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Sexual selection research on spiders: progress and biases

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ABSTRACT

The renaissance of interest in sexual selection during the last decades has fuelled an extraordinary increase of scientific papers on the subject in spiders. Research has focused both on the process of sexual selection itself, for example on the signals and various modalities involved, and on the patterns, that is the outcome of mate choice and competition depending on certain parameters. Sexual selection has most clearly been demonstrated in cases involving visual and acoustical signals but most spiders are myopic and mute, relying rather on vibrations, chemical and tactile stimuli. This review argues that research has been biased towards modalities that are relatively easily accessible to the human observer. Circumstantial and comparative evidence indicates that sexual selection working *via* substrate-borne vibrations and tactile as well as chemical stimuli may be common and widespread in spiders. Pattern-oriented research has focused on several phenomena for which spiders offer excellent model objects, like sexual size dimorphism, nuptial feeding, sexual cannibalism, and sperm competition. The accumulating evidence argues for a highly complex set of explanations for seemingly uniform patterns like size dimorphism and sexual cannibalism. Sexual selection appears involved as well as natural selection and mechanisms that are adaptive in other contexts only. Sperm competition has resulted in a plethora of morphological and behavioural adaptations, and simplistic models like those linking reproductive morphology with behaviour and sperm priority patterns in a straightforward way are being replaced by complex models involving an array of parameters. Male mating costs are increasingly being documented in spiders, and sexual selection by male mate choice is discussed as a potential result. Research on sexual selection in spiders has come a long way since Darwin, whose spider examples are reanalysed in the context of contemporary knowledge, but the same biases and methodological constraints have persisted almost unchanged through the current boom of research.

Key words: sexual selection, spiders, signals, modalities, sexual size dimorphism, cannibalism, sperm competition, male mate choice, biases, constraints.

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I. INTRODUCTION

Sexual selection was Darwin's (1871) answer to three major questions: why are males and females often so different, how can we explain exaggerated male sexual traits, and how can we explain the existence of characters that would seem detrimental to survival? Due to the evidence available at the time, Darwin's emphasis was largely on birds, mammals, and insects (Fig. 1). Only a few pages were dedicated to spiders even though Darwin remarked that 'spiders are possessed of acute senses, and exhibit much intelligence'. Indeed, some spiders for example have complex display repertoires, with repertoire sizes comparable to the maximum repertoire sizes recorded for mammals, birds, and social insects (Jackson *et al.*, 1990). Darwin's postulation of animal aesthetic senses earned him much criticism. However, recent research rather suggests that his "idea that a 'sense of the beautiful' is an inherent … property of animal nervous systems may be not far from the truth" (Enquist & Arak, 1993), and that 'human beauty and obsession with bodily beauty are mirrored in analogous traits and tendencies throughout the plant and animal kingdoms' (Grammer *et al.*, 2003).

Not much has changed since Darwin regarding the relative importance of animal groups in the study of sexual selection. The right panel of Fig. 1 is derived from Andersson (1994) who listed 232 publications that demonstrate a statistically significant relationship between some character and mating success, and that identify a mechanism of sexual selection. It is evident that some changes have occurred with respect to groups like fishes and amphibians, but arachnids and other non-insect arthropods continue to be a marginal group in the study of sexual selection.

It may be unlikely that this will change significantly in the future, but the last decades have seen a steady increase of papers dedicated to sexual selection in spiders (Fig. 2), and the number of papers on the subject has almost doubled since Elgar's (1998) review. However, the main focus of the present paper is not only an update of evidence, ideas and speculations. I will first focus on female choice and male competition working in the various sensory modalities, with the main conclusion that sexual selection in spiders may predominantly work *via* channels of communication that are not as easily accessible to the human observer as bird plumage, mammal weapons, and insect stridulation (*cf.* Andersson, 1994; Uetz & Taylor, 2003). Mate choice often seems to be based on multiple cues (Candolin, 2003), and spider communication also tends to be multimodal (Uetz, 2000; Uetz & Roberts, 2002). However, most spiders are nocturnal hunters, and it is vibrations, pheromones and tactile signals that play the major roles, in courtship as much as in foraging. Another part of this review will consider some topics for which spiders offer particularly useful model organisms, like sexual size dimorphism, cannibalism, and sperm competition. The picture that is emerging is a highly complex one, with seemingly homogenous characteristics resulting from a variety of evolutionary and mechanistic causes (Hormiga, Scharff & Coddington, 2000; Elgar & Schneider, 2004), and with relatively simple problems resulting in a multitude of solutions (as for example predicted for sperm competition by Parker, 1970). Finally, this review also has a minor historical component. Darwin's (1871) spider examples have apparently never been reanalysed in the context of contemporary knowledge. This review presents the current taxonomic status of the species cited by Darwin, and shows that some of his examples appear better explained by natural than by sexual selection.

II. FEMALE CHOICE AND MALE COMPETITION: THE COMMUNICATORY CHANNELS

(1) Visual signals

A prerequisite for sexual selection to operate *via* the visual channel is a sensory system that is capable of perceiving these signals. However, most spiders are myopic (Land, 1985). The spiders with the best visual system are probably the salticids. Their anterior median eyes have muscles that move the eye tube in complicated ways, complex layered retinae with receptors on one of these layers arranged in a 'staircase' manner allow the lack of accommodation to be overcome (Land, 1969*b*; Blest *et al.*, 1981). The presence of receptors sensitive for different frequencies, as well as behavioural experiments, suggest colour vision (Blest *et al.*, 1981; Peaslee & Wilson, 1989; Harland & Jackson, 2000; Nakamura & Yamashita, 2000). The spatial acuity in *Portia* spp. is 0.04°, which is not much worse than human eye acuity (Williams & McIntyre, 1980; Harland & Jackson, 2000). The field of view is small, but this is partly compensated by movements of the retinae (Land, 1969*a*). Other spiders that are heavily reliant on vision are the deinopids, but it is only the sensitivity that is high (Laughlin, Blest & Stowe, 1980), allowing them to hunt visually at night, while the resolution is bad (angle distance approximately 1.5°). Lycosids, thomisids, and a few other families have a fairly good resolution, but limited colour perception (Foelix, 1996).

However, good eyesight and sexual dimorphisms in visual signals do not automatically mean that sexual selection is involved. Oxford & Gillespie (1998) identified five selective forces acting on spider coloration, and most or all of these might also be responsible for sexually dimorphic coloration: crypsis, mimicry, aposematism, thermoregulation, and sexual selection. The first four factors result from ecological differences between males and females, as for example from the males being vagrant and the females stationary. It seems

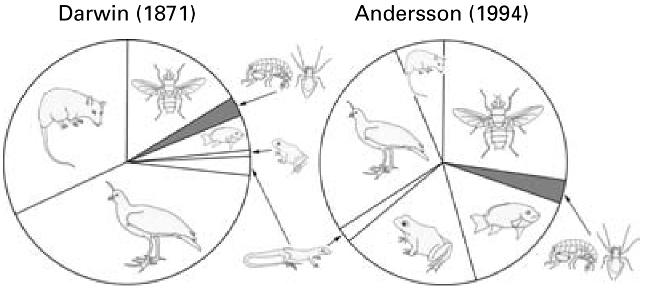

Fig. 1. Diagrams illustrating the taxonomic bias in sexual selection studies. The left diagram is based on Darwin's (1871) seminal book, counting the pages dedicated to each of several taxa. The right diagram is based on Andersson's (1994) review of sexual selection, and on his selection of publications treating sexual selection in a quantitative way. The grey slices include all non-insect invertebrates.

that at least one of Darwin's (1871) examples pertains to this category of characters under natural selection: the dimorphism in *Misumena vatia* (Thomisidae; cited as *Thomisus citraeus*) and other thomisids, may be rather explained by male defensive and female aggressive crypsis (Foelix, 1996), with visually hunting birds and visual insect prey as major selective agents. However, no experimental work has been done related to the coloration of this species, nor on the other example cited by Darwin for visual signals (*Micrommata virescens*, Sparassidae; cited as *Sparassus smaragdulus*). In this species, the conspicuous male visual cues do not seem to play any significant role in mate searching, courtship is very short, rather resembling an assault, and once in copula, the female is in a position that makes it impossible for her to see the male dorsal coloration (Bristowe, 1926; Crome, 1962).

What about positive evidence for sexual selection on visual signals in spiders? Comparative data on salticids strongly suggest that sexual selection is involved. Usually it is the males that carry the signals, the ornaments are primarily situated on the frontal side that faces the female during precopulatory courtship, and in some cases the signals are covered by the palps and exposed during courtship (Peckham & Peckham, 1889, 1890; Bristowe & Locket, 1926; Maddison & McMahon, 2000). Even more suggestive are cases of abdominal exposure, where the abdomen is held downward, upward, or to the side depending on the location of characteristic abdominal surfaces (Taylor, Hasson & Clark, 2000). The problem with comparative data such as these is that other functions of the ornaments cannot be excluded, as for example species recognition, where the roles of ecological divergence and sexual selection are hard to disentangle (Andersson, 1994). However, Masta & Maddison (2002) provide genetic, behavioural, and simulation data evidence that the striking divergence in traits of male behaviour and morphology in *Habronattus pugillis* is due to sexual selection.

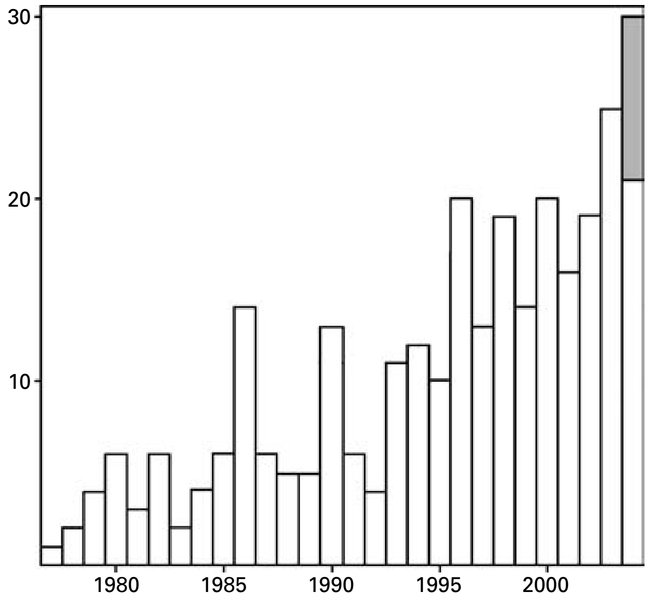

Fig. 2. Scientific literature on sexual selection in spiders since 1977. As an objective criterion, all papers listed herein in the References section were included, but it is obvious that the selection is incomplete and not strictly limited to papers dealing explicitly with sexual selection in spiders. The grey bar represents papers 'in press' as of November 2004.

Indirect evidence comes from detailed investigations of salticid courtship behaviour. Males of a single species may perform over 20 major visual and other displays, (Jackson, 1986*c*, 1988; Jackson & Macnab, 1989*a*, *b*). Such complex display repertoires seem to reflect the action of sexual selection rather than a need for reproductive isolation or reduction of cannibalism (Jackson, 1986*b*; Jackson & Hallas, 1986; Jackson *et al.*, 1990). Interestingly, some of the displays observed were also used by females.

It is surprising that 'remarkably little of the literature on salticid behaviour has been directly relevant to understanding exactly how important [sexual selection] may be in the Salticidae' (Jackson, 1982*a*), as this was one of the first groups of animals that were the subject of sexual selection studies (Peckham & Peckham, 1889, 1890). In a study on *Phidippus johnsoni*, Jackson (1981) demonstrated that females tend to mate preferentially with dancing males rather than with males that do not dance, and that the female's tendency to make this choice is more pronounced when she is non-virgin than when she is virgin. The latter observation is explained by a compromise females need to make between rejecting a male and the need to obtain sperm to fertilize their eggs.

The data that show most clearly the action of sexual selection on visual signals in spiders come from work on wolf spiders of the genus *Schizocosa* (Lycosidae). Clark and Uetz (1990) developed the technique of video animations, working on the salticid *Maevia inclemens*, and later used this technique in *Schizocosa*. In *Maevia inclemens*, an unusual species with two male morphs, experiments suggested that females have no preference for either morph but simply for the male that moves first (Clark & Uetz, 1992). Different morphs appear to use alternative strategies to stimulate different fields of the female visual range, using different postures at different distances from the female (Clark & Uetz, 1993; Clark

& Morjan, 2001; Clark & Biesiadecki, 2002). In *Schizocosa*, female receptivity can even increase with manipulation of the visual signal (McClintock & Uetz, 1996; Hebets & Uetz, 2000). When brushes (tufts) were added to the legs of *S. stridulans* and *S. rovneri* males (two species with visual courtship but without tufts), female receptivity increased significantly. In both cases, the visual signal was modified to resemble that of a third species (*S. ocreata*), meaning that species recognition cannot be the sole function of the visual courtship display. Either the males are exploiting pre-existing female biases, or sexual selection is favouring a novel visual stimulus (McClintock & Uetz, 1996). Further experiments suggest that the male visual stimulus is condition dependent, and may thus serve as an honest indicator of male quality in mate choice (Uetz, 2000; Uetz, Papke & Kilinic, 2002). *Schizocosa ocreata* males with larger ornaments do not only profit from female choice but they are also less likely to fall victim to sexual cannibalism (Persons & Uetz, 2005). However, the causality in this correlation remains unclear.

Other experiments demonstrate that the relative importance of visual signals varies in relation to other modalities. When conflicting (conspecific and allospecific) vibratory and visual signals were presented to females, *S. ocreata* females did not accept the male, while in *S. rovneri* vibratory signals were dominant in affecting female decision (Uetz, 2000, and references therein).

Uetz *et al.* (1996) and Uetz & Smith (1999) demonstrated female choice based on the asymmetry of the leg tufts in *S. ocreata*. This applied to fluctuating asymmetry that was the result of both developmental instability and leg loss with subsequent regeneration. With manipulated video images, all variables were held constant with the exception of tuft asymmetry. There was a significant correlation between symmetry and female receptivity.

As in salticids, comparative data in lycosids also indicate that visual signals are under sexual selection. Hebets & Uetz (2000) found a significant correlation between visual courtship and ornamentation in various groups of wolf spiders. As above, this does not exclude alternative or additional functions in the context of species isolation.

With respect to conflicts between males, there is limited evidence that visual signals play a significant role. Taylor, Hasson & Clark (2001) found no evidence that visual signals decide on the outcome of male–male interactions in the salticid *Plexippus paykulli*. It was not the size difference that determined persistence and escalation but the absolute size of the minor male. However, Jackson (1982 *b*) suggested that in *Myrmarachne lupata*, a salticid with enlarged male chelicerae, smaller males might detect cheliceral size visually and decamp before the fight escalates. Observations of Braun (1958) on *Diaea dorsata* (Thomisidae) and Dijkstra (1970) on *Pardosa amentata* (Lycosidae) also suggest that visual signals do play a role in male battles in some species, at least during the early, non-contact phases of interactions.

Above, I depicted visual signals as being easily accessible to research. A recently discovered exception is ultraviolet (UV) coloration in a salticid where extreme UV sexual dimorphism and substantial inter-male variation suggest the action of sexual selection (Matthew Lim, personal communication). Whether this is a more common phenomenon or not remains to be explored.

Concluding, there is strong experimental, comparative, and circumstantial evidence for intersexual selection (female choice) acting on visual signals in lycosids and salticids, but it appears that visual signals in spiders in general do not play a role comparable to that in other groups like mammals, birds, and insects.

(2) Acoustic signals

Acoustic signals have traditionally played a central role in the study of sexual selection, primarily in birds, insects and amphibians (review in Andersson, 1994). This is partly because these signals can be easily recorded with a minimum of interference, they can be quantified (volume, frequency, duration of syllables and pauses, *etc.*), digitised, and modified for experiments. In reality, there is no clear boundary between acoustic (air-borne) and vibratory (substrate-borne) signals. Vibratory signals may have components transmitted through the air and others travelling through the substratum (Rovner, 1967, 1975, 1980; Kronestedt, 1973; Rivero *et al.*, 2000), and the actual receiving mode of acoustic signals may be substrate vibrations generated by the airborne sound (Kotiaho *et al.*, 2004). Moreover, in spiders it is partly the same receptors for both kinds of signals, i.e. the slit sensilla on the legs and to a lesser degree the proprioreceptors and (only for air-borne waves) the trichobothria on the legs (Foelix, 1996; Barth, 2001). The reason to treat both kinds of signals separately is the fact that acoustic signals are much more easily accessible for human observers.

One type of acoustic communication that is very common in spiders is stridulation (Uetz & Stratton, 1982; Uhl & Schmitt, 1996). Up to eight morphological types of stridulation have been described in spiders (Starck, 1985), indicating that spiders are preadapted to use this channel of communication that evidently evolved several times convergently. However, in only a small minority of cases are the vibrations audible for humans (e.g. Gwinner-Hanke, 1970; Hinton & Wilson, 1970; Rovner, 1975; Edwards, 1981; Uhl & Schmitt, 1996), and it may be that in most cases it is the substrate-borne component that is relevant for communication, and no significant acoustic signal is involved (Braun, 1956). In some cases it has been demonstrated that the female can perceive the signal without substrate connection between male and female (e.g. Gwinner-Hanke, 1970 on *Steatoda bipunctata*, Theridiidae).

Sexual dimorphisms are very common, even in cases where both sexes have the same type of stridulatory organ (e.g. *Physocyclus globosus*, Pholcidae: Huber & Eberhard, 1997). However, as in visual signals, various biological contexts may be responsible for sexual dimorphisms, and some do not involve sexual selection (Uetz & Stratton, 1982). For example, *Micrathena gracilis* (Araneidae) females produce a signal that is probably defensive (Hinton & Wilson, 1970), directed towards predators like birds. Certain acoustic signals may play a role in reproductive isolation and thus be largely under natural selection (Uetz & Stratton, 1982). This applies both for stridulation and for other types of spider sound production, like percussion and vibration (Rovner, 1980).

Most of the evidence for sexual selection acting on spider acoustic signals comes from studies on a lycosid, *Hygrolycosa rubrofasciata*. Males of this species produce drums by vibrating the abdomen against the ground, preferably on dry leaves (Kronestedt, 1996; Kotiaho *et al.*, 2000). The resulting signal can be heard from a distance of up to several meters (by humans). Experiments have shown that the traditional interpretation of spider acoustic signals as species isolation mechanisms is inadequate. Rather than that, there is variation in the male signal that results in variation in the female response. Females respond more rapidly to drums of high volume, long duration, and to high drumming rates (Parri *et al.*, 1997, 2002). Interestingly, signal frequency has a low repeatability and does not convey honest information on male size or viability (Rivero *et al.*, 2000). Drumming activity rather than male body size is a good predictor of male viability (Mappes *et al.*, 1996), and females actively choose the most actively drumming males rather than larger males (Kotiaho *et al.*, 1996). A correlation between drumming rate and a measure of immune function suggests that females might use male courtship as a signal for choosing mates with good immunocompetence (Ahtiainen *et al.*, 2004). Moreover, signalling seems to involve a significant cost, as predicted by the good genes model of sexual selection: mortality, metabolic rate and risk of predation increase with drumming rate in both laboratory and field conditions (Mappes *et al.*, 1996; Kotiaho *et al.*, 1998*a*, *b*, 1999*b*; Ahtiainen *et al.*, 2001). A positive relationship between metabolic rate per unit mass and absolute body mass may compensate any disadvantage of small male size (Kotiaho *et al.*, 1998*a*). Sexual selection is also likely to favour synchronous chorusing in this species (Kotiaho *et al.*, 2004).

The majority of spider acoustic signals is much less audible to humans, and in those cases where the signals are audible, there is no clear evidence on the function of the signals. This is also true for the examples presented by Darwin (1871) under *Theridion* (now representatives of the genera *Steatoda* and *Crustulina*). Studies on the stridulation of *Steatoda bipunctata* (Gwinner-Hanke, 1970; Lee *et al.*, 1986) do not allow a decision about the involvement of sexual selection. However, the observations that males of this and related species stridulate not only before but also during copulation (Gwinner-Hanke, 1970; Knoflach, 2004) suggest that species recognition is not the only factor and sexual selection remains a plausible explanation. Considerable intraspecific variation in several signal parameters in *Steatoda* (Lee *et al.*, 1986) supports this possibility.

Stridulation has also been shown to occur in male–male agonistic interactions (Rovner, 1967; Lee *et al.*, 1986). Aggressive acoustic signalling (agonistic drumming) has also been observed between *H. rubrofasciata* males (Kotiaho *et al.*, 1997, 1999*a*) but the importance of agonistic interactions compared to that of courtship drumming is controversial (Kotiaho *et al.*, 1997, 1999*a versus* Ahtiainen *et al.*, 2001). Agonistic drumming has also been observed in *Leucorchestris arenicola* (Sparassidae) (Henschel, 2002), but the signal transmitted may be rather substrate-borne than air-borne.

(3) **Chemical signals**

Andersson (1994) considered chemical signals to be 'the third major channel of animal communication', following visual and acoustic signals. This sequence sounds anthropocentric, and is quite certainly not true for spiders. It is mainly for technical reasons that we know relatively little about communication using the chemical channel in spiders, and the available data are largely limited to female pheromones (e.g. Tietjen, 1979; Suter & Hirscheimer, 1986; Watson, 1986; Jackson, 1986*d*; Lopez, 1987; Pollard, Macnab & Jackson, 1987; Suter, Shane & Hirscheimer, 1987; Barth, 1993; Trabalon, Bagnères & Roland, 1997; Prouvost *et al.*, 1999; Searcy, Rypstra & Persons, 1999; Tichy *et al.*, 2001; Costa & Pérez-Miles, 2002; Haupt, 2003; reviews in Robinson, 1982; Tietjen & Rovner, 1982; Schulz, 2004*a*). In only a few cases have the pheromones been identified (Schulz & Toft, 1993; Papke *et al.*, 2000; Papke, Riechert & Schulz, 2001).

It has long been known that males of several families can distinguish between draglines and webs of males and females (Bristowe & Locket, 1926; Dondale & Hegdekar, 1973; Blanke, 1974; further references in Clark & Jackson, 1995*b*; Schulz, 2004*a*). However, a series of experiments on the salticid *Portia labiata* suggests that these spiders use a much more sophisticated system of communication *via* pheromones. *Portia labiata* females discriminate between their own eggsacs and draglines and those of conspecifics (self-recognition; Clark & Jackson, 1994*a*, *b*), they distinguish between draglines of unknown females and of females against which they have lost an agonistic encounter (Clark & Jackson, 1995*a*), and they can assess by the draglines alone the agonistic abilities of unknown females (Clark, Jackson & Waas, 1999). These data do not document sexual selection, but they indicate that there may be a system of signals and receptors perfectly adequate to serve as a basis for sexual selection.

Most studies on spider pheromones are on female substances that function in the context of male attraction, in triggering courtship behaviour, and in species recognition (Schulz, 2004*a*). In *Metellina segmentata* (Tetragnathidae), the assessment of female quality (size and hence fecundity, as well as her nearness to moult) by males seems to be based on pheromonal cues (Prenter, Elwood & Montgomery, 1994). Sexual selection more probably acts on male signals, but male spider pheromones have barely been studied (Ross & Smith, 1979; Ayyagari & Tietjen, 1986). Ross & Smith (1979) suggest that *Latrodectus hesperus* (Theridiidae) females chemically validate the identity of the male by contact with the 'bridal veil' that males throw over females before copulation.

One phenomenon suggesting the action of sexual selection on chemical signals in spiders is gustatorial courtship. Transfer of male glandular products and possibly of haemolymph to the female mouth during copulation is documented in erigonine (and suggested in linyphiine) linyphiids (Schaible, Gack & Paulus, 1986; Blest, 1987; Schaible & Gack, 1987; Hormiga, 1999) in *Argyrodes* (Theridiidae) (Legendre & Lopez, 1974; Lopez & Emerit, 1979; Whitehouse, 1987; Whitehouse & Jackson, 1994), and in one species of pholcid (Huber, 1997). The substances transferred have not been identified in any case, and might involve pheromones as well as nutrients. In the male-dimorphic linyphiid *Oedothorax gibbosus*, different gland cells occur in the head region of the 'gibbosus' morph, and robbing of the secretions by conspecific males and even heterospecific males and females suggests that gibbosus males produce a valuable secretion including more than just pheromones (Vanacker *et al.*, 2003*a*, *b*). Further experiments have indicated that the chance of being accepted by non-virgin females is significantly higher for gibbosus males (Vanacker *et al.*, 2004). Interestingly, mynoglenine linyphiids also have clypeal glands, but in this case both sexes and even juveniles are equipped with these modifications, and gland ultrastructure rather suggests a defensive function (Blest & Taylor, 1977).

Pheromones might also be produced by sexually dimorphic glands other than those on the head, as for example gnathocoxal glands (Lopez & Emerit, 1978; Juberthie-Jupeau & Lopez, 1991), epiandrous glands (Lopez & Emerit, 1988), tibial glands (Kronestedt, 1986; Juberthie-Jupeau, Lopez & Kronestedt, 1990), and metatarsal glands (Kropf, 2004). Spider surface lipids probably serve a variety of functions, but their diversity and apparent species-specificity (Schulz, 2004*b*) hints to sexual selection as one potential factor driving the evolution of these components. Another field that in spiders remains unstudied is the signalling (and other) functions of male seminal products ('chemical genitalia', Eberhard & Cordero, 1995). Theory predicts that under sexual selection, these seminal products should evolve and diversify relatively rapidly. In fact, a comparative analysis of seminal fluid ultrastructure has revealed an astounding diversity among species (Peter Michalik, personal communication). The lack of experimental research is remarkable, because at least some compounds of the semen are unusually easy to collect, study, and manipulate when males charge their pedipalps with a droplet of semen deposited on a small web.

(4) Vibratory signals

It may well be that substrate-borne vibrations are the most important modality for spiders in general (Uetz, 2000). In many groups of spiders, vibrations are fundamental in the perception of prey and in intraspecific interactions. This is not only true for web-borne spiders but also for the more basal mesothelid and mygalomorph spiders (Costa & Pérez-Miles, 2002; Haupt, 2003), and even for cursorial spiders with acute vision, like salticids (Jackson, 1988; Elias *et al.*, 2003). In the ctenid *Cupiennius salei*, Barth & Libera (1970) counted approximately 3300 slit sense organs per individual. Spider lyriform organs are among the most sensitive receptors in any organism (Barth, 2001). Displacement of the metatarsus by 1×10^{-7} cm elicits a response in the lyriform organ in *C. salei*. This amounts to a 1 mm displacement in a spider with 100 km leg span (Barth, 2001).

Considering the obvious importance of vibrations for spiders, it is surprising that few studies exist that explicitly investigate the function of vibrations in the context of sexual selection. Technical difficulties of recording vibrations may be a major reason, but methods like laser doppler vibrometry promise to improve drastically our understanding of vibratory courtship signals (Tarsitano & Kirchner, 2001; Elias *et al.*, 2003). Refined techniques may even justify reconsideration of species where previous study has revealed no evidence for male vibrations being under sexual selection by female choice (e.g. Maklakov, Bilde & Lubin, 2003, on *Stegodyphus lineatus*).

Two groups of researchers have contributed most significantly to our knowledge about vibratory communication in spiders, the groups of F. Barth and G. Uetz. Most experiments were carried out within the conceptual frameworks of species isolation and recognition, sexual arousal, and suppression of aggressive behaviour (reviews in Barth & Schmitt, 1991; Barth, 1993, 2001), or with the aim of documenting the relative importance of visual *versus* vibratory signals (see above), with less attention paid to possible sexual selection (see also Suter & Renkes, 1984). However, circumstantial evidence indicates the potential for sexual selection on vibratory signals: both spectral and temporal characteristics of manipulated male vibratory signals determined female responses in *Cupiennius* spp. (Barth, 1990). Equally, manipulation of electronically synthesised vibrations improved the efficiency of the signal in *Cupiennius salei* above the level of natural signals (Schüch & Barth, 1990). There appears to be a cost involved in the increase of carrier frequency and syllable repetition rate, as these parameters are below the optimum in natural signals (Schüch & Barth, 1990). This means that certain signal parameters might constitute a valuable criterion for the female, comparable to the drums of *Hygrolycosa rubrofasciata* mentioned above. By contrast, *C. getazi* females did not discriminate between high and low amplitudes, long and short signals, or frequently or rarely repeated signals, but only between conspecific and heterospecific signals (Schmitt, Schuster & Barth, 1994).

Suggestive but inconclusive evidence also comes from studies on *Schizocosa ocreata* wolf spiders. Usually, tufts on male *S. ocreata* legs had no effect on female receptivity. However, when vibrations were artificially excluded, there was a significant correlation between male optical signal (tufts) and female receptivity (Scheffer, Uetz & Stratton, 1996). This means that the female based her decision on optical signals only when vibrations could not be perceived. In other words, in certain natural circumstances, the female might base her decision primarily on vibrations.

In certain salticids, males employ different tactics depending on where they meet a female (Jackson, 1978, 1982*b*). Outside nests, visual signalling is used, but if the female is inside her nest, the male uses primarily vibratory signals. If visual signals are indeed under sexual selection in salticids (see above) and if the two male courtship tactics have the same function(s), then this suggests sexual selection on male vibratory signals.

Courting male *Frontinella communis* (Linyphiidae) produce a variety of web-borne vibrations, some of which carry information about the male (Suter & Renkes, 1984, as *F. pyramitela*). Larger spiders oscillate longer and at lower frequencies. Suter & Renkes (1984) argue against sexual selection as shaping courtship in this species because females were never seen to reject a male, but the possibility of cryptic female choice (see below) was not considered. Males of

Zygiella x-notata (Araneidae) produce a rhythmical pulling signal only after walking across the web, arguing against a predatory inhibition function of the signal (Tarsitano & Kirchner, 2001). The authors suggest that information about the male's status contained in the vibratory signals could influence the female's decision whether to mate with him or not.

Vibratory courtship on mating threads produced by males is widespread in araneid orb-weavers (Robinson, 1982), but no study has investigated in detail both the vibratory signals involved and their potential effect on the male's success.

Finally, courtship may be complex in spiders other than the visually oriented salticids above. For example, Whitehouse & Jackson (1994) documented 32 major displays in the theridiid *Argyrodes antipodiana*, involving mostly vibratory and tactile signals. They argue that sexual selection is a more likely explanation than species recognition or defence against cannibalism.

(5) **Tactile signals**

Eberhard (1994) documented courtship during and after copulation in 81 % of 131 species of insects and spiders. Most of the signals involved were tactile, and the author concluded that female choice was the most probable explanation, rather than alternative functions like sperm displacement or courtship for additional copulations. This suggests that cryptic female choice (Thornhill, 1983) is a common phenomenon in spiders, and that tactile male signals may significantly affect female processes and behaviours (Eberhard, 1996) that in turn affect paternity. Cryptic female choice in spiders might involve mechanisms like early termination of copulation, remating likelihood, manipulation of sperm (transport to storage or fertilisation site, dumping, digestion), preventing certain male processes (complete intromission, ejaculation, plugging), biasing sperm storage by body position, and others (Eberhard, 1996; Gunnarsson & Andersson, 1996; Bukowski & Christenson, 1997, 2000; Eberhard & Huber, 1998; Uhl, 2000; Burger, Nentwig & Kropf, 2003). Cryptic female choice is of course not limited to tactile signals, but it is particularly evident in these signals that are often transmitted during or even after sperm transfer.

One type of tactile signal apparently ubiquitous in spiders is rhythmical movements of the genitalia during copulation, either in the form of repeated insertions and withdrawals or as rhythmic movements during insertion (Huber, 1998*b*). Insertion patterns evolve relatively rapidly (Huber, 1998*b*; Knoflach, 2004), suggesting sexual selection. In *Physocyclus globosus* (Pholcidae), morphological evidence suggests that rhythmical movements do not function in the context of sperm ejaculation or displacement (Huber & Eberhard, 1997). Instead, these movements probably transmit a tactile signal to the female, affecting cryptic female choice (A. Peretti, W. G. Eberhard & R. D. Briceño, in preparation).

The signal parameters used by the female are unknown. Data on *Neriene litigiosa* (Linyphiidae) suggest that they may simply judge persistence, *i.e.* metabolic competence. Watson & Lighton (1994) used CO_2 respirometry to measure energy consumption during the 2–6 h of continuous insertions and retractions of the genitalia during copulation in *N. litigiosa*. It turned out that energy consumption rises up to seven times above resting metabolic rate. Additionally or alternatively, females might use tactile stimuli resulting directly from each single movement, but the sensory system of female spider genitalia has never been the subject of any detailed investigation. In any case, Watson & Lighton (1994) found a significant correlation between frequency of insertions and paternity, suggesting that genital movements are under sexual selection. In another linyphiid, *Florinda coccinea*, lengthy pseudocopulations (approximately 500 insertions in approximately 20 min) have also been considered to function as a form of internal courtship and to be under sexual selection (Willey-Robertson & Adler, 1994). Similar results were obtained in *Pholcus phalangioides* (Pholcidae) by Schäfer & Uhl (2002). In that study, several variables affected reproductive success, but the number of male palpal movements was the only one with a significant effect on paternity.

Another stimulus might stem from the precision of male movements, *i.e.* from the 'flubs' (Watson, 1991*b*), or unsuccessful intromission attempts by males. Such flubs are common in spiders (Huber, 1998*b*), and if they reflect the male's competency in copulation (Watson, 1991*b*), females are predicted to be under selection to use the flub to hit ratio as a criterion in cryptic female choice. In *Pardosa milvina*, predation risk is correlated with significantly higher numbers of failed insertions, possibly due to increased predator vigilance (Taylor, Persons & Rypstra, in press). Whether or not this affects female choice in unknown.

Tactile stimuli used by males to court females are usually not obviously related to male vigour (Eberhard, 1994). Pholcid spiders might be an exception, as in some genera the palps have very large muscles and palpal strength seems to be under sexual selection (Huber, 1996, 1998*a*, 1999; Huber & Eberhard, 1997). In *Metagonia mariguitarensis* (Pholcidae), the only known spider with directionally asymmetric male genitalia, the strong right palp seems to have assumed the display function while the weak left palp has the larger sperm reservoir and might be the main sperm transfer organ (Huber, 2004).

Sexual selection on the tactile stimuli generated by the genitalia during copulation may explain the extremely widespread phenomenon of rapid divergent evolution of genitalia (Eberhard, 1985, 2004*a*, *b*; Arnqvist, 1998; Arnqvist & Danielsson, 1999; Hosken & Stockley, 2004). The same may apply to species-specific contact and grasping structures other than genitalia (Eberhard, 1985; Coyle, 1985, 1986; Huber, 1995, 1999; Yoward & Oxford, 1997). For example, clasping behaviour, where males use modifications on their first legs to hold on to females during copulation, is widespread in mygalomorphs. Jackson & Pollard (1990) summarised the available evidence and concluded that a stimulatory function is more probable than physical restraint of a predatory female. However, both for genitalia and other contact structures, sexual selection by mechanical fit (Eberhard, 1985) might be an alternative mechanism that need not be tied to stimuli. This might be more common in spiders and other arachnids than in insects, especially because spider female external genitalia are often rigid and apparently devoid of receptors (Huber, 1993*a*, *b*; Peretti, 2003; Berendonck & Greven, 2005). Exaggeration of genitalic morphology may be a result of sexual selection (Eberhard, 1985), and accordingly it is widespread in males but not in females (Huber, Brescovit & Rheims, in press).

Tactile stimuli might also convey information on male fluctuating asymmetry, and therefore on male individual quality. However, a study on *Hygrolycosa rubrofasciata* found only a weak correlation between pedipalp fluctuating asymmetry and male sexual performance, suggesting it is an unreliable measure of individual quality in this species (Ahtiainen *et al*., 2003). Similarly, no female discrimination against males with experimentally asymmetric legs was observed in the linyphiid *Pityohyphantes phrygianus*, possibly due to a female-biased sex ratio (Stålhandske & Gunnarsson, 1996).

Tactile stimuli are probably the major component of most male–male interactions (e.g. Billaudelle, 1957; Braun, 1958; Robinson & Robinson, 1980; Jackson, 1982*b*; Suter & Keiley, 1984; Dodson & Beck, 1993; Méndez, 2002; Hu & Morse, 2004). The energetic cost of escalated fighting (which involves physical contact) in *Neriene litigiosa* has been shown to be approximately 7 to 12-fold above resting metabolic rate (Decarvalho, Watson & Field, 2004). In *Linyphia triangularis*, males first approach each other using vibratory signalling, then possibly visual threat displays, and finally physical contact, and several encounters were resolved in the tactile phase (Rovner, 1968). Male *L. triangularis* use their chelicerae for fighting, larger males displace smaller males (Toft, 1989), and the male chelicerae have high allometric values, indicating directional selection (Funke & Huber, in press). In some spiders, male armaments are developed to a degree that probably incurs costs to the male (Pollard, 1994).

III. SEXUAL SIZE DIMORPHISM

Traditionally, males in extremely size dimorphic spider species were often considered dwarfs (e.g. Elgar, Ghaffar & Read, 1990; Main, 1990; Vollrath & Parker, 1992), implying an evolutionary scenario where the males had changed their size rather than the females. This view has been questioned recently, both by reconstructions of ancestral sizes in cladistic analyses (Coddington, Hormiga & Scharff, 1997; Hormiga *et al*., 2000) and by comparative studies (Head, 1995; Prenter, Elwood & Montgomery, 1999). It turned out that in the majority of cases, size dimorphism is better explained by female size increase by fecundity selection than by male size decrease. This would imply that sexual selection may not necessarily be involved in the origin or maintenance of the dimorphism in *Nephila* (Tetragnathidae; the genus that Darwin, 1871, used as an example) and in the majority of other cases in which sexual size dimorphism occurs.

However, this has not solved the problem entirely. Usually there is also strong selection favouring large males (Elgar, 1998). In *Nephila* spp., for example, large males displace smaller ones towards the periphery of the web (Christenson & Goist, 1979; Vollrath, 1980; Elgar & Fahey, 1996; Elgar, Champion de Crespigny & Ramamurthy, 2003*b*). This means that there is still a force to be explained that is hindering males from following their females in increasing their size. In other words, the correct question in many cases seems not to be why males became small, but why they remained small (*cf*. Maklakov, Bilde & Lubin, 2004). In other cases it may actually have been the males that became small (e.g. *Tidarren*, Theridiidae, Knoflach & van Harten, 2000; *Kaira*, Araneidae: Hormiga *et al*., 2000; *Misumena* and *Misumenops*, Thomisidae: LeGrand & Morse, 2000).

The model of differential mortality of males and females by Vollrath & Parker (1992) explains male dwarfism by invoking sexual selection by scramble competition. According to this model, vagrant males suffer higher mortality, resulting in a female-biased operational sex ratio. This in turn reduces the intensity of male competition that would otherwise select for large males. If, at the same time, selection continues to favour the male that arrives first (e.g. by first male sperm priority, see below), this will result in increased selection for protandry and necessarily for males with short ontogeny and small size. In contrast to other models (see below), the advantage lies not in small size *per se* but in the short ontogeny. One central assumption made by Vollrath and Parker (1992) is that there is a link between behaviour and mortality across taxa. Recent data on lycosid spiders indicate that this assumption may not hold in all cases, and that further research on the relationship between size, fitness, and mobility is needed (Walker & Rypstra, 2003). Another prediction of the Vollrath and Parker (1992) ideas, concerning an association between predatory strategy and sexual size dimorphism (sit-and-wait predators should be more dimorphic than actively hunting predators) was also not fulfilled (Prenter, Montgomery & Elwood, 1997; Prenter, Elwood & Montgomery, 1998). On the other hand, a study on three *Metepeira* (Araneidae) species with different ecologies found a correlation between male mobility and sexual size dimorphism (Piel, 1996). Whether increased mortality is involved or not is unknown, and mobility might select directly for smaller males. The latter mechanism implies that male dwarfism may also result from natural rather than sexual selection (analogous to fecundity selection resulting in female gigantism). Similarly, small males might avoid moulting risks during growth and reduce competition with females during development (Vollrath, 1998), and small size could give an advantage in avoiding visual predators and in coping with environmental hazards like drought and flooding (Elgar & Nash, 1988; Main, 1990; Gunnarsson, 1998). One aspect of the Vollrath & Parker (1992) model, namely the advantage of protandry rather than of small size *per se*, has been supported by recent studies on *Stegodyphus lineatus* (Schneider & Lubin, 1996, 1997; Maklakov *et al*., 2004).

Another option involving sexual selection was presented by Schneider *et al*. (2000) who suggested sperm competition and perhaps cryptic female choice as possible mechanisms in *Nephila edulis*. They found a correlation between copulation duration and paternity, and it was the smaller males that copulated for longer periods of time. Schneider *et al.* (2000) suggest that different strategies may be the reason for variation in copulation duration: large males copulate through a hole in the web while small males sit directly on the female's abdomen. Alternatively, it might be the female that decides on copulation duration. In any case, sexual selection seems to be involved. The same conclusion may hold for *Nephila plumipes*, where smaller males seem to have an advantage that they are not as easily detected and cannibalised by the females as larger males (Elgar & Fahey, 1996). In *Argiope keyserlingi* (Araneidae), females copulating with smaller males delay cannibalism, thereby prolonging copulation duration and increasing the percentage of eggs fertilised by these smaller males (Elgar, Schneider & Herberstein, 2000). Comparative data have also indicated a close relationship between sexual dimorphism and cannibalism in certain taxa. Males of species that court at the female hub are relatively smaller in relation to females than males that court on a mating thread, *i.e.* in a relatively secure position (Elgar, 1991). Thus, small size seems to be beneficial for some reason, but only males courting in a secure position can afford to be small. Sexual cannibalism has also been argued to select simultaneously for relatively longer male legs and small body size in Araneinae (Elgar *et al.*, 1990).

A further hypothesis explaining sexual size dimorphism in spiders is the 'gravity hypothesis' (Moya-Laraño, Halaj & Wise, 2002). According to this model, small males are favoured in species in which males have to climb to reach females for simple biomechanical reasons. This kind of sexual selection by scramble competition is seen as complementary to both the fecundity selection model and the differential mortality model. The crab spider *Misumena vatia*, where females are much larger and heavier than males but males have longer legs and are much more agile (LeGrand & Morse, 2000), may fit this hypothesis. Intense scramble competition also occurs in *Tidarren sisyphoides* where female body mass is about 80 times male body mass and the first male to reach the female abdomen usually copulates (Ramos, Irschick & Christenson, 2004). Males further increase their maximum speed and endurance by removing one of their pedipalps (Ramos *et al.*, 2004).

In the end, it may well be that Darwin (1871) was right when using *Nephila* as an example for size dimorphism resulting from sexual selection. However, several kinds of data indicate that various evolutionary pathways may lead to female-biased sexual size dimorphism, and some of these may be driven by natural rather than sexual selection (see above). The cladistic analysis of Coddington *et al.* (1997) and Hormiga *et al.* (2000) suggests that several scenarios have actually happened in orb-weaving spiders, like female size increase coupled with male decrease, female increase alone, male increase alone, male and female decrease, *etc.* This variety of evolutionary pathways means that sexual size dimorphism in spiders 'is complex and unlikely to be explained by simplistic selectionist arguments applied wholesale' (Hormiga *et al.*, 2000).

The water spider, *Argyroneta aquatica* (Cybaeidae), represents one of a few cases in spiders where the male is overall larger than the female. In contrast to vertebrates, where this kind of dimorphism usually results from sexual selection (Andersson, 1994), experimental data indicate that in *A. aquatica* it is as a result of natural selection that males are larger than females. Schütz & Taborsky (2003) found evidence for two mechanisms of natural selection responsible in this case: males, being the more mobile sex, gain an advantage by being larger because mobility is positively correlated with size. Depending on the advantage mobility offers them with regard to reproduction, the selective pressure is entirely or partly natural (as opposed to sexual). At the same time, females need larger air bells than males, and a correlation between body size and bell size (in females only) results in selection for smaller females. As a result, the dimorphism in this species may partly or entirely be due to natural selection.

Sexual selection for large male size occurs both as inter- and intrasexual selection. In *Agelenopsis aperta* (Agelenidae), females prefer heavier males for the genes for behavioural aggressiveness they offer their offspring (Riechert & Johns, 2003). In *Neriene litigiosa*, females rely 'blindly' on the outcome of inter-male fights to determine their major sire (Watson, 1990, 1991*a*). In some highly sexually size-dimorphic orb-weavers, several males may be found on the web of a single female (Robinson, 1982), indicating a high potential for male–male competition counteracting the selective forces that keep males small.

In most cases of male–male competition, selection is particularly strong on the fighting structures *per se* (e.g. chelicerae in certain linyphiid and salticid spiders: Toft, 1989; Funke & Huber, in press; Pollard, 1994) rather than on overall body size. Abdomens of *Mecolaesthus longissimus* (Pholcidae) males are on average more than twice as long as in females, and circumstantial evidence suggests that males use their abdomens in male–male fights (B. A. Huber, in preparation). In *Hygrolycosa rubrofasciata*, larger males win male–male contests, but only courtship drumming activity determines male mating success (Kotiaho *et al.*, 1997). In general, small males lose in direct interactions, but may still successfully mate with the female by using alternative strategies, by simply waiting and searching for whatever limited opportunities arise, or when male density is very low (Christenson & Goist, 1979; Suter & Keiley, 1984; Toft, 1989; Nielsen & Toft, 1990; Faber, 1994; LeGrand & Morse, 2000; Prenter, Elwood & Montgomery, 2003).

Most comparative studies have used rather simple measures of size that can be readily taken from the taxonomic literature (e.g. total body length). In species that are only slightly dimorphic, this common practice may easily produce a simplified and sometimes mistaken picture of sexual dimorphism as it fails to account for the multivariate nature of dimorphism (Prenter, Montgomery & Elwood, 1995). For example, using single measures in *Metellina segmentata* could result in either males or females being the larger sex, and in this species it is shape rather than size that is the major factor in sexual dimorphism (Prenter *et al.*, 1995). In *Pholcus phalangioides*, males grow larger (in terms of leg length) but females gain more body mass (Uhl *et al.*, 2004).

IV. NUPTIAL FEEDING AND SEXUAL CANNIBALISM

Nuptial feeding in the form of prey items ceded to the female by the male (for gustatorial courtship see above) is widespread in insects (Vahed, 1998) but rare in spiders. The best known case, *Pisaura mirabilis* (Pisauridae), has attracted considerable attention for a long time (e.g. Gerhardt, 1923; Austad & Thornhill, 1986; Nitzsche, 1988; Drengsgaard & Toft, 1999; Stålhandske, 2001, 2002). Other than that, the occurrence of wrapped prey used as a gift during courtship has only been documented in a few other members of the same family Pisauridae (Nitzsche, 1988; Itakura, 1993, 1998). Male chivalry, or ceding of prey to the female by a dominant male, has been reported for pholcid spiders (Eberhard & Briceño, 1983), and this might represent yet another form of nuptial feeding. A potentially much more common but barely studied form of nuptial feeding may occur *via* the transfer of nongametic ejaculatory substances (Suter & Parkhill, 1990).

Experiments indicate that in *P. mirabilis*, the nuptial gift is not a male strategy to appease the female, as cannibalism is very rare (1.5 % of mating situations in Drengsgaard & Toft, 1999), does usually not happen to males without a gift (Stålhandske, 2001), and is sometimes even caused by struggles over nuptial prey (Austad & Thornhill, 1986). There was also no correlation between presence or size of the gift and female fecundity or progeny size (Stålhandske, 2001; but see Austad & Thornhill, 1986). But there were significant correlations between (1) presence of the gift and chance of being accepted by the female, (2) size of the gift and copulation duration, (3) copulation duration and proportion of eggs fertilised (Austad & Thornhill, 1986; Stålhandske, 2001). The conclusion is that the gift presents a mating effort rather than a paternal investment, maintained by sexual selection. A similar conclusion may also hold for the silk that the male uses to wrap up the nuptial gift. Higher amounts of silk resulted in longer copulations but seemed to provide no significant nutritional benefit to the female (Lang, 1996).

Additional experiments (Stålhandske, 2002) indicate that male gifts and female preferences in *P. mirabilis* may have originated *via* sexual selection by sensory exploitation (Ryan *et al.*, 1990). Females of this species carry the eggsac in their chelicerae, and male gifts more or less resemble eggsacs. Stålhandske (2002) observed a correlation between similarity of the gift to an eggsac and female reaction towards the male.

Sexual cannibalism is relatively rare taxonomically but common or even obligatory in several spider species (Elgar, 1992). It may be seen as an extreme form of nuptial feeding (Vahed, 1998), but there is a fundamental difference between offering of prey or secretions on one hand and being cannibalised on the other. The first is probably always an adaptive male strategy, *via* mating effort or paternal investment, while cannibalism may or may not be adaptive from the male perspective. There are probably various evolutionary pathways towards cannibalism (Morse, 2004; Morse & Hu, 2004; Elgar & Schneider, 2004), and some of these do not involve male adaptive strategies and sexual selection. For example, Arnqvist & Henriksson (1997) proposed an entirely non-adaptive model for cannibalism in *Dolomedes fimbriatus* (Pisauridae). According to their 'aggressive-spillover hypothesis', aggressive behaviour is adaptive in juveniles and maintained in adults by some unknown constraints even though it is not adaptive any more. To the contrary, it is even maladaptive because some females remain virgin after cannibalising their suitors instead of copulating with them. According to the 'economic' or 'adaptive foraging hypothesis' of Newman & Elgar (1991), females cannibalise the males if males are abundant and other prey is scarce. In this model, cannibalism is adaptive, but only from the female perspective. For example, in *Araneus diadematus*, some males are cannibalised before copulation, and cannibalism increases female fecundity (Elgar & Nash, 1988). Further supporting evidence for both the 'aggressive-spillover hypothesis' and the 'adaptive foraging hypothesis' came from studies on *Dolomedes triton*, where sequential behavioural components seem best explained by one or the other hypothesis (Johnson, 2001). A similar situation occurs in *Argiope keyserlingi*, except that female benefit is apparently not related to nutrients provided by the male but results from the control of paternity *via* timing of cannibalism (Elgar *et al.*, 2000). Paternal investment is probably not a general explanation for sexual cannibalism, especially in species with pronounced sexual size dimorphism (Elgar, 1992, 1998; Schneider & Elgar, 2002; Fromhage, Uhl & Schneider, 2003; Elgar & Schneider, 2004).

In *Schizocosa uetzi*, females are more likely to cannibalise males of an unfamiliar phenotype (Hebets, 2003). However, it is not clear whether mate choice in this case occurs in the context of reproductive isolation or sexual selection. In *S. ocreata*, both female choice (see above) and sexual cannibalism result in selection for large male body size and large male ornaments (hair tufts) (Persons & Uetz, 2005). However, due to multiple intercorrelations of several variables, the causal relationships remain obscure.

Finally, there are cases where cannibalism represents an adaptive male strategy under sexual selection. An adaptive strategy implies male complicity, i.e. the male offers himself instead of trying to escape. In *Argiope aemula* and *A. aurantia*, males copulate making two insertions, one with each palp. They try to escape after the first, but show complicity (*i.e.* die without being bitten) during the second (Sasaki & Iwahashi, 1995; Foellmer & Fairbairn, 2003). Similar variation in male behaviour occurs in *Nephila plumipes*, but in this case depending on the reproductive status of the female. The male gains nothing by being eaten after copulation with a virgin female, but after copulation with a non-virgin female the male can increase his paternity by offering himself as prey (Schneider & Elgar, 2001). However, by removing the potential nutritional benefit of cannibalism, Schneider & Elgar (2002) could show that cannibalism *per se* may be relatively unimportant in the process of resource accumulation in *N. plumipes*. They suggest that sexual cannibalism in this species may be simply a consequence of increased foraging vigour of small, poor-condition females. In *Argiope bruennichi*, complicity was not observed, but cannibalism was associated with prolonged copulations, suggesting a sexually selected benefit of cannibalism for males (Fromhage *et al.*, 2003).

In *Latrodectus hasselti* (Theridiidae), males show complicity by positioning their abdomens in front of the female fangs, and 65 % (11/17) of observed copulations resulted in cannibalism (Andrade, 1996). Ecological factors might be involved, as 80 % of males died without finding a potential mate in nature (Andrade, 2003), and males are functionally sterile after mating with both palps (Andrade & Banta, 2002). However, the causality in this obvious correlation between low residual reproductive value of non-virgin males and cannibalism is unclear. Experiments have shown that the male body offers no significant nutrition to the female (Andrade, 1996). However, copulations with males being cannibalised (1) decrease the likelihood that the female will remate, (2) take about twice as long, and (3) result in twice as many eggs fertilised. The link between copulation duration and paternity may be owing to cryptic female choice or the transfer of nongametic ejaculatory substances rather than to the number of sperm transferred (Snow & Andrade, 2004). As for cannibalism in this species, the conclusion is that the male employs an adaptive strategy maintained by sexual selection.

Finally, in three species of the genera *Echinotheridion* and *Tidarren* (Theridiidae), males are apparently always cannibalised (Knoflach & van Harten, 2000, 2001; Knoflach, 2002). There are no experiments, but 25 to 45 copulations were observed per species, and all males were cannibalised. Either the males employ an adaptive strategy, or they have evidently lost the arms race.

V. SPERM COMPETITION

The basis for Parker's (1970) idea on sperm competition is female polygamy. Apart from numerous observations in spiders, there are good theoretical reasons for female polygamy to be common in general even in the absence of direct benefits, like offspring genetic diversity and viability, insurance against male sterility or genetic incompatibility, high costs of rebuking males, *etc.* (Austad, 1984; Watson, 1991*b*, 1993, 1998). For the male, female polygamy creates both a problem and an opportunity: other males might displace or dilute his sperm in the female receptacle or reduce his paternity in some other way, and he himself can do the same things to other males. This selects for two kinds of diametrically opposed adaptations (Parker, 1970, 1984; Simmons, 2001), both present in spiders: males will try to make it difficult for successors, for example by prolonged copulations, non-contact mate guarding, or copulatory plugs (defensive adaptations). And they will try to steal the previous male's investments, for example by displacing his sperm, by inducing the female to dump it herself, or by displacing copulatory plugs left by previous males (aggressive adaptations).

Details of aggressive adaptations indicate that this kind of male–male competition is not resolved among males alone, but it is the female that provides the arena and decides on the 'rules of the game' (Eberhard, 1996). For example, gamasomorphine oonopid females seem to have a mechanism that allows them to dump sperm from their spermathecae (Burger *et al.*, 2003). A rather controversial example for such female 'rules' is the morphology of her internal genitalia. Austad (1984) suggested that some spermathecae will favour first males because the flow-through morphology results in a first-in-first-out situation. By contrast, one-way (*cul-de-sac*) spermathecae will favour last males because the last in will be the first out. This might explain why in some spiders but not in others the males guard penultimate females (Austad, 1984; Jackson, 1986*a*; Toft, 1989; Watson, 1990; Dodson & Beck, 1993; Stumpf & Linsenmair, 1996; Fahey & Elgar, 1997).

However, in reality the situation is more complicated, and Austad's (1984) model has been modified accordingly. For example, Jackson (1980) showed an extreme variation in sperm priority in *Phidippus johnsoni* (Salticidae). In 55 % of cases, there was no sperm displacement, in 27 % there was complete sperm displacement. Equally extreme degrees of variation have also been found in other families of spiders (Eberhard, Guzmán-Gómez & Catley, 1993; Andrade, 1996; Kaster & Jakob, 1997; Yoward, 1998; Schäfer & Uhl, 2002), indicating that female morphology is not the sole predictor of sperm priority. Factors that complicate the situation are intermediate and additional types of morphologies, sperm mixing, size differences among males, variation in copulation duration, the time it takes for sperm capacitation (spiders transfer encapsulated sperm which subsequently emerge from their capsules in the female), the degree of sperm depletion of the male palp, copulations without sperm transfer, the interval between matings, and the number of copulations by the female (Brown, 1985; Christenson & Cohn, 1988; Andrade, 1996; Schneider & Lubin, 1996; Yoward, 1996; Elgar, 1998; Uhl & Vollrath, 1998; Drengsgaard & Toft, 1999; West & Toft, 1999; Uhl, 2000, 2002; Elgar *et al.*, 2003*a*; Danielson-François, in press).

A common male spider strategy possibly explained by sperm competition is the production of copulatory plugs, defined here as any mass or structure that appears to seal the female gonopore or to block access to the spermatheca. Plugs may consist of male secretions produced in special glands, as for example bulbal glands (Suhm, Thaler & Alberti, 1995; Knoflach, 2004), glands in the mouth area (Braun, 1956; Knoflach, 2004), or glands from the genital tract (Knoflach, 1998, 2004). They may consist of sperm (Huber, 1995), or it may be that the entire male genital bulb, the intromittent organ (embolus), or parts of it break and remain more or less firmly locked in the female insemination duct or her spermatheca (Abalos & Baez, 1963; Wiehle, 1967; Levi, 1970; Knoflach & van Harten, 2001, 2002; Berendonck & Greven, 2002; Knoflach, 2002). In *Argiope argentata* and *Tidarren sisyphoides*, males invariably die during copulation and their corpses have been suggested to form short-term mating plugs (Foellmer & Fairbairn, 2003; Knoflach & Benjamin, 2003). The extent to which such plugs impede access to further males is largely unknown. Alternative functions, like prevention of sperm backflow during oviposition, sperm desiccation (Huber, 1995), or genitalic infections (Eberhard, 2004*c*) remain unexplored. In some cases, male ectomised structures have been shown to present no barriers for further males, as for example in *Nephila plumipes* (Schneider, Thomas & Elgar, 2001). However, whether or not they originally evolved as barriers is unknown. Suhm *et al.* (1995) listed 14 families of spiders in which copulatory plugs had been described (further records: Jackson & Hallas, 1986; Patel & Bradoo, 1986; Whitehouse & Jackson, 1994; Eberhard, 1996; Eberhard & Huber, 1998; Knoflach, 1998, 2004; Knoflach & van Harten, 2001, 2002; Berendonck & Greven, 2002; Méndez, 2002), but few studies have documented their function in detail.

In *Phidippus johnsoni*, plugs of first males remained intact in 30% of copulation attempts by second males (Jackson, 1980). Apparently, the strategy of the plugging male works, even though not perfectly, suggesting sexual selection favouring males that produce more durable plugs. In *Agelena limbata*, Masumoto (1993) distinguished between incomplete and complete plugs. Large males were better able to produce complete plugs, and these presented insuperable barriers for subsequent males. However, incomplete plugs could be eliminated by subsequent males who then fertilised an average of 63% of the eggs. Several different kinds of plugs have been described in *Leucauge mariana* females (Méndez, 2002). In 10 of 29 copulations involving females with the 'transparent whitish' type of plug, the second male was unable to remove the plug despite persistent attempts (Méndez, 2002).

Barely studied is the female influence on the production and the fate of mating plugs. In theory, selection on polygamy should result in selection on female abilities to manipulate the plug. Scattered observations of supposed female origins of plugs have existed for a long time (e.g. Strand, 1906; Engelhardt, 1910; Gerhardt, 1924), but the prevalent tendency of studies continues to be male-centred. Eberhard & Huber (1998) and Méndez (2002) demonstrated that the female of *Leucauge mariana* contributes a liquid, apparently from within the insemination duct or deeper, which is crucial to the formation of a plug that will be effective against further intromissions (the 'transparent whitish' type above). Similarly, Knoflach (1998) observed apparent female additions to plug material deposited by the male in several *Theridion* species. In these spiders, females even seem to provide the main material of the plug, while the male components from his palp and/or genital tract are necessary for hardening of the female material (Knoflach, 1998). In *Argyrodes antipodiana*, the male interrupts copulation and leaves the female between sperm transfer and plug formation (Knoflach, 2004), suggesting that the female could easily avoid being plugged. Instead, the female continues to cooperate, which is evidence for the plug being also a female strategy. Finally, in *Latrodecus revivensis* (Theridiidae), it may be the female herself that actively prevents the male from withdrawing the embolus after copulation, thus promoting fracture of the embolus within her genitalia (Berendonck & Greven, 2005).

Direct physical manipulation or removal of sperm may not be a common phenomenon in spiders because the male genitalia do not usually reach the spermathecae, at least not with structures that would permit sperm displacement (Huber & Eberhard, 1997). However, Schäfer & Uhl (2002) found suggestive evidence in *Pholcus phalangioides* for sperm displacement by the second male's palpal movements though they did not eliminate the possibility of active female participation. Suggestive brush-like structures on the male intromittent genitalia occur in several spiders (e.g. Davies, 1999; Hormiga, 2000; Huber, 2000; Griswold, 2001) but their function remains unknown, and their design suggests that they could function to remove sperm as well as to stimulate.

Copulation duration may also be intimately tied to sperm competition (for several other factors influencing copulation duration see Elgar, 1995). *Nephila edulis* and *Pholcus phalangioides* males increase the duration of copulation when the risk of sperm competition is high, *i.e.* when a rival male is present (Schaefer & Uhl, 2003; Elgar *et al.*, 2003*b*). Small *N. edulis* males are at a disadvantage in male–male competition, but this may partly be offset by longer copulations (Schneider *et al.*, 2000). Parker (1970) suggested that copulating males could be considered as living mating plugs. In accordance with this idea, some spiders copulate for hours even though most sperm is transferred within a few minutes or less (Austad, 1982; Willey-Robertson & Adler, 1994; Knoflach, 2004; A. Sziranyi, personal communication; see also Snow and Andrade, 2004). However, other functions of prolonged copulations, like prolonged stimulation and transfer of nutrients or pheromones may also be involved (Suter & Parkhill, 1990). Post-copulation associations are not as common in spiders as in insects (Alcock, 1994), possibly because first male sperm priority is the predominant pattern in spiders but not in insects. Short-term guarding may be quite common and may reflect the time it takes the female to become non-receptive (Elgar & Bathgate, 1996). In pholcid spiders, where second males often sire a significant proportion of the female's offspring (Eberhard *et al.*, 1993; Kaster & Jakob, 1997; Yoward, 1998; Schäfer & Uhl, 2002), male associations with mature females are widespread (Eberhard & Briceño, 1985; Merrigan, 1995 cited in Kaster & Jakob, 1997; B. A. Huber, in preparation).

Finally, it must be noted that polygamy may be prevalent in female spiders, but numerous observations indicate that remating may be very rare or even absent in some species (Muniappan & Chada, 1970; Blanke, 1973; Patel & Bradoo, 1986; Pollard *et al.*, 1987; Huber, 1993*b*; Riechert & Singer, 1995; Haupt, 2003). Proving lack of remating in females is very difficult to do, however, since females of many species may be more (or less) reluctant to remate in captivity than they are in nature (see Eberhard, 1996 for a list of failed claims for monogamy in a variety of animal groups).

VI. MALE MATE CHOICE

Theoretical considerations suggest that, in general, females are the choosier sex and males rather increase their reproductive output by mating with multiple females (Andersson, 1994; for a review of male–female conflict in spiders, see Schneider & Lubin, 1998). Male mate choice has received relatively little empirical study, but available evidence suggests that it is widespread among insects and other animals (Bonduriansky, 2001). Few experimental data exist for spiders, but there is evidence that male choice could be important in certain taxa. For example, males that are obligatorily cannibalised or invariably die during or after copulation (Blanke, 1974; Sasaki & Iwahashi, 1995; Knoflach & van Harten, 2000, 2001; Knoflach, 2002; Foellmer & Fairbairn, 2003; Knoflach & Benjamin, 2003) or are functionally sterile after a single copulation using both palps (Andrade & Banta, 2002; Knoflach & van Harten, 2002), are predicted to be choosy, especially if female density and quality variance are high enough. In fact, *Cyrtophora cicatrosa* (Araneidae) and *Tidarren* spp. (Theridiidae) females were observed to court males (Blanke, 1974; Knoflach & van Harten, 2000, 2001). Female courtship was also described for a theraphosid spider, where operational sex-ratios tend to be female-biased due to the short life span of males compared to females (Costa & Pérez-Miles, 2002). In *Lycosa tarantula*, several lines of evidence suggest sex-role reversal, including high variance of female mating success, female intense coloration, and low density of males due to sexual cannibalism and other forms of predation (Moya-Laraño, Pascual & Wise, 2003; J. Moya-Laraño, personal communication). Functional sterility by sperm depletion was observed in *Nephila clavipes* (Christenson, 1989). The author doubted that males would have ample opportunity to chose, but considered further study to be warranted. However, the male-biased operational sex ratio of *N. clavipes* may override any effect of mating being costlier to males than to females (Schneider & Lubin, 1998). Highly female-biased sex ratios (up to 10:1) have been reported for social spiders (e.g. Avilés & Salazar, 1999; Avilés *et al.*, 2000), creating a scenario that potentially favours male choice.

Quality variance is evidenced by the strong correlation between female fecundity and size: a 17% increase in carapace width in *Misumenoides formosipes* (Thomisidae) resulted in a 100% increase in fecundity (Beck & Connor, 1992). This would strongly benefit male bias favouring larger females. In fact, *M. formosipes* females below a certain size were never found to reproduce. Whether or not males copulated with such females is unknown. In *Pholcus phalangioides*, smaller females are visited less frequently than larger females (Uhl, 1998) and males perform more pedipalp movements (resulting in more sperm transferred) when mating with larger females (G. Uhl, personal communication). In *Tetragnatha elongata*, males prefer heavier females and females with higher body condition indices, traits that are correlated with the volume of her egg load and the proximity of oviposition (Danielson-François, Fetterer & Smallwood, 2002). In *Metellina segmentata*, males assess female quality (size and nearness to moult) before deciding on whether to guard or leave the female (Prenter *et al.*, 1994). In the congeneric *M. mengei*, the guarding male adjusts his fight tactics against intruders according to the reproductive value of the female, increasing fight intensity and duration with his mate's body mass (Bridge, Elwood & Dick, 2000). Other cases of male mate choice have been reported, but these need not result in sexual selection for any female trait. An obvious and common example is male preference of virgin females over non-virgin females which evidently does not select for virginity (e.g. Suter, 1990; Riechert & Singer, 1995; Bukowski & Christenson, 1997; Herberstein, Schneider & Elgar, 2002; Rypstra *et al.*, 2003; Gaskett *et al.*, 2004).

Indirect evidence for male choice comes from a rare case of genital dimorphism. Usually, intrasexual dimorphisms are thought to imply alternative strategies, and this usually involves strategies for access to a limited resource, for example to females. Thus, male dimorphisms are often a consequence of sexual selection (Gadgil, 1972). However, in *Ciboneya antraia* (Pholcidae) it is the females that are dimorphic (Huber & Pérez, 2001), suggesting that there are alternative female strategies for access to a limited resource. Since it is the genitalia that are dimorphic, it seems probable that the limited resource is linked to the male. What kind of resource the males might offer, or even what the mechanical consequences of the female dimorphism for copulation and sperm transfer are, remains to be established.

VII. CONCLUSIONS

(1) The large amount of valuable research on spiders of the last decades has greatly improved but at the same time biased our perception of the spiders' world. While it is true that 'courtship is conspicuous to us' (Platnick, 1971), it is also true that 'watching araneids court could be compared to watching a symphony orchestra and hearing no sound' (Robinson, 1982).

(2) Our understanding of sexual selection in spiders has grown significantly since Darwin, partly due to approaches like experimental manipulation, quantitative analysis, sterile male technique, video animations, *etc*. Fundamental issues have been addressed, as for example the relative importance of competing ideas explaining female choice (Watson & Lighton, 1994; Mappes *et al.*, 1996; Watson, 1998; Kotiaho *et al.*, 1998*a*; Uetz *et al.*, 2002), or the origin of female preferences (Stålhandske, 2002; Hebets, 2003). Comparative evidence argues for sexual selection as the driving force behind the rapid diversification of traits ranging from the composition of surface lipids and seminal products to genital morphology, copulatory patterns, and courtship signals (Eberhard, 1985, 2004*a*, *b*; Huber, 1998*b*; Masta & Maddison, 2002; Knoflach, 2004; Schulz, 2004*b*; P. Michalik, personal communication).

(3) It seems that to appreciate properly spider communication in its complexity and to get a more complete picture of the targets of sexual selection, considerable amounts of technology will be necessary, especially regarding vibratory and pheromonal signals (Barth, 2001; Schulz, 2004*a*).

(4) It appears that a large proportion of research on spiders, and on sexual selection in particular, has been done on exceptions: on conspicuous visual and acoustic signals, on extreme size dimorphism and cannibalism in *Nephila* spp. and *Latrodectus* spp., on the dimorphic males of *Maevia inclemens*, on the nuptial gift in *Pisaura mirabilis*, on cognitive

abilities in *Portia* spp., *etc*. This is not to be critical of what has been achieved, and notable exceptions exist, like the work of F. G. Barth and colleagues (Barth, 2001) on vibratory communication. However, much of the research available results in a misperception of the spiders' world as similar to ours. Much more remains to be learned about the mainstream spider phenomena like vibratory, tactile, and chemical communication, and the action of sexual selection in shaping these signals. And finally, research on sexual selection in spiders is almost completely focused on araneomorph spiders, largely ignoring the more primitive liphistiomorph and mygalomorph spiders.

(5) Spiders may not rival insects and vertebrates in numbers of studies, but several aspects make spiders especially useful candidates for particular research questions (see also Eberhard, 2004*c*). For example, all male and most female spiders have paired genitalia, allowing for experimental manipulation of one side only, or for studies of fluctuating asymmetry in genitalia. Spider males deposit sperm on a sperm web before taking it up into their palpal copulatory organs, allowing for easy collection of pure, uncontaminated samples of sperm. The substances transferred to the female and their physiological effects on the female are two potential areas of research building on this methodological advantage. For example, are there 'exaggerated' chemical compounds or bouquets analogous to exaggerated male morphologies? A further unstudied question concerns the effect of sperm competition on sperm morphology (*cf.* Simmons, 2001 on insects). The ability to electronically simulate male vibratory signals in spiders offers a better chance for experimental study of different signal traits than in many other groups. Further, though less unique, features that make spiders intruiging objects of research are listed in Elgar (1998).

(6) Many other fields also await further study and promise interesting new insights. Among the key challenges for future studies will be the mechanisms of sexual selection (e.g. antagonistic coevolution *vs.* Fisherian *vs.* a variety of good genes models; *cf.* Watson, 1998; Eberhard, 2004*a*, *b*; Mays & Hill, 2004), the proper identification of conflict and cooperation between the sexes, and the female perspective of sexual selection, including mechanisms of cryptic female choice, the mechanics and physiology of sperm transport and capacitation, and female neurophysiology (*cf.* Méndez & Córdoba-Aguilar, 2004). At the current rate of research, the present review will probably be outdated rather quickly.

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IX. REFERENCES

Abalos, J. W. & Baez, E. C. (1963). On spermatic transmission in spiders. *Psyche* **70**, 197–207.

Ahtiainen, J. J., Alatalo, R. V., Kortet, R. & Rantala, M. J. (2004). Sexual advertisement and immune function in an arachnid species (Lycosidae). *Behavioral Ecology* **15**, 602–606.

Ahtiainen, J. J., Alatalo, R. V., Kotiaho, J. S., Mappes, J., Parri, S. & Vertainen, L. (2001). Sexual selection in the drumming wolf spider *Hygrolycosa rubrofasciata*. In *European Arachnology 2000* (eds. S. Toft and N. Scharff), pp. 129–137. Aarhus University Press, Aarhus.

Ahtiainen, J. J., Alatalo, R. V., Mappes, J. & Vertainen, L. (2003). Fluctuating asymmetry and sexual performance in the drumming wolf spider *Hygrolycosa rubrofasciata*. *Annales Zoologici Fennici* **40**, 281–292.

Alcock, J. (1994). Postinsemination associations between males and females in insects: the mate-guarding hypothesis. *Annual Review of Entomology* **39**, 1–21.

Andersson, M. (1994). *Sexual Selection*. Monographs in Behavior and Ecology. Princeton University Press, Princeton, NJ.

Andrade, M. C. B. (1996). Sexual selection for male sacrifice in the Australian redback spider. *Science* **271**, 70–72.

Andrade, M. C. B. (2003). Risky mate search and male self-sacrifice in redback spiders. *Behavioral Ecology* **14**, 531–538.

Andrade, M. C. B. & Banta, E. M. (2002). Value of male remating and functional sterility in redback spiders. *Animal Behaviour* **63**, 857–870.

Arnqvist, G. (1998). Comparative evidence for the evolution of genitalia by sexual selection. *Nature* **393**, 784–786.

Arnqvist, G. & Danielsson, I. (1999). Copulatory behavior, genital morphology, and male fertilization success in water striders. *Evolution* **53**, 147–156.

Arnqvist, G. & Henriksson, S. (1997). Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evolutionary Ecology* **11**, 255–273.

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 *Sperm competition and the evolution of animal mating systems* (ed. R. L. Smith), pp. 223–249. Academic Press, Inc.

Austad, S. N. & Thornhill, R. (1986). Female reproductive variation in a nuptial-feeding spider, *Pisaura mirabilis*. *Bulletin of the British arachnological Society* **7**, 48–52.

Avilés, L. & Salazar, P. (1999). Notes on the social structure, life cycle, and behavior of *Anelosimus rupununi*. *Journal of Arachnology* **27**, 497–502.

Avilés, L., McCormack, J., Cutter, A. & Bukowski, T. (2000). Precise, highly female-biased sex ratios in a social spider. *Proceedings of the Royal Society of London B* **267**, 1445–1449.

Ayyagari, L. R. & Tietjen, W. J. (1986). Preliminary isolation of male inhibitory pheromone of the spider *Schizocosa ocreata* (Araneae, Lycosidae). *Journal of Chemical Ecology* **13**, 237–244.

Barth, F. G. (1990). Spider courtship: male vibrations, female responsiveness and reproductive isolation. In *Sensory systems and communication in arthropods* (eds. F. G. Gribakin, K. Wiese and A. V. Popov), pp. 161–166. Birkhäuser, Basel.

Barth, F. G. (1993). Sensory guidance in spider pre-copulatory behaviour. *Comparative Biochemistry and Physiology* **104A**, 717–733.

Barth, F. G. (2001). *Sinne und Verhalten: aus dem Leben einer Spinne*. Springer Verlag, Berlin.

Barth, F. G. & Libera, W. (1970). Ein Atlas der Spaltsinnesorgane von *Cupiennius salei* Keys. Chelicerata (Araneae). *Zeitschrift für Morphologie der Tiere* **68**, 343–369.

Barth, F. G. & Schmitt, A. (1991). Species recognition and species isolation in wandering spiders (*Cupiennius* spp.; Ctenidae). *Behavioral Ecology and Sociobiology* **29**, 333–339.

Beck, M. W. & Connor, E. F. (1992). Factors affecting the reproductive success of the crab spider *Misumenoides formosipes*: the covariance between juvenile and adult traits. *Oecologia* **92**, 287–295.

Berendonck, B. & Greven, H. (2002). Morphology of female and male genitalia of *Latrodectus revivensis* Shulov, 1948 (Araneae, Theridiidae) with regard to sperm priority patterns. In *European Arachnology 2000* (eds. S. Toft and N. Scharff), pp. 157–167. Aarhus University Press, Aarhus.

Berendonck, B. & Greven, H. (2005). Genitalic structures in the entelegyne widow spider *Latrodectus revivensis* (Arachnida; Araneae; Theridiidae) indicate a low ability for cryptic female choice by sperm manipulation. *Journal of Morphology* **263**, 118–132.

Billaudelle, H. (1957). Zur Biologie der Mauerspinne *Dictyna civica* (H. Luc.) (Dictynidae, Araneida). *Zeitschrift für angewandte Entomologie* **41**, 474–512.

Blanke, R. (1973). Neue Ergebnisse zum Sexualverhalten von *Araneus cucurbitanus* Cl. (Araneae, Araneidae). *Forma et Functio* **6**, 279–290.

Blanke, R. (1974). Untersuchungen zum Sexualverhalten von *Cyrtophora cicatrosa* (Stoliczka) (Araneae, Araneidae). *Zeitschrift für Tierpsychologie* **37**, 62–74.

Blest, A. D. (1987). The copulation of a linyphiid spider, *Baryphyma pratense*: does a female receive a blood meal from her mate? *Journal of Zoology, London* **213**, 189–191.

Blest, A. D., Hardie, R. C., McIntyre, P. & Williams, D. S. (1981). The spectral sensitivities of identified receptors and the function of retinal tiering in the principal eyes of a jumping spider. *Journal of Comparative Physiology* **145**, 227–239.

Blest, A. D. & Taylor, H. H. (1977). The clypeal glands of *Mynoglenes* and of some other linyphiid spiders. *Journal of Zoology, London* **183**, 473–493.

Bonduriansky, R. (2001). The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biological Reviews* **76**, 305–339.

Braun, R. (1956). Zur Biologie von *Teutana triangulosa* (Walck.) (Araneae; Theridiidae, Asageneae). *Zeitschrift für wissenschaftliche Zoologie* **159**, 255–318.

Braun, R. (1958). Das Sexualverhalten der Krabbenspinne *Diaea dorsata* (F.) und der Zartspinne *Anyphaena accentuata* (Walck.) als Hinweis auf ihre systematische Eingliederung. *Zoologischer Anzeiger* **160**, 119–134.

Bridge, A. P., Elwood, R. W. & Dick, J. T. A. (2000). Imperfect assessment and limited information preclude optimal strategies in male–male fights in the orb-weaving spider *Metellina mengei*. *Proceedings of the Royal Society of London B* **267**, 273–279.

Bristowe, W. S. (1926). The mating habits of British thomisid and sparassid spiders. *Annals and Magazine of Natural History* **18**, ser. 9, nr. 103, 114–131.

Bristowe, W. S. & Locket, G. H. (1926). The courtship of British lycosid spiders, and its probable significance. *Proceedings of the Zoological Society* **22**, 317–347.

Brown, S. G. (1985). Mating behavior of the golden-orb-weaving spider, *Nephila clavipes*: II. Sperm capacitation, sperm competition, and fecundity. *Journal of Comparative Psychology* **99**, 167–175.

Bukowski, T. C. & Christenson, T. E. (1997). Determinants of sperm release and storage in a spiny orbweaving spider. *Animal Behaviour* **53**, 381–395.

Bukowski, T. C. & Christenson, T. E. (2000). Determinants of mating frequency in the spiny orbweaving spider, *Micrathena gracilis* (Araneae: Araneidae). *Journal of Insect Behavior* **13**, 331–352.

Burger, M., Nentwig, W. & Kropf, C. (2003). Complex genital structures indicate cryptic female choice in a haplogyne spider (Arachnida, Araneae, Oonopidae, Gamasomorphinae). *Journal of Morphology* **255**, 80–93.

Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews* **78**, 575–595.

Christenson, T. E. (1989). Sperm depletion in the orb-weaving spider *Nephila clavipes* (Araneae, Araneidae). *Journal of Arachnology* **17**, 115–118.

Christenson, T. E. & Cohn, J. (1988). Male advantage for egg fertilization in the golden orb-weaving spider (*Nephila clavipes*). *Journal of Comparative Psychology* **102**, 312–318.

Christenson, T. E. & Goist, K. C. (1979). Costs and benefits of male–male competition in the orbweaving spider, *Nephila clavipes*. *Behavioral Ecology and Sociobiology* **5**, 87–92.

Clark, D. L. & Biesiadecki, B. (2002). Mating success and alternative reproductive strategies of the dimorphic jumping spider, *Maevia inclemens* (Araneae, Salticidae). *Journal of Arachnology* **30**, 511–518.

Clark, D. L. & Morjan, C. L. (2001). Attracting female attention: the evolution of dimorphic courtship displays in the jumping spider *Maevia inclemens* (Araneae: Salticidae). *Proceedings of the Royal Society of London B* **268**, 2461–2465.

Clark, D. L. & Uetz, G. W. (1990). Video image recognition by the jumping spider, *Maevia inclemens* (Araneae: Salticidae). *Animal Behaviour* **40**, 884–890.

Clark, D. L. & Uetz, G. W. (1992). Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video-controlled courtship behaviour. *Animal Behaviour* **43**, 247–254.

Clark, D. L. & Uetz, G. W. (1993). Signal efficacy and the evolution of male dimorphism in the jumping spider, *Maevia inclemens*. *Proceedings of the National Academy of Sciences USA* **90**, 11954–11957.

Clark, R. J. & Jackson, R. R. (1994*a*). *Portia labiata*, a cannibalistic jumping spider, discriminates between own and foreign eggsacs. *International Journal of Comparative Psychology* **7**, 38–43.

Clark, R. J. & Jackson, R. R. (1994*b*). Self recognition in a jumping spider: *Portia labiata* females discriminate between their own draglines and those of conspecifics. *Ethology Ecology & Evolution* **6**, 371–375.

Clark, R. J. & Jackson, R. R. (1995*a*). Araneophagic jumping spiders discriminate between the draglines of familiar and unfamiliar conspecifics. *Ethology Ecology & Evolution* **7**, 185–190.

Clark, R. J. & Jackson, R. R. (1995*b*). Dragline-mediated sex recognition in two species of jumping spiders (Araneae, Salticidae), *Portia labiata* and *P. fimbriata*. *Ethology Ecology & Evolution* **7**, 73–77.

Clark, R. J., Jackson, R. R. & Waas, J. R. (1999). Draglines and assessment of fighting ability in cannibalistic jumping spiders. *Journal of Insect Behaviour* **12**, 753–766.

Coddington, J. A., Hormiga, G. & Scharff, N. (1997). Giant female or dwarf male spiders? *Nature* **385**, 687–688.

Costa, F. G. & Pérez-Miles, F. (2002). Reproductive biology of Uruguayan theraphosids (Araneae, Mygalomorphae). *Journal of Arachnology* **30**, 571–587.

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

Coyle, F. A. (1986). Courtship, mating, and the function of male-specific leg structures in the mygalomorph spider genus *Euagrus* (Araneae, Dipluridae). In *International Congress of Arachnology 9* (*Panama*) (eds. W. G. Eberhard, Y. D. Lubin and B. C. Robinson), pp. 33–38. Smithsonian Institution Press, Washington, D.C.

Crome, W. (1962). Die Paarung bei *Micromata rosea* (Clerck). *Abhandlungen und Berichte für Naturkunde und Vorgeschichte, Magdeburg* **11**, 43–64.

Danielson-François, A. (in press). Natural history, mating behavior and sperm release in the haplogyne *Glenognatha emertoni* (Araneae, Tetragnathidae). *Journal of Arachnology*.

Danielson-François, A., Fetterer, C. A. & Smallwood, P. D. (2002). Body condition and mate choice in *Tetragnatha elongata* (Araneae, Tetragnathidae). *Journal of Arachnology* **30**, 20–30.

Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. Murray, London.

Davies, V. T. (1999). *Carbinea*, a new spider genus from North Queensland, Australia (Araneae, Amaurobioidea, Kababininae). *Journal of Arachnology* **27**, 25–36.

Decarvalho, T. N., Watson, P. J. & Field, S. A. (2004). Costs increase as ritualized fighting progresses within and between phases in the sierra dome spider, *Neriene litigiosa*. *Animal Behaviour* **68**, 473–482.

Dijkstra, H. (1970). Comparative research of the courtship behaviour in the genus *Pardosa* (Arachn., Araneae) III. Agonistic behaviour in *Pardosa amentata*. *Bulletin du Muséum national d'Histoire naturelle*, 2^{e} ser, **41** (suppl. 1), 91–97.

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

Dondale, C. D. & Hegdekar, B. M. (1973). The contact sex pheromone of *Pardosa lapidicina* Emerton (Araneida: Lycosidae). *Canadian Journal of Zoology* **51**, 400–401.

Drengsgaard, I. L. & Toft, S. (1999). Sperm competition in a nuptial feeding spider, *Pisaura mirabilis*. *Behaviour* **136**, 877–987.

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

Eberhard, W. G. (1994). Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. *Evolution* **48**, 711–733.

Eberhard, W. G. (1996). *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton University Press, Princeton, NJ.

Eberhard, W. G. (2004*a*). Male–female conflict and genitalia: failure to confirm predictions in insects and spiders. *Biological Reviews* **79**, 121–186.

Eberhard, W. G. (2004*b*). Rapid divergent evolution of sexual morphology: comparative tests of antagonistic coevolution and traditional female choice. *Evolution* **58**, 1947–1970.

Eberhard, W. G. (2004*c*). Why study spider sex: Special traits of spiders facilitate studies of sperm competition and cryptic female choice. *Journal of Arachnology* **32**, 545–556.

Eberhard, W. G. & Briceño, L. R. D. (1983). Chivalry in pholcid spiders. *Behavioral Ecology and Sociobiology* **13**, 189–195.

Eberhard, W. G. & Briceño, L. R. D. (1985). Behavior and ecology of four species of *Modisimus* and *Blechroscelis* (Araneae, Pholcidae). *Revue arachnologique* **6**, 29–36.

Eberhard, W. G. & Cordero, C. (1995). Sexual selection by cryptic female choice on male seminal products – a new bridge between sexual selection and reproductive physiology. *TREE* **10**, 493–496.

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

Eberhard, W. G. & Huber, B. A. (1998). Courtship, copulation, and sperm transfer in *Leucauge mariana* (Araneae, Tetragnathidae) with implications for higher classification. *Journal of Arachnology* **26**, 342–368.

Edwards, G. B. (1981). Sound production by courting males of *Phidippus mystaceus* (Araneae: Salticidae). *Psyche* **88**, 199–214.

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

Elgar, M. A. (1992). Sexual cannibalism in spiders and other invertebrates. In *Cannibalism: ecology and evolution among diverse taxa* (eds. M. A. Elgar and B. J. Crespi), pp 128–155. Oxford University Press, Oxford.

Elgar, M. A. (1995). The duration of copulation in spiders: comparative patterns. *Records of the Western Australian Museum, Supplement* **52**, 1–11.

Elgar, M. A. (1998). Sperm competition and sexual selection in spiders and other arachnids. In *Sperm Competition and Sexual Selection* (eds. T. R. Birkhead and A. P. Møller), pp. 307–339. Academic Press.

Elgar, M. A. & Bathgate, R. (1996). Female receptivity and male mate-guarding in the jewel spider *Gasteracantha minax* Thorell (Araneidae). *Journal of Insect Behavior* **9**, 729–738.

Elgar, M. A., Bruce, M. J., Champion de Crespigny, F. E., Cutler, A. R., Cutler, C. L., Gaskett, A. C., Herberstein, M. E., Ramamurthy, S. & Schneider, J. M. (2003*a*). Male mate choice and patterns of paternity in the polyandrous, sexually cannibalistic orb-web spider *Nephila plumipes*. *Australian Journal of Zoology* **51**, 357–365.

Elgar, M. A., Champion de Crespigny, F. E. & Ramamurthy, S. (2003*b*). Male copulation behaviour and risk of sperm competition. *Animal Behaviour* **66**, 211–216.

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

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

Elgar, M. A. & Nash, D. R. (1988). Sexual cannibalism in the garden spider *Araneus diadematus*. *Animal Behaviour* **36**, 1511–1517.

Elgar, M. A. & Schneider, J. M. (2004). The evolutionary significance of sexual cannibalism. In *Advances in the Study of Behaviour* **34**, 135–163.

Elgar, M. A., Schneider, J. M. & Herberstein, M. E. (2000). Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. *Proceedings of the Royal Society of London B* **267**, 2439–2443.

Elias, D. O., Mason, A. C., Maddison, W. P. & Hoy, R. R. (2003). Seismic signals in a courting male jumping spider (Araneae: Salticidae). *Journal of Experimental Biology* **206**, 4029–4039.

Engelhardt, V. von (1910). Beiträge zur Kenntnis der weiblichen Copulationsorgane einiger Spinnen. *Zeitschrift für wissenschaftliche Zoologie* **96**, 32–117.

Enquist, M. & Arak, A. (1993). Selection of exaggerated male traits by female aesthetic senses. *Nature* **361**, 446–448.

Faber, D. B. (1994). Przibram's rule and male body-size dimorphism in *Zygoballus rufipes* (Araneae: Salticidae). *Journal of Zoology, London* **232**, 191–198.

Fahey, B. F. & Elgar, M. A. (1997). Sexual cohabitation as mate-guarding in the leaf-curling spider *Phonognatha graeffei* Keyserling (Araneoidea, Araneae). *Behavioral Ecology and Sociobiology* **40**, 127–133.

Foelix, R. F. (1996). *Biology of spiders*. 2nd edition. Oxford University Press, Oxford, Georg Thieme Verlag, Berlin.

Foellmer, M. W. & Fairbairn, D. J. (2003). Spontaneous male death during copulation in an orb-weaving spider. *Proceedings of the Royal Society of London B* **270**, S183–S185.

Fromhage, L., Uhl, G. & Schneider, J. M. (2003). Fitness consequences of sexual cannibalism in female *Argiope bruennichi*. *Behavioral Ecology and Sociobiology* **55**, 60–64.

Funke, S. & Huber, B. A. (in press). Allometry of genitalia and fighting structures in *Linyphia triangularis* (Araneae: Linyphiidae). *Journal of Arachnology*.

Gadgil, M. (1972). Male dimorphism as a consequence of sexual selection. *American Naturalist* **106**, 574–580.

Gaskett, A. C., Herberstein, M. E., Downes, B. J. & Elgar, M. A. (2004). Changes in male mate choice in a sexually cannibalistic orb-web spider (Araneae: Araneidae). *Behaviour* **141**, 1197–1210.

Gerhardt, U. (1923). Weitere sexualbiologische Untersuchung an Spinnen. *Archiv für Naturgeschichte* **89**, 1–225.

Gerhardt, U. (1924). Weitere Studien über die Biologie der Spinnen. *Archiv für Naturgeschichte* **90**, 85–192.

Grammer, K., Fink, B., Møller, A. P. & Thornhill, R. (2003). Darwinian aesthetics: sexual selection and the biology of beauty. *Biological Reviews* **78**, 385–407.

Griswold, C. E. (2001). A monograph of the living world genera and Afrotropical species of cyatholipid spiders (Araneae, Orbiculariae, Araneoidea, Cyatholipidae). *Memoirs of the California Academy of Sciences* **26**, 1–251.

Gunnarsson, B. (1998). Bird predation as a sex- and size-selective agent of the arboreal spider *Pityohyphantes phrygianus*. *Functional Ecology* **12**, 453–458.

Gunnarsson, B. & Andersson, A. (1996). Sex ratio variation in sheet-web spiders: options for female control? *Proceedings of the Royal Society of London B* **263**, 1177–1182.

Gwinner-Hanke, H. (1970). Zum Verhalten zweier stridulierender Spinnen *Steatoda bipunctata* Linné und *Teutana grossa* Koch (Theridiidae, Araneae), unter besonderer Berücksichtigung des Fortpflanzungsverhaltens. *Zeitschrift für Tierpsychologie* **27**, 649–678.

Harland, D. P. & Jackson, R. R. (2000). 'Eight-legged cats' and how they see – a review of recent research on jumping spiders (Araneae: Salticidae). *Cimbebasia* **16**, 231–240.

Haupt, J. (2003). The Mesothelae – a monograph of an exceptional group of spiders (Araneae: Mesothelae). *Zoologica* **154**, 1–102.

Head, G. (1995). Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (class Araneae). *Evolution* **49**, 776–781.

Hebets, E. A. (2003). Subadult experience influences adult mate choice in an arthropod: exposed female wolf spiders prefer males of a familiar phenotype. *Proceedings of the National Academy of Science USA* **100**, 13390–13395.

Hebets, E. A. & Uetz, G. W. (2000). Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). *Behavioral Ecology and Sociobiology* **47**, 280–286.

Henschel, J. R. (2002). Long-distance wandering and mating by the dancing white lady spider (*Leucorchestris arenicola*) (Araneae, Sparassidae) across Namib dunes. *Journal of Arachnology* **30**, 321–330.

Herberstein, M. E., Schneider, J. M. & Elgar, M. A. (2002). Costs of courtship and mating in a sexually cannibalistic orb-web spider: female mating strategies and their consequences for males. *Behavioral Ecology and Sociobiology* **51**, 440–446.

Hinton, H. E. & Wilson, R. S. (1970). Stridulatory organs in spiny orb-weaver spiders. *Journal of Zoology, London* **162**, 481–484.

Hormiga, G. (1999). Cephalothoracic sulci in linyphiine spiders (Araneae, Linyphiidae, Linyphiinae). *Journal of Arachnology* **27**, 94–102.

Hormiga, G. (2000). Higher level phylogenetics of erigonine spiders (Araneae, Linyphiidae, Erigoninae). *Smithsonian Contributions to Zoology* **609**, 1–160.

Hormiga, G., Scharff, N. & Coddington, J. A. (2000). The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). *Systematic Biology* **49**, 435–462.

Hosken, D. J. & Stockley, P. (2004). Sexual selection and genital evolution. *TREE* **19**, 87–93.

Hu, H. H. & Morse, D. H. (2004). The effect of age on encounters between male crab spiders. *Behavioral Ecology* **15**, 883–888.

Huber, B. A. (1993*a*). Female choice and spider genitalia. *Bollettino dell' Accademia Gioenia di Scienze Naturali* (*Catania*) **26**, 209–214.

Huber, B. A. (1993*b*). Genital mechanics and sexual selection in the spider *Nesticus cellulanus* (Araneae: Nesticidae). *Canadian Journal of Zoology* **71**, 2437–2447.

Huber, B. A. (1995). The retrolateral tibial apophysis in spiders – shaped by sexual selection? *Zoological Journal of the Linnean Society* **113**, 151–163.

Huber, B. A. (1996). Genitalia, fluctuating asymmetry, and patterns of sexual selection in *Physocyclus globosus* (Araneae: Pholcidae). *Revue Suisse de Zoologie* (suppl. 1996), 289–294.

Huber, B. A. (1997). Evidence for gustatorial courtship in a haplogyne spider (*Hedypsilus culicinus*: Pholcidae: Araneae). *Netherlands Journal of Zoology* **47**, 95–98.

Huber, B. A. (1998*a*). On the 'valve' in the genitalia of female pholcids (Pholcidae, Araneae). *Bulletin of the British arachnological Society* **11**, 41–48.

Huber, B. A. (1998*b*). Spider reproductive behaviour: a review of Gerhardt's work from 1911–1933, with implications for sexual selection. *Bulletin of the British arachnological Society* **11**, 81–91.

Huber, B. A. (1999). Sexual selection in pholcid spiders (Araneae, Pholcidae): artful chelicerae and forceful genitalia. *Journal of Arachnology* **27**, 135–141.

Huber, B. A. (2000). New World pholcid spiders (Araneae: Pholcidae): a revision at generic level. *Bulletin of the American Museum of Natural History* **254**, 1–348.

Huber, B. A. (2004). Evidence for functional segregation in the directionally asymmetric male genitalia of the spider *Metagonia mariguitarensis* (González-Sponga) (Pholcidae: Araneae). *Journal of Zoology, London* **262**, 317–326.

Huber, B. A., Brescovit, A. D. & Rheims, C. (in press). Exaggerated female genitalia in two new spider species (Araneae: Pholcidae), with comments on genital evolution by female choice versus antagonistic coevolution. *Insect Systematics and Evolution.*

Huber, B. A. & Eberhard, W. G. (1997). Courtship, copulation, and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). *Canadian Journal of Zoology* **74**, 905–918.

Huber, B. A. & Pérez, G. A. (2001). Female genital dimorphism in a spider (Araneae: Pholcidae). *Journal of Zoology, London* **255**, 301–304.

Itakura, Y. (1993). The life history and nuptial feeding of a nursery web spider, *Pisaura lama*. *Insectarium* **30**, 88–93.

Itakura, Y. (1998). Discovery of nuptial feeding in the spider, *Perenethis fascigera* (Araneae: Pisauridae). *Acta Arachnologica* **47**, 173–175.

Jackson, R. R. (1978). An analysis of alternative mating tactics of the jumping spider *Phidippus johnsoni* (Araneae, Salticidae). *Journal of Arachnology* **5**, 185–230.

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. (1981). Relationship between reproductive security and intersexual selection in a jumping spider *Phidippus johnsoni* (Araneae: Salticidae). *Evolution* **35**, 601–604.

Jackson, R. R. (1982*a*). The behavior of communicating in jumping spiders (Salticidae). In *Spider Communication: Mechanisms and Ecological Significance* (eds. P. N. Witt and J. S. Rovner), pp. 213–247. Princeton University Press, Princeton, NJ.

Jackson, R. R. (1982*b*). 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. (1986*a*). Cohabitation of males and juvenile females: a prevalent mating tactic of spiders. *Journal of Natural History* **20**, 1193–1210.

Jackson, R. R. (1986*b*). The display behaviour of *Bavia aericeps* (Araneae: Salticidae), a jumping spider from Queensland. *Australian Journal of Zoology* **34**, 381–409.

Jackson, R. R. (1986*c*). The display behaviour of *Cyllobelus rufopictus* (Simon) (Araneae, Salticidae), a jumping spider from Kenya. *New Zealand Journal of Zoology* **13**, 27–43.

Jackson, R. R. (1986*d*). Use of pheromones by males of *Phidippus johnsoni* (Araneae, Salticidae) to detect subadult females that are about to molt. *Journal of Arachnology* **14**, 137–139.

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

Jackson, R. R. & 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. & Macnab, A. M. (1989*a*). Display behaviour of *Corythalia canosa*, an ant-eating jumping spider (Araneae: Salticidae) from Florida. *New Zealand Journal of Zoology* **16**, 169–183.

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

Jackson, R. R. & 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., Pollard, S. D., Macnab, A. M. & Cooper, K. J. (1990). The complex communicatory behaviour of *Marpissa marina*, a New Zealand jumping spider (Araneae: Salticidae). *New Zealand Journal of Zoology* **17**, 25–38.

Johnson, J. C. (2001). Sexual cannibalism in fishing spiders (*Dolomedes triton*): An evaluation of two explanations for female aggression towards potential mates. *Animal Behaviour* **61**, 905–914.

Juberthie-Jupeau, L. & Lopez, A. (1991). Sexual dimorphism of gnathocoxal glands of the spider *Leptyphantes sanctivincentii. Tissue and Cell* **23**, 423–426.

Juberthie-Jupeau, L., Lopez, A. & Kronestedt, T. (1990). Structure et ultrastructure de la glande tibiale chez le mâle d'*Alopecosa cuneata* (Clerck) (Araneae, Lycosidae). *Revue arachnologique* **9**, 63–77.

Kaster, J. L. & Jakob, E. M. (1997). Last-male sperm priority in a haplogyne spider (Araneae: Pholcidae): correlations between female morphology and patterns of sperm usage. *Annals of the Entomological Society of America* **90**, 254–259.

Knoflach, B. (1998). Mating in *Theridion varians* Hahn and related species (Araneae: Theridiidae). *Journal of Natural History* **32**, 545–604.

Knoflach, B. (2002). Copulation and emasculation in *Echinotheridion gibberosum* (Kulczynski, 1899) (Araneae, Theridiidae). In *European Arachnology 2000* (eds. S. Toft and N. Scharff), pp. 139–144. Aarhus University Press, Aarhus.

Knoflach, B. (2004). Diversity in the copulatory behaviour of comb-footed spiders (Araneae, Theridiidae). *Denisia* **12**, 161–256.

Knoflach, B. & Benjamin, S. P. (2003). Mating without sexual cannibalism in *Tidarren sisyphoides* (Araneae, Theridiidae). *Journal of Arachnology* **31**, 445–448.

Knoflach, B. & van Harten, A. (2000). Palpal loss, single palp copulation and obligatory mate consumption in *Tidarren cuneolatum* (Tullgren, 1910) (Araneae, Theridiidae). *Journal of Natural History* **34**, 1639–1659.

Knoflach, B. & van Harten, A. (2001). *Tidarren argo* sp. nov. (Araneae: Theridiidae) and its exceptional copulatory behaviour: emasculation, male palpal organ as a mating plug and sexual cannibalism. *Journal of Zoology, London* **254**, 449–459.

Knoflach, B. & van Harten, A. (2002). The genus *Latrodectus* (Araneae: Theridiidae) from mainland Yemen, the Socotra Archipelago and adjacent countries. *Fauna of Arabia* **19**, 321–361.

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

Kotiaho, J., Alatalo, R. V., Mappes, J. & Parri, S. (1997). Fighting success in relation to body mass and drumming activity in the male wolf spider *Hygrolycosa rubrofasciata*. *Canadian Journal of Zoology* **75**, 1532–1535.

Kotiaho, J. S., Alatalo, R. V., Mappes, J., Nielsen, M. G., Parri, S. & Rivero, A. (1998*a*). Energetic costs of size and sexual signalling in a wolf spider. *Proceedings of the Royal Society of London B* **265**, 2203–2209.

Kotiaho, J., Alatalo, R. V., Mappes, J., Parri, S. & Rivero, A. (1998*b*). Male mating success and risk of predation in a wolf spider: a balance between sexual and natural selection? *Journal of Animal Ecology* **67**, 287–291.

Kotiaho, J. S., Alatalo, R. V., Mappes, J. & Parri, S. (1999*a*). Honesty of agonistic signalling and effects of size and motivation asymmetry in contests. *Acta Ethologica* **2**, 13–21.

Kotiaho, J. S., Alatalo, R. V., Mappes, J. & Parri, S. (1999*b*). Sexual signalling and viability in a wolf spider (*Hygrolycosa* *rubrofasciata*): measurements under laboratory and field conditions. *Behavioral Ecology and Sociobiology* **46**, 123–128.

Kotiaho, J. S., Alatalo, R. V., Mappes, J. & Parri, S. (2000). Microhabitat selection and audible sexual signalling in the wolf spider *Hygrolycosa rubrofasciata* (Araneae, Lycosidae). *Acta Ethologica* **2**, 123–128.

Kotiaho, J. S., Alatalo, R. V., Mappes, J. & Parri, S. (2004). Adaptive significance of synchronous chorusing in an acoustically signalling wolf spider. *Proceedings of the Royal Society of London B* **271**, 1847–1850.

Kronestedt, T. (1973). Study of a stridulatory apparatus in *Pardosa fulvipes* (Collett) (Araneae, Lycosidae) by scanning electron microscopy. *Zoologica Scripta* **2**, 43–47.

Kronestedt, T. (1986). A presumptive pheromone-emitting structure in wolf spiders (Araneae, Lycosidae). *Psyche* **93**, 127–131.

Kronestedt, T. (1996). Vibratory communication in the wolf spider *Hygrolycosa rubrofasciata* (Araneae, Lycosidae). *Revue Suisse de Zoologie*, suppl. 1996, 341–354.

Kropf, C. (2004). Eine interessante Kleinspinne: *Comaroma simonii* Bertkau 1889 (Arachnida, Araneae, Anapidae). *Denisia* **12**, 257–270.

Land, M. F. (1969*a*). Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *Journal of Experimental Biology* **51**, 471–493.

Land, M. F. (1969*b*). Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *Journal of Experimental Biology* **51**, 443–470.

Land, M. F. (1985). The morphology and optics of spider eyes. In *Neurobiology of Arachnids* (ed. Barth, F. G.), pp. 53–78. Springer Verlag, Berlin.

Lang, A. (1996). Silk investment in gifts by males of the nuptial feeding spider *Pisaura mirabilis* (Araneae: Pisauridae). *Behaviour* **133**, 697–716.

Laughlin, S., Blest, A. D. & Stowe, S. (1980). The sensitivity of receptors in the posterior median eye of the nocturnal spider, *Dinopis*. *Journal of Comparative Physiology A* **141**, 53–65.

Lee, R. C. P., Nyffeler, M., Krelina, E. & Pennycook, B. W. (1986). Acoustic communication in two spider species of the genus *Steatoda* (Araneae, Theridiidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **59**, 337–348.

Legendre, R. & Lopez, A. (1974). Étude histologique de quelques formations glandulaires chez les Araignées du genre *Argyrodes* (Theridiidae) et description d'un nouveau type de glande: la glande clypéale des males. *Bulletin de la Société Zoologique de France* **99**, 453–460.

LeGrand, R. S. & Morse, D. H. (2000). Factors driving extreme sexual size dimorphism of a sit-and-wait predator under low density. *Biological Journal of the Linnean Society* **71**, 643–664.

Levi, H. W. (1970). Problems in the reproductive physiology of the spider palpus. *Bulletin du Muséum national d'Histoire naturelle*, 2e ser., **41** (suppl. 1), 108–111.

Lopez, A. (1987). Glandular aspects of sexual biology. In *Ecophysiology of Spiders* (ed. W. Nentwig), pp. 121–132. Springer Verlag, Berlin.

Lopez, A. & Emerit, M. (1978). Le dimorphisme sexuel gnathocoxal de *Leptoneta microphtalma* Simon, 1872 (Araneae, Leptonetidae). *Revue arachnologique* **2**, 1–15.

Lopez, A. & Emerit, M. (1979). Données complémentaires sur la glande clypéale des *Argyrodes* (Araneae, Theridiidae). *Revue arachnologique* **2**, 143–153.

Lopez, A. & Emerit, M. (1988). New data on the epigastric apparatus of male spiders. *Bulletin of the British arachnological Society* **7**, 220–224.

Maddison, W. & McMahon, M. (2000). Divergence and reticulation among montane populations of a jumping spider (*Habronattus pugillis* Griswold). *Systematic Biology* **49**, 400–421.

Main, B. Y. (1990). Dwarf males in mygalomorph spiders: adaptation to environmental hazards. *Acta Zoologica Fennica* **190**, 273–278.

Maklakov, A. A., Bilde, T. & Lubin, Y. (2003). Vibratory courtship in a web-building spider: signalling quality or stimulating the female? *Animal Behaviour* **66**, 623–630.

Maklakov, A. A., Bilde, T. & Lubin, Y. (2004). Sexual selection for increased male body size and protandry in a spider. *Animal Behaviour* **68**, 1041–1048.

Mappes, J., Alatalo, R. V., Kotiaho, J. & Parri, S. (1996). Viability costs of condition-dependent sexual male display in a drumming wolf spider. *Proceedings of the Royal Society of London B* **263**, 785–789.

Masta, S. E. & Maddison, W. P. (2002). Sexual selection driving diversification in jumping spiders. *Proceedings of the National Academy of Science USA* **99**, 4442–4447.

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

Mays, H. L. & Hill, G. E. (2004). Choosing mates: good genes versus genes that are a good fit. *Trends in Ecology and Evolution* **19**, 554–559.

McClintock, W. J. & Uetz, G. W. (1996). Female choice and pre-existing bias: visual cues during courtship in two *Schizocosa* wolf spiders (Araneae: Lycosidae). *Animal Behaviour* **52**, 167–181.

Méndez, V. (2002). Comportamiento sexual y dinamica de población en *Leucauge mariana*. Master thesis, University of Costa Rica.

Méndez, V. & Córdoba-Aguilar, A. (2004). Sexual selection and animal genitalia. *Trends in Ecology and Evolution* **19**, 224–225.

Morse, D. H. (2004). A test of sexual cannibalism models, using a sit-and-wait predator. *Biological Journal of the Linnean Society* **81**, 427–437.

Morse, D. H. & Hu, H. H. (2004). Age affects the risk of sexual cannibalism in male crab spiders (*Misumena vatia*). *American Midland Naturalist* **151**, 318–325.

Moya-Laraño, J., Halaj, J. & Wise, D. H. (2002). Climbing to reach females: Romeo should be small. *Evolution* **56**, 420–425.

Moya-Laraño, J., Pascual, J. & Wise, D. H. (2003). Mating patterns in late-maturing female Mediterranean tarantulas may reflect the costs and benefits of sexual cannibalism. *Animal Behaviour* **66**, 469–476.

Muniappan, R. & Chada, H. L. (1970). Biology of the crab spider, *Misumenops celer*. *Annals of the Entomological Society of America* **63**, 1718–1722.

Nakamura, T. & Yamashita, S. (2000). Learning and discrimination of colored papers in jumping spiders (Araneae, Salticidae). *Journal of Comparative Physiology A* **186**, 897–901.

Newman, J. A. & Elgar, M. A. (1991). Sexual cannibalism in orb-weaving spiders: an economic model. *American Naturalist* **138**, 1372–1395.

Nielsen, N. & Toft, S. (1990). Alternative male mating strategies in *Linyphia triangularis* (Araneae, Linyphiidae). *Acta Zoologica Fennica* **190**, 293–297.

Nitzsche, R. (1988). 'Brautgeschenk' und Umspinnen der Beute bei *Pisaura mirabilis*, *Dolomedes fimbriatus* und *Thaumasia uncata*

(Arachnida, Araneida, Pisauridae). *Verhandlungen des naturwissenschaftlichen Vereins Hamburg* **30**, 353–393.

Oxford, G. S. & Gillespie, R. G. (1998). Evolution and ecology of spider coloration. *Annual Review of Ecology and Systematics* **43**, 619–643.

Papke, M., Schulz, S., Tichy, H., Gingl, E. & Ehn, R. (2000). Identifizierung eines neuen Sexualpheromons aus Sicherungsfäden der tropischen Jagdspinne *Cupiennius salei*. *Angewandte Chemie* **112**, 4517–4518.

Papke, M. D., Riechert, S. E. & Schulz, S. (2001). An airborne female pheromone associated with male attraction and courtship in a desert spider. *Animal Behaviour* **61**, 877–886.

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

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

Parri, S., Alatalo, R. V., Kotiaho, J. & Mappes, J. (1997). Female choice for male drumming in the wolf spider *Hygrolycosa rubrofasciata*. *Animal Behaviour* **53**, 305–312.

Parri, S., Alatalo, R. V., Kotiaho, J. S., Mappes, J. & Rivero, A. (2002). Sexual selection in the wolf spider *Hygrolycosa rubrofasciata*: female preference for drum duration and pulse rate. *Behavioral Ecology* **13**, 615–621.

Patel, B. H. & Bradoo, B. L. (1986). Observations on sperm induction, courtship, and mating behavior of *Uloborus ferokus* Bradoo (Araneae: Uloboridae). In *International Congress of Arachnology 9* (*Panama*) (eds. W. G. Eberhard, Y. D. Lubin and B. C. Robinson), pp. 181–191. Smithsonian Institution Press, Washington, D.C.

Peaslee, A. G. & Wilson, G. (1989). Spectral sensitivity in jumping spiders (Araneae, Salticidae). *Journal of Comparative Physiology A* **164**, 359–363.

Peckham, G. W. & Peckham, E. G. (1889). Observations on sexual selection in spiders of the family Attidae. *Occasional Papers of the Wisconsin Natural History Society* **1**, 3–60.

Peckham, G. W. & Peckham, E. G. (1890). Additional observations on sexual selection in spiders of the family Attidae. *Occasional Papers of the Wisconsin Natural History Society* **1**, 117–151.

Peretti, A. V. (2003). Functional morphology of spermatophores and female genitalia in bothriurid scorpions: genital courtship, coercion and other possible mechanisms. *Journal of Zoology, London* **261**, 135–153.

Persons, M. H. & Uetz, G. W. (2005). Sexual cannibalism and mate choice decisions in wolf spiders: influence of male size and secondary sexual characters. *Animal Behaviour* **69**, 83–94.

Piel, W. H. (1996). Ecology of sexual dimorphism in spiders of the genus *Metepeira* (Araneae: Araneidae). *Revue Suisse de Zoologie*, suppl. 1996, 523–529.

Platnick, N. (1971). The evolution of courtship behaviour in spiders. *Bulletin of the British Arachnological Society* **2**, 40–47.

Pollard, S. D. (1994). Consequences of sexual selection on feeding in male jumping spiders (Araneae: Salticidae). *Journal of Zoology, London* **234**, 203–208.

Pollard, S. D., Macnab, A. M. & Jackson, R. R. (1987). Communication with chemicals: pheromones and spiders. In *Ecophysiology of Spiders* (ed. W. Nentwig), pp. 133–141. Springer Verlag, Berlin.

Prenter, J., Elwood, R. W. & Montgomery, W. I. (1994). Assessments and decisions in *Metellina segmentata* (Araneae: Metidae): evidence of a pheromone involved in mate guarding. *Behavioral Ecology and Sociobiology* **35**, 39–43.

Prenter, J., Elwood, R. W. & Montgomery, W. I. (1998). No association between sexual size dimorphism and life histories in spiders. *Proceedings of the Royal Society of London B* **265**, 57–62.

Prenter, J., Elwood, R. W. & Montgomery, W. I. (1999). Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. *Evolution* **53**, 1987–1994.

Prenter, J., Elwood, R. W. & Montgomery, W. I. (2003). Mate guarding, competition and variation in size in male orb-web spiders, *Metellina segmentata*: a field experiment. *Animal Behaviour* **66**, 1053–1058.

Prenter, J., Montgomery, W. I. & Elwood, R. W. (1995). Multivariate morphometrics and sexual dimorphism in the orb-web spider *Metellina segmentata* (Clerck, 1757) (Araneae, Metidae). *Biological Journal of the Linnean Society* **55**, 345–354.

Prenter, J., Montgomery, W. I. & Elwood, R. W. (1997). Sexual dimorphism in northern temperate spiders: implications for the differential mortality model. *Journal of Zoology, London* **243**, 341–349.

Prouvost, O., Trabalon, M., Papke, M. & Schulz, S. (1999). Contact sex signals on web and cuticle of *Tegenaria atrica* (Araneae, Agelenidae). *Archives of Insect Biochemistry and Physiology* **40**, 194–202.

Ramos, M., Irschick, D. J. & Christenson, T. E. (2004). Overcoming an evolutionary conflict: Removal of a reproductive organ greatly increases locomotor performance. *Proceedings of the National Academy of Sciences USA* **101**, 4883–4887.

Riechert, S. E. & Johns, P. M. (2003). Do female spiders select heavier males for the genes for behavioral aggressiveness they offer their offspring? *Evolution* **57**, 1367–1373.

Riechert, S. E. & Singer, F. D. (1995). Investigation of potential male mate choice in a monogamous spider. *Animal Behaviour* **49**, 715–723.

Rivero, A., Alatalo, R. V., Kotiaho, J. S., Mappes, J. & Parri, S. (2000). Acoustic signalling in a wolf spider: can signal characteristics predict male quality? *Animal Behaviour* **60**, 187–194.

Robinson, M. H. (1982). Courtship and mating behavior in spiders. *Annual Review of Entomology* **27**, 1–20.

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

Ross, K. & Smith, R. L. (1979). Aspects of the courtship behavior of the black widow spider, *Latrodectus hesperus* (Araneae: Theridiidae), with evidence for the existence of a contact sex pheromone. *Journal of Arachnology* **7**, 69–77.

Rovner, J. S. (1967). Acoustic communication in a lycosid spider (*Lycosa rabida* Walckenaer). *Animal Behaviour* **15**, 273–281.

Rovner, J. S. (1968). Territoriality in the sheet-web spider *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). *Zeitschrift für Tierpsychologie* **25**, 232–242.

Rovner, J. S. (1975). Sound production by Nearctic wolf spiders: A substratum-coupled stridulatory mechanism. *Science* **190**, 1309–1310.

Rovner, J. S. (1980). Vibration in *Heteropoda venatoria* (Sparassidae): A third method of sound production in spiders. *Journal of Arachnology* **8**, 193–200.

Ryan, M. J., Fox, J. H., Wilczynski, W. & Rand, A. S. (1990). Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* **343**, 66–67.

Rypstra, A. L., Wieg, C., Walker, S. E. & Persons, M. H. (2003). Mutual mate assessment in wolf spiders: differences in the cues used by males and females. *Ethology* **109**, 315–325.

Sasaki, T. & Iwahashi, O. (1995). Sexual cannibalism in an orb-weaving spider *Argiope aemula*. *Animal Behaviour* **49**, 1119–1121.

Schaefer, D. & Uhl, G. (2003). Male competition over access to females in a spider with last-male sperm precedence. *Ethology* **109**, 385–400.

Schäfer, M. A. & Uhl, G. (2002). Determinants of paternity success in the spider *Pholcus phalangioides* (Pholcidae: Araneae): the role of male and female mating behaviour. *Behavioral Ecology and Sociobiology* **51**, 368–377.

Schaible, U. & Gack, C. (1987). Zur Morphologie, Histologie und biologischen Bedeutung der Kopfstrukturen einiger Arten der Gattung *Diplocephalus* (Araneida, Linyphiidae, Erigoninae). *Verhandlungen des naturwissenschaftlichen Vereins Hamburg NF* **29**, 171–180.

Schaible, U., Gack, C. & Paulus, H. F. (1986). Zur Morphologie, Histologie und biologischen Bedeutung der Kopfstrukturen männlicher Zwergspinnen (Linyphiidae, Erigoninae). *Zoologisches Jahrbuch für Systematik* **113**, 389–408.

Scheffer, S. J., Uetz, G. W. & Stratton, G. E. (1996). Sexual selection, male morphology, and the efficacy of courtship signalling in two wolf spiders (Araneae: Lycosidae). *Behavioral Ecology and Sociobiology* **38**, 17–23.

Schmitt, A., Schuster, M. & Barth, F. G. (1994). Vibratory communication in a wandering spider, *Cupiennius getazi*: female and male preferences for features of the conspecific male's releaser. *Animal Behaviour* **48**, 1155–1171.

Schneider, J. M. & Elgar, M. A. (2001). Sexual cannibalism and sperm competition in the golden orb-web spider *Nephila plumipes* (Araneoidea): female and male perspectives. *Behavioral Ecology* **12**, 547–552.

Schneider, J. M. & Elgar, M. A. (2002). Sexual cannibalism in *Nephila plumipes* as a consequence of female life history strategies. *Journal of Evolutionary Biology* **15**, 84–91.

Schneider, J. M., Herberstein, M. E., de Crespigny, F. C., Ramamurthy, S. & Elgar, M. A. (2000). Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. *Journal of Evolutionary Biology* **13**, 939–946.

Schneider, J. M. & Lubin, Y. (1996). Infanticidal male eresid spiders. *Nature* **381**, 655–656.

Schneider, J. M. & Lubin, Y. (1997). Infanticide by males in a spider with suicidal maternal care, *Stegodyphus lineatus* (Eresidae). *Animal Behaviour* **54**, 305–312.

Schneider, J. M. & Lubin, Y. (1998). Intersexual conflict in spiders. *Oikos* **83**, 496–506.

Schneider, J. M., Thomas, M. L. & Elgar, M. A. (2001). Ectomised conductors in the golden orb-web spider, *Nephila plumipes* (Araneoidea): a male adaptation to sexual conflict? *Behavioral Ecology and Sociobiology* **49**, 410–415.

Schüch, W. & Barth, F. G. (1990). Vibratory communication in a spider: female responses to synthetic male vibrations. *Journal of Comparative Physiology A* **166**, 817–826.

Schulz, S. (2004*a*). Semiochemistry of spiders. In *Advances in Insect Chemical Ecology* (eds. R. T. Cardé and J. G. Millar), pp. 110–150. Cambridge University Press, Cambridge.

Schulz, S. (2004*b*). Structural diversity of surface lipids from spiders. In *Advances in Chemical Ecology*. In press.

Schulz, S. & Toft, S. (1993). Identification of a sex pheromone from a spider. *Science* **260**, 1635–1637.

Schütz, D. & Taborsky, M. (2003). Adaptations to an aquatic life may be responsible for the reversed sexual size dimorphism in the water spider, *Argyroneta aquatica*. *Evolutionary Ecology Research* **5**, 105–117.

Searcy, L. E., Rypstra, A. L. & Persons, M. H. (1999). Airborne chemical communication in the wolf spider *Pardosa milvina*. *Journal of Chemical Ecology* **25**, 2527–2533.

Simmons, L. W. (2001). *Sperm competition and its evolutionary consequences in the insects*. Princeton University Press, Princeton and Oxford.

Snow, L. S. E. & Andrade, M. C. B. (2004). Pattern of sperm transfer in redback spiders: implications for sperm competition and male sacrifice. *Behavioral Ecology* **15**, 785–792.

Stålhandske, P. (2001). Nuptial gift in the spider *Pisaura mirabilis* maintained by sexual selection. *Behavioral Ecology* **12**, 691–697.

Stålhandske, P. (2002). Nuptial gifts of male spiders function as sensory traps. *Proceedings of the Royal Society of London B* **269**, 905–908.

Stålhandske, P. & Gunnarsson, B. (1996). Courtship behaviour in the spider *Pityohyphantes phrygianus* (Linyphiidae, Araneae): do females discriminate injured males? *Revue Suisse de Zoologie* (suppl. 1996), 617–625.

Starck, J. M. (1985). Stridulationsapparate einiger Spinnen – Morphologie und evolutionsbiologische Aspekte. *Zeitschrift für zoologische Systematik und Evolutionsforschung* **23**, 115–135.

Strand, E. (1906). Studien über den Bau und die Entwicklung der Spinnen. I. Über die Geschlechtsorgane von *Agelena labyrinthica* (L.). *Zeitschrift für wissenschaftliche Zoologie* **80**, 515–543.

Stumpf, H. & Linsenmair, K. E. (1996). Observations on the mating systems of two spiders, *Linyphia hortensis* Sund. and *L. triangularis* (Cl.) (Linyphiidae: Araneae). *Revue Suisse de Zoologie*, suppl. 1996, 627–634.

Suhm, M., Thaler, K. & Alberti, G. (1995). Glands in the male palpal organ and the origin of the mating plug in *Amaurobius* species (Araneae: Amaurobiidae). *Zoologischer Anzeiger* **234**, 191–199.

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

Suter, R. B. & Hirscheimer, A. J. (1986). Multiple web-borne pheromones in a spider *Frontinella pyramitela* (Araneae, Linyphiidae). *Animal Behaviour* **34**, 748–753.

Suter, R. B. & Keiley, M. (1984). Agonistic interactions between male *Frontinella pyramitela* (Araneae, Linyphiidae). *Behavioral Ecology and Sociobiology* **15**, 1–7.

Suter, R. B. & Parkhill, V. S. (1990). Fitness consequences of prolonged copulation in the bowl and doily spider. *Behavioral Ecology and Sociobiology* **26**, 369–373.

Suter, R. B. & Renkes, G. (1984). The courtship of *Frontinella pyramitela* (Araneae, Linyphiidae): patterns, vibrations and functions. *Journal of Arachnology* **12**, 37–54.

Suter, R. B., Shane, C. M. & Hirscheimer, A. J. (1987). Communication by cuticular pheromones in a linyphiid spider. *Journal of Arachnology* **15**, 157–162.

Tarsitano, M. & Kirchner, W. H. (2001). Vibrational courtship signals of *Zygiella x-notata* (Clerck) (Araneae: Araneidae). *Bulletin of the British arachnological Society* **12**, 26–32.

Taylor, A. R., Persons, M. H. & Rypstra, A. L. (in press). The effect of perceived predation risk on male courtship and copulatory behavior in the wolf spider *Pardosa milvina* (Araneae, Lycosidae). *Journal of Arachnology*.

Taylor, P. W., Hasson, O. & Clark, D. L. (2000). Body postures and patterns as amplifiers of physical condition. *Proceedings of the Royal Society of London B* **267**, 917–922.

Taylor, P. W., Hasson, O. & Clark, D. L. (2001). Initiation and resolution of jumping spider contests: roles for size, proximity, and early detection of rivals. *Behavioral Ecology and Sociobiology* **50**, 403–413.

Thornhill, R. (1983). Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *American Naturalist* **122**, 765–788.

Tichy, H., Gingl, E., Ehn, R., Papke, M. & Schulz, S. (2001). Female sex pheromone of a wandering spider (*Cupiennius salei*): identification and sensory reception. *Journal of Comparative Physiology A* **187**, 75–78.

Tietjen, W. J. (1979). Tests for olfactory communication in four species of wolf spiders (Araneae: Lycosidae). *Journal of Arachnology* **6**, 197–206.

Tietjen, W. J. & Rovner, J. S. (1982). Chemical communication in lycosids and other spiders. In *Spider communication: Mechanisms and ecological significance* (eds. P. N. Witt and J. S. Rovner), pp. 249–279. Princeton University Press, Princeton, NJ.

Toft, S. (1989). Mate guarding in two *Linyphia* species (Araneae: Linyphiidae). *Bulletin of the British arachnological Society* **8**, 33–37.

Trabalon, M., Bagnères, A. G. & Roland, C. (1997). Contact sex signals in two sympatric spider species, *Tegenaria domestica* and *Tegenaria pagana*. *Journal of Chemical Ecology* **23**, 747–758.

Uetz, G. W. (2000). Signals and multi-modal signaling in spider communication. In *Animal Signals: Signalling and Signal Design in Animal Communication* (eds. Y. Espmark, T. Amundsen and G. Rosenqvist), pp. 387–405. Tapir Academic Press, Trondheim, Norway.

Uetz, G. W., McClintock, W. J., Miller, D., Smith, E. I. & Cook, K. K. (1996). Limb regeneration and subsequent asymmetry in a male secondary sexual character influences sexual selection in wolf spiders. *Behavioral Ecology and Sociobiology* **38**, 253–257.

Uetz, G. W., Papke, R. & Kilinic, B. (2002). Influence of feeding regime on body size, body condition and a male secondary sexual character in *Schizocosa ocreata* wolf spiders (Araneae, Lycosidae): condition-dependence in a visual signaling trait. *Journal of Arachnology* **30**, 461–469.

Uetz, G. W. & Roberts, J. A. (2002). Multisensory cues and multimodal communication in spiders: insights from video/audio playback studies. *Brain, Behavior and Evolution* **59**, 222–230.

Uetz, G. W. & Smith, E. I. (1999). Asymmetry in a visual signaling character and sexual selection in a wolf spider. *Behavioral Ecology and Sociobiology* **45**, 87–93.

Uetz, G. W. & Stratton, G. E. (1982). Acoustic communication and reproductive isolation in spiders. In *Spider Communication: Mechanisms and Ecological Significance* (eds. P. Witt and J. Rovner), pp 123–159. Princeton Univ. Press, Princeton, N.J.

Uetz, G. W. & Taylor, P. W. (2003). Developmental instability and animal communication – fluctuating asymmetry as a signal and as an influence on the signaling process. In *Developmental Instability: Causes and Consequences* (ed. M. Polak). Oxford University Press, Oxford.

Uhl, G. (1998). Mating behaviour in the cellar spider, *Pholcus phalangioides*, indicates sperm mixing. *Animal Behaviour* **56**, 1155–1159.

Uhl, G. (2000). Two distinctly different sperm storage organs in female *Dysdera erythrina* (Araneae: Dysderidae). *Arthropod Structure and Development* **29**, 163–169.

Uhl, G. (2002). Female genital morphology and sperm priority patterns in spiders (Araneae). In *European Arachnology 2000* (eds. S. Toft and N. Scharff), pp. 145–156. Aarhus University Press, Aarhus.

Uhl, G. & Schmitt, M. (1996). Stridulation in *Palpimanus gibbulus* Dufour (Araneae: Palpimanidae). *Revue Suisse de Zoologie*, suppl. 1996, 649–660.

Uhl, G., Schmitt, S., Schäfer, M. A. & Blanckenhorn, W. (2004). Food and sex-specific growth strategies in a spider. *Evolutionary Ecology Research* **6**, 523–540.

Uhl, G. & Vollrath, F. (1998). Genital morphology of *Nephila edulis*: implications for sperm competition in spiders. *Canadian Journal of Zoology* **76**, 39–47.

Vahed, K. (1998). The function of nuptial feeding in insects: a review of empirical studies. *Biological Reviews* **73**, 43–78.

Vanacker, D., Hendrickx, F., Maes, L., Verraes, P. & Maelfait, J.-P. (2004). Can multiple mating compensate for slower development and shorter adult life in a male dimorphic dwarf spider? *Biological Journal of the Linnean Society* **82**, 269–273.

Vanacker, D., Borre, J. V., Jonckheere, A., Maes, L., Pardo, S., Hendrickx, F. & Maelfait, J.-P. (2003*a*). Dwarf spiders (Erigoninae, Linyphiidae, Araneae): good candidates for evolutionary research. *Belgian Journal of Zoology* **133**, 145–151.

Vanacker, D., Maes, L., Pardo, S., Hendrickx, F. & Maelfait, J.-P. (2003*b*). Is the hairy groove in the gibbosus male morph of *Oedothorax gibbosus* (Blackwall 1841) a nuptial feeding device? *Journal of Arachnology* **31**, 309–315.

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

Vollrath, F. (1998). Dwarf males. *TREE* **13**, 159–163.

Vollrath, F. & Parker, G. A. (1992). Sexual dimorphism and distorted sex ratios in spiders. *Nature* **360**, 156–159.

Walker, S. E. & Rypstra, A. L. (2003). Sexual dimorphism and the differential mortality model: is behaviour related to survival? *Biological Journal of the Linnean Society* **78**, 97–103.

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). *Behavioral Ecology and Sociobiology* **26**, 77–90.

Watson, P. J. (1991*a*). Multiple paternity and first mate sperm precedence in the sierra dome spider, *Linyphia litigiosa* Keyserling (Linyphiidae). *Animal Behaviour* **41**, 135–148.

Watson, P. J. (1991*b*). Multiple paternity as genetic bet-hedging in female sierra dome spiders, *Linyphia litigiosa* (Linyphiidae). *Animal Behaviour* **41**, 343–360.

Watson, P. J. (1993). Foraging advantage of polyandry for female sierra dome spiders (*Linyphia litigiosa*: Linyphiidae) and assessment of alternative direct benefit hypotheses. *American Naturalist* **141**, 440–465.

Watson, P. J. (1998). Multi-male mating and female choice increase offspring growth in the spider *Neriene litigiosa* (Linyphiidae). *Animal Behaviour* **55**, 387–403.

Watson, P. J. & Lighton, J. R. B. (1994). Sexual selection and the energetics of copulatory courtship in the Sierra dome spider, *Linyphia litigiosa*. *Animal Behaviour* **48**, 615–626.

West, H. P. & Toft, S. (1999). Last-male sperm priority and the mating system of the haplogyne spider *Tetragnatha extensa* (Araneae: Tetragnathidae). *Journal of Insect Behavior* **12**, 433–450.

Whitehouse, M. E. A. (1987). The external structural detail of the protrusions on the cephalothorax of male *Argyrodes antipodiana*. *Bulletin of the British arachnological Society* **7**, 142–144.

Whitehouse, M. E. A. & Jackson, R. R. (1994). Intraspecific interactions of *Argyrodes antipodiana*, a kleptoparasitic spider from New Zealand. *New Zealand Journal of Zoology* **21**, 253–268.

Wiehle, H. (1967). Steckengebliebene Emboli in den Vulven von Spinnen (Arach., Araneae). *Senckenbergiana biologica* **48**, 197–202.

Willey-Robertson, M. & Adler, P. H. (1994). Mating behavior of *Florinda coccinea* (Hentz) (Araneae: Linyphiidae). *Journal of Insect Behavior* **7**, 313–326.

Williams, D. S. & McIntyre, P. (1980). The principal eyes of a jumping spider have a telephoto component. *Nature* **228**, 578–580.

Yoward, P. J. (1996). Spider sperm competition: the condiut/cul-de-sac hypothesis – a route to understanding or a dead end? PhD thesis, University of York.

Yoward, P. J. (1998). Sperm competition in *Pholcus phalangioides* (Fuesslin, 1775) (Araneae, Pholcidae) – shorter copulations gain higher paternity reward than first copulations. In *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997* (ed. P. A. Selden), pp. 176–170. British Arachnological Society, Burnham Beeches, Bucks.

Yoward, P. & Oxford, G. (1997). Involvement of grasping mechanisms in copulation in spiders. *Newsletter of the British Aarachnological Society* **78**, 12–14.