerolycosa miniata	6.0	5.0	0.5	No	Bristowe (1958)
Metidae					
Herennia ornatissima	12.0	3.0	6.3	No	Robinson and Robinson (1980)
Metellina segmentata	6.0	5.0	2.7	Yes	Prenter *et al.* (1994)
Nephila clavipes	25.0	6.0	25.6	Yes	Christenson *et al.* (1985)
Nephila plumipes	22.0	5.0	0.9	Yes	Present study
Nephila maculata	43.0	5.0	17.0	Yes	Robinson and Robinson (1980)
Nephila pilipes	40.0	4.5	20.0	No	Robinson and Robinson (1980)
Nephila senegalensis	24.7	4.6	8.0	No	Clausen (1987)
Nephilengys malabarensis	16.7	4.8	1.5	No	Robinson and Robinson (1980)
Nesticidae					
Nesticus cellulanus	5.0	4.0	7.0	No	Bristowe (1958)
Pisauridae					
Dolomedes fimbriatus	22.0	12.0	0.9	Yes	Arnqvist (1992)
Pisaura mirabilis	13.5	11.0	58.0	Yes	Bristowe (1958)

Taxa	Body length (mm)		Copulation duration (min)	Sexual cannibal	Source
	Male	Female			
Tetragnathidae					
Phonognatha graeffei	8.0	5.0	111.0	Rare	Fahey (1992)
Salticidae					
Asemonea tenuipes	4.5	3.5	4.4		Jackson and Macnab (1991)
Cobanus mandibularis			7.1	No	Jackson (1989)
Euophrys frontalis	4.0	3.0	45.0	No	Bristowe (1958)
Evarcha falcata	7.0	5.0	200.0		Bristowe (1958)
Goleba puella	4.5	4.5	1.3		Jackson and Macnab (1991)
Holoplatys sp.	5.0	4.4	17.0	No	Jackson and Harding (1982)
Jacksonoides queenslandica	6.0	6.0	3.1	No	Jackson (1988)
Lyssomanes viridis	7.5	5.5	14.5	No	Jackson and Macnab (1991)
Marpissa muscosa	8.0	8.0	20.0		Bristowe (1958)
Marpissa nivoyi	5.0	4.0	47.0	No	Bristowe (1958)
Menemerus sp.	3.5	3.5	9.0	No	Jackson (1986)
Mopsus mormon	12.0	12.0	44.4	No	Jackson (1983)
Myrmarachne lupata	5.0	5.0	10.9	No	Jackson (1982a)
Phiddipus femoratus	10.0	7.0	12.0	No	Jackson (1982c)
Phiddipus johnsoni	9.0	8.0	179.0	Yes	Jackon (1980)
Plexippus paykulli			0.7	Yes	Jackson and Macnab (1989)
Portia fimbriata	8.5	5.5	6.0	Yes	Jackson (1982b)
Portia sp.			1.7	Yes	Jackson and Hallas (1986)
Pseudicius sp. #1	3.5	3.5	9.0	No	Jackson (1986a)
Pseudicius sp. #2	3.5	3.5	900.0	No	Jackson (1986a)
Simaetha paetula	7.0	7.0	12.7	Yes	Jackson (1985)
Thorellia ensifera	5.0	5.0	5.8	No	Jackson and Whitehouse (1989)
Theridiidae					
Achaearanea lunata	3.0	2.5	0.2		Bristowe (1958)
Achaearanea tepidariorum	7.0	4.0	0.2		Bristowe (1958)
Achaearanea wau	4.5	1.9	0.7	No	Lubin (1986)
Argyrodes antipodiana	3.0	2.5	21.3		Whitehouse (1991)
Enoplagnatha ovata	5.0	4.0	15.0		Bristowe (1958)
Episinus truncatus	4.0	4.0	5.0		Bristowe (1958)
Latrodectus hasselti	10.0	5.0	27.0	Yes	Forster (1992)
Steatoda bipunctata	7.0	5.0	100.0	No	Bristowe (1958)
Steatoda nobilis	12.0	9.2	25.0		Snazell and Jones (1993)
Thomisidae					
Diaea dorsata	6.0	4.0	5.0		Bristowe (1958)
Diaea socialis	6.6	5.6	30.0	No	T. Evans (pers comm)
Misumenoides formosipes			4.4		Dodson and Beck (1993)
Philodromus dispar	5.0	4.0	0.5		Bristowe (1958)
Philodromus fallax	6.0	5.0	4.0		Bristowe (1958)
Xysticus cristatus	7.0	5.0	90.0	No	Bristowe (1958)
Xysticus lanio	7.0	5.0	110.0		Bristowe (1958)
Uloboridae					
Uloborus walckenaerius	5.0	3.5	10.0	No	Bristowe (1958)
Zoridae					
Zora spinimana	6.0	4.5	6.0		Bristowe (1958)