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Authors
Elias, Damian O
Andrade, Maydianne CB
Kasumovic, Michael M

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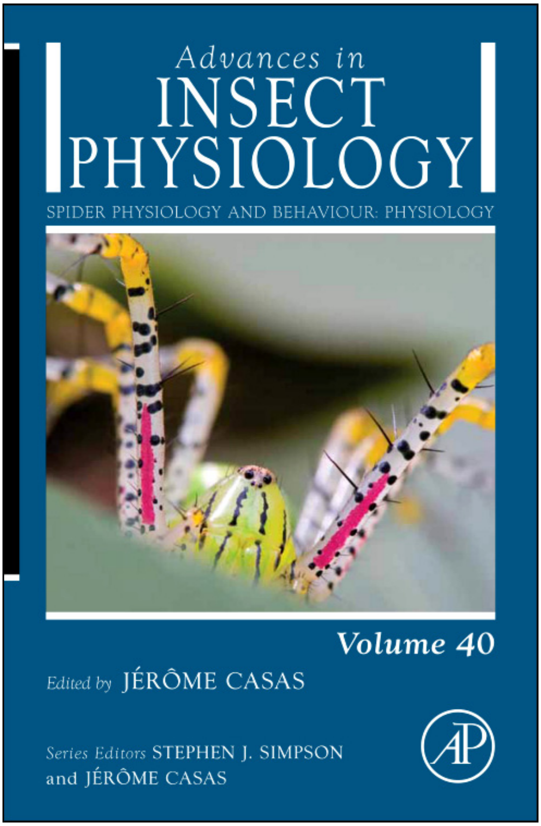

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Dynamic Population Structure and the Evolution of Spider Mating Systems

Damian O. Elias,* Maydianne C. B. Andrade,† and
Michael M. Kasumovic‡

*Department of Environmental Science, Policy and Management,
University of California, Berkeley, California, USA
†Integrative Behaviour and Neuroscience Group, University of Toronto
Scarborough, Toronto, Ontario, Canada
‡Evolution & Ecology Research Centre, School of Biological, Earth, and
Environmental Sciences, The University of New South Wales, Sydney,
New South Wales, Australia

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Abstract

Classic explanations of variation in mating systems critically depend on variation in demography. Here, we emphasize how understanding dynamic links between fluctuating population structure and mating tactics, life history, morphology, and sensory capabilities may be advanced using spiders as models. The impressively diverse range of mating systems and tactics among spiders, coupled with unique and manipulable aspects of their biology, may yield important insights into mating system evolution.

1 Introduction

Temporal variation in demography between or within populations has long been known to play a crucial role in evolutionary processes (Emlen and Oring, 1977; Stamps *et al.*, 1997). One particular aspect of demography that has recently become a focus in ecological, evolutionary, and behavioural research is spatio-temporal variation in population structure (i.e. density and age distribution) within and between breeding seasons. Understanding how population structure varies is important as empirical studies demonstrate that fluctuations in the density of males and females in the environment (Kasumovic *et al.*, 2008; Punzalan *et al.*, 2010) and the age structure of the population (Dreiss *et al.*, 2010) affect small-scale variation in the intensity and direction of sexual selection encountered by individuals. These effects can shape variation in phenotypic distributions and ultimately evolutionary trajectories (Kasumovic and Andrade, 2006, 2009a,b). The relative importance of such small-scale variation will depend on the natural history of the species under study and variation in microhabitat features such as resource availability, as this has the potential to accentuate or dampen effects of interactions between individuals (Gwynne, 1985; Gwynne *et al.*, 1998; Jann *et al.*, 2000; Petersen *et al.*, 2010). We suggest that understanding the scale of fluctuations in population structure relative to the life history of the organism under study can provide important insights into the evolution of the variety of mating systems and mating strategies we see in nature. We believe that these links may be especially transparent in spiders as the life history and reproductive biology of spiders can result in rapid shifts in the social environment and population structure, and therefore, selection. In spiders, several variables that are critically important to the intensity of selection show broad fluctuations of the type we highlight here. These include the tertiary sex ratio (sex ratio of individuals that reach sexual maturity), the density of males (i.e. intensity of sexual competition), the density of reproductively available females, and the absolute and relative timing of maturation for males and females (Table 1). Here, we argue that rapid fluctuations in sexual selection as a function of demography has led to the evolution of an amazing diversity of adaptations and behaviours in spiders.

TABLE 1
Spider mating systems

Species	Family	Sperm priority	Mate guarding	Protandry	Density	Maturation synchrony bias	References
Agelena limbata	Agelinidae	Last (0.63)	None	Yes	n/a	None	Masumoto (1991, 1993)
Agelenopsis aperta	Agelinidae	n/a	None	n/a	Dispersed	n/a	Becker *et al*. (2005), Papke *et al*. (2001), Riechert and Singer (1995), Singer *et al*. (2000), and Singer and Riechert (1994, 1995)
Dolomedes triton	Pisauridae	n/a	Pre-copulatory	Yes	Patchy	Female	Johnson (personal communication) and Johnson (2001
Frontinella communis	Linyphiidae	First ($P2 = 0.05$)	Both	Yes	Patchy	None	Suter (personal communication), Suter (1985), Suter and Keiley (1984), and Suter and Renkes (1982, 1984)
Holocnemus pluchei	Pholcidae	Last ($P2 = 0.74$)	Postcopulatory	No	Patchy	None	Jakob (personal communication), Calbacho-Rosa *et al*. (2010), Huber (1999), and Kaster and Jakob (1997)
Latrodectus hasselti	Theridiidae	First ($P2 = 0.11$)	Pre-copulatory	Yes	Patchy	None	Andrade (1996, 2003), Andrade and Banta (2002), Forster (1995), Kasumovic and Andrade (2006), Snow and Andrade (2005), and Stoltz *et al*. (2008)

(*continues*)

TABLE 1 (*Continued*)

Species	Family	Sperm priority	Mate guarding	Protandry	Density	Maturation synchrony bias	References
Latrodectus hespersus	Theridiidae	First	Postcopulatory	Yes	Patchy	None	Macleod (personal communication)
Linyphia triangularis	Linyphiidae	First ($P2 = 0.20$)	Pre-copulatory	Yes	n/a	n/a	Toft (1989) and Weldingh *et al*. (2011)
Misumena vatia	Thomisidae	n/a	Pre-copulatory	Yes	Dispersed	Female	Morse (personal communication), Anderson and Morse (2001), Holdsworth and Morse (2000), Legrand and Morse (2000), Morse and Fritz (1982), Morse (2010), and Morse and Hu (2004)
Misumenoides formosipes	Thomisidae	n/a	Pre-copulatory	Yes	Patchy	Female	Dodson (personal communication), Dodson and Beck (1993), Dodson and Schwaab (2001), Hoefler (2002), and Stellwag and Dodson (2010)
Nephila clavipes	Nephilidae	First ($P2 = 0.18$)	None	No	Patchy	None	Christenson *et al*. (1985), Linn (2001), Moore (1977), Rittschof (2010), Rittschof and Ruggles (2010), and Vincent and Lailvaux (2006)
Nephila edulis	Nephilidae	Last ($P2 = 0.66$)	None	No	Dispersed	None	Schneider *et al*. (2000a) and Uhl and Vollrath (1998)

Nephila plumipes	Nephilidae	Mixing	None	No	Patchy	None	Elgar and Fahey (1996), Kasumovic *et al*. (2007a,b, 2008), Schneider *et al*. (2008), andSchneider and Elgar (2001, 2002)
Neriene litigiosa	Linyphiidae	First ($P2 = 0.35$)	Pre-copulatory	Yes	High	Male	Watson (personal communcation), Keil and Watson (2010), and Watson (1986, 1990, 1991, 1998)
Pardosa milvina	Lycosidae	n/a	None	n/a	Patchy	None	Rypstra (personal communication), Hoefler *et al*. (2008, 2009), Marshall *et al*. (2002), Marshall and Rypstra (1999), Rypstra *et al*. (2003, 2009), Schmidt and Rypstra (2010), and Wilder and Rypstra (2008a)
Phidippus clarus	Salticidae	n/a	Pre-copulatory	Yes	High	Female	Elias *et al*. (2008, 2010b), Hoefler (2007, 2008), and Kasumovic *et al*. (2009b, 2010)
Phidippus johnsoni	Salticidae	Mixing	Pre-copulatory	Yes	Patchy	Female	Jackson (personal communication) and Jackson (1977, 1978a,b, 1980a,b, 1981, 1986b)
Pholcus phalangioides	Pholcidae	Last ($P2 = 0.82$)	Both	No	High	None	Uhl (personal communication), Hoefler *et al*. (2010), Schäfer and Uhl (2002), Uhl (1994, 1998), and Uhl *et al*. (2004, 2005)

(*continues*)

TABLE 1 (*Continued*)

Species	Family	Sperm priority	Mate guarding	Protandry	Density	Maturation synchrony bias	References
Physocyclus globosus	Pholcidae	Mixing	Both	No	n/a	None	Eberhard (personal communication), Eberhard (1992), Huber (1995), and Huber and Eberhard (1997)
Schizocosa ocreata	Lycosidae	n/a	None	Yes	High	Female	Hebets (personal communication), Miller *et al*. (1998), Stratton (1983, 2005), and Uetz and Denterlein (1979)
Schizocosa rovneri	Lycosidae	n/a	None	Yes	High	Female	Hebets (personal communication), Stratton and Uetz (1986), and Uetz and Denterlein (1979)
Stegodyphus lineatus	Eresidae	Mixing	None	No	Patchy	None	Lubin and Schneider (personal communication), Erez *et al*. (2005), Maklakov *et al*. (2004), Schneider (1997, 1999), and Schneider and Lubin (1996, 1997)
Tetragnatha extensa	Tetragnathidae	Last ($P2 = 0.7$)	None	No	Dispersed	None	Toft (personal communication) and West and Toft (1999)

Spiders provide excellent systems for studying variation in demography and its results on mating systems for three key reasons. First, all spiders produce silk, and silk can provide reliable, short-lived cues about demographic variables in the local environment. Cues on silk, or the silk itself, could be used to estimate current or predict future competitive environments. As such cues are often separate from the spider after they are deposited; there is also the opportunity for manipulation of information by competitors. Second, the genitalic morphology of most spider groups favours intense post-copulatory sexual selection and sexual conflict and can generate wide variance in reproductive success in many groups. Male monogamy and female polyandry have been observed in several spider systems (Elgar, 1991b, 1998; Fromhage *et al*., 2005, 2008; Schneider and Andrade, 2011). Further, the overall structure of the genitalic morphology in many species allows males to manipulate female sperm use patterns through the use of mating plugs (Uhl, 2002; Uhl *et al*., 2010). Third, spiders are solitary and cannibalistic resulting in mating opportunities that may be rare and dangerous for males (Elgar, 1992, 1998; Elgar and Fahey, 1996), and sometimes for females (Aisenberg *et al*., 2009; Cross *et al*., 2007). This has resulted in the evolution of diverse male mating strategies tuned to the possibility that only one or a few mating opportunities may be secured. Changes in the availability of receptive, unplugged females and density of surviving males will result in rapid spatio-temporal shifts in selective pressures. The resulting variation in the competitive environment spiders will encounter at maturity may nevertheless be detected by individuals via silk cues. The interplay between these forces has led to some of the most exceptional mating system adaptations known in nature.

In recent years, spiders have received increasing attention as models in the study of behavioural ecology and neuroethology (Barth, 2002; Elgar, 1992, 1998; Elias and Mason, 2011; Huber, 2005; Schneider and Andrade, 2011; Uetz and Roberts, 2002; Uetz and Stratton, 1982; Uhl and Elias, 2011; Uhl *et al*., 2010). In particular, the three common features of the Order Araneae outlined above have been the focus of many excellent reviews (e.g. Eberhard and Huber, 2010; Elgar, 1992; Elgar and Fahey, 1996; Herberstein and Tso, 2011; Huber, 2005; Schneider and Andrade, 2011; Thery and Casas, 2009; Uhl *et al*., 2010). This review is unique in emphasizing how these traits make spiders excellent models for studying demographic and environmental effects on behaviour and mating system evolution. We review these traits, in turn, focusing on several key characteristics that set the stage for adaptations to demographic variation. We then discuss how spider systems may be particularly sensitive to variation in demographic structure and discuss possible adaptations seen in spider systems. With this review, we hope to trigger more studies on how demographic and environmental fluctuations can shape behavioural and life-history adaptation and to highlight the utility of spider models for this work.

2 Spider reproductive and life-history traits

2.1 SILK AND CHEMICAL CUES

All spiders possess silk glands and silk is used in a variety of contexts from lining burrows and foraging through the use of webs, to the production of egg sacs and sperm webs for reproduction, to the use of draglines for locomotion (Foelix, 1996). In addition to these functions, chemicals on the silk provide information on location (Aisenberg *et al*., 2010; Baruffaldi and Costa, 2010; Clark and Jackson, 1995; Cross and Jackson, 2010; Kasumovic and Andrade, 2004; Papke *et al*., 2001; Taylor, 1998; Xiao *et al*., 2010; Yoshida and Suzuki, 1981), species identity (Kasumovic and Andrade, 2004), reproductive state (Baruffaldi and Costa, 2010; Gaskett *et al*., 2004; Koh *et al*., 2009; Miyashita and Hayashi, 1996; Riechert and Singer, 1995; Roberts and Uetz, 2005; Rypstra *et al*., 2003; Searcy *et al*., 1999; Stoltz *et al*., 2007), size/fecundity/age (Hoefler, 2007; Jackson, 1986b), competitive environment (De Meester and Bonte, 2010; Kasumovic and Andrade, 2006; Nessler *et al*., 2009b; Trabalon and Assi-Bessekon, 2008), and predation pressures (Folz *et al*., 2006; Holler and Persons, 2009; Li, 2002a; Persons and Rypstra, 2000; Persons *et al*., 2002; Storm and Lima, 2010; Taylor *et al*., 2005). In some instances, it is unknown whether these cues are released through glands found on the spider's body (Miyashita and Hayashi, 1996; Riechert and Singer, 1995) or whether they are solely properties of the silk itself (Gaskett, 2007). Regardless, spiders leave behind ''traces'' of information which are short lived and potentially contain reliable information about recent events (Andrade and Kasumovic, 2005; Baruffaldi *et al*., 2010; Gaskett, 2007; Miyashita and Hayashi, 1996). This information may be used by individuals to make mating or foraging decisions.

The relative importance of silk cues in the evolution of mating systems and behaviour in spiders will depend on the life history of the spiders under study. Spiders can be divided into two general groups based on lifestyle: wandering and web-building spiders. Wandering spiders do not use webs to forage and instead either actively hunt prey (e.g. jumping spiders, Salticidae) or find suitable foraging sites where they use ''sit and wait'' predatory strategies (e.g. crab spiders, Thomisidae). Wandering spiders often have well-developed sensory systems across a range of modalities (chemical, vibratory, visual), and males may locate females using silken draglines left by foraging females. In general, wandering spider males can discriminate between conspecific males and females using these draglines (Clark and Jackson, 1995; Cross and Jackson, 2009) based on the physical structure of the silk alone (Anderson and Morse, 2001) but more commonly based on pheromones (Gaskett, 2007). For example, in the jumping spider *Carrhotus xanthogramma*, males that detect the presence of female silk slow down their movement to more efficiently search for hidden females (Yoshida and Suzuki, 1981). In a crab spider, *Misumena vatia*, males respond to mechanical cues of silk alone and follow draglines indiscriminately (Anderson and Morse, 2001). Anderson and Morse (2001) suggested that following draglines to large concentrations of silk would likely maximize the number of females encountered. Wandering males may also search for relatively sedentary females using web-based pheromones as seen in wolf spiders (Baruffaldi *et al*., 2010; Fernandez-Montraveta and Ruano-Bellido, 2000; Searcy *et al*., 1999). The opposite occurs in the sex role-reversed wolf spider species *Allocosa brasiliensis* and *Allocosa alticeps*, where males build burrows and emit a pheromone that females use to locate them (Aisenberg *et al*., 2010).

Unlike wandering spiders, web-building spiders use webs as hunting snares and spend most of their lives on or near their web constructions. While web structures vary widely across groups (Barth, 2002; Foelix, 1996), most web-builders are dependent on web vibrations for detecting prey and conspecifics (Barth, 1998, 2002). These spiders are thus very sensitive to vibratory as well as chemical stimuli but tend to have poor vision (Foelix, 1982). The main exception to the sedentary lifestyle of the web-builder arises when males become sexually mature and begin searching for potential mates. During mate searching, males often cease foraging and devote all their resources to locating mates (Elgar, 1998). In most species, long-distance chemical signals emitted from webs (pheromones) are used to locate females (Kasumovic and Andrade, 2004; Papke *et al*., 2001; Searcy *et al*., 1999).

In addition to the importance of silk for mate location, in many species, silk-based cues are used for distinguishing among potential mates. Males are able to detect female age based purely on silk cues and often exhibit male mate choice for females that are closer to maturation (Hoefler, 2007). The moulting hormone, ecdysone, accumulates in the haemolymph several days prior to moulting (Bonaric and Dereggi, 1977) and could be detected via cues deposited in silk or faeces that adhere to the silk. In many species of spiders, virgin females are more receptive than mated females (Christenson *et al*., 1985; Jackson, 1981; Schäfer and Uhl, 2005; Schneider and Lesmono, 2009; Sivalinghem *et al*., 2010) and males can detect differences between mated and virgin females through body and silk-borne chemical cues (Andrade and Kasumovic, 2005; Baruffaldi and Costa, 2010; Bukowski *et al*., 2001; Gaskett *et al*., 2004; Jackson, 1986b; Roberts and Uetz, 2005). Virgin females are often courted for longer durations suggesting higher investment by males. For example, in the orb weaver *Argiope keyserlingi*, virgin males prefer the silk of virgin females and preferentially venture onto those webs (Herberstein *et al*., 2002). In some species, however, particularly ones with last male sperm precedence, males are attracted to mated females and silk may also mediate this preference (Klein *et al*., 2005). Females can also use silk-based chemical cues to assess mating status. For example, in the spitting spider *Scytodes* sp., females are less attracted to, and more likely to kill mated rather than virgin males even in the absence of courtship displays, suggesting chemical assessment via silken cues (Koh *et al*., 2009). In this species, Koh and colleagues (2009) suggested that females modulate their reproductive investment based on odour cues as they laid more and heavier eggs after mating with preferred (virgin) males.

Silk may also reliably indicate the nature or intensity of future competitive (see below) and predatory environments. For example, spiderlings of *Erigone atra* that encounter more draglines from conspecifics are more likely to disperse for long distances than those that encounter few (De Meester and Bonte, 2010). De Meester and Bonte (2010) suggested that long distance dispersal served as a mechanism to avoid competition from conspecifics. In the subsocial spider *Coelotes terrestris*, silken cues mediate spatial distribution and potentially serve to reduce competition (Trabalon and Assi-Bessekon, 2008). Cues in silk also contain information about predatory environments. For example, female *Gryllus pennsylvanicus* crickets that experience silken cues from the spider *Hogna helluo* have offspring that are more immobile than the offspring of females not exposed to such cues. This maternal effect increases the survival offspring in the presence of *Hogna* predators (Storm and Lima, 2010). *H. helluo*, however, are attracted to silk cues deposited by *Pardosa milvina* spiders, a common prey item (Persons and Rypstra, 2000). *P. milvina* can also detect differences in silk between *Hogna* that have fed on *P. milvina* versus other prey and respond accordingly (Persons *et al.*, 2001). The possibility of maternal effects on offspring, comparable to that seen in crickets (Storm and Lima, 2010), has not been investigated in spiders.

2.2 GENITALIA

Males store sperm independently in paired, anterior appendages known as pedipalps. Sperm is ejaculated from the gonads on to a ‘‘sperm web’’ prior to copulation, and males collect the sperm within their pedipalps (pedipalp charging). Pedipalps are used as intromittent organs and are usually inserted independently through the female’s epigynum (Foelix, 1996). The most anterior portion of the palp is the embolus—a sclerotized structure used to deliver sperm to the female. Different species have very different pedipalp morphology and many have peculiar embolus structures that may be adaptations for sperm competition or sexual conflict (Miller, 2007; Uhl, 2002; Uhl *et al.*, 2010; see Uhl and Vollrath, 1998). In some species, the embolus breaks off inside the female, serving as a plug that prevents mating or successful insemination of the sperm storage organs (Uhl *et al.*, 2010). In one species *Harpactea sadistica*, the embolus has evolved a needle-like point that is used to puncture the female’s exoskeleton, allowing males to bypass the traditional means of inseminating the spermatheca to directly fertilize eggs (Řezáč, 2009). For a recent review on structures and functions of male genitalia, see Eberhard and Huber (2010).

The genitalia of female spiders are also complex with variable arrangements and structures. In his seminal review, Austad (1984) hypothesized a connection between female genital morphology and sperm priority patterns in the two main Araenomorph groups, the Haplogynae and the Entelgynae. Haplogyne spiders were predicted to exhibit last male sperm precedence, as the last sperm to enter their ''cul-de-sac''-type spermathecae lies closest to a single combined fertilization/insemination duct (assuming no sperm mixing, Austad, 1984). In contrast, entelegyne spiders have separate insemination and fertilization ducts and were described as having ''conduit'' spermathecae. For these spiders, Austad (1984) predicted first male sperm precedence (Austad, 1984; Snow and Andrade, 2005; Uhl, 2000; Uhl *et al*., 2010), as the last sperm to enter would lie most distal to the fertilization duct (Austad, 1984).

These predictions have been met in some species and not in others (Uhl, 2002). The details of gross morphology deviate from expected patterns in most of the cases under investigation (Uhl, 2002; see Burger, 2009; Burger and Kropf, 2007; Burger and Michalik 2010; Burger *et al*., 2010; Eberhard and Huber, 2010; Huber and Eberhard, 1997; Coddington and Levi, 1991). In *Nephila edulis*, for example, the fertilization and seminal ducts are so close together that a ''cul-de-dac'' pattern is suggested (Uhl and Vollrath, 1998); consistent with this, a last male sperm precedence pattern has been documented (Schneider *et al*., 2000b).

Although the phylogenetic categorization of Austad (1984) is apparently too broad, spermathecal morphology nevertheless has important implications to spider mating systems, and in the following sections, we review some of the literature on sperm competition, sperm priority patterns, and genitalic adaptations. Much more work is needed to understand this important topic, and research in this area suggests a strong diversity in sperm utilization patterns, post-copulatory (cryptic) female choice mechanisms, and antagonistic co-evolution of male and female reproductive traits across spider species. For recent reviews on female genital morphology and sperm priority patterns, see Uhl (2002, 2010) and Schneider and Andrade (2011). For ease of reference in this review, we will refer to the ''haplogyne type'' as instances where there is a single spermathecal duct and the ''entelegyne type'' as instances where spermathecae have separate insemination and fertilization ducts, after Uhl (2002).

2.3 HAPLOGYNE-TYPE GENITALIA

Relative to studies on entelegyne-type species, few studies exist on haplogyne-type species. In the only major study on a haplogyne, experiments demonstrated that in matings with two male *Pholcus phalangioides*, 88% of offspring are sired by the last male to copulate (Schäfer and Uhl, 2002). There was, however, considerable variation in the second male's paternity, and evidence suggests that this variation is controlled by female behaviour after mating (Schäfer *et al*., 2008). Interestingly, while female *P. phalangioides* nearly always mate with the first male they encounter, 20–30% of females never remate (Schäfer and Uhl, 2002). Currently, these studies suggest that last male sperm priority may be augmented by mechanisms promoting sperm removal by males and sperm dumping by females (Schäfer and Uhl, 2002). Sperm dumping and selective dumping of male ejaculates may also be important in other haplogynes (Burger, 2007, 2010; Burger *et al.*, 2006). Last sperm priority would predict mated females would be more choosy closer to egg laying and males would engage in post-copulatory mate guarding in order to safeguard their paternity (Alcock, 1994). Males of the Oonopid *Orchestina* genus show post-copulatory mate guarding (Burger *et al.*, 2010). Males of the Pholcid spider *Holocnemus pluchei* also showed pronounced mate guarding for 14 h after mating, which corresponds to the period during which females are likely to remate (Calbacho-Rosa *et al.*, 2010). Second-mating males that copulated within 6 h of the first male showed elevated levels of paternity (70% last male sperm precedence; Kaster and Jakob, 1997).

2.4 ENTELEGYNE-TYPE GENITALIA

Multiple sperm storage organs and/or selective sperm use set the stage for intense sperm competition (Elgar, 1998). In most entelegynes for which sperm use patterns have been documented, paired genital morphology in both males and females leads to unusual mating pattern possibilities. For example, at any encounter with a potential mate, one or both of the male's palps may have been previously used, and females may have one or both spermathecae previously inseminated. Each individual spermathecae can be fertilized by a different male (or combination of males), and evidence exists that males can detect the presence of previously inseminated spermathecae (Snow *et al.*, 2006) and release sperm differentially to virgin and previously inseminated spermathecae (Bukowski and Christenson, 2000; Bukowski *et al.*, 2001; Morse, 2010). These patterns have been used experimentally to successfully disentangle sources of variation in sperm use patterns (see Schneider and Lesmono, 2009; Snow and Andrade, 2004, 2005), and evidence exists that females may exercise choice by killing males after a single insemination (Stoltz *et al.*, 2008, 2009) or that males may strategically use different palps on different females (Fromhage *et al.*, 2005, 2008; Herberstein *et al.*, 2005a). Of the studies on sperm priority in species with entelegyne-type genitalia, only 4 of 10 species showed first male sperm priority (reviewed in Elgar, 1998; Schneider and Andrade, 2011; Uhl, 2002). For some of these species, cryptic female choice is a likely explanation for observed sperm priority patterns. For example, in *Argiope bruennichi*, if males perform costly courtship displays, paternity increases dramatically from 50% to 80% (Schneider and Lesmono, 2009).

Whether first male sperm precedence is common in entelegyne spiders is not yet clear, as relatively few species have been studied (Schneider and Andrade, 2011). However, if there is first male sperm precedence, males mating with virgin females will have more favourable paternity outcomes than males mating with previously mated females. This predicts the evolution of protandry (males maturing first) as early-maturing males will find valuable virgin females before competitors (Simmons, 2001; Thornhill and Alcock, 1983). In this scenario, pre-copulatory mate guarding of immature females will be favoured assuming that females are receptive after maturation. Protandry and pre-copulatory mate guarding have been found in a wide variety of spider groups (Table 1), although sperm use patterns are unknown for most of these. Even a slight paternity bias may be sufficient to favour these patterns. For example, in the Linyphid, *Neriene litigiosa*, the first male's paternity is 61% (61% first male paternity; Watson, 1991) and protandrous males find immature females and defend them against intruding males (cohabitation) (Keil and Watson, 2010). Contests are more likely to escalate in the presence of females and are most often won by larger males (Keil and Watson, 2010; Watson, 1990).

The presence of separate copulatory and fertilization ducts in entelegyne-type spiders makes it possible for males to block subsequent fertilization attempts using plugs (Miller, 2007; Uhl *et al*., 2010). Mating plugs (reviewed in Uhl *et al*., 2010) can consist of secretions produced by the male (Jackson, 1980a; Suhm *et al*., 1996; Uhl *et al*., 2010), parts of the male genitalia broken off inside the female reproductive tract (Kuntner *et al*., 2009b; Miller, 2007; Uhl *et al*., 2010), the entire male palp (Knoflach and van Harten, 2001), and in some cases, the carcass of the dead male (Foellmer and Fairbairn, 2003; Knoflach and Benjamin, 2003; Knoflach and Van Harten, 2000). Evidence suggests that the efficacy of mating plugs can be extremely variable and subject to selection. In *Latrodectus hasselti*, males use the tip of their embolus as mating plugs and plug efficacy was strongly location dependent as only plugs deposited at the entrance to the spermathecae were successful at securing paternity for the plugging male (Snow *et al*., 2006). Males that spent a longer time in copula were better able to position the mating plug (Snow *et al*., 2006). In some species, it appears that females contribute to the formation of plugs (Aisenberg and Eberhard, 2009; Eberhard, 2004), suggesting the deterrence of subsequent mating attempts may be beneficial for females. In the spider *Leucauge mariana*, successful plugs are only formed when the female adds her own chemical substance to a substance transferred by the male during copulation (Mendez, 2002 cited in Eberhard, 2004). Copulatory courtship by the male increases the likelihood that the females will cooperate in plug formation (Aisenberg and Eberhard, 2009). Further, in many species, it is evident that females can easily remove mating plugs (Jackson, 1980a; Uhl, 2002; Uhl *et al*., 2010).

2.5 SOLITARY BEHAVIOUR AND CANNIBALISM

Spiders live under constant threat of predation from conspecifics, and evidence exists that population size and age distribution are strongly influenced by cannibalism (Rabaneda-Bueno *et al*., 2008). While the prevalence of cannibalism during mating in spiders is often overstated, the majority of spiders are fiercely solitary (Elgar, 1998), with a few notable exceptions (i.e. the social spiders; Bilde and Lubin, 2011). In general, there are two life stages when spiders tolerate conspecifics: as newly hatched spiderlings and during reproduction. Even during these phases, however, cannibalism may still occur and behaviours may rapidly shift back to solitary/cannibalistic behaviour after successful mating. In some species, cannibalism is an important part of mating behaviour (sexual cannibalism) (reviewed in Elgar, 1992, 1998) and male self-sacrifice can be an adaptation that increases copulation time and favourably biases sperm usage patterns (see Andrade, 1996; Elgar, 1991a; Herberstein *et al*., 2005c; Miller, 2007; Nessler *et al*., 2009a; Welke and Schneider, 2010). Since mating is potentially extremely costly, selection should favour males that are able to assess female aggression levels rapidly.

In situations where mate searching is costly, and more importantly, when there is a male-biased tertiary sex ratio and fierce competition, male monogamy without parental care (which is the general rule for spiders) is predicted to evolve (Fromhage *et al*., 2005, 2008). Extreme male monogamy (by self-sacrifice) is expected when the fitness benefits exceed the costs of foregoing future matings (see Andrade, 1996, 2003; Schneider and Elgar, 2001). However, for males to accrue any fitness benefits, self-sacrifice behaviour must occur after copulation has taken place and in most cases, after both spermathecae have been inseminated. In the redback spider (*L. hasselti*), for example, Snow and Andrade (2005) calculate that males cannibalized by females after they copulate twice receive the vast majority of paternity (80% paternity; Snow and Andrade, 2004, 2005). Females, however, punish males with premature sexual cannibalism (cannibalism before both spermathecae are inseminated) when males do not court for a sufficient length of time, thus capping paternity to a maximum of 50% (Stoltz *et al*., 2008, 2009).

Several hypotheses have been proposed to explain cannibalism and sexual cannibalism in spiders (see Elgar, 1992, 1998). One proposed hypotheses is that cannibalism evolved as an extreme form of mate rejection because courtship performed by poor males is costly to females as it increases the visibility of females to predators as well as decreasing the efficiency of predatory behaviours (Pruden and Uetz, 2004). Pre-copulatory cannibalism is thus a way to ''silence'' poor-quality males while allowing females a meal (Elgar, 1992). In the crab spider, *M. vatia*, field and laboratory studies concluded that poorer condition males were attacked and cannibalized more (Morse and Hu, 2004). The intensity and frequency of cannibalism may also be a function of the environment where the utility of consuming males as prey for nutrient-stressed females. Spiders often live in poor-quality environments where prey items are few and far between (Moya-Larano 2002). In a few spiders, cannibalism is observed to increase female fecundity (Rabaneda-Bueno *et al*., 2008). Pre-copulatory sexual cannibalism may thus reflect a trade-off between acquiring sperm and acquiring food (Newman and Elgar, 1991). For example, in the fishing spider *Dolomedes triton*, females that cohabited with males (a cue suggesting a high availability of mates) were more likely to cannibalize potential suitors (Johnson, 2001). In another experiment, in field enclosures with higher male sex ratios, females were more likely to cannibalize potential mates

(Rabaneda-Bueno *et al*., 2008). However, sexual cannibalism is most common when there is female-biased size dimorphism (Wilder and Rypstra, 2008b), and in most such cases, results suggest that eating males confers little if any fecundity benefits (Andrade, 1996; Elgar *et al*., 2000; Schneider and Elgar, 2002). Nevertheless, cannibalism can occur at sufficiently high frequencies to have dramatic effects on the structure of spider populations. In some wandering species, males make up a significant proportion of the female's diet (Moya-Larano, 2002; Zimmermann and Spence, 1992) and are an order of magnitude more profitable than the most commonly found prey item (Moya-Larano, 2002). Sexual cannibalism itself can thus lead to major, systematic shifts in sex ratio within mating seasons (Zimmermann and Spence, 1992).

2.6 VARIATION IN POPULATION STRUCTURE

In classic behavioural ecology theory, sex ratio is an important determinant of the evolution of mating systems. Extreme male-biased sex ratios are predicted to lead to strong male competition as many males fight for few available females. As sex ratios become more equal, competition is predicted to be weaker and in cases of extremely female-biased sex ratios, a shift towards female competition for few male mates. In the crab spider *M. vatia*, spiders are sparsely distributed and the local measured sex ratios in the field are female biased (Holdsworth and Morse, 2000). Observed incidences of mate guarding is low, and few fights have been observed even in staged interactions (Holdsworth and Morse, 2000). Males of this species are extremely polygynous, mating up to 14 times (Legrand and Morse, 2000). In the related *Misumenoides formosipes*, however, tertiary sex ratio in the field is highly male biased and males vigorously defend females against rival males, often engaging in lethal fighting (Dodson and Beck, 1993).

As the breeding season progresses, the tertiary sex ratio could remain static or it could shift. Static tertiary sex ratios would be predicted if males and females continually mature throughout the breeding season. In many spider species, however, males are protandric (maturing first) and females mature synchronously (Table 1), so the tertiary sex ratio is known to shift over time. In these groups, there is a generally a high proportion of mature males early in the season, when the proportion of immature females is also high. Later in the season, all females are mature and males begin to die off thus leading to tertiary sex ratio shifts. Although a given system may show static or systematically shifting sex ratios and age structure on average through the season, the local conditions experienced by individuals may be more dynamic than this suggests (Kasumovic *et al*., 2009a). For example, variation in ecological factors can affect the spatial patterning of the population, and sex differences in a variety of life-history traits can lead to both temporal and spatial variation in population structure. Understanding how these factors shift is important as local variation in mating status, and age structure within populations can have a significant effects on the strength and direction of selection (Dreiss *et al*., 2010; Kasumovic *et al*., 2008; Punzalan *et al*., 2010).

3 Spatial variation

3.1 ECOLOGICAL VARIATION

Spatial variation in spider population structure stems mainly from the interaction of habitat structure and availability with the hunting practices of spiders. Orb-weaving species require substrate to which they can attach their webs. The density of individuals in any given population is thus likely to depend on the density of the necessary habitat structures. The availability of these structures within a particular habitat will limit the overall density and patchiness of individuals of both sexes, likely leading to strong variation in the spatial structure of the population. For example, in *Nephila plumipes*, two neighbouring populations inhabiting the same park, less than 50 m from one another, differed strongly in the density of females, and this was correlated with differences in the density of the trees (Kasumovic *et al*., 2008). Similarly, patchy distributions are expected for any species that use particular types of physical structures for nests, such as black widows (*Latrodectus hesperus*) that build refugia in abandoned tunnels built by small mammals (E. Macleod, personal communication) or in crevices in rock (Kasumovic and Andrade, 2004). Such patchiness may be accentuated in the many species that now use human structures as substrates and inhabit manicured parks or the walls of buildings. For example, *A. keyserlingi* use many different low-lying structures but prefer using low-lying *Lomandra* spp. plants that are commonly used in Australian parks (Herberstein and Fleisch, 2003). As a result, density depends strongly on how the parks are designed and the planting regime. A second example is *Zygiella x-notata* which frequently inhabits the underside of roofs on buildings, so density depends on the frequency and size of buildings (Bel-Venner and Venner, 2006; Bel-Venner *et al*., 2008). Other factors that could influence spatial structure of populations are the affinity of individuals for conspecifics. For example, in a cobweb species (*L. hesperus*), spiders are attracted to areas with established webs and may live in groups of up to eight individuals (Salomon *et al*., 2010). Once females are established, they are unlikely to move until they are ready to lay eggs (Salomon, 2009; Salomon *et al*., 2010). Web clustering may have interesting effects on sexual selection, particularly if the affinity for neighbours fluctuates in response to mating status. For example, in the spider *C. terrestris*, silk-based cues affect the spatial distribution of females as gravid females are attracted to webs of mated females while these same webs repel virgin females (Trabalon and Assi-Bessekon, 2008).

Wandering spiders may not experience the same level of spatial heterogeneity as web-building species as both sexes wander in search of food and mates (Foelix, 1982). However, a number of ecological factors can affect the distributions of wandering spiders as well. For example, if male wandering species aggregate around the nests of females, this can immediately change the spatial organization of the population, as nests can be dependent upon habitat structure and refuge availability. This is common in mate guarding species such as *Phidippus clarus* where males mature earlier than females and then guard females at nests (Hoefler, 2007; Holdsworth and Morse, 2000; Jackson, 1986a). In addition, many wandering spiders show habitat-dependent mating behaviour. In the jumping spider *Habronattus dossenus*, even though spiders were observed foraging in a variety of habitats, mating behaviour only occurred in a subset of those habitats (Elias *et al*., 2004). Similar habitat preferences have been shown in wolf spiders (Elias and Mason, 2011; Elias *et al*., 2010a; Hebets *et al*., 2008) suggesting that many wandering spiders have evolved mating behaviours tuned to specific ‘‘signalling microhabitats’’. Some crab spiders also show preferences for specific habitats (or plant species), and spatial heterogeneity may play an important role in mating behaviour. In the crab spider *M. formosipes*, males use floral cues to locate the preferred foraging habitats of females (Stellwag and Dodson, 2010). Preferred foraging sites are patchy in distribution and this leads to a patchy population distribution (Heiling *et al*., 2005). These effects may be amplified if female distribution is dependent on female quality as in *Metellina segmentata* (Rubenstein, 1987), where larger more fecund females monopolize better feeding territories and are found in large aggregations, while smaller females are found in lower-quality sites and are sparsely distributed (Rubenstein, 1987).

Once documented, habitat constraints and preferences can be used by researchers to test hypotheses about the effect of spatial organization on mating tactics and behaviours, and therefore, selection. Already-manipulated habitats, such as manicured parks with alternative planting schemes, can provide useful experimental comparisons, or researchers can manipulate the availability of necessary structures in natural populations. This was done successfully by Hoefler and Jakob (2006b) who provided female *P. clarus* with opaque tubes that females preferred to natural structures for the construction of their hibernacula. Either of these approaches provides powerful tools for the experimental examination of how local and broad-scale population densities affect selection.

4 Temporal variation

4.1 DEVELOPMENT TIME

Temporal variation in the distribution of sexually mature males and females is expected as a consequence of species- and sex-specific differences in life-history traits. Even if the primary sex ratio is equal at hatching, there may still be sex-specific differences in development that can lead to variation in the relative number of mature males and females in a population at any given time (tertiary sex ratio). Such differences have particularly pronounced effects in many species of web-building spiders that show female-biased size dimorphism, as males develop much more quickly and may mature before any females are available (e.g. Fromhage *et al*., 2003; Kasumovic and Andrade, 2006; Knoflach and van

Harten, 2001; Schneider *et al*., 2000a). The degree of dimorphism and the rate of maturation, however, can vary due to factors such as food availability and temperature (Kleinteich and Schneider, 2010; Li, 2002b). Moreover, the sexes may follow different developmental trajectories (Uhl *et al*., 2004), inhabit different niches, and behave differently to capture prey (Walker and Rypstra, 2001, 2002) due to different dietary requirements (Fernandez-Montraveta and Moya-Larano, 2007; Higgins and Goodnight, 2010; Uhl *et al*., 2004).

In addition to differences in male and female development, there may differences in the window of time individuals of the same sex mature. For example, individuals could mature relatively synchronously or relatively dispersed throughout the breeding season. Sex differences in the synchrony of maturation may lead to variation in the type of competition, and the intensity of sexual selection males will encounter. For example, in *P. clarus*, females mate multiply (Sivalinghem *et al*., 2010) and mature relatively synchronously compared to males (Hoefler, 2007) leading to a pattern where differential reproduction depends mainly on the outcome of male–male competition early in the breeding season but depends on male courtship and female choice later in the breeding season (Elias *et al*., 2010b; Sivalinghem *et al*., 2010). As male *P. clarus* can only guard a single female at a time, no single male can monopolize access to multiple females. However, in *N. litigiosa*, females mate only once and mature relatively asynchronously such that mature females are available throughout the breeding season (Watson, 1990). In this example, the vast majority of males have already matured before females start to mature, and the asynchrony of female maturation allows the potential for male monopolization of multiple females (Emlen and Oring, 1977), leading to strong male–male competition throughout the entire breeding season (Keil and Watson, 2010; Watson, 1990, 1991, 1998). Understanding how ecological factors influence development rates and maturation times between the sexes can provide insight into the evolution of the mating system of the species under examination.

4.2 MORTALITY RATES

Sex differences in mortality rates should have a strong effect on population age structure. In most spiders, behaviours of juvenile males and females are similar, suggesting mortality rates may also be similar at this life-history stage. In wandering spiders, both sexes actively hunt for food while immature and this continues after maturity while males simultaneously search for females which may result in similar mortality between the sexes (Prenter *et al*., 1997; Walker and Rypstra, 2001), although males may still be more active as they search for available females (Framenau, 2005). Females of many species of wandering spiders, however, provide parental care to egg sacs and spiderlings (Foelix, 1982), and this may make them more conspicuous to predators. A secondary cost that females of wandering spiders may incur includes a higher incidence of predation when they are being courted (Su and Li, 2006).

In contrast to wandering spiders, web-building spiders are generally sedentary for much of their life time, with individuals of some species travelling short to moderate distances to move web sites each night, when prey availability shifts, or in response to encroachment of conspecifics (Chmiel *et al*., 2000; Jakob *et al*., 2001; Lubin *et al*., 1993; Nakata and Ushimaru, 1999; Rayor and Uetz, 2000; Riechert, 1976; Smith, 2009; Vollrath, 1985; Ward and Lubin, 1993; Wherry and Elwood, 2009). After maturity, however, female web-building spiders continue to build webs and capture prey, while males leave their natal web and begin searching for females. Web-building spiders have evolved several traits that make them inconspicuous, simultaneously facilitating prey attraction and predator avoidance (Hauber, 2002; Herberstein and Tso, 2011; Higgins, 1992; Rao *et al*., 2007; Thery and Casas, 2002). After maturity females remain inconspicuous on webs while males abandon their webs. Searching for females thus results in two costs paid by males. First, as web-building spiders require webs to catch food, adult males cannot truly feed until they reach a female's web where they can steal food (kleptoparasitism) from the female (Agnarsson, 2002; Elgar, 1989; Kasumovic and Andrade, 2009a; McCrate and Uetz, 2010), although there is evidence that males may be able to subsist on flower nectar (Pollard *et al*., 1995). Second, there is an increased risk of predation as males are relatively conspicuous while mate searching. The mate-searching period is thus an extremely risky time for males of web-building species where there is a high mortality rate (Anava and Lubin, 1993; Andrade, 2003; De Mas *et al*., 2009; Kasumovic *et al*., 2007b; Prenter *et al*., 1997; Segev *et al*., 2003; Walker and Rypstra, 2003). The opposite is true for sex role-reversed spiders (*A. brasiliensis*; *A. alticeps*) where females perish more often due to mate searching (Aisenberg and Costa 2008; Aisenberg *et al*., 2007, 2009).

This difference in mortality between the sexes has been argued to explain why female-biased size dimorphism is more often seen in orb-weaving spiders than in wandering spiders (Vollrath, 1998; Vollrath and Parker, 1992), although this claim has since been revaluated (Prenter *et al*., 1998). Regardless, sex differences in mortality rates, especially due to the increased mortality males face due to mate-searching behaviour, can cause local or broad-scale fluctuations in the sex ratio at any given time. This will therefore change the selective pressures males will encounter (Kasumovic *et al*., 2008). Moreover, it has the potential to decrease competition between males (Vollrath and Parker, 1992) and can theoretically lead to the evolution of monogyny (Fromhage *et al*., 2005), although intense competition can still exist if males are attracted to a limited number of sexually receptive females (Kasumovic *et al*., 2007b).

4.3 MOVEMENT WITHIN AND BETWEEN POPULATIONS

Emigration and immigration of adults between populations have the potential to significantly alter population structure during the breeding season (Clutton-Brock *et al*., 1997; Matter and Roland, 2002; Wauters and Dhondt, 1993).

The role of either factor is difficult to surmise in spiders as only a few studies have examined movement patterns in spiders and those that have focus on web-building species (but see Henschel, 2002; Hoefler and Jakob, 2006; Nihei *et al.*, 2003, 2004). Here, we consider movement of adults and spiderlings separately. Large-scale movement of adults between populations could cause sudden and significant shifts in tertiary sex ratio and local density. The few studies that have marked adult males and followed their movements demonstrate that males usually move short distances and visit the nearest (Andrade, 2003; Lubin *et al.*, 1993) or nearby (Kasumovic *et al.*, 2007b) available females. Given that males are moving such short distances, even in larger populations, it may be the sub-population structure that is more relevant for examinations of mating patterns and selection (Kasumovic *et al.*, 2008). Movement of adults between populations may be unlikely due to habitat constraints, particularly for species with specific microhabitat requirements or species that live in anthropogenically disturbed (fragmented) areas. For example, a study involving movement patterns of *N. plumipes* showed that single lane roads acted as effective population barriers (Kasumovic *et al.*, 2007b). In the social spider, *Stegodyphus dumicola*, males frequently move among close neighbouring colonies, but this was not observed to facilitate gene flow between populations (Lubin *et al.*, 2009). Overall, although there are relatively little data available, it seems unlikely that population structure will change significantly within a breeding season as a function of emigration and immigration of adults (but see Uhl, 1998). More studies using larger sample sizes are still needed.

Movement patterns during the early life-history stages of a spider's lifetime vary significantly from adult movement patterns as many spiders use silk to travel on air currents when very young (i.e. ballooning). The success of ballooning depends on the patchiness of the population and wind velocity (Bonte *et al.*, 2007; Bonte and Lens, 2007) and may allow movement through habitat barriers (Ramirez and Haakonsen, 1999), although fragmentation may still limit ballooning success (Reed *et al.*, 2011). In multivoltine (multiple generations) species, large-scale movement by juveniles may change the population structure as the breeding season progresses. This will be more likely if the stochastic nature of ballooning means that immigration and emigration rates are not balanced, and if spiderlings balloon at a range of developmental stages or as a function of local conditions. A study examining sex-specific dispersal behaviour under laboratory conditions demonstrated that juvenile females dispersed shorter distances when they experienced increased female densities during development, whereas males dispersed further distances when they experienced high male and low female densities during development (De Meester and Bonte, 2010). The fact that individual spiderlings demonstrated differential dispersal behaviour as a function of conspecific densities suggests that population structure could change quite dramatically through ballooning. Studies examining juvenile movement patterns in the field (which are undoubtedly difficult) are required to examine the extent to which movement patterns of individuals within and between populations may significantly affect population structure and how this shapes the strength and direction of selection in natural populations. The use of genetic techniques will undoubtedly provide greater insight into variation in migration than typical behavioural studies (e.g. Ramirez and Haakonsen, 1999; Reed *et al*., 2011).

4.4 GENITALIA AND MATING SYSTEM

Although both sexes mate multiply in the majority of animals, males have higher variance in mating opportunities and on average, it is generally believed that males mate more often than females (Jones *et al*., 2002). In most species, the marginal fitness returns of multiple mating reaches an asymptote for females while there is no such asymptote for males (Bateman, 1948; Jones *et al*., 2002). This sex difference may not be as drastic in many spiders, due to spider genitalic morphology, sperm use patterns, and life history. First, one major determinant of the rate of change in fitness with mating opportunities is the number of individuals who never mate (Shuster, 2009; Shuster and Wade, 2003); where typically the skew in mating opportunities is greater for males than females (Bateman, 1948; Jones *et al*., 2002). However, in spiders, some females may never mate or have only rare mating opportunities in nature (Andrade and Kasumovic, 2005). This may be a risk for web-building species, in particular, where mate attraction largely depends on the detection of pheromones by males. Consistent with this idea, female pheromone production increases when males are scarce in *N. litigiosa* (Watson, 1986). This may generate significant skew among females if some females are consistently superior in mate attraction. Second, males of many well-studied species have an upper limit to the number of mating opportunities because they (i) cannot or do not recharge their pedipalps with sperm after their first mating (Andrade and Banta, 2002), (ii) irreparably damage their pedipalps by breaking them during copulation (Andrade and Banta, 2002; Herberstein *et al*., 2005b; Kuntner *et al*., 2009a,b; Miller, 2007; Schneider *et al*., 2008; Snow *et al*., 2006; Uhl *et al*., 2010), (iii) are cannibalized by females (Elgar, 1992; Elgar *et al*., 2000; Fromhage *et al*., 2003; Schneider and Elgar, 2001; Segoli *et al*., 2006; Welke and Schneider, 2010) or die spontaneously during their first mating (Foellmer and Fairbairn, 2003; Sasaki and Iwahashi, 1995), (iv) suffer high mortality rates during mate searching (Andrade, 2003; Kasumovic *et al*., 2007b; Segoli *et al*., 2006), and/or (v) have such energetically costly courtship that male longevity is significantly reduced after a mating attempt (independent of copulation; Hoefler, 2008; Kotiaho, 2000). In species that fit these descriptors, males will typically copulate only once with each pedipalp, and after mating with only one or a few females, the male will be removed from the mating pool. As a result, interactions with females that either end with a mating (successful) or end in pre-mating cannibalism (unsuccessful) can immediately change the density of males within the population, and therefore, the competitive environment a newly matured male will encounter.

A successful mating also affects the density and availability of females within a population. First, females that mate may quickly change pheromone release such that they are no longer attractive to males (Stoltz *et al*. 2007), effectively removing them from the mating population. Second, although females of many species mate multiply (see Aisenberg, 2009; Cross *et al*., 2008; Elgar, 1992, 1998; Schäfer and Uhl, 2005; Uhl *et al*., 2005; Welke and Schneider, 2010), if males can successfully plug both entrances of a female's genital tract, they may be able to successfully ensure that any mating attempts from subsequent males are unsuccessful (Schneider and Andrade, 2011; Schneider and Elgar, 2001; Snow *et al*., 2006; Uhl and Vollrath, 1998; Uhl *et al*., 2010). Females that have attracted multiple males (Miller, 2007) also alter the competitive environment of the remaining virgin males in three ways: first, in populations where the tertiary sex ratio is equal, males accumulating on one web may lead to female-skewed sex ratios elsewhere; second, females will be removed from the mating pool if they successfully mate with the first male; and third, the remaining males on the web that do not get the chance to mate with the female may not leave to find other virgin females. Successful and unsuccessful matings can thus rapidly alter the density of virgin males and females within a population depending on the mating system, behaviour, and reproductive biology of the species under study.

4.5 BREEDING SEASON LENGTH

As discussed, sex-specific differences in the above factors can lead to fluctuations in the number of available females and the density of rival males resulting in variation in competitive challenges encountered by males maturing at different times of the season. If temporal factors interact with spatial variation, this could lead to a large amount of variance in population structure at any given time in the breeding season. The relative importance of life-history traits, however, could also be affected by the length of the breeding season as this has the potential to change the number of mating opportunities, the number of generations per year (univoltine to multivoltine), and whether generations overlap. The length of the breeding season is one ecological factor that is likely to have a strong affect on the mating system of a species.

A short breeding season is defined as a small window in which males and females mature and in which they have the opportunity to mate. Short breeding seasons impose temporal limits on polygyny for males (Emlen and Oring, 1977) due to intense competition for females and often lead to mate guarding which could potentially lead to size-assortative pairing (Burley, 1983; Crespi, 1989; Hoefler, 2007). For example, in many Salticid (Hoefler, 2007; Jackson, 1986a) and Linyphiid species (Austad, 1983; Weldingh *et al*., 2011), mature males guard nearly mature females to ensure a mating.

As the length of the breeding season increases, there is not only a greater likelihood that multiple generations can occur in a single breeding season but also the possibility that the second generation may not have the time or resources to successfully reach maturity, mate, and produce offspring. This could result in two separate cohorts. For example, in *Pardosa agrestis*, individuals hatching early in the breeding season follow one of two trajectories: they either mature near the end of the breeding season with time to breed in the current season or do not mature and overwinter as juveniles, maturing earlier in the following breeding season mature more slowly (Kiss and Samu, 2005). This results in two distinct peaks of adults due to the overwintering individuals. The developmental trajectory is in part determined by signals of photoperiod and temperature (Kiss and Samu, 2002), although individuals from the same egg sac can follow different developmental trajectories (Kiss and Samu, 2005). Individuals preparing to overwinter may also allocate resources differentially as seen in *Pardosa pseudoannulata* (Iida and Fujisaki, 2007) or may move to a different habitat to increase overwintering success (Kraus and Morse, 2005). This may change dramatically for larger spiders as a single breeding season may not be long enough to mature. In *Pardosa moesta* and *Pardosa mackenziana* wolf spiders that can weigh up to 80 and 60 mg, respectively, and have a two-year life cycle where immature individuals overwinter twice before maturing (Buddle, 2000). Although most examples of overwintering species occur in temperate zones where breeding seasons are relatively short, examples of cohort-splitting or life-cycle polymorphism also occurs in species in more tropical zones (Framenau and Elgar, 2005).

During longer breeding seasons, females may reach maturity asynchronously either because there is sufficient time for multiple generations each season or because spatio-temporal variation in resource acquisition will allow divergent growth trajectories. Asynchronous maturity will typically allow males the potential to find second mates (Emlen and Oring, 1977) leading to an increase in the variance in male reproductive success. Longer breeding seasons may also allow the earlier generations to produce offspring that can reach maturity before the breeding season ends. This can result in several generations (multivoltine) where individuals from the different generations may overlap and compete against one another.

Although the variability seen in these factors within and between populations and species of spiders can be extreme, this variability allows researchers wide latitude in testing specific predictions regarding the evolution of mating systems and strategies. The key is to choose species that have life-history and ecological features that allow comparative and experimental focus on the questions of interest.

5 Adaptations towards an uncertain world

5.1 EXPERIENCE THROUGH PHEROMONES

As the availability of mates and the density of rivals fluctuate throughout the breeding season, and as age and mating structure of the population change, the phenotypic optima for successful competition will also change. As males are the mate-searching sex in the vast majority of species, and females are either sedentary (Foelix, 1982) or return to the same nest each night (Hoefler and Jakob, 2006), spatio-temporal shifts in population structure will affect a male's reproductive success more than a female's.

In this uncertain landscape, males have one significant edge—chemical cues produced by females to attract mates, in addition to chemicals produced by other males (Gaskett, 2007), can provide a substantial amount of accurate information about their competitive environment (see above). Thus we predict that male spiders should have developmental and behavioural traits that anticipate the features of the competitive arena they are entering, and that allow them to take maximum advantage of the current population structure or minimize competition for available females. Below, we discuss a range of male mating strategies for which there is now growing evidence that information in airborne chemicals is used to make developmental and/or behavioural decisions.

5.1.1 *Stopping the transmission of attractive pheromones*

Competition between males can be extremely intense and is not only energetically costly (Kotiaho *et al*., 1996, 1997, 1998) but can also lead to death (Elias *et al*., 2008; Kasumovic *et al*., 2009b; Leimar *et al*., 1991). One method for a male to decrease the level of competition is to reduce a female's ability to transmit attractive pheromones. In at least one species (*L. hasselti*), evidence suggests that females discontinue producing attractive pheromones very soon after mating (Jerhot *et al*., 2010; Stoltz *et al*., 2007) such that males searching for virgins are not attracted to newly mated females (Kasumovic and Andrade, 2009a). Although it is not known whether it is the result of a pheromonal signal, the webs of mated females of other species are also not attractive and may sometimes be a deterrent to males (Dodson and Beck, 1993; Gaskett *et al*., 2004; Hoefler, 2007; Miyashita and Hayashi, 1996; Papke *et al*., 2001; Riechert and Singer, 1995; Rypstra *et al*., 2003). This suggests that males can reduce competition with rivals simply by mating with females as quickly as possible. Mating with females may not be simple, however, particularly in species where one of the following occurs: (1) females are aggressive and may cannibalize males before the opportunity to mate arises (Elgar, 1991b, 1992), (2) females show unpredictable variation in receptivity resulting in variable periods of cohabitation prior to mating (Anava and Lubin, 1993; Masumoto, 1991; Suter and Keiley, 1984; Suter and Renkes, 1984), or (3) females are unlikely to mate or allow a complete copulation unless the male engages in prolonged courtship (Snow and Andrade, 2005; Stoltz *et al*., 2008, 2009), increasing the risk of usurpation. In a recent study on mating behaviour in *L. hasselti*, for example, Stoltz and Andrade (2010) showed that males may parasitize previous courtship effort from rival males. *L. hasselti* males have very long courtship displays (6 h), and if males attempt to copulate too soon, they are killed by the female before mating is complete. However, when a resident male has been courting for at least 100 min, rivals can successfully mate with the female instantly with no repercussions (Stoltz and Andrade, 2010). Thus selection may favour males with a secondary means of limiting rivals from locating the female with which they are attempting to mate.

In some species, males have evolved a behaviour in which they cut the female's web and bind it with their own. This web-reduction behaviour is documented in several species (Forster, 1995; Harari *et al*., 2009; Schulz and Toft, 1993; Watson, 1986). Males cut and bind the threads of females that are actively releasing attractive pheromones until the male has an opportunity to mate with the female (Watson, 1986). In an elegant set of laboratory experiments, Watson (1986) showed that reduced webs are less attractive to rivals than intact webs.

5.1.2 *Developmental tactics*

As changes in population structure affect within-season variation in the intensity and direction of selection, the fitness of any given phenotype is context dependent (e.g. Kasumovic and Andrade, 2009a; Lailvaux and Kasumovic, 2010; Moya-Laraño *et al*., 2007). As a result, there may be strong selection for adaptive developmental plasticity by which individuals can match their phenotype to variable competitive contexts (Berrigan and Scheiner, 2004; Garland and Kelly, 2006; Kasumovic and Brooks, 2010). For such a strategy to evolve, however, developing males would require reliable cues of the surrounding competitive challenges (Lively, 1986). Again, the changes in airborne chemical cues produced by surrounding males and females potentially provide the information necessary for this type of developmental strategy to evolve.

One such example comes from the Australian redback spider (*L. hasselti*). As in most web-building spiders, male redbacks do not feed after maturity (Foelix, 1982) and therefore have fixed resources at maturity that must be used to search for and court females, and compete with other males. In a laboratory study, penultimate instar males were reared in the presence or absence of female's pheromones and at differing densities of immature males. In this study, male redbacks modified their allocation towards development rate, body size, and body condition (Kasumovic and Andrade, 2006), traits that are correlated with fitness in different competitive environments (Andrade, 2003; Snow and Andrade, 2005; Stoltz *et al*., 2008). Males matured significantly faster in the presence of females but were smaller and in poorer body condition (Kasumovic and Andrade, 2006). Although smaller, this shift is adaptive as there is strong first male precedence (Snow and Andrade, 2005; Snow *et al*., 2006), so rapidly developing males would mate with virgin females quickly, and outcompete larger, more slowly developing competitors (Kasumovic and Andrade, 2009a; Snow and Andrade, 2004, 2005). When females were absent and rivals present at high density, males took longer to mature but were larger and in better condition as adults; traits that increase fitness in competition against rivals

(Stoltz *et al.*, 2009). This example demonstrates that males can alter allocation across life-history traits as a function of relatively short-term changes in their environment. More studies of this type are necessary to determine the phylogenetic and ecological distribution of this form of plasticity.

There are two further examples of strong correlations between phenotypes and local population structure in field populations of two species of spiders: the golden orb-web spider (*N. plumipes*) and the St. Andrew's cross spider (*A. keyserlingi*). In *N. plumipes*, females produce webs either singly or in aggregations of up to nine females (Herberstein and Elgar, 1994; Kasumovic *et al.*, 2007b). Males mature either within or near these aggregations and then search for females. While searching, males preferentially settle on the webs of adult females (Kasumovic *et al.*, 2008), but those in better body condition prefer penultimate instar females (Kasumovic *et al.*, 2007b). Due to the intense cannibalism faced by males, most males only have a single opportunity to mate in their lifetime (Schneider and Elgar, 2001). A male's fitness is thus maximized by successfully finding and monopolizing a virgin female. Kasumovic and colleagues (2009a) found that a male's size and weight were positively correlated with the number of males and negatively correlated with the number of females within an aggregation (but not across the entire population). Such a pattern would be expected if males develop more quickly when competition is low, but mature larger and heavier when more rivals are present as larger size increases competitive success against rivals (Elgar and Fahey, 1996).

This is in contrast to male *A. keyserlingi* that have a very different life history and mating strategy. First, males attempt to mate multiply (Herberstein *et al.*, 2005b). Second, although virgin male *A. keyserlingi* prefer virgin females (Herberstein *et al.*, 2002), mated males have no such preference and attempt to mate with (and subsequently guard; Herberstein *et al.*, 2005a) any female they can find (Gaskett *et al.*, 2004). As a result, a male's fitness is determined by finding and mating with different females. In *A. keyserlingi*, male size and weight was positively correlated with male density as larger and heavier males are better equipped to outcompete rivals (Herberstein *et al.*, 2005a). As expected, female density was not correlated with male phenotypic traits as fitness is not as constrained by the availability of virgins as it is in *N. plumipes*. Although the results are only correlative and no data were available on development time, the population structure was a far stronger correlate of a male's phenotype than any other measured environmental variable. Direct experimental tests in these two species would be welcomed, as would similar studies across a range of spiders with a diversity of mating systems.

5.1.3 *Behavioural tactics*

Apart from developmental tactics, the structure of the population can also determine a male's mating tactics. For example, in *A. bruennichi*, copulation duration is positively correlated with paternity (Schneider *et al.*, 2006), but longer matings carry a higher risk of cannibalism (Nessler *et al.*, 2007; Schneider *et al.*, 2006). Although males are commonly cannibalized after mating, some males also attempt to survive the first cannibalistic attempt in order to mate a second time (Nessler *et al.*, 2009a; Schneider *et al.*, 2006), after which they succumb to cannibalism without attempting to escape (Foellmer and Fairbairn, 2003; Gaskett *et al.*, 2004; Nessler *et al.*, 2007). Nessler and colleagues (Nessler *et al.*, 2009a,b) found that the variation in escape attempts between males can be explained by the presence of females during rearing (Nessler *et al.*, 2009b). Males that experienced females and their pheromones while immature were more likely to succumb to female attacks (and copulate for longer) during the first copulation than males that were reared in the absence of females and their pheromones (Chinta *et al.*, 2010). Although the fitness effect of such a shift is unknown, it is clear the perception of the availability of females while immature can affect adult male mating strategies.

5.2 EXPERIENCE THROUGH SOCIAL INTERACTIONS

Although accurate assessment of competitive environments can be facilitated by pheromones, other modalities may be important particularly for wandering spiders. Direct social interactions may provide more salient estimates of the social environment for these species and may be a secondary mechanism used to estimate/predict competitive environments. In the following sections, we will explore the role of experience as an indicator of future and current environments and its effects on spider behaviour and mating system evolution.

5.2.1 *Juvenile experience*

Wolf spiders of the genus *Schizocosa* have received a lot of attention particularly in studies on mating behaviour. Three species that have been the focus of intense research have been *Schizocosa ocreata*, *Schizocosa rovneri*, and *Schizocosa uetzi* (see Hebets, 2003, 2005; Hebets and Uetz, 2000; Hebets and Vink, 2007; Norton and Uetz, 2005; Roberts and Uetz, 2008; Shamble *et al.*, 2009; Uetz *et al.*, 2009). Male wolf spiders produce courtship signals consisting of visual leg waving, visual ornaments, and substrate borne vibrations (Elias and Mason, 2011; Hebets and Papaj, 2005; Hebets and Uetz, 2000; Shamble *et al.*, 2009; Uetz and Roberts, 2002), and female spiders have been demonstrated to choose males based on properties of vibratory (Gibson and Uetz, 2008; Hebets, 2005; Shamble *et al.*, 2009) and visual displays (Persons and Uetz, 2005; Scheffer *et al.*, 1996; Shamble *et al.*, 2009; Stratton, 2005; Uetz and Norton, 2007; Uetz and Roberts, 2002; Uetz and Smith, 1999; Uetz *et al.*, 2002). Lab-raised females of these species exhibit preferences for species-specific male displays (Hebets and Uetz, 2000; Hebets *et al.*, 2006; Stratton and Uetz, 1981, 1983).

In *Schizocosa*, juvenile experience has major effects on mating preferences (Hebets, 2003, 2007; Hebets and Vink, 2007; Rutledge *et al*., 2010). In laboratory experiments with *S. uetzi*, Hebets (2003) demonstrated that females that had experienced courtship from males with manipulated visual traits as juveniles preferred those traits after sexual maturation. Females were more likely to mate with males with familiar traits and more likely to cannibalize males with unfamiliar traits (Hebets, 2003). Similarly, in experiments with Mississippi populations of *S. rovneri*, females with no juvenile experience showed no preferences between an *ocreata*-like morph (brush-legged) and a *rovneri*-like morph (non-ornamented). However, females that had been courted by either brush-legged or non-ornamented morphs as juveniles significantly preferred brush-legged males (Hebets and Vink, 2007). Interestingly, in experiments with manipulated *S. rovneri* from Ohio populations, a much different pattern was observed (Rutledge *et al*., 2010). In this laboratory study, *S. rovneri* juveniles experiencing courtship from males with highly modified phenotypes, preferred unfamiliar phenotypes over familiar phenotypes (Rutledge *et al*., 2010). The different patterns observed between these studies may result from genetic differences between populations, methodological differences, or from natural selection stemming from different demographic patterns of sympatrically occurring species (Rutledge *et al*., 2010). Regardless, this set of studies suggests juvenile experience, in this case, courtship and visual contact, can have strong effects on female choice. This has important implications. As the relative density of males increases, social interactions between juvenile females and males will also increase. Thus experience effects could amplify the effect of sexual selection and could promote species maintenance/diversification (Rutledge *et al*., 2010). Experience-dependent mechanisms could be plastic and such mechanisms could evolve as a response to local demographic patterns. In several studies, preferences for particular male phenotypes only emerged with juvenile experience suggesting that experience-mediated effects are context dependent (Hebets and Vink, 2007; Rutledge *et al*., 2010).

Juvenile experience can also affect several other behaviours associated with reproduction. In the fishing spider *D. triton*, Johnson (2005) demonstrated that when juvenile females had experience with males (cohabitation), those females were more likely to cannibalize courting males as adults, regardless of mating status. The presence or number of cohabiting males apparently serves as a cue to local mate availability and thus affects female ''choosiness'' as adults (Johnson, 2005). When males are rare, cohabitation is rare as well thus pre-copulatory cannibalism of potential mates is costly as the female could remain unmated (Arnqvist and Henriksson, 1997; Johnson, 2001, 2005). However, because cannibalizing males increases female fecundity, when the perception of male density is higher and the female is likely to have multiple suitors, a higher rate of pre-copulatory cannibalism may be adaptive (Johnson, 2005). By tuning mating and cannibalistic behaviours to local demographic factors, females can thus compensate for spatio-temporal variations in male density.

5.2.2 *Adult experience*

While experience-related learning by adults is believed to be an important aspect of mating behaviour in most vertebrates (see Dugatkin, 1992; Jennions and Petrie, 1997), experience/learning effects have been overlooked in most arthropods, perhaps because it is assumed to be unlikely due to the relatively small size of the nervous system and short lifespan (Dukas, 2007). However, learning/experience-modified behaviour may be superior to innate behaviour in variable environments and has been shown to be significant in several arthropods (Dukas, 2007). Experience would allow spiders to adaptively change their behaviours in a variety of scenarios, and modifications of behaviour based on experience have been demonstrated to be a major part of the biology of several spider species.

One class of experience that may have significant effects across spider taxa is that derived from fight outcomes. Experience-dependent effects on fighting behaviour have been documented in many systems (Hsu *et al*., 2009). Winning a contest often increases the probability of winning future contests (winner effect), while losing a contest decreases the probability of winning future contests (loser effect) (reviewed in Hsu *et al*., 2006). In fact, many of the classic examples of this phenomenon come from spiders (Austad, 1983; Dodson and Beck, 1993; Riechert, 1988). Here, we outline a recent set of studies examining this phenomenon in *P. clarus* (Salticidae) and argue that experience effects allow males to assess their own ability relative to the field of likely competitors—a field that constantly shifts over the breeding season. Males in this species are protandrous, and males seek out and find immature females to cohabit with early in the breeding season (Hoefler, 2007). At this point in the breeding season, demographic structure is strongly biased towards mature males (male-biased operational sex ratio) and males fiercely defend immature female resources (Elias *et al*., 2008; Hoefler, 2007). Heavier males are more likely to win contests during this time (Elias *et al*., 2008; Hoefler, 2007; Kasumovic *et al*., 2009b). Near the middle of the season, females mature relatively synchronously leading to a predictable and rapid demographic shift from male-biased tertiary sex ratio to equal tertiary sex ratio (Elias *et al*., 2010b; Hoefler, 2007). At this point in the breeding season, sexual selection shifts from male–male competition for immature females (Hoefler, 2007; Kasumovic *et al*., 2011) to female mate choice based on male courtship (Elias *et al*., 2010b; Sivalinghem *et al*., 2010). Male size/weight is extremely variable during the breeding season and males tend to get bigger as the season progresses (Elias *et al*., 2010b; Hoefler, 2007, 2008; Kasumovic *et al*., 2010). The competitive environment as well as the relative competitive ability of an individual male is thus expected to fluctuate through the breeding season. Because males actively choose larger, more fecund females that are closer to maturing and because females mature relatively synchronously (Hoefler, 2007), it is important for males to choose only females they can successfully defend within the intense male–male competition selection window. However, a male's ability to defend a chosen female is wholly dependent on his competitive ability relative to the pool of local opponents, which can shift as males move over time. Thus a running estimate of relative competitive ability would give males a strategic advantage over local competitors. One proposed mechanism for keeping this kind of ''running tally'' is experience-dependent changes in fighting ability (winner and loser effects; Hsu *et al*., 2006; Kasumovic *et al*., 2010).

As predicted, Kasumovic *et al*. (2009b) determined that experience played a significant role in contest success in *P. clarus* using a mixed tournament design (Stuart-Fox, 2006); Winner and loser effects were not permanent, however, and disappeared over the course of 24 h (Kasumovic *et al*., 2010). Kasumovic *et al*. (2010) suggested that retention time of experience effects was dependent on the expected encounter rates of competitors and that a ''leaky integrator'' type mechanism could serve to track the relative status of fighting ability of the local pool of competitors (Hsu *et al*., 2009; Kasumovic *et al*., 2010). If subsequent contests occur before the effects of prior experience decay, then experience effects may accumulate (Hsu *et al*., 2006). Over repeated encounters an individual's estimate of his own competitiveness should float to a level that represents his actual fighting ability relative to that of his pool of competitors as the ratio of successful (incrementing) and unsuccessful (decrementing) encounters will be determined by his resource-holding potential (Arnott and Elwood, 2009) relative to competitors. Time-dependent experience affects, therefore, should provide a male with a running average of the competitive level of their local population of rivals. This may be especially important because the competitive environment is likely to fluctuate widely because resource-holding potential (weight; Elias *et al*., 2008; Hoefler, 2007) changes depending on current feeding history (Elias *et al*., 2008; Kasumovic *et al*., 2010) and time of the season (Elias and Kasumovic, unpublished observation).

In *P. clarus*, adult male experience is also likely to mediate the shift from male–male competition behaviours (aggressive signalling and resource defence behaviours) to courtship behaviours (courtship signalling). Signalling is distinct in each context and females prefer males that court at higher rates and have longer legs (Elias *et al*., 2010b; Sivalinghem *et al*., 2010). Males that act aggressively towards females are less likely to mate (Sivalinghem *et al*., 2010), and males are commonly seen being cannibalized in the field by females (Elias and Kasumovic, unpublished observation). Accurately assessing the current selective environment and suites of behaviours more likely to ensure reproductive success at that point in time is critical (defend vs. court free roaming females). Flexible behaviours dependent on experience with the local demographic and environmental conditions is likely to be common across spider taxa, but we predict strongest effects for wandering rather than web-building spiders. Wandering spiders are likely to have higher encounter rates with conspecifics, and thus the opportunity for salient experiences is higher.

Experience with the local competitive environment has also been shown to shift mate choice behaviour in male spiders. In field studies on *Z. x-notata*, several populations were examined which varied in the level of competition; in high competition populations where the sex ratio was heavily male biased, most females were guarded by males, and guarding success was low. In contrast, in a low competition population where the sex ratio was even, 70% of females were guarded, and guarding success was high (Bel-Venner *et al.*, 2008). In high competition environments, large males chose larger, more fecund females and smaller males chose poorer-quality females leading to a pattern of size-assortative mating (Bel-Venner *et al.*, 2008). Bel-Venner *et al.* (2008) proposed that smaller males chose small females as a way to avoid futile and costly competition with large males. In low competition environments, however, no male mate choice was observed and it was suggested that males in these environments pair opportunistically to maximize reproductive opportunities (Bel-Venner *et al.*, 2008). Size assortative pairing was also observed in *P. clarus* but in that species, all males preferred larger, more fecund females but only large males could compete successfully for them (Hoefler, 2007).

Not surprisingly, mating experience often changes subsequent mating behaviour. The most commonly observed pattern in spiders is that females become less receptive after both spermathecae have been filled (see Aisenberg and Costa, 2005; Baruffaldi and Costa, 2010; Molina and Christenson, 2008; Wilder and Rypstra, 2008a). Recent work suggests that males transfer considerable volumes of seminal fluids to females suggesting the potential for chemical manipulation of female receptivity (Michalik *et al*., 2010). However, there is debate on whether this commonly observed pattern is adaptive for both sexes or whether it is the outcome of sexual conflict between males and females (see Kuntner *et al*., 2009b; Maklakov and Lubin, 2004). Many female spiders will still mate multiply even though receptivity patterns have been changed, and this has often been interpreted as a shift in the ''choosiness'' of females (see Cross *et al*., 2007; Jackson, 1981; Sivalinghem *et al*., 2010). In the spider *L. mariana*, larger females are more likely to choose smaller males and males that signal more after their initial matings even though second matings are less frequent than first matings (Aisenberg, 2009). In *Stegodyphus lineatus*, females mate with up to five males but behave aggressively to all males after the first mate (Maklakov and Lubin, 2004). The success of the second mate is determined by male body mass with larger males being more likely to mate again (Schneider and Lubin, 1996, 1997). In this species, this pattern results from sexual conflict and not increased choosiness as females experienced lower fitness when they mated multiply (Maklakov and Lubin, 2004).

Males have also been shown to modify their behaviour based on mating experience. In the case of *A. keyserlingi*, males exhibit preferences to virgin webs but after mating do not show any preference for immature, virgin, or mated females (Gaskett *et al*., 2004). In *Pisaura mirabilis*, males that successfully mated with more than one female provided more courtship effort for every individual female than monogamous males (Tuni and Bilde, 2010). In the cellar spider *P. phalangioides*, Hoefler *et al.* (2010) demonstrated that males that had experienced female silk courted non-virgin females more suggesting that males bias mating investment (courtship) based on some estimate of female density.

One potentially important aspect of adult experience that could drastically affect future mating opportunities and by extension mating system evolution is maternally derived effects on hatching in response to predators. Li (2002a) showed that in the spider *Scytodes pallida*, pregnant females experiencing cues from predators (jumping spiders) pass on a maternal cue that causes faster egg hatching. Spiderlings hatching in areas with high predators in general hatch sooner and the spiderlings are smaller (Li, 2002a). Variation in the population structure of predators can thus also have dramatic effects on mating systems as spiders from predator-rich environments may be weaker competitors than those from predator-poor environments. Alternatively, if there are advantages to emerging sooner (see Kasumovic and Andrade, 2006), then spiders from predator-rich environments may have an advantage in securing mates and may gain an ownership advantage which may outweigh the competitive disadvantages (Hack *et al.*, 1997; Kasumovic *et al.*, 2011; Leimar *et al.*, 1991).

6 Conclusions and future directions

Research on spiders has often concentrated on the lurid and extravagant traits that seem to be common in spider mating systems (e.g. genital mutilation, mating plugs, extreme monogyny, sexual cannibalism). These behaviours have offered a means to test general hypotheses about sexual selection and behavioural ecology. Here, we argue that the unique nature of spider mating systems and the adaptations that defines them as a group gives scientists the opportunity to explore how environmental variations may affect behaviour and life history. While this line of research is not novel, the idea that environments vary at very short temporal and spatial scales has only recently been explored theoretically and empirically. In order to fully understand adaptation, it is important to understand not only how selection operates on phenotypic distributions, but also how selective environments change, at what scales they change, and how animals may or may not be adapted to change in their selective environments. Changes in population structure are an excellent opportunity to investigate dynamic environments because of their strong role in determining selection pressures.

Here, we focus on three demographic variables that we argue can have wide-ranging effects on selection in spiders, and more critically, are likely to vary over relatively short spatio-temporal scales: tertiary sex ratio, density, and sex biases in development time (Table 1). We suggest several avenues of research that are missing in the literature. First, more studies that measure demographic patterns (spatial distribution, tertiary sex ratio, density, etc.) in the field as well as how development, experience, and predatory pressures shape population distributions and structure across the landscape. Second, it is important to expand our knowledge-base on sperm competition patterns in more species. More studies examining sperm precedence, genitalic morphology, and mating patterns are needed. To date, too few studies in spiders have explored this in detail, and understanding sperm patterns is key to deciphering mating patterns in the field. Third, it is important to understand the different competitive contexts that spiders face in nature. Scientists must take care to design experiments that are grounded in the ecology and biology of the study species in nature. Manipulations are critical, but when these cannot be done in the field, they should at least be paired with complementary data acquired under field conditions—and these must be interpreted in their particular spatio-temporal context. Fourth, one challenge with making broad conclusions based on the literature in this area is the strong tendency of researchers to focus on a few, showy taxa. While it is clear that broader taxonomic coverage is needed, we urge researchers to choose species as a function of the questions they wish to answer whenever possible, rather than the reverse.

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