

Spider sex pheromones: emission, reception, structures, and functions

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ABSTRACT

Spiders and their mating systems are useful study subjects with which to investigate questions of widespread interest about sexual selection, pre- and post-copulatory mate choice, sperm competition, mating strategies, and sexual conflict. Conclusions drawn from such studies are broadly applicable to a range of taxa, but rely on accurate understanding of spider sexual interactions. Extensive behavioural experimentation demonstrates the presence of sex pheromones in many spider species, and recent major advances in the identification of spider sex pheromones merit review. Synthesised here are the emission, transmission, structures, and functions of spider sex pheromones, with emphasis on the crucial and dynamic role of sex pheromones in female and male mating strategies generally. Techniques for behavioural, chemical and electrophysiological study are summarised, and I aim to provide guidelines for incorporating sex pheromones into future studies of spider mating.

In the spiders, pheromones are generally emitted by females and received by males, but this pattern is not universal. Female spiders emit cuticular and/or silk-based sex pheromones, which can be airborne or received *via* contact with chemoreceptors on male pedipalps. Airborne pheromones primarily attract males or elicit male searching behaviour. Contact pheromones stimulate male courtship behaviour and provide specific information about the emitter's identity. Male spiders are generally choosy and are often most attracted to adult virgin females and juvenile females prior to their final moult. This suggests the first male to mate with a female has significant advantages, perhaps due to sperm priority patterns, or mated female disinterest. Both sexes may attempt to control female pheromone emission, and thus dictate the frequency and timing of female mating, reflecting the potentially different costs of female signalling and/or polyandry to both sexes. Spider sex pheromones are likely to be lipids or lipid soluble, may be closely related to primary metabolites, and are not necessarily species specific, although they can still assist with species recognition. Newer electrophysiological techniques coupled with chemical analyses assist with the identification of sex pheromone compounds. This provides opportunities for more targeted behavioural experimentation, perhaps with synthetic pheromones, and for theorising about the biosynthesis and evolution of chemical signals generally. Given the intriguing biology of spiders, and the critical role of chemical signals for spiders and many other animal taxa, a deeper understanding of spider sex pheromones should prove productive.

Key words: sex pheromones, chemical signalling, behaviour, mating strategies, sperm priority, sexual conflict, spiders, Araneae.

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I. INTRODUCTION

Intersexual communication involves signals and cues in visual, tactile, auditory, and chemical modes, which can be used to attract, find, or assess the qualities of potential mating partners. Signals have coevolved in the emitter and receiver, and stimulate specific behavioural responses (Maynard-Smith & Harper, 2003). Cues, such as female body size, may be used by a receiver to gather information, but are not the result of evolution driven by their effects on others (Maynard-Smith & Harper, 2003). Pheromones are chemical signals that elicit generally mutually beneficial responses from intraspecific receivers (Karlson & Butenandt, 1959; Wyatt, 2003). Pheromone communication has perhaps been most comprehensively studied in the phylum Arthropoda, with particular focus on crustaceans and insects (Wyatt, 2003; Cardé & Millar, 2004). Amongst the Chelicerata, sex pheromones are reported in mites (Acari; Sonenshine, 1985; Kuwahara, 2004) and scorpions (Scorpionida; Gaffin & Brownell, 2000). Extensive behavioural experimentation and some chemical studies demonstrate that sex pheromones are also common in spiders (Araneae; Kaston, 1936; Krafft, 1982; Tietjen & Rovner, 1982; Witt, 1982; Nentwig, 1987; Schulz, 2004). The absence of sex pheromones in a spider species is reported only rarely, e.g. in some jumping spiders (Salticidae; Jackson, 1978, 1987), the orb-web spider *Nephila plumipes* (Latreille) (Sparassidae; Elgar *et al.*, 2003), and the crab spider *Misumena vatia* (Clerck) (Thomisidae; LeGrand & Morse, 2000; Anderson & Morse, 2001).

Spiders are often solitary with a widely dispersed or low-density population, lack permanent home sites or are wandering, have poor vision, or are aggressive and cannibalistic (Elgar, 1992; Foelix, 1996). These behavioural and ecological factors may exert strong selection for communication modes such as chemical signalling that can function over long distances, without necessarily involving contact between the emitter and the receiver. Perhaps the three most important functions of female spider sex pheromones are: (1) long-range attraction of conspecific males, (2) short-range signalling of female identity, and (3) stimulation of male courtship behaviour (Table 1). Mating behaviour in spiders often involves behavioural tactics and conflict between the sexes (Schneider & Lubin, 1998), and communication with pheromones is also intriguingly complicated by phenomena

such as strategic pheromone emission by females, and male sabotage or inhibition of female pheromone emission (e.g. Watson, 1986).

Spiders and their mating behaviour have become popular subjects for evolutionary research (Eberhard, 2004). Several recent publications use spiders as model systems to investigate significant topics such as sexual selection, sperm competition, sexual conflict, cryptic female choice, and male and female mate choice and mating strategies (e.g. Eberhard, 2004; Maklakov & Lubin, 2004; Fromhage, Elgar & Schneider, 2005; Huber, 2005; Roberts & Uetz, 2005; Snow & Andrade, 2005). Given the usefulness of spiders for studying topics applicable to a broad range of taxa and the crucial role of chemical signals in mating systems, a deeper understanding of spider sex pheromones should prove rewarding. Increasingly sophisticated chemical techniques used in analyses of spider and insect sex pheromones permit accurate identification of sex pheromones, allowing elegant and targeted behavioural assays. Knowledge of the functions and structures of pheromones contributes significantly to general theories as to the evolution and biosynthesis of chemical signals.

Synthesised here is the current literature investigating sex pheromones in spiders. The emission, transmission, reception and structures of spider sex pheromones are discussed, and methods used for chemical and electrophysiological analyses and behavioural assays are assessed. I use the spider literature to examine how the emission of female sex pheromones can vary with female age, sexual maturity, and sexual status, and how this interacts with male mate choice and behaviour. Finally, the potential for exploitation of pheromones by predators and the possible role of pheromones in species recognition are considered. This review aims to demonstrate the importance of sex pheromones in mating strategies, and provide guidelines for better incorporating sex pheromones into future studies in this field. All species names are according to Platnick (2006).

II. EMISSION AND TRANSMISSION OF SEX PHEROMONES

Studies of spider pheromones generally focus on pheromones emitted by females and received by males (see Table 1). This is appropriate for species in which males only respond to female pheromones and females do not respond to female or male

Table 1. Emission, transmission, and functions of female sex pheromones in spiders (Araneae). Cells are left blank where the information is unknown. ‘Adult’ denotes adult females of unknown mating history, ‘virgin’ denotes adult, not juvenile, virgins, and ‘juv.’ indicates a juvenile. Tests are considered ‘direct’ if controlled behavioural experiments were used or ‘indirect’ if the presence of sex pheromones was concluded from observations only (exp., experiment). “Choice exp.” refers to whether males were simultaneously exposed to more than one type of pheromone in controlled trials (Y, yes; N, no). Species names are according to Platnick (2006).

Spider taxa	Status of attractive female	Pheromone substratum	Transmission mode	Male response	Tests	Choice exp.	Source
Araneomorphae							
Agelenidae							
<i>Agelenopsis aperta</i> (Gertsch)	older virgins	cuticle & silk	airborne & contact	attraction	Direct (lab. experiments)	Y	Riechert & Singer (1995); Papke et al. (2001)
<i>Tegenaria atrica</i> C. L. Koch	virgin	cuticle & silk	contact	attraction	Direct (lab. experiments) Chemical analyses	N	Prouvost et al. (1999); Trabalon et al. (2005)
<i>Tegenaria domestica</i> (Clerck)		cuticle & silk	contact	attraction	Direct (lab. experiments) Chemical analyses	N	Roland (1984); Trabalon et al. (1997)
<i>Tegenaria pagana</i> (C. L. Koch)		cuticle & silk	contact	courtship	Direct (lab. experiments) Chemical analyses	N	Roland (1984); Trabalon et al. (1997)
<i>Tegenaria parietina</i> (Fourcroy)		silk	contact	courtship	Indirect (lab. observations)	N	Krafft (1978)
Amaurobiidae							
<i>Amaurobius fenestralis</i> (Ström)		silk	contact	courtship	Indirect (lab. observations)	N	Krafft (1978)
<i>Amaurobius similis</i> (Blackwall)		silk	contact	courtship	Indirect (lab. observations)	N	Locket & Bristowe (1926); Krafft (1978)
<i>Coelotes terrestris</i> (Wider)		silk	contact	attraction & courtship	Direct (lab. experiments)	N	Krafft (1978); Roland (1984)
Araneidae							
<i>Araneus trifolium</i> (Hentz)	juv. & virgin		airborne	attraction	Direct (field experiment)	N	Olive (1982)
<i>Argiope aurantia</i> Lucas		cuticle	airborne	attraction	Indirect (field observation)	N	Enders (1975); Olive (1982)
<i>Argiope keyserlingi</i> Karsch	juv. & virgin	cuticle & silk	airborne & contact	attraction & courtship	Direct (lab. & field experiments)	Y	Herberstein et al. (2002); Gaskett et al. (2004)
<i>Argiope trifasciata</i> (Forskål)	juv. & virgin		airborne	attraction	Direct (field experiment)	N	Olive (1982)
<i>Cyrtophora cicatrosa</i> (Stoliczka)	young virgins	cuticle & silk	airborne	attraction	Indirect (lab. observations)	N	Blanke (1975)
<i>Larinioides</i> (= <i>Araneus</i>) <i>sclopetarius</i> (Clerck)		silk	contact	attraction	Direct (lab. experiments)	N	Roland (1984)
<i>Zygiella</i> (= <i>Zilla</i>) <i>x-notata</i> (Clerck)		silk	contact	courtship	Indirect (lab. observation)	N	Locket & Bristowe (1926)
Atypidae							
<i>Sphodros abboti</i> Walckenaer	adult	silk	contact	attraction	Indirect (field observation)	N	Coyle & Shear (1981)
<i>Sphodros niger</i> (Hentz)			contact		Indirect (field observation)	N	Edwards & Edwards (1990)

Table 1 (cont.)

Spider taxa	Status of attractive female	Pheromone substratum	Transmission mode	Male response	Tests	Choice exp.	Source
Clubionidae							
<i>Clubiona cambridgei</i> L. Koch		silk	contact	courtship	Indirect (field & lab. observations)	N	Pollard <i>et al.</i> (1987)
Ctenidae							
<i>Cupiennius cocineus</i> F. O. P. –Cambridge	virgin	silk	contact	searching & courtship	Indirect (field & lab. observations) Direct (lab. experiments) Chemical analyses	Y	Barth & Schmitt (1991); Barth (1993); Schuster <i>et al.</i> (1994); Schulz (2004)
<i>Cupiennius getazi</i> Simon	virgin	silk	contact	searching & courtship	Indirect (field & lab. observations) Direct (lab. experiments) Chemical analyses	Y	Barth & Schmitt (1991); Barth (1993); Schuster <i>et al.</i> (1994); Schulz (2004)
<i>Cupiennius salei</i> (Keyserling)	adult	silk	contact	searching & courtship	Indirect (field & lab. observations) Direct (lab. experiments) Chemical & Electro-physiological analyses	Y	Barth & Schmitt (1991); Barth (1993); Schuster <i>et al.</i> (1994); Papke <i>et al.</i> (2000, 2001); Tichy <i>et al.</i> (2001); Schulz (2004)
Dictynidae							
<i>Dictyna calcarata</i> Banks	virgin	silk	contact	courtship	Indirect (lab. observation)	N	Jackson (1978)
<i>Dictyna latens</i> (Fabricius)		silk	contact	courtship	Indirect (lab. observation)	N	Lockett & Bristowe (1926)
<i>Dictyna volucripes</i> Keyserling	virgin	silk	contact	courtship	Indirect (lab. observation)	N	Starr (1988)
<i>Mexillia trivittata</i> (= <i>Mallos trivittatus</i>) (Banks)	virgin	silk	contact	courtship	Indirect (lab. observation)	N	Jackson (1978)
Dysderidae							
<i>Dysdera crocata</i> C. L. Koch		cuticle & silk	contact	courtship	Direct (lab. experiments)	N	Jackson & Pollard (1982)
Eresidae							
<i>Stegodyphus sarasinorum</i> Karsch		silk	contact	attraction	Direct (lab. experiment)	N	Roland (1984)
Hexathelidae							
<i>Hadronyche infensa</i> (= <i>Atrax infensus</i>) Hickman			airborne	attraction	Indirect (field observation)	N	Hickman (1964)
Linyphiidae							
<i>Frontinella communis</i> (Hentz) (= <i>F. pyramitela</i>)	juv. & virgin	cuticle & silk	contact	attraction, orientation & courtship	Direct (field experiments)	N	Suter & Renkes (1982); Suter & Hirscheimer (1986); Suter <i>et al.</i> (1987)
<i>Linyphia tenuipalpis</i> Simon	juv. & virgin	silk	contact	attraction & web damage	Direct (lab. experiment) Chemical analyses	N	Schulz & Toft (1993)

<i>Linyphia triangularis</i> (Clerck)	juv. & virgin	silk	contact	attraction & web damage	Indirect (lab. observations) Direct (lab. experiments) Chemical analyses	N	Locket & Bristowe (1926); Schulz & Toft (1993)
<i>Microlinyphia impigra</i> (O. P. -Cambridge)	virgin	silk			Indirect (chemical analyses)	N	Schulz & Toft (1993)
<i>Neriene clathrata</i> (Sundevall)	virgin	silk			Indirect (chemical analyses)	N	Schulz & Toft (1993)
<i>Neriene emphana</i> (Walckenaer)	virgin	silk			Indirect (chemical analyses)	N	Schulz & Toft (1993)
<i>Neriene</i> (= <i>Linyphia</i>) <i>lütigiosa</i> (Keyserling)	juv. & virgin	cuticle & silk	airborne & contact	attraction & web damage	Direct (field & lab. exp.) Indirect (field observations)	Y	Watson (1986); Watson (1990)
Lycosidae							
<i>Alopecosa</i> (= <i>Tarentula</i>) <i>barbipes</i> (Walckenaer)			contact	courtship	Indirect (lab. observations)	N	Bristowe & Locket (1926)
<i>Alopecosa</i> (= <i>Tarentula</i>) <i>pulverulenta</i> Clerck			contact	courtship	Indirect (lab. observations)	N	Bristowe & Locket (1926)
<i>Arctosa perita</i> (Latreille) (as <i>Trochosa picta</i> Simon)			contact	searching & courtship	Indirect (lab. observations)	N	Bristowe & Locket (1926)
<i>Geolycosa turricola</i> (Treat)	adult	silk		courtship	Indirect (single field observation)	N	Miller & Miller (1986)
<i>Lycosa carbonelli</i> Costa & Capocasa			contact	courtship	Direct (lab. experiments)	N	Costa, Viera & Francescoli (2000)
<i>Lycosa helluo</i> (Walckenaer)		cuticle	contact	courtship	Indirect (lab. observations)	N	Kaston (1936)
<i>Lycosa longitarsis</i> F. P. -Cambridge	juv. & adult	silk	contact	attraction & courtship	Direct (lab. experiments) Solvent extractions	N	Lizotte & Rovner (1989)
<i>Lycosa punctulata</i> Hentz		silk	contact	courtship	Direct (lab. experiments)	N	Tietjen (1979 <i>b</i>)
<i>Lycosa rabida</i> Walckenaer		cuticle & silk	contact	courtship	Indirect (lab. observation) Direct (lab. experiments)	N	Kaston (1936); Tietjen (1979 <i>a</i> , 1979 <i>b</i>)
<i>Lycosa thorelli</i> (Keyserling)			contact	courtship	Direct (lab. experiments)	N	Costa <i>et al.</i> (2000)
<i>Lycosa</i> (= <i>Schizocosa</i>) <i>tristani</i> Banks	adult	silk	contact	attraction & courtship	Direct (lab. experiments) Solvent extractions	N	Lizotte & Rovner (1989)
<i>Pardosa amentata</i> (Clerck)	adult	silk	contact	courtship	Direct (lab. experiments)	N	Richter, Stolting & Vlijm (1971)
<i>Pardosa lapidicina</i> Emerton		cuticle & silk	contact	courtship	Direct (lab. experiments)	N	Dondale & Hegdekar (1973)
<i>Pardosa milvina</i> (Hentz)	adult	cuticle	airborne & contact	attraction & courtship	Direct (lab. experiments) Indirect (lab. observations) Indirect (field collections with females as bait)	Y	Kaston (1936); Hegdekar & Dondale (1969)
<i>Pardosa modica</i> (Blackwall)		cuticle	contact	courtship	Indirect (lab. observations)		Kaston (1936)
<i>Pardosa moesta</i> Banks	adult	cuticle & silk	contact	courtship	Direct (lab. experiments)	N	Hegdekar & Dondale (1969)
<i>Pardosa saxatilis</i> (Hentz)	adult	cuticle & silk	contact	courtship	Indirect (lab. observations) Direct (lab. experiments)	N	Kaston (1936); Hegdekar & Dondale (1969)
<i>Pardosa xerampelina</i> (Keyserling)		silk	contact	searching & courtship	Direct (lab. experiments)	N	Dumais & Perron (1973)

Table 1 (cont.)

Spider taxa	Status of attractive female	Pheromone substratum	Transmission mode	Male response	Tests	Choice exp.	Source
<i>Schizocosa avida</i> (Walckenaer)	virgin	cuticle & silk	contact	courtship	Direct (lab. experiments)	N	Hegdekar & Dondale (1969)
<i>Schizocosa crassipalpa</i> Roewer (as <i>S. crassipalpis</i> [Emerton])	virgin	cuticle & silk	contact	courtship	Direct (lab. experiments)	N	Hegdekar & Dondale (1969)
<i>Schizocosa crassipes</i> (Walckenaer)		silk	contact	courtship	Indirect (lab. observations)	N	Kaston (1936)
<i>Schizocosa ocreata</i> (Hentz)	older virgins	cuticle & silk	airborne & contact	attraction & courtship	Direct (lab. experiments) Indirect (field experiments)	Y	Tietjen (1979 <i>b</i>); Uetz & Denterlein (1979); Tietjen & Rovner (1982); Ayyagari & Tietjen (1986); Roberts & Uetz (2004 <i>a</i> , 2004 <i>b</i> , 2005)
<i>Schizocosa retrorsa</i> (Banks)		silk	contact	courtship	Indirect (lab. observations)	N	Hebets <i>et al.</i> (1996)
<i>Schizocosa rovnerei</i> Uetz & Dondale		silk	contact	searching & courtship	Direct (lab. experiments)		Uetz & Denterlein (1979); Roberts & Uetz (2004 <i>a</i> , 2004 <i>b</i>)
<i>Schizocosa saltatrix</i> (Hentz)		cuticle	airborne	searching	Direct (lab. experiments) Indirect (field experiments)	Y	Tietjen (1979 <i>b</i>); Tietjen & Rovner (1982)
<i>Trochosa ruficola</i> (De Geer)		silk	contact	courtship	Indirect (lab. observations)	N	Bristowe & Locket (1926)
Metidae							
<i>Metellina segmentata</i>		silk			Indirect (another lab. experiment)	Y	Prenter <i>et al.</i> (1994)
Philodromidae							
<i>Tibellus oblongus</i> (Walckenaer)		cuticle	contact	courtship	Indirect (lab. observations)	N	Kaston (1936)
Pisauridae							
<i>Dolomedes fimbriatus</i> (Clerck)		silk	contact	attraction	Direct (lab. experiments)	N	Arnqvist (1992)
<i>Dolomedes scriptus</i> Hentz		cuticle	contact	courtship	Indirect (lab. observations)	N	Kaston (1936)
<i>Dolomedes triton</i> (Walckenaer)	adult	cuticle & silk	waterborne & contact	attraction & courtship	Indirect (lab. experiments)	N	Roland & Rovner (1983)
<i>Pisaura mirabilis</i> (Clerck)			contact	courtship	Indirect (lab. observations)	N	Bristowe & Locket (1926)
Salticidae							
<i>Anasaitis</i> (= <i>Corythalia</i>) <i>canosa</i> (Walckenaer)		silk	contact	courtship	Direct (lab. experiments)	N	Jackson (1987)
<i>Ashtabula furcillata</i> Crane			contact		Indirect (lab. observations)	N	Crane (1949)
<i>Bavia aericeps</i> Simon		silk	contact	courtship	Direct (lab. experiments)	N	Jackson (1987)
<i>Brettus cingulatus</i> Thorell			airborne	searching	Direct (lab. experiments)	N	Pollard <i>et al.</i> (1987)
<i>Carrhotus xanthogramma</i> (Latreille)		silk	contact	searching & courtship	Indirect (field observations) Direct (lab. experiments)	Y	Yoshida & Suzuki (1981)
<i>Corythalia chalcea</i> Crane			contact		Indirect (lab. observations)	N	Crane (1949)

<i>Corythalia tropica</i> (Mello-Leitão) (= <i>C. fulgipedia</i> Crane)		contact		Indirect (lab. observations)	N	Crane (1949)
<i>Corythalia xanthopa</i> Crane		contact		Indirect (lab. observations)	N	Crane (1949)
<i>Cosmophasis micarioides</i> (L. Koch)		silk	contact	courtship	Direct (lab. experiments)	N Jackson (1987)
<i>Cyrba algerina</i> (Lucas)		silk	airborne & contact	courtship		Jackson (1987); Pollard <i>et al.</i> (1987)
<i>Euryattus</i> sp.		silk	contact	courtship		N Jackson & Li (1997)
<i>Euryattus</i> sp.			airborne	searching	Direct (lab. experiment)	N Pollard <i>et al.</i> (1987)
<i>Heliophanus flavipes</i> (Hahn)		silk	contact	courtship	Indirect (lab. observations)	N Bristowe & Lockett (1926)
<i>Helpis minitabunda</i> (L. Koch)		silk	contact	courtship	Direct (lab. experiments)	N Jackson (1987)
<i>Jacksonoides</i> (= <i>Lagnus</i>) <i>kochi</i> Simon		silk	contact	courtship	Direct (lab. experiments)	N Jackson (1987)
<i>Lyssomanes viridus</i> (Walckenaer)			airborne	courtship	Direct (lab. experiments)	Y Pollard <i>et al.</i> (1987)
<i>Marpissa marina</i> Goyen		silk	contact	courtship	Direct (lab. experiments)	N Jackson (1987); Jackson & Cooper (1990)
<i>Menemerus</i> sp.		silk	contact	courtship	Direct (lab. experiments)	N Jackson (1987)
<i>Menemerus bivittatus</i> (Dufour)			contact		Indirect (lab. observations)	N Crane (1949)
<i>Mopsus mormon</i> Karsch		silk	contact	courtship	Direct (lab. experiments)	N Jackson (1987)
<i>Mymarachne lupata</i> (L. Koch)		silk	contact	courtship	Direct (lab. experiments)	N Jackson (1987)
<i>Natta horizontalis</i> Karsch (= <i>N. rufopictus</i> Simon)		silk	contact	courtship		Jackson & Cooper (1990)
<i>Pachomius</i> (= <i>Phiale</i>) <i>dybowskii</i> (Taczanowski)			contact		Indirect (lab. observations)	Crane (1949)
<i>Phidippus audax</i> (Hentz)		silk	contact		Direct (lab. experiments)	see summaries in Roland & Rovner (1983) and Pollard <i>et al.</i> (1987)
<i>Phidippus johnsoni</i> (Peckham & Peckham)	juv. & adult	silk	contact	attraction & courtship	Direct (lab. experiments)	N Jackson (1981, 1986b, 1987)
<i>Phidippus octopunctatus</i> (Peckham & Peckham) (= <i>P. opifex</i> McCook)		silk	contact	courtship	Direct (lab. experiments)	N Jackson (1987)
<i>Phidippus otiosus</i> (Hentz)		silk	contact	courtship	Direct (lab. experiments)	N Jackson (1987)
<i>Phidippus regius</i> C. L. Koch		silk	contact	courtship	Direct (lab. experiments)	N Jackson (1987)
<i>Phidippus whitmani</i> Peckham & Peckham		silk	contact	courtship	Direct (lab. experiments)	N Jackson (1987)
<i>Plexippus paykulli</i> (Andouin)		silk	contact	courtship	Direct (lab. experiments)	N Jackson (1987); Jackson & Cooper (1990)
<i>Portia africana</i> (Simon)				courtship	Indirect (lab. observations)	N Willey & Jackson (1993)
<i>Portia fimbriata</i> (Doleschall)		silk	airborne & contact	attraction & courtship	Indirect (lab. observations) Direct (lab. experiments)	Y Pollard <i>et al.</i> (1987); Willey & Jackson (1993); Clark & Jackson (1995)
<i>Portia labiata</i> (Thorell)		silk	airborne & contact	attraction & courtship	Indirect (lab. observations) Direct (lab. experiments)	Y Pollard <i>et al.</i> (1987); Willey & Jackson (1993); Clark & Jackson (1995)

Table 1 (cont.)

Spider taxa	Status of attractive female	Pheromone substratum	Transmission mode	Male response	Tests	Choice exp.	Source
<i>Portia schultzi</i> Karsch		silk	airborne & contact	attraction & courtship	Direct (lab. experiments)	N	Pollard <i>et al.</i> (1987); Willey & Jackson (1993); Clark & Jackson (1995)
<i>Pseudicius</i> spp.		silk	contact	courtship	Direct (lab. experiments)	N	Jackson (1987)
<i>Semorina brachychelyne</i> Crane			contact		Indirect (lab. observations)	N	Crane (1949)
<i>Simaetha paetula</i> (Keyserling)		silk	contact	courtship	Direct (lab. experiments)	N	Jackson (1987); Jackson & Cooper, 1990)
<i>Simaetha thoracica</i> Thorell		silk	contact	courtship	Direct (lab. experiments)	N	Jackson (1987)
<i>Thiodena sylvana</i> (Hentz)		silk	contact	courtship	Direct (lab. experiments)	N	Jackson (1987)
<i>Trite auricoma</i> (Urquhart)		silk	contact	courtship	Direct (lab. experiments)	N	Jackson (1987); Jackson & Cooper (1990)
<i>Trite</i> (= <i>Euophrys</i>) <i>parvula</i> (Bryant)		silk	contact	courtship	Direct (lab. experiments)	N	Jackson (1987)
<i>Trite planiceps</i> Simon	virgin	silk	contact	attraction	Direct (lab. experiments)	N	Jackson (1987); Taylor (1998)
<i>Uspachus ministerialis</i> (C. L. Koch) (= <i>Phiale flammea</i> Crane)			contact		Indirect (lab. observations)		Crane (1949)
Sparassidae							
<i>Micrommata virescens</i> (Clerck)					Indirect (lab. observations)	N	Bristowe (1926)
Tetragnathidae							
<i>Nephila clavata</i> L. Koch	virgin	cuticle	airborne	attraction			Miyashita & Hayashi (1996)
<i>Nephila edulis</i> (Labillardière)	virgin	silk	contact	courtship	Direct (lab. experiments)	Y	A. C. Gaskett (unpublished data)
Theridiidae							
<i>Achaearanea wau</i> Levi	juv. & adult		airborne & contact	attraction & courtship	Indirect (field observations)	N	Lubin (1986)
<i>Anelosimus cf. jucundus</i> (O. P. -Cambridge)			airborne	courtship	Indirect (lab. observation)	N	Bukowski & Avilés (2002)
<i>Argyrodes antipodanus</i> (O. P. -Cambridge) (= <i>A. antipodiana</i>)	adult	silk	contact	courtship & web damage	Direct (lab. experiments)	N	Whitehouse & Jackson (1994)
<i>Latrodectus hasselti</i> Thorell	virgin	silk	airborne & contact	attraction & courtship	Direct (field & lab. experiments)	Y	Andrade & Kasumovic (2005); Kasumovic & Andrade (2006)
<i>Latrodectus hesperus</i> Chamberlin & Ivie	virgin, mated & juv.	silk	airborne & contact	attraction & courtship	Direct (field experiments) Indirect (lab. observations)	Y	Ross & Smith (1979); Kasumovic & Andrade (2004)

<i>Latrodectus mactans</i> Fabricius	adult & juv.	silk	contact	courtship & web damage	Indirect (lab. observations) Direct (lab. experiments)	N	Ross & Smith (1979); Breene & Sweet (1985)
<i>Latrodectus revivensis</i> Shulov	adult	silk	airborne & contact	courtship & web damage	Indirect (field observations) Direct (lab. experiments)	N	Anava & Lubin (1993); Segev et al. (2003); Schulz (2004)
<i>Theridion sisyphium</i> (Clerck)		silk	contact	attraction	Indirect (lab. observations)	N	Locket & Bristowe (1926)
Thomisidae							
<i>Diaea dorsata</i> (Fabricius)					Indirect (lab. observation)	N	Bristowe (1926)
<i>Misumena vatia</i>					Indirect (lab. observation)	N	Bristowe (1926), but see Anderson & Morse (2001)
<i>Xysticus auctificus</i> Keyserling				attraction	Indirect (field collection with synthetic compounds)	N	Aldrich & Barros (1995)
<i>Xysticus cristatus</i> (Clerck)			contact		Indirect (lab. observation)	N	Bristowe (1926)
<i>Xysticus discursans</i> Keyserling				attraction	Indirect (field collection with synthetic compounds)	N	Aldrich & Barros (1995)
<i>Xysticus ferox</i> (Hentz)				attraction	Indirect (field collection with synthetic compounds)	N	Aldrich & Barros (1995)
<i>Xysticus triguttatus</i> Keyserling			contact	attraction & courtship	Indirect (lab. observation & field collection with synthetic compounds)	N	Kaston (1936); Aldrich & Barros (1995)
Mygalomorphae							
Antrodiaetidae							
<i>Aliatyopus gulosus</i> Coyle		silk	contact		Indirect (field observations)	N	Coyle & Icenogle (1994)
Theraphosidae							
<i>Acanthoscurria</i> <i>suina</i> Pocock		silk	contact	courtship	Indirect (lab. observations)	N	Costa & Pérez-Miles (2002)
<i>Catumiri</i> (= <i>Oligoxystre</i>) <i>argentinense</i> (Mello-Leitão)		silk	contact	courtship	Indirect (lab. observations)	N	Costa & Pérez-Miles (2002)
<i>Eupalaestrus</i> <i>weijenberghi</i> (Thorell)		silk	contact	courtship	Indirect (lab. observations)	N	Costa & Pérez-Miles (2002)
<i>Grammostola iheringi</i> (Keyserling)		silk	contact	courtship	Indirect (lab. observations)	N	Costa & Pérez-Miles (2002)
<i>Grammostola mollicoma</i> (Ausserer)		silk	contact	courtship	Indirect (lab. observations)	N	Costa & Pérez-Miles (2002)
<i>Plesiopelma</i> <i>longisternale</i> (Schiapelli & Gerschman)		silk	contact	courtship	Indirect (lab. observations)	N	Costa & Pérez-Miles (2002)

pheromones, as occurs for the salticids *Portia labiata* (Thorell), *Portia fimbriata* (Doleschall) (Clark & Jackson, 1995), and *Trite planiceps* Simon (Taylor, 1998). In several spider species however, both females and males emit and respond to pheromones. For example, the silk from females of the social spider *Stegodyphus sarasinorum* Karsch (Eresidae) attracts other females (Roland, 1984), and male silk attracts females in the web-building spiders *Tegenaria domestica* (Clerck) (Agelenidae) and *Coelotes terrestris* (Wider) (Amaurobiidae, previously Agelenidae; Roland, 1984). Male silk affects the courtship behaviour of conspecific males in a widow spider *Latrodectus hesperus* Chamberlin & Ivie (Theridiidae; Ross & Smith, 1979), a sheet-web spider *Frontinella communis* (Hentz) (= *F. pyramitela*, Linyphiidae; Suter, Shane & Hirscheimer, 1987), a wolf spider *Schizocosa ocreata* (Hentz) (Lycosidae; Ayyagari & Tietjen, 1986), and a jumping spider *Carrhotus xanthogramma* (Latreille) (Salticidae; Yoshida & Suzuki, 1981). Thus, comprehensive assessments of pheromone use by a species should avoid any assumptions as to the roles of the sexes in communication.

(1) Sources of sex pheromones

Female spiders emit sex pheromones from their body cuticle and/or web silk (Table 1). Spider silk is a well-known vector for chemical, vibratory, tactile, and visual signals (e.g. Stowe, Tumlinson & Heath, 1987; Craig & Bernard, 1990; Singer *et al.*, 2000; Anderson & Morse, 2001). Sex pheromones from spider silk have been studied more assiduously, and are more widely reported, than sex pheromones emitted directly from spider cuticles (Table 1). Using silk or webs for pheromone transmission may provide females with the advantage of continuous pheromone emission without the need actively to emit pheromones from glands, which may hinder other activities such as catching prey (Schulz, 1997), or attract predators directly to the spider's body; see Zuk & Kolluru (1998) for a general review of signal exploitation by parasitoids. Silk pheromones may be produced in the silk glands (Schulz, 2004), or could be cuticular in origin, and only applied to the silk during web construction (Trabalon, Niogret & Legrand-Frossi, 2005).

Cuticular pheromones may be synthesised near the integument and transported to the epicuticle for emission (Trabalon *et al.*, 1996), possibly *via* modified cuticular wax glands or abdominal organs (Tietjen & Rovner, 1982; Pollard, Macnab & Jackson, 1987). The specific glands that secrete pheromones in spiders are unknown (Papke, Riechert & Schulz, 2001), although some putative structures have been identified for the wolf spider *Alopecosa cuneata* (Clerck) (Lycosidae; Kronstedt, 1986).

The genetics and regulation of pheromone production in spiders remain largely unstudied (Schulz, 2004), although a hormone involved in the synthesis or release of female sex pheromones has been identified for the agelenid *Tegenaria atrica* C.L. Koch (Trabalon *et al.*, 2005). Injection of the ecdysteroid 20-hydroxyecdysone (20E), normally only found in virgin female *T. atrica* during oocyte development, stimulated vitellogenesis, increased the quantity of male-attracting compounds on female silk and cuticle, decreased female cannibalism, and increased her sexual receptivity (Trabalon *et al.*, 2005).

(2) Sex pheromone transmission

Female spiders may emit volatile, airborne pheromones and/or pheromones that require contact between emitter and receiver (Table 1). Pheromones with these transmission modes may have different functions: airborne sex pheromones typically attract males, but rarely elicit courtship (Table 1). Airborne pheromones may function primarily as long-range attractants that cannot accurately indicate the emitter's location, especially if females aggregate. Species with airborne cuticular pheromones include the funnel-web spider *Hadronyche infensa* Hickman (Hexathelidae, as *Atrax infensus* [Dipluridae]; Hickman, 1964), the wolf spider *Pardosa milvina* (Hentz) (Lycosidae; Searcy, Rypstra & Persons, 1999), and the orb-web spiders *Nephila clavata* L. Koch (Tetragnathidae; Miyashita & Hayashi, 1996), *Argiope keyserlingi* Karsch (Araneidae; Gaskett *et al.*, 2004), and potentially, *Argiope trifasciata* (Forskål) and *Araneus trifolium* (Hentz) (Araneidae; Olive, 1982).

Airborne pheromones appear to be largely absent in the jumping spiders (Salticidae; e.g. Crane, 1949; Jackson, 1987). Salticids are renowned for their excellent vision, and visual signals are often sufficient to stimulate male courtship (Crane, 1949). However, contact pheromones in silk draglines are very common amongst the Salticidae and typically elicit male courtship (Table 1). Pheromones may assist communication at salticid nests, which are usually concealed beneath rocks or in rolled leaves that hinder visual display (Pollard *et al.*, 1987). Wolf spiders (Lycosidae) also use silk contact pheromones extensively, but airborne pheromone use is occasionally reported, e.g. by *Schizocosa saltatrix* (Hentz) (Table 1; Tietjen, 1979b). Habitat differences such as dampness and foliage density, which may influence silk deposition, could limit contact silk pheromone use in the Lycosidae (Tietjen & Rovner, 1982).

Contact pheromones may provide the receiver with more specific information about the emitter than is available *via* airborne signals. For example, males of web-building species may use airborne silk or cuticular pheromones to determine a female's general location, and contact pheromones from silk for further details about her species identity or quality as a mate (Krafft, 1982; Tietjen & Rovner, 1982; Gaskett *et al.*, 2004). This could be vital for cannibalistic or aggressive species because males that can correctly identify a female's qualities from her silk have the strong selective advantage of being able to reject an unattractive female before entering her web and risking death. This pattern is apparent in the ground-dwelling lycosid *Schizocosa ocreata*, in which airborne pheromones from hidden females elicit male searching behaviour (Tietjen & Rovner, 1982), whereas contact with female silk elicits both searching and courtship (Roberts & Uetz, 2005). Male *S. ocreata* respond most quickly to the silk of virgin, adult females, which are more sexually receptive and less aggressive than mated females (Roberts & Uetz, 2005).

III. RECEPTION OF SEX PHEROMONES

After emission, pheromones are detected by the receiver's chemosensitive cells. In the chelicerates these are located in

specialised abdominal appendages, palps, or walking legs (Strausfeld *et al.*, 1987). For example, in the whip spiders (Amblypygidae) and whip scorpions (Uropygidae) the forelegs have hundreds of sensilla and convoluted mushroom bodies, and function as antenniform chemoreceptors (Strausfeld *et al.*, 1987; Hebets & Chapman, 2000). Scorpions have a pair of specialised chemosensitive pectines attached to the first abdominal segment (Strausfeld *et al.*, 1987) and chemosensory sensilla on their pedipalps (Melville, Tallarovic & Brownell, 2003). In spiders, the probable location of male chemoreceptors is on the pedipalps, which are used to transfer sperm, or on the forelegs or tarsi. There are several examples of male spiders using their pedipalps, forelegs or tarsi to handle female silk during courtship, e.g. the wolf spiders *Pardosa lapidicina* Emerton (Dondale & Hegdekar, 1973), *Schizocosa retrorsa* (Banks) (Hebets, Stratton & Miller, 1996), and several other lycosid species (Bristowe & Locket, 1926). When contacting female silk, male spiders frequently groom their own legs and pedipalps, e.g. *Agelenopsis aperta* (Gertsch) (Agelenidae; Papke *et al.*, 2000), and *Argiope keyserlingi* (Araneidae; Gaskett *et al.*, 2004). Self-grooming of the palps, tarsal or palpal rubbing of the female, and gustation, or tasting, of female silk all indicate male sexual stimulation in spiders (Bristowe & Locket, 1926; Locket & Bristowe, 1926; Robinson & Robinson, 1980).

Putative chemoreceptive sensilla have been identified *via* scanning electron microscopy on the tarsi and pedipalps of male *Latrodectus hesperus* (Theridiidae; Ross & Smith, 1979), and the pedipalps of male *Cupiennius salei* (Kerserling) (Ctenidae; Tichy *et al.*, 2001). For *C. salei*, the chemoreceptive role of these sensilla was confirmed by electrophysiological recordings made during exposure to female silk, male silk, and synthetic female sex pheromone (Tichy *et al.*, 2001). The chemoreceptive sensilla of *C. salei* were each tipped with a pore, similar to structures identified as putative chemoreceptors in the orb-web spider *Araneus diadematus* Clerck (Araneidae), and in some lycosids and other arthropods (Foelix & Chu-Wang, 1973; Kronstedt, 1979). The location of olfactory chemoreceptors for airborne, volatile pheromones is currently unknown (Foelix, 1996). Female spiders lack pedipalps, but putative chemoreceptors on their legs have been examined by electron microscopy (Ross & Smith, 1979). There is strong behavioural evidence that females of various spider species can detect odours from males (Ross & Smith, 1979; Roland, 1984), females (Suter, Shane & Hirscheimer, 1989; Anava & Lubin, 1993), offspring (Trabalon *et al.*, 1996), prey (Allan, Elgar & Capon, 1996), predators (Persons & Rypstra, 2001), and kleptoparasites (Suter *et al.*, 1989). The locations and structures of female chemoreceptors could be surmised from further studies performed on male spiders, which may be the easier sex to study given the strong responses elicited from males by female pheromones.

In the chelicerates, olfactory stimuli are generally processed in mushroom-body-like neuropils in the supraoesophageal ganglion (Strausfeld *et al.*, 1987). These are not necessarily homologous to the mushroom bodies of insects, but serve similar functions (Foelix, 1996). Insect mushroom bodies are neuropils composed of thousands of densely packed parallel neurons or Kenyon cells, separated from the

rest of the brain by a thin layer of glia lamellae, and located only two synapses away from the antennal chemoreceptors (Heisenberg, 1998). Insect mushroom bodies have been associated with learning, memory function and spatial orientation, which may indicate that behavioural responses to odours arise from learned associations (Strausfeld *et al.*, 1987; Hebets & Chapman, 2000). Insect mushroom bodies are also essential for short-term memory in odour discrimination (Heisenberg, 1998).

IV. SEX PHEROMONE STRUCTURE AND IDENTITY

Currently, sex pheromones have been conclusively identified in only three spider species: the sheet-web spider *Linyphia triangularis* (Clerck) (Linyphiidae; Schulz & Toft, 1993b), the wandering spider *Cupiennius salei* (Ctenidae; Papke *et al.*, 2000), and the orb-web spider *Agelenopsis aperta* (Agelenidae; Papke *et al.*, 2001). Female *L. triangularis* attract males to their webs with airborne (*R*)-3-hydroxybutyric acid (HBA) and crotonic acid, also known as 2-butenic acid (Fig. 1; Schulz, 2004). Once a male arrives on a web, a second compound, (3*R*,3*R'*)-3-(3-hydroxybutyryloxy)-butyric acid (HBBA), stimulates him to damage and roll up the web, reducing the emission of pheromones that may attract other males (Fig. 1; Schulz & Toft, 1993b; Schulz, 2004). After mating, female *L. triangularis* rebuild their webs without HBA or HBBA (Schulz & Toft, 1993b). HBA and HBBA have also been found in the silk of virgin females of other species in the genera *Linyphia*, *Microlinyphia*, and *Neriene* (Schulz, 1997).

Interestingly, the web-damage pheromone HBBA degrades under natural conditions to form the airborne attractant pheromones (HBA and crotonic acid), thus if HBBA is applied during web construction, there will be a steady release of male-attractants from the web over time (Schulz & Toft, 1993b; Schulz, 1997, 2004). HBBA is a long-chain-methyl-branched 1-methoxyalkane, a class of ether lipids first found in spider silk (Schulz & Toft, 1993a).

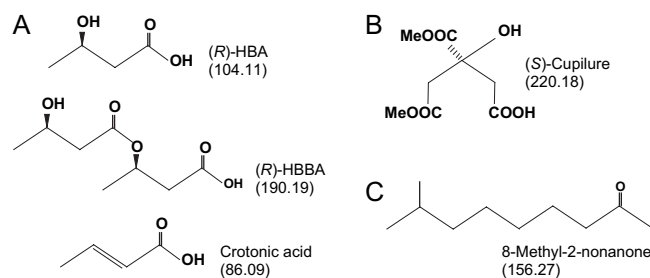


Fig. 1. Structure of sex pheromones of three spiders (Araneae). A) *Linyphia triangularis* (Linyphiidae; Schulz, 2004; Schulz & Toft, 1993a, 1993b), B) *Cupiennius salei* (Ctenidae; Tichy *et al.*, 2001), and C) *Agelenopsis aperta* (Agelenidae; Papke *et al.*, 2001). Values in parentheses are relative molecular masses (u). (*R*)-HBA is (*R*)-3-hydroxybutyric acid; (*R*)-HBBA is (3*R*,3*R'*)-3-(3-hydroxybutyryloxy)-butyric acid; Crotonic acid is 2-butenic acid; (*S*)-Cupilure is (*S*)-1'-dimethyl citrate [also known as (*S*)-3,4-di(methoxycarbonyl)-3-hydroxybutanoic acid].

Trials with 1-methoxyalkanes from the silk of female *Latrodectus rewilvensis* Shulov demonstrated that they also attract conspecific males (Schulz, 2004). It was originally thought that 1-methoxyalkanes were unique to spiders and may assist in conspecific recognition because they could not be confused or contaminated with compounds from other sources such as captured prey (Schulz, 1997). However, HBA and HBBA are also produced by a fungus (Quang *et al.*, 2003), which perhaps emphasises the ubiquity of chemical compounds used for signalling by diverse taxa (see Wyatt, 2003).

Spider sex pheromones may have evolved from metabolic by-products, or compounds produced during silk manufacture or moulting (Kittredge & Takahashi, 1972; Ross & Smith, 1979; Miyashita & Hayashi, 1996; Schulz, 2004). The production of HBA and HBBA by female spiders may be closely linked to primary metabolism because HBA is an intermediate of fatty acid biosynthesis (Tichy *et al.*, 2001). Intriguingly, micro-organisms could be involved in the production of HBBA. Micro-organisms commonly store carbon as a polymer of HBBA, and some produce enzymes that selectively cleave the polymer into HBBA (Schulz & Toft, 1993b). However, these micro-organisms have not been identified on the silk of *L. triangularis* or any other spider thought to use HBA and HBBA as sex pheromones.

The sex pheromone on the silk of female *Cupiennius salei* can also be closely related to primary metabolites (Papke *et al.*, 2000). (*S*)-Cupilure, or (*S*)-1'1-dimethyl citrate [also known as (*S*)-3,4-di(methoxycarbonyl)-3-hydroxybutanoic acid], can be formed from citric acid by double methylation, resulting in two esterified carboxyl groups that provide volatility (Fig. 1). Cupilure is received by males *via* direct contact, and stimulates male courtship and vibratory signalling (Papke *et al.*, 2000). Cupilure has also been found in the silk of females from sympatric congeners *Cupiennius getazi* Simon and *Cupiennius coccineus* F.O.P. –Cambridge (Schulz, 2004). Silk from females of these species often elicits courtship from male *C. salei* (Barth, 1993).

The only other spider sex pheromone identified thus far is produced by adult female *Agelenopsis aperta* (Papke *et al.*, 2001). Two methylated ketones, 8-methyl-2-nonanone and 6-methyl-3-heptanone, were found only in the cuticles of sexually receptive virgin females, but tests with synthetic versions determined that only the former attracted males and elicited courtship (Fig. 1; Papke *et al.*, 2001).

The relative molecular masses of these spider sex pheromone compounds (see Fig. 1) are slightly below the typical range for insect sex pheromones (200–300u; Wyatt, 2003). The carbon chain lengths of spider pheromones (Fig. 1) are similar to those of ant alarm pheromones, which are generally short-lived and highly volatile (Wyatt, 2003). The double bonds and chirality observed in the three known spider sex pheromones (Fig. 1) are also common in hymenopteran sex pheromones (Ayasse, Paxton & Tëngo, 2001).

Most of the spider sex pheromones identified thus far are lipids or lipid soluble. Both spider silk and spider cuticles are covered in a lipid layer, which is protective and regulates water balance (Schulz, 1997; Prouvost *et al.*, 1999). This lipid layer would also act as a solvent for any lipid-based pheromones (Schulz, 1997). Several studies suggest a lipid form for spider sex pheromones. For example, males of *Dysdera*

crocata C.L. Koch (Dysderidae; Jackson & Pollard, 1982), *Linyphia triangularis* (Linyphiidae; Schulz, 2004), the wolf spider *Pardosa milvina* (Lycosidae), and the fishing spider *Dolomedes scriptus* Hentz (Pisauridae; Kaston, 1936) respond to extracts of female cuticle or silk made with lipophilic solvents such as diethyl ether or dichloromethane. However, males of another lycosid, *Schizocosa crassipalpa* Roewer (as *S. crassipalpis*) did not respond to extracts of female silk made with the lipid solvents benzene or ether; thus the pheromones of *S. crassipalpa* may be highly polar lipids, which could be better extracted with chloroform (Hegdekar & Dondale, 1969).

Other species with sex pheromones that are soluble in water or other polar solvents (e.g. methanol) include the lycosid *Pardosa lapidicina* (Dondale & Hegdekar, 1973), the agelenid *Tegenaria atrica* (Prouvost *et al.*, 1999), the red-back spider *Latrodectus hasselti* Thorell (Theridiidae; J. A. Stoltz, J. McNeil & M. C. B. Andrade, unpublished data), the linyphiid *Frontinella communis* (Suter & Renkes, 1982), and several species of Salticidae (Jackson, 1987). Furthermore, quantitative changes in polar compounds on the silk and cuticles of females correlate significantly with changes in female sexual receptivity in *Tegenaria atrica* and *Tegenaria domestica* (Trabalon *et al.*, 1996, 2005; Prouvost *et al.*, 1999), and also with the likelihood of male courtship in *T. atrica* (Trabalon *et al.*, 2005). However, the pheromones of female fishing spiders (*Dolomedes* spp.: Pisauridae) spread on the surface of water in the manner of a mildly polar or non-polar compound, possibly a lipid or steroid (Roland & Rovner, 1983). The silk pheromones of female lycosids of *Lycosa tristani* Banks and *Lycosa longitarsis* F.P. –Cambridge are also unaffected by water (Lizotte & Rovner, 1989), and those of male *Schizocosa ocreata* have both polar and non-polar lipid components (Ayyagari & Tietjen, 1986). Since the polarity of spider pheromones appears to vary (possibly according to habitat and ecology), several different solvents should be tested when attempting to extract sex pheromones from silk or cuticles. The current literature may also be somewhat misleading given that mechanical features of the silk can be affected by extraction with solvents, including water (see Shao & Vollrath, 1999; Schulz, 2004), and that mechanical stimuli alone may encourage males to follow silk in some circumstances (Anderson & Morse, 2001). However, the frequency of water exposure in natural circumstances suggests that wetting with water or similar solvents must have negligible or manageable effects on sex pheromone function.

V. ELECTROPHYSIOLOGICAL METHODS FOR IDENTIFYING SEX PHEROMONES

Identification and quantification of spider pheromones is an important contribution to understanding spider behaviour and mating. This has been notoriously difficult because many compounds of unknown function are typically present in extracts of spider cuticles and silk (e.g. Trabalon *et al.*, 1996; Trabalon, Bagnères & Roland, 1997). Potentially time-consuming methods for identifying sex pheromones have involved comparison of gas chromatograph output for

extracts prepared from attractive and unattractive females (e.g. Prouvost *et al.*, 1999), or separating, identifying and testing every compound from an extract for behavioural responses from the receiver (Cork *et al.*, 1990). Some studies of olfactory stimulants in various taxa combine gas-chromatography and electrophysiological recordings to identify accurately which extracted compounds are olfactory stimulants (Cork *et al.*, 1990; Schiestl & Marion-Poll, 2002). Electrophysiological measurements of this type were first applied to a spider species by Tichy *et al.* (2001). Compounds present on the silk of female wandering spiders of *Cupiennius salei* (Ctenidae) were initially extracted, separated, and then identified with gas chromatography and mass spectrometry (Papke *et al.*, 2000). Putative chemoreceptive sensory cells on the pedipalps of male spiders were then identified with scanning and transmission electron microscopy (Tichy *et al.*, 2001). A recording electrode was inserted into the chemoreceptors while they were exposed to the putative pheromone, to monitor the generation of action potentials indicating a positive chemo-response.

Greater parsimony may be achieved by coupling the electrophysiological measurements directly with simultaneous gas chromatography, as occurs in insect studies with gas chromatography-electroantennography, or GC-EAD (Cork *et al.*, 1990; Jones & Oldham, 1999; Schiestl & Marion-Poll, 2002). Mounting an insect antenna between electrodes in a GC-EAD apparatus allows chemoreceptor responses to be tested with every chemical compound in an extract at the same time as the compounds are separated by the gas chromatograph (Cork *et al.*, 1990; Jones & Oldham, 1999). In this way, compounds that stimulate chemoreceptor responses can be identified from multiple non-target compounds sampled during extraction, although this prevents study of responses to multiple compounds received simultaneously in blends (Schiestl & Marion-Poll, 2002). Once physiologically active compounds have been identified, their structure could be determined with mass spectrometry, and the compounds may be synthesised for use in behavioural experiments. These behavioural assays are essential because chemoreception of a compound does not necessarily indicate its behavioural relevance or role (Schiestl & Marion-Poll, 2002). Application of such electrophysiological techniques to studies of spider sex pheromones promises some interesting results and elegant experimental opportunities, particularly for the identification of airborne pheromones which have so far proved more difficult to study than pheromones received *via* contact. As more spider pheromones are identified, general patterns of pheromone structure and identity may become apparent, contributing to understanding of pheromone biosynthesis and the evolution of chemical communication.

VI. BEHAVIOURAL ASSAYS TESTING FOR SEX PHEROMONES

Circumstantial evidence of sex pheromones in spiders has been gathered from observations of male responses to serendipitous contact with silk draglines in the field, or

during staged matings in the laboratory (e.g. Coyle & Shear, 1981; Yoshida & Suzuki, 1981; Edwards & Edwards, 1990; Costa & Pérez-Miles, 2002; see Table 1). Placing males in boxes previously inhabited by females and recording male behaviour and courtship (e.g. Bristowe & Lockett, 1926) also provides indirect evidence of sex pheromones. Drawing strong conclusions from indirect tests can be problematic because of the lack of control for mechanical cues provided by the silk, which may also elicit male searching behaviour (Platnick, 1971; Anderson & Morse, 2001). More compelling evidence of contact sex pheromones has been gathered by exposing spiders to silk draglines in controlled experiments (e.g. Hegdekar & Dondale, 1969; Lizotte & Rovner, 1989; Clark & Jackson, 1995; Anderson & Morse, 2001; Roberts & Uetz, 2005; see Table 1). Testing for airborne pheromones has involved placing caged females or female silk in the field to attract wild males (e.g. Olive, 1982; Searcy *et al.*, 1999; Gaskett *et al.*, 2004; Kasumovic & Andrade, 2004).

Exposing spiders to solvent extracts of silk or cuticle removes potentially confounding behavioural signals or mechanical cues. Extracts should be made with both polar and non-polar solvents to ensure the pheromones have been dissolved (e.g. Ayyagari & Tietjen, 1986; Lizotte & Rovner, 1989; Schulz & Toft, 1993*b*; but see Shao & Vollrath, 1999). Male responses to silk or cuticular extracts can be quantified by measuring male courtship behaviours. For example, comparisons of palpal drumming by male *Tegenaria atrica* when exposed to full or fractionated extracts of female silk or cuticle, or to synthetic or control compounds, elegantly revealed which compounds or classes of compounds act as sex pheromones in this species (Trabalon *et al.*, 2005).

The functions and roles of spider pheromones in mating strategies have often been investigated using choice tests, in which animals are exposed to more than one signal simultaneously (Table 1). Olfactometers for typical choice tests are made from glass or plastic and consist of a central hub with radiating arms leading to various options between which the test animal can choose (Fig. 2). The choice may be between live animals, or silk or exuviae, which may vary according to sex, conspecific or heterospecific status, and sexual maturity or age. Between assays, the apparatus must be washed to remove any pheromones or silk deposited by the test animal or the choice options. Test animals are sometimes introduced into the choice apparatus *via* an entry arm (e.g. Riechert & Singer, 1995; Taylor, 1998; Searcy *et al.*, 1999; Gaskett *et al.*, 2004), are placed directly into the central hub (e.g. Riechert & Singer, 1995; Searcy *et al.*, 1999), or are positioned initially with a randomly chosen option and monitored to determine whether they move or stay (e.g. Prenter, Elwood & Montgomery, 1994). Some studies using Lycosidae provided males with one large arena in which the test options were evenly spaced (Ayyagari & Tietjen, 1986; Roberts & Uetz, 2004*a*, 2005; Fig. 2). For the semi-aquatic fishing spiders, *Dolomedes* spp., experiments have been carried out in aquaria, with floating blocks covered in silk draglines (Roland & Rovner, 1983; Arnqvist, 1992).

An inherent problem with the design of a choice test apparatus is the risk that test animals may simply follow a wall into its corresponding choice arm thus appearing to make

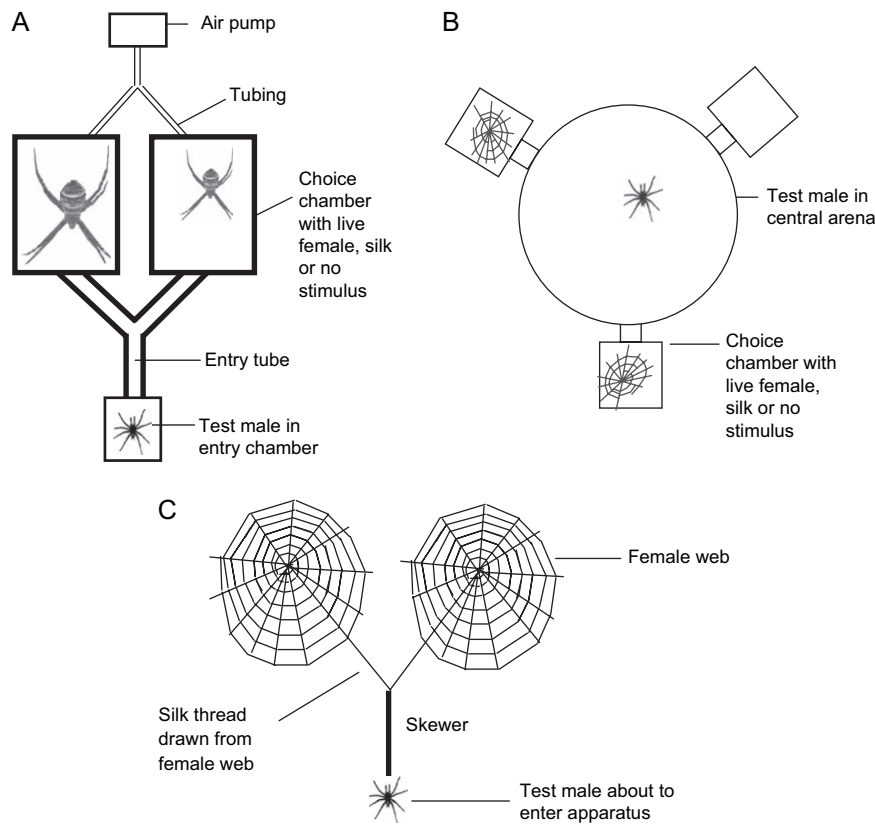


Fig. 2. Typical choice test designs for assessing spider sex pheromones. Equipment for investigating airborne pheromones from cuticle or silk (A), contact pheromones from cuticle or silk (B), and contact pheromones from silk (C).

a choice without actually requiring a specific behavioural response to a signal (Hegdekar & Dondale, 1969). For orb-web species (Araneidae), a thread can be strung through the entry and choice arms of the olfactometer from a knot in the central hub (e.g. Gaskett *et al.*, 2004). Male spiders hang from the string and cannot touch or follow the walls as they explore the apparatus. If the test animal reaches the knot, he can proceed down either of the 'choice' arms, or return to the entry chamber. However, perhaps the most effective safeguard against such biases are large sample sizes, adequate controls, and careful experimental design and statistical analyses.

Some studies include choice tests with an empty control arm (e.g. Tietjen, 1979*b*; Roland, 1984; Searcy *et al.*, 1999; Gaskett *et al.*, 2004). This tests for male ability to detect signals emitted by a test option, or whether males will accept a less-attractive female if no others are available. For example, in choice tests males of some agelenid and araneid species chose conspecifics over heterospecifics, but chose a heterospecific female if she was paired with an empty control arm (Roland, 1984). This may reflect strategic male mate choice according to the costs of searching for a mate. For example, although male red-back spiders (*Latrodectus hasselti*; Theridiidae) prefer the silk of virgin females (Andrade & Kasumovic, 2005), males have very high mate search costs (Andrade & Banta, 2002), which may mean they will accept a mated female if no other females are immediately available.

In some studies, females are assigned the status of 'attractive' or 'unattractive' before experimentation by

exposing them to males and monitoring male responses (e.g. Jackson & Pollard, 1982; Riechert & Singer, 1995). However, individual females of various spider taxa vary in their attractiveness to males over short time periods (Crane, 1949; Krafft, 1982; Tietjen & Rovner, 1982; Jackson & Cooper, 1990). Females may also be most attractive for specific periods such as just after moulting to adulthood, e.g. *Nephila clavata* (Miyashita & Hayashi, 1996), or more than one week after moulting, e.g. *Schizocosa ocreata* (Roberts & Uetz, 2005). Thus, females should ideally be collected from the field during their early instars and choice tests should involve females before and after their final moult (i.e. before and after they have reached sexual maturity), at different ages, and before and after mating to ensure testing occurs during the pheromone emission period.

Male sexual status and previous experience can also influence male mate choice behaviour and this must be controlled for carefully. For example, virgin male *Argiope keyserlingi* are strongly attracted to the silk and bodies of virgin but not mated females (Gaskett *et al.*, 2004). However, after a male has mated, he is equally attracted to virgin and mated females. If the males had been collected as adults rather than juveniles, they could have already mated, and thus the choice test results would incorrectly suggest that male *A. keyserlingi* do not choose females according to their mating status, or that the species lacks female sex pheromones. Controlling for male sexual status is most pertinent when studying species such as *A. keyserlingi*

(Araneidae) and the red-back spider *Latrodectus hasselti* (Theridiidae), in which males are limited to very few copulations (Andrade & Banta, 2002; Herberstein *et al.*, 2005) and thus a male's mate choice is likely to be affected by his potential for future matings.

Choice tests can use different definitions of 'choice'. Some studies record the first choice of a test animal (e.g. Riechert & Singer, 1995; Gaskett *et al.*, 2004), however, this assumes that the male spider has been able to assess both options adequately before making his choice. Other studies use the male's final choice, or the option with which he spent the most time (e.g. Tietjen, 1979*b*; Prenter *et al.*, 1994; Taylor, 1998), but this may involve some subjectivity from the observer when deciding if the final choice has been made, or the duration of each trial. However, studies that compare males' first choices with the choice with which males spent most time found no significant differences (e.g. Gaskett *et al.*, 2004; Andrade & Kasumovic, 2005). The observer could use a reliable indicator of male mate choice such as the commencement of male courtship behaviour. Other behavioural changes used as indicators of male awareness of pheromones include increased searching behaviour and slower locomotion (e.g. Yoshida & Suzuki, 1981; Tietjen & Rovner, 1982; Roberts & Uetz, 2004*a*). Rigorous studies could include more than one indicator of male choice, and compare the results gained for each indicator.

VII. FEMALE PHEROMONE EMISSION AND MATING BEHAVIOUR

Female pheromones may be specific to female age, level of sexual maturity and/or mating history. For example, for sheet-web spiders of *Tegenaria atrica* the composition of cuticular pheromones changes with age (Trabalon *et al.*, 1996). Males that recognise female reproductive maturity or mating history according to female pheromones can choose mates that provide a higher reproductive success. Male mate choice is likely to reflect the risk of sperm competition, which is expected to vary with female sexual maturity or sexual status (Bonduriansky, 2001).

(1) Pheromone emission by juvenile females

In species with first-male sperm priority the first male to mate with a female sires the majority of her offspring. A male spider can ensure he is a female's first partner by responding to the pheromones of a juvenile female, waiting on her web, and mating with her as soon as she has her final moult. Cohabitation with juvenile females is common in several spider taxa (Robinson, 1982; Jackson, 1986; Pollard *et al.*, 1987). First-male sperm priority and attraction to juvenile females occur in the linyphiids *Frontinella communis* (as *F. pyramitela*; Suter & Renkes, 1982), *Linyphia tenuipalpis* Simon and *Linyphia triangularis* (Toft, 1989; Schulz & Toft, 1993*a*), and *Neriene litigiosa* (Keyserling) (as *Linyphia l.*; Watson, 1986). Males may also benefit from cohabiting with juvenile females if they can mate with the female

during her final moult and avoid her aggression or resistance, as occurs in the social spider *Achaearanea wau* Levi (Theridiidae; Lubin, 1986). A single report of a male mating with a soft-cuticled and recently moulted female exists for the salticid *Corythalia tropica* (Mello-Leitão) (as *C. fulgipedia* Crane; Crane, 1949).

Male preference for juvenile rather than adult females was absent in tests with the lycosids *Pardosa milvina* (Searcy *et al.*, 1999), *Pardosa saxatilis* (Hentz), and *Schizocosa avida* (Walckenaer) (Hegdekar & Dondale, 1969). For all three species, female mating status (i.e. virgin or previously mated) did not affect male response. However, this does not prove an absence of first-male sperm priority. The entelogyne structure of female lycosid genitalia has been associated with first-male sperm priority (Austad, 1982), although genital morphology is not necessarily a reliable predictor of sperm use patterns (see Uhl, 2000). Furthermore, some male lycosids have behavioural strategies that are typical of species with first-male sperm priority, such as cohabitation with juveniles until mating has occurred, e.g. *Geolycosa turricola* (Treat) and *Lycosa tarantula* (Linnaeus) (Miller & Miller, 1986; Fernández-Montraveta & Cuadrado, 2003), and possibly, transferral of ejaculate products that inhibit female remating (Aisenberg & Costa, 2005). Male lycosids will also court juvenile females upon contact with the females' bodies (Bristowe & Lockett, 1926; Kaston, 1936) or silk (Lizotte & Rovner, 1989). It may be that male lycosids cannot identify when females reach sexual maturity. If so, cohabitation with penultimate females may function to ensure a male is a female's first mate (Fernández-Montraveta & Cuadrado, 2003).

Juvenile females may benefit from emitting pheromones because they can mate with a male immediately upon maturity, or if competition between the attracted males selects for high mate quality. For example, juvenile female sierra dome spiders *Neriene litigiosa* attract males to their webs with airborne pheromones (as *Linyphia l.*; Watson, 1990). As males arrive at a female's web, they fight to expel all other potential suitors. When the female becomes sexually mature she copulates immediately with the male who has successfully evicted all other males. Thus, by signalling prior to sexual maturity, she encourages male-male competition and indirectly selects for male fighting ability. However, attracting males may be costly for juvenile females if courting males take prey, inhibit prey capture, or attract predators (e.g. Herberstein, Schneider & Elgar, 2002; Erez, Schneider & Lubin, 2005). Subadult female salticids (*Corythalia* spp.) can respond aggressively to male courtship (Crane, 1949) and subadult female widow spiders *Latrodectus revivensis* often relocate their webs within a few days of a male arriving, (Segev, Ziv & Lubin, 2003), suggesting that male presence or courtship may be costly for females.

(2) Pheromone emission and adult female mating history

After mating, females of many spider species are no longer attractive to males (Table 1; Tietjen & Rovner, 1982). Mated females can have a different blend of pheromone compounds, as identified for virgin and mated female

Tegenaria atrica (Agelenidae; Trbalon, Pourie & Hartmann, 1998). Alternatively, mated females could stop producing the attractants they emit when virgin, e.g. *Linyphia triangularis* (Schulz & Toft, 1993b) and *Agelenopsis aperta* (Papke *et al.*, 2001). Mated female spiders could conceivably emit compounds to repel males, as occurs for mated female solitary bees, *Andrena nigroaenea* (Kirby) (Apoidea, Andrenidae; Schiestl & Ayasse, 2000). In insects, male preference for the pheromones of adult virgin rather than mated females is common, and is often associated with avoidance of sperm competition (Bonduriansky, 2001). This seems also to be the case for many spiders (Table 1). For example, male red-back spiders (*Latrodectus hasselti*; Theridiidae) are more attracted to virgin than mated female silk pheromones (Andrade & Kasumovic, 2005). Furthermore, male red-backs that sacrifice themselves to female cannibalism induce females to resist remating in the future, and thus secure 100% paternity (Andrade & Banta, 2002). Male spiders also choose virgin rather than mated females when females are likely to mate only once, e.g. *Agelenopsis aperta* (Riechert & Singer, 1995), or if mated or older females are aggressive and less sexually receptive, e.g. the cellar spider *Pholcus phalangioides* (Fuesslin) (Pholcidae; Schäfer & Uhl, 2002), *Argiope keyserlingi* (Araneidae; Herberstein *et al.*, 2002), *Schizocosa ocreata* (Roberts & Uetz, 2005), and *Tegenaria atrica* (Agelenidae; Trbalon *et al.*, 1998; also see Elgar, 1998).

VIII. CONTROL OF FEMALE SEX PHEROMONE EMISSION

Post-mating changes in female pheromone emission are generally associated with increased aggression and cannibalistic behaviour, e.g. *Clubiona cambridgei* L. Koch (Clubionidae; Pollard *et al.*, 1987), *Tegenaria atrica* (Agelenidae; Trbalon *et al.*, 1998), and *Argiope keyserlingi* (Araneidae; Herberstein *et al.*, 2002), or decreased receptivity to subsequent courting males (see Elgar, 1998). It is unclear whether these changes in female pheromone emission and behaviour are controlled autonomously by females, or are due to interference by her mate. Males that prevent their partners remating avoid sperm competition and the associated reduction in their share of paternity (Thornhill & Alcock, 1983; Simmons & Siva-Jothy, 1998). Males can thwart their mating partners' attempts to attract another male by reducing female sex pheromone emission. For example, in the sierra dome spider *Neriene litigiosa* there is strong first-male sperm priority and males are attracted by airborne pheromones from the webs of virgin females (as *Linyphia l.*; Watson, 1986). When a male locates a virgin female, he immediately destroys her web, which removes the pheromone source and significantly decreases the attraction of other males (Watson, 1986). Web damage is also performed by males of *Linyphia triangularis*, *L. tenuipalpis* (Schulz & Toft, 1993b), and the black widow spider *Latrodectus mactans* Fabricius (Theridiidae; Breene & Sweet, 1985). Comparable, but less extensive web damage by males is reported for other theridiids: the black widow spiders *Latrodectus hesperus* (Ross & Smith, 1979) and

Latrodectus revivensis (Anava & Lubin, 1993), the social spider *Achaearanea wau* (Lubin, 1986), and the kleptoparasitic *Argyrodes antipodianus* (O.P. -Cambridge) (as *A. antipodiana*; Whitehouse & Jackson, 1994). Web damage in these species may not necessarily function to limit female sex pheromone emission. Anava and Lubin (1993) suggest that when male *Latrodectus revivensis* damage webs and replace the silk with their own, this exposes females to male silk and possibly male sex pheromones, which might stimulate female receptivity. However, when tested with male silk, female *L. revivensis* gave no response (Anava & Lubin, 1993). Alternatively, damaging a female's web could fulfil functions unrelated to chemical communication, e.g. hampering access for other males that may interrupt, or limiting female movement or cannibalism.

Amongst the insects, there are examples of chemically mediated male strategies to control female remating. For example, in the corn earworm *Heliothis zea* (Boddie) (Lepidoptera: Noctuidae), male accessory gland secretions transferred to the female during mating prevent her producing sex pheromones that may attract other males (Raina, 1989). The cuticular hydrocarbons of male *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) appear to induce females to emit scents inhibiting courtship by other males (Scott & Jackson, 1990). Similar chemically mediated strategies may be used by male spiders. Female *Schizocosa malitiosa* (Tullgren) (Lycosidae) that do not receive sperm from a copulation maintain their sexual receptivity (Aisenberg & Costa, 2005). This may be because males transfer compounds with their sperm during copulation that limit female receptivity to subsequent males. However, it may also be that females can detect when insemination has failed to occur, and thus remain receptive to future matings.

Alternatively, a post-mating change in female sex pheromone emission may be a female strategy to gain control over the timing and frequency of mating; a significant factor underlying sexual conflict in spiders (Elgar, 1998; Schneider & Lubin, 1998). Females may halt their pheromones after mating to avoid the attention of subsequent males. This may occur if polyandry is impossible or risky (e.g. Chapman *et al.*, 1995), or if the benefits of polyandry are outweighed by costs imposed by males such as reduced or hindered prey capture or web-building, kleptoparasitism, web damage, or infanticide (Schneider & Lubin, 1996, 1998; Herberstein *et al.*, 2002; Erez *et al.*, 2005). Emitters of chemical signals also risk detection by parasites and predators (Zuk & Kolluru, 1998). For example, yellowjacket wasps *Vespula germanica* (Fabricius) (Hymenoptera: Vespidae) find prey by following the sex pheromones emitted by lekking male dipterans (Hendrichs *et al.*, 1994; Hendrichs & Hendrichs, 1998). Exploitation of spider sex pheromones by parasitoids is rare (Zuk & Kolluru, 1998). However, an eggsac parasitoid wasp species is attracted to the silk from its host, the linyphiid *Erigone atra* Blackwall (van Baarlen, Topping & Sunderland, 1996), and there are several wasp species that parasitise spiders (e.g. Colville, 1987; Elgar & Jebb, 1999; Blackledge & Pickett, 2000). Thus, parasitism is a feasible cost for sexually advertising female spiders.

If female spiders remain receptive to males for some hours after their first copulation, as occurs in the jewel

spider *Gasteracantha minax* Thorell (Araneidae; Elgar & Bathgate, 1996), they could continue to emit attractive pheromones and encourage polyandry. Females that subsequently halt pheromone emission could then limit costs such as male harassment and exposure to chemotactic parasites or predators. Continuous emission of pheromones may also be physiologically costly. A recent study reports a trade-off between body mass and alarm pheromone production in an aphid (Byers, 2005). Such costs could also limit sex pheromone emission by spiders.

IX. SEX PHEROMONES AND SPECIES RECOGNITION

Spider sex pheromones have been considered species specific and crucial for the reinforcement of reproductive isolation (e.g. Tietjen & Rovner, 1982). The plentiful case studies now available indicate that pheromones can be shared between species (Schulz, 1997, 2004) and can stimulate courtship by heterospecific males (Ross & Smith, 1979; Roland, 1984; Roberts & Uetz, 2004a). Nonetheless, pheromones may still assist in species recognition, and this may be dependent on whether the pheromone is airborne and potentially long-range, or if it requires contact and thus operates only over short distances. For example, females of some species in the closely related genera *Linyphia*, *Microlinyphia* and *Neriere* share a long-range pheromone that attracts both conspecific and heterospecific males (Schulz & Toft, 1993b). Females in this group appear to have additional species-specific pheromones that males use to recognise conspecific females at short-range (Schulz & Toft, 1993b). Short-range species recognition *via* cuticular pheromones also occurs in the closely related and morphologically similar agelenids *Tegenaria domestica* and *T. pagana* (C. L. Koch). These species have quantitative and qualitative differences in cuticular pheromone composition (Trabalon *et al.*, 1997) and males respond to cuticular pheromones only from conspecific females (Roland, 1984). Perhaps similarly, almost all male salticids in Jackson's (1987) extensive survey react to the draglines of both conspecific and heterospecific females, yet when tested with whole webs and nests, males reacted only to those produced by conspecific females.

The degree of relatedness between the pheromone emitter and the receiver may also influence the potential for reproductive isolation. For example, male *Latrodectus hesperus* are more attracted to the webs of conspecific females from their own geographic location than to webs of conspecific females from other regions (Kasumovic & Andrade, 2004). Male *Schizocosa ocreata* respond to the sex pheromones of heterospecific females with searching behaviour (Uetz & Denterlein, 1979; Roberts & Uetz, 2004b), but court more actively with conspecifics and closely related heterospecifics (e.g. *Schizocosa royneri* Uetz & Dondale) than with less related species (e.g. *Schizocosa crassipes*; Roberts & Uetz, 2004b). Lycosids in particular are renowned for their multimodal communication that involves vibratory, visual, tactile, and chemical elements

(Krafft, 1982; Uetz & Roberts, 2002). In many cases, a combination of signals and cues may be required to identify conspecific mates, e.g. pheromone and visual signals as for *Pardosa moesta* Banks and *Schizocosa crassipalpa* (Hegdekar & Dondale, 1969), or pheromone and vibratory signals as for *Cupiennius* spp. (Ctenidae; Barth & Schmitt, 1991; Barth, 1993; Papke *et al.*, 2001). There are several reports of interspecific matings between lycosids in captivity (Kronstedt, 1994). Captive spiders may not be able to use their full signalling repertoire and thus may misidentify heterospecifics as mates. Alternatively, the lack of conspecific mating partners may lead to acceptance of heterospecifics. When it occurs, species specificity in sex pheromones may be due to mutual sexual selection between females and males, rather than natural selection for reproductive isolation (Ayasse *et al.*, 2001).

X. CONCLUSIONS

(1) Sex pheromones are almost ubiquitous in spiders, and most female spiders are likely to have both airborne and contact pheromones, emitted from both the cuticle and silk. Pheromones from silk are better studied than cuticular pheromones.

(2) Although female spiders are typically the pheromone emitters, and male spiders the receivers, this pattern is not universal.

(3) Airborne pheromones of female spiders primarily attract males or elicit male searching behaviour, whereas contact pheromones stimulate male courtship behaviour and appear to provide specific information about the releaser's sexual status.

(4) In males, chemoreceptors are found on the pedipalps and forelegs. Female perception of sex pheromones, and the genetics and regulation of pheromone production require investigation.

(5) Whilst spider pheromones are generally lipids or lipid soluble, polarity appears to depend on the species' ecology, although there are more reports of successful pheromone extraction with polar rather than non-polar solvents. In the spider sex pheromones identified thus far, there are strong links to primary metabolism.

(6) Recent chemical analyses, sometimes coupled with electrophysiological measurements, have conclusively identified some spider sex pheromones. Behavioural experimentation with synthetic pheromones has commenced and future studies using such techniques will contribute significantly towards more general theories about the biosynthesis and evolution of chemical signals.

(7) Behavioural assays with choice tests provide extensive data for assessing spider sex pheromones. However, experimental designs must ensure that the age and sexual status of both males and females are adequately controlled and that sample sizes and statistical analyses are sufficient to reveal any biases due to the shape of the choice apparatus.

(8) Male spiders are typically most attracted to adult virgin females and juveniles before their final moult. This may be due to sperm competition and the influence of

first-male sperm priority, or the aggressive behaviour of mated females. Attraction to mated females does occur in some species, and male lycosids in particular do not seem to distinguish between juvenile, adult virgin and mated females.

(9) Females and males can use sophisticated pheromone-based strategies to communicate location and sexual receptivity, choose mates, gain control of the timing and frequency of mating, improve fertilisation success, and promote or avoid sperm competition.

(10) Investigation of the potential for signal exploitation by non-target receivers such as parasites could be a productive new avenue for research.

(11) Sex pheromones are not necessarily species specific, but may still assist with species recognition depending on whether the signals are long- or short-range and the degree of relatedness between the emitter and receiver.

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