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REVIEW

A review of the mechanisms and functional roles of male silk use in spider courtship and mating

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Abstract. Spiders are well known for using chemical, vibratory, tactile, and visual signals within mating contexts. All spiders produce silk, and even in non-web building spiders, silk is intimately tied to courtship and mating. Silk produced by females provides a transmission channel for male vibratory courtship signals, while webs and draglines provide a substrate for female sex pheromones. Observations of male spiders producing silk during sexual interactions are also common across phylogenetically widespread taxa. However, the function of male-produced silk in mating has received very little study. Exploring the function of male silk use during mating will provide a deeper understanding of the complex mating systems of spiders and allow tests of hypotheses about the evolution of male and female traits under sexual selection and/or conflict. In this review, we outline functional hypotheses that may explain each of the following three main categories of silk deposition males exhibit during courtship and mating: (1) silk deposition on females' webs or other silk structures, (2) silk deposition on females ('bridal veils') and (3) silk associated with nuptial gifts. We then summarize the current knowledge of silk use by male spiders within these three categories and the types of mechanisms that may lead to functional effects, and discuss areas where future work can be targeted.

Keywords: Nuptial gifts, web modification, bridal veils, mating behavior, sexual selection

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1. INTRODUCTION

1.1 Overview.—Mating in animals that are generally solitary, like spiders, necessarily involves a number of shifts in behavior to facilitate locating, approaching, and mating with the opposite sex (Elias et al. 2011; Schneider & Andrade 2011). These shifts provide interesting opportunities to test general aspects of theory related to communication (Hauser 1996; Bradbury & Vehrencamp 2011; Herberstein et al. 2014), mate choice (Bateson 1983), sexual conflict (Arnqvist & Rowe 2005), and sexual selection (Andersson 1994). In many species, males use a range of behavioral, morphological, sensory, and physiological traits when approaching females to seek matings (Andersson 1994). These traits may enhance the success of the male through their effects on the behavior of potential mates or rivals. For example, females' mating decisions may be based on the nature or intensity of male courtship displays or ornaments if these reflect desirable (female-fitness-enhancing) characteristics in a potential mate (Bateson 1983; Andersson 1994; Jennions & Petrie 1997; York & Baird, 2017). Moreover, in many taxa, courtship is a public event (Herberstein et al. 2002), vulnerable to interruption or interference by other males (e.g., Hibler & Houde 2006; Stoltz & Andrade 2009). Sexual selection on males to achieve matings is often intense and may lead to the evolution of remarkable adaptations to overcome competition or persuade females to mate (Andersson 1994). In addition, it is now clear that males may adjust investment in courtship as a function of the perceived fitness payoff (quality or risk) associated with approaching or mating with a given female (Johnson et al. 2011; Moskalik & Uetz 2011; Lane et al. 2015; McGhee et al. 2015; Rundus et al. 2015; Cross 2016; Rypstra et al. 2016). In cannibalistic spiders, there is an added dimension of risk to the male associated with approaching the wrong female (Herberstein et al. 2002; Johnson et al. 2011; Kralj-Fiser et al. 2016). The result is a rich interplay of male and female fitness interests that may be intertwined in different ways at different stages of courtship.

In general, spiders offer interesting opportunities for studying the 'mating dance' between the sexes in detail, since mating behavior varies considerably among taxa (Schneider & Andrade 2011), and courtship often includes multimodal communication (e.g., visual, vibratory, chemical, and tactile; Witt & Rovner 1982). Silk is a tangible, measurable, and manipulable medium that can convey information in all of these modalities and thus has been frequently studied in this context—but almost exclusively from the perspective of females. Thus, it is well known that female silk plays a central role in many aspects of communication and mating outcomes across spider taxa (Gaskett 2007; Elias & Mason 2010; Uhl & Elias 2011; Schulz 2013). In addition to its communicative role, for many spider species female silk is the substrate on which mating interactions occur (Foelix 2011) and this also has implications for its functional role.

What is less well known is the variety of ways in which male silk may mediate sexual interactions in spiders. In this review, we highlight accumulating evidence, from a variety of spider taxa, that male silk also has a significant role in mate attraction, courtship, and mating. We outline the ways in which male silk is used in these interactions and suggest tractable approaches to testing a range of hypotheses to explain the evolution of male silk use in terms of sexual selection and/or sexual conflict. Finally, we identify, where possible, taxa where additional study may be particularly illuminating, both in terms of our understanding of silk use in spiders, and in terms of a more general understanding of male and female mating tactics.

We start by briefly summarizing some salient features of spider silk, and the well-known uses of silk by females during mating interactions. We then provide an overview of the main functional hypotheses for male silk use in mating, and the mechanisms that may lead to functional outcomes. We follow this with a description of the ways males use silk in mating, split into three broad categories (silk deposition on the female's web or other silk structures, silk deposition on the female, and silk associated with nuptial gifts), with examples from a range of taxa. Each category ends with a qualitative evaluation of the hypotheses given the available data. Finally, we briefly discuss a few other ways males use silk in mating interactions (e.g., sperm webs).

1.2 Properties of spider silk.—Spider silk consists of protein-based fibers, is energetically costly to produce (Peakall & Witt 1976; Prestwich 1977), is unique in its combination of strength and elasticity, and is one of the toughest known biological substances (Gosline et al. 1999; Rising et al. 2011). The physical properties of spider silk vary among taxa and among contexts within taxa (Craig 2003). Years of research show the biophysical properties of silk are strongly dependent on links between ecological context, evolutionary history (e.g., Wolff et al. 2017), and the physiology of the spider at the time of silk production (Blamires et al. 2017). This may explain why, despite recent progress (Rising et al. 2011; Hsia et al. 2012), attempts to develop industrial production methods to synthesize spider silk have been challenging (Kluge et al. 2008; Koeppel & Holland 2017). Features such as the silk tensile strength and elasticity depend on which glands are used to produce the silk (e.g., aciniform, ampullate, flagelliform, tubuliform, or piriform) and how it is extruded, which varies with use (e.g., egg sacs, structural web silk, capture silk, or drag lines; Vollrath & Knight 2001; Foelix 2011).

Spiders produce silk at every life history phase, and in most cases, leave silk draglines behind them as they move through their habitat (Foelix 2011). Thus, most spider behaviors have the potential to create and leave behind information associated with silk in a variety of modalities. Variation in reflectance properties (Blackledge & Wenzel 2000; Barrantes

et al. 2013) and color (e.g., Craig et al. 1996) of silk can have implications for visibility or attractiveness to prey, predators and conspecifics under a variety of light conditions. However, functional effects have primarily been investigated with regard to predator/prey dynamics (e.g., Craig & Barnard 1990; Blackledge 1998; Persons & Rypstra 2001; Rypstra & Buddle 2013; Bucher et al. 2014; Lai et al. 2017). The structure of silk makes it well-suited as a delivery vehicle for contact or airborne semiochemicals (Gaskett 2007; Schulz 2013; Henneken et al. 2017a) with interesting implications for function arising from variation in how long pheromones remain active after deposition, and whether rain (i.e., a polar solvent) can wash them away (e.g., water soluble pheromones in some wolf spiders: Dondale & Hegdekar 1973; Tietjen 1977; Baruffaldi et al. 2010; water-resistant pheromones in fishing spiders and some wolf spiders: Roland & Rovner 1983; Lizotte & Rovner 1989). Finally, silk also serves as a medium for vibratory communication and detection of vibratory cues, particularly in web-building species (Uhl & Elias 2011).

1.3 Female silk and mating.—As a substrate for pheromones, transmission of vibratory signals, and the structure on which mating may take place, female silk is well known for its role within courtship and mating contexts in web-building spiders (Locket 1926; Foelix 2011). Webs or other silk structures (e.g., the silk associated with burrows) provide the stage for vibratory courtship displays by males in many spider taxa in which females are sedentary (Uhl & Elias 2011). Similarly, among cursorial spiders, female drag-line silk provides information to conspecific males (Bristowe & Locket 1926; Kaston 1936; Anderson & Morse 2001; Nelson et al. 2012; Rundus et al. 2015; Bell & Roberts 2017). Draglines can convey chemical (chemo-tactile; e.g., Nelson et al. 2012) or tactile (mechanical; e.g., Anderson & Morse 2001; Leonard & Morse 2006) information about the location and identity of the signaler.

1.3.1 Substrate for pheromones: Spiders are predatory and generally solitary, and thus face the challenge of attracting or finding mates. Behavioral evidence indicates that sex pheromones provide the solution to this problem in many spiders (Gaskett 2007; Uhl & Elias 2011; Trabalon 2013). Indeed, since chemical signaling is the most ancient form of communication (Wyatt 2014), sex pheromone production is likely ubiquitous in spiders. Pheromones associated with female silk include those that release volatile, airborne chemicals, and those that require contact by the receiver (Gaskett 2007; Schulz 2013).

Airborne sex pheromones typically attract mates at long range and may also reveal information about the identity and quality of the signaler (Gaskett 2007; Uhl & Elias 2011; Uhl 2013). Volatile, attractive sex pheromones have been identified from the bodies and/or silk of females in only three species: *Argiope bruennichi* (Scopoli, 1772) (Araneidae; Chinta et al. 2010), *Agelenopsis aperta* (Gertsch, 1934) (Agelenidae; Papke et al. 2001), and *Pholcus beijingensis* Zhu & Song, 1999 (Pholcidae; Xiao et al. 2009). Although these chemically identified pheromones come from web-builders, cursorial spiders including lycosids and salticids also produce volatile sex attractants associated with their bodies and/or silk (e.g., Searcy et al. 1999; Nelson et al. 2012). Behavioral studies with *Latrodectus* Walckenaer, 1805 spp. (Theridiidae) indicate that volatile, silk-borne female pheromones allow males to discriminate between females of different age, mating status, body condition, and population of origin (Kasumovic & Andrade 2004; Andrade & Kasumovic 2005; MacLeod & Andrade 2014).

Silk-borne contact pheromones elicit male searching and courtship behavior in both cursorial and web-building spiders (e.g., Tietjen 1978; Suter & Renkes 1982; Taylor 1998), and may provide information about female identity, mating status, receptivity, diet, gravidity, and reproductive potential (Riechert & Singer 1995; Roberts & Uetz 2005; Baruffaldi & Costa 2010; Trabalon 2013; Henneken et al. 2015, 2017b). Contact sex pheromones have been identified from the silk of female spiders in four families: *Linyphia triangularis* (Clerck, 1757) (Linyphiidae; Schulz & Toft 1993), *Latrodectus hasselti* Thorell, 1870 and *L. hesperus* Chamberlin & Ivie, 1935 (Theridiidae; Jerhot et al. 2010; Scott et al. 2015a), *Eratigena atrica* (C.L. Koch, 1843) (Agelenidae; Prouvost et al. 1999), and *Cupiennius salei* (Keyserling, 1877) (Ctenidae; Papke et al. 2000).

1.3.2 Substrate for transmission of vibratory signals: Substrate-borne vibrations are extremely important for spiders (Barth 2002; Elias & Mason 2010), which are highly sensitive to vibrations detected via receptors on their legs (Barth 1982; Foelix 2011). Spiders that build webs or snares or simply extend the silk lining of their burrow can essentially expand their field of sensory perception and create their own specialized signaling environments (Elias & Mason 2010; Krafft & Cookson 2012). The silk in these contexts transmits vibrations both from prey and courting males. The types of vibratory behaviors in spiders include percussion, stridulation, and tremulation, and these may transmit seismic and/or near-field airborne vibratory signals (reviewed in Uhl & Elias 2011). Vibratory courtship signals produced on webs have been recorded in only a small number of studies (Masters & Markl 1981; Masters 1984; Suter & Renkes 1984; Naftilan 1999; Wignall & Herberstein 2013a; Vibert et al. 2014). However, our understanding of the biomechanical properties of spider silk with respect to vibration transmission has expanded rapidly in recent years (primarily for orb-webs, e.g., Landolfa & Barth 1996; Watanabe 2000; Alam et al. 2007; Mortimer et al. 2014, 2015, 2016). For example, Mortimer and colleagues (2016) examined trade-offs between signal transmission and the structure of orb-webs; their work led them to conclude that silk tension and stiffness can affect vibration amplitude. This led them to the intriguing suggestion that females could construct webs to optimally balance multiple signal transmission functions (Mortimer et al. 2016).

1.3.3 Structural effects on courtship & mating activity: In web-building spiders, the female's web and/or retreat is often the location of courtship and mating. Thus, the structure of the web or retreat may constrain the type of courtship, approach vector, or mobility of males. For example, in some species females rest with their genital opening in close proximity to dense silk sheets such that mating requires a postural change (e.g., *Latrodectus*; Andrade & MacLeod 2015). Similarly, mating by non-web-building spiders may take place inside the female's burrow or silk retreat, where the movement of males and females is constrained (e.g., *Phidippus* C.L. Koch, 1846; Hoefler 2007). To our knowledge, there has

been no investigation of female web or retreat structure in relation to mobility during mating.

2. MALE SILK AND MATING

2.1 Overview.—Male spiders from diverse and distantly related families use silk during courtship and mating (Fig. 1). We review the main contexts in which males use silk in mating, with an emphasis on what is known about the effects of silk on males and/or females (Table 1). We start with a brief overview of the general types of effects that are recurrent themes, which suggest a number of (non-exclusive) hypotheses about male silk use in mating. We then arrange existing data on male silk use during mating into three main categories: (I) silk addition to females' webs (with or without web reduction; Table 2), (II) application of silk to female mating partners ('bridal veils'; Table 3), and (III) presentation of silk associated with nuptial gifts (or silk itself) to females (Table 4). For each type of silk use, we end by considering the specific types of effects predicted by each hypothesis and suggest where additional study would be fruitful. We then briefly discuss other ways silk is used by males during mating interactions that do not fall into these categories (Table 5). Finally, we provide general conclusions and suggestions for future directions.

2.2 Fitness effects of silk use.—There are a number of different hypotheses for the function of male silk use during mating interactions (Table 1). These are not mutually exclusive; as male silk use could have multiple functions in a given species. We consider these in terms of the way in which the behavior may increase the fitness of the silk-laying male, and the mechanism that leads to effects on fitness.

2.2.1 Fitness effects—current mating: Silk may increase a male's fitness if it increases his mating success with a given female (see columns 1–3 in Table 1). We consider three ways males might use silk to increase their fitness during interactions with a potential mate. (1) Silk may increase the likelihood of copulation by increasing or accelerating female receptivity to mating (i.e., affect female preference). More receptive females may also copulate more quickly. Rapid copulation may decrease the risk of interference by other males or by predators, and/or reduce the energetic investment in courtship. (2) Silk use may increase male fitness if it increases sperm transfer via longer or more frequent copulations (total copulation duration is linked to paternity or fertilization success in some species; Andrade 1996; Elgar et al. 2000; Anderson & Hebets 2017). We predict these functions would have the most significant effects on male fitness in species in which females are very choosy, courtship is costly and possibly prolonged, where rival males commonly approach females that are being courted by other males, and/or where copulation frequency or duration is related to paternity or fertilization success. (3) Silk use might increase male fitness by reducing the risk of male injury or death. These effects may arise through decreased risk of sexual cannibalism or attacks by rival males. Clearly, these effects would be most important in species where females frequently attack males during courtship or copulation, and/or where direct or escalated inter-male competition is coincident with courtship and mating attempts.

2.2.2 Fitness effects—decreased polyandry: Males may also benefit from silk use through a reduced risk of polyandry and thus a reduced risk of losing paternity to rival males (see columns 4–5 in Table 1). We divide this fitness benefit into two categories. (4) Silk use may decrease the risk of rival males courting or mating by interfering with the female's attractiveness to rivals, causing ineffective courtship by rivals, or decreasing physical access to females for rival males. (5) Alternatively, male silk use may decrease the likelihood of females remating by decreasing the receptivity of mated females. These effects would be most significant in species where females typically have the opportunity for polyandry, where sperm of rival males mix or last-male sperm precedence is relatively common (so males that mate after the first male will secure some paternity).

2.3 Mechanisms of effect.—In terms of mechanisms of effect (Table 1), fitness benefits of silk use can be derived indirectly through communication, where beneficial changes in the behavior of females or rival males arise from assessment of the information content of silk use. Information may be encoded in chemical, visual, tactile, or vibratory modalities. This may involve assessment of qualities of the male silk in itself (chemical, visual, and/or tactile modalities), or assessment of the performance of male behaviors involved in silk addition (vibratory and/or visual modalities). Finding evidence for fitness consequences of silk addition, or understanding the implications in terms of vibrations, may be less challenging than unravelling underlying mechanism(s) related to chemical or tactile signalling. Demonstrating the presence of pheromones on silk and differentiating between chemical and tactile cues requires carefully designed experiments (e.g., Anderson & Morse 2001). While identifying spider pheromones remains a challenge, other approaches include temporary or permanent ablation of the female's tactile or chemosensory receptors (Zhang et al. 2011; Aisenberg et al. 2015).

Fitness benefits may also derive directly through physical effects of male silk addition to the female, her web, or a nuptial gift. This may arise if structural changes to the web affect courtship and mating mobility, if silk acts as a physical constraint on movement, or if it functions to hide the contents of a nuptial gift (deception). In this category, we also include effects of silk addition on efficacy of communication that may arise through structural changes to the web.

2.3.1 Indirect effects—chemical signals/cues: Behavioral evidence suggests that, like female silk, silk produced by males can transmit chemical information as part of intersexual communication. Only one male spider pheromone has been chemically identified to date, an aphrodisiac isolated from whole-body extracts of *Pholcus beijingensis* (Pholcidae) males (Xiao et al. 2010). However, behavioral evidence demonstrates or supports the existence of silk-borne male sex pheromones in seven families (Fig. 1; Table 6). Like female pheromones, these putative male pheromones have diverse functions. Contact with male silk elicits courtship behavior in female *L. hesperus* (Theridiidae; Ross & Smith 1979). A pheromone from the male's body and/or silk induces quiescence in female *Agelenopsis aperta* (Agelenidae; Becker et al. 2005). Tactile and/or chemical information on male silk facilitates orientation in female *Tegenaria domestica* (Clerck, 1757) and *Coelotes terrestris* (Wider, 1834) (Agelenidae; Roland 1983). Similarly, in the lycosid spider *Pardosa milvina*

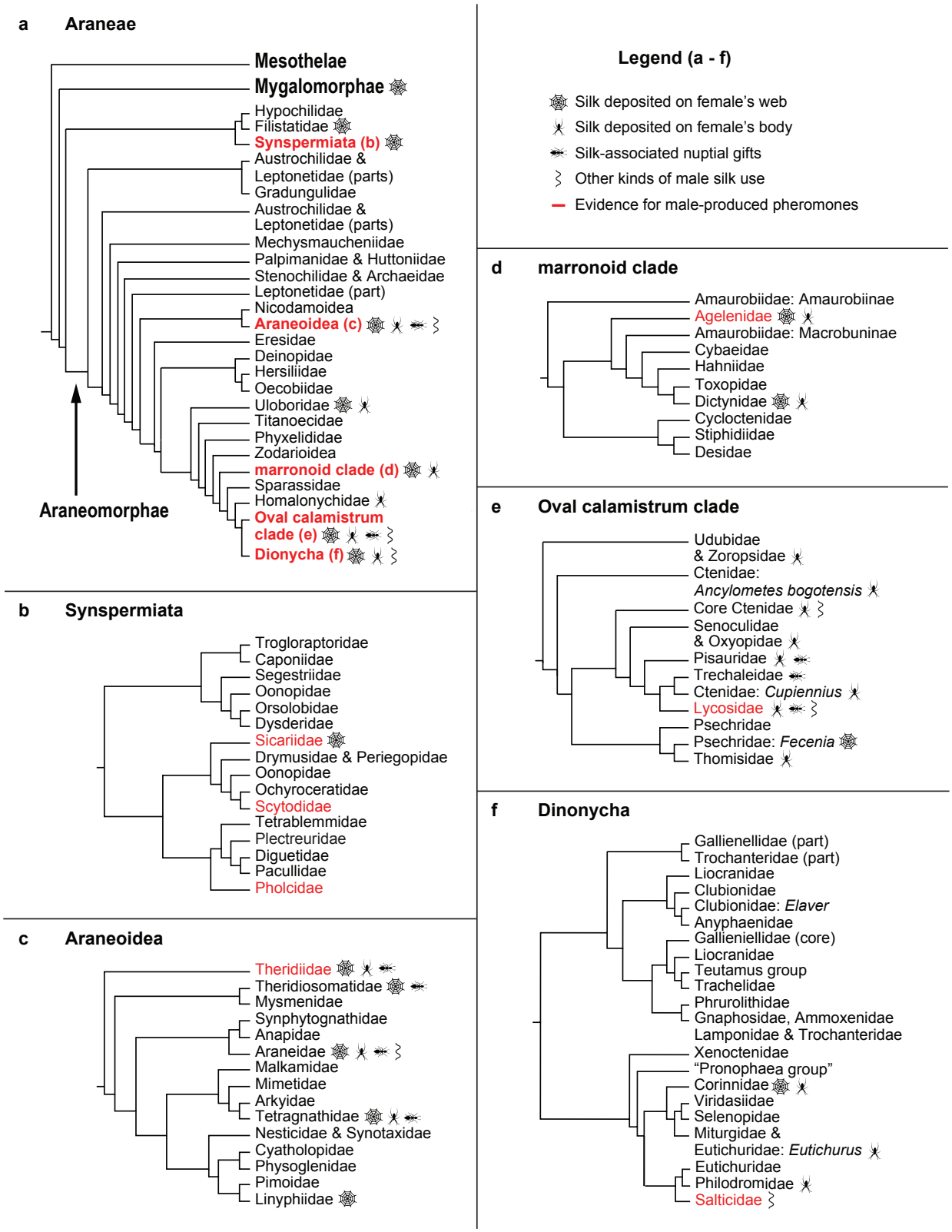

Figure 1.—Cladograms illustrating relationships between araneomorph spider families (based on Wheeler et al. 2016) and the occurrence of male silk and pheromone use. (a) Overview of the order Araneae. (b) Families in clade Synspermiata. (c) Families in clade Araneoidea. (d) Families in the marronoid clade. (e) Families in the Oval Calamistrum clade. (f) Families in clade Dionycha. Red type or symbols next to a clade (see legend) indicates that there is evidence for a given type of male silk use or the presence of male pheromones in at least one species in that clade (see Tables 2–5 for lists of species and references). Note that in the Mygalomorphae (families not shown on the figure) there are records of male silk deposition on the female's web or silk for species in the following three families: Dipluridae, Porrhothelidae, and Theraphosidae.

Table 1.—Cross tabulation of potential functions (columns) and mechanisms (rows) of silk use by male spiders in courtship and mating. Symbols in filled cells indicate functions and their mechanisms for which there is experimental evidence. Symbols are as in Fig. 1 (web indicates silk addition to or reduction of the female's web; spider indicates silk deposition on the female's body; insect indicates silk-associated nuptial gift). ✗ indicates experimental evidence against a specific function/mechanism and "nt" indicates that, to our knowledge, no test has been conducted.

Function →	Increased success: current mating			Decreased polyandry	
Mechanisms	Increased female receptivity/ probability of mating	Increased sperm transfer (copulation # or duration)	Decreased risk of injury or death	Decreased risk of rival males courting/mating	Decreased female receptivity to remating
INDIRECT: Communication					
Chemical	(1)	(2)	(2)	(3,4)	nt
Visual	(5-7)			nt	nt
Tactile	nt	(2)	(2)	nt	nt
Vibratory (correlated effect)	nt	nt	nt	nt	nt
DIRECT: Structural effects					
Mobility	nt	nt	nt	nt	nt
Signal Transmission	nt	nt	nt	(3,4)	nt
DIRECT: Physical effects					
Physical constraints	✗ (8)	(8)	(9)	nt	nt
Deceit	(10,11)	(10,11)	nt	nt	nt

(1) *Paratrechalea ornata* (Trechaleidae); Brum et al. 2012 (silk extract alone is sufficient to elicit female gift acceptance)
(2) *Nephila pilipes* (Araneidae); Zhang et al. 2011 (chemical and tactile effects of veil on cannibalism and sperm transfer duration)
(3) *Neriene litigiosa* (Linyphiidae); Watson 1986 (female pheromone emission/attractiveness decreased by web reduction and females remain unattractive after mating)
(4) *Latrodectus hesperus* (Theridiidae); Scott et al. 2015b (female pheromone emission/attractiveness decreased by web reduction and females remain unattractive after mating)
(5) *Pisaura mirabilis* (Pisauridae); Stålhandske 2002 (females accept brighter gifts more quickly)
(6) *Paratrechalea ornata* (Trechaleidae); Trillo et al. 2014 (males with white painted chelicerae had higher mating success than those without, in absence of prey item)
(7) *Paratrechalea ornata* (Trechaleidae); Klein et al. 2014 (small bright gifts accepted more quickly than large dark ones, but does not exclude chemical/tactile cues)
(8) *Pisaurina mira* (Pisauridae); Anderson & Hebets 2017 (male silk does not affect copulation success but males that produce a bridal veil achieve increased sperm transfer and fertilization success)
(9) *Pisaurina mira* (Pisauridae); Anderson & Hebets 2016 (silk wrapping physically restrains females, reducing male's risk of cannibalism following/during sperm transfer and increasing the number of insertions achieved)
(10) *Pisaura mirabilis* (Pisauridae); Albo et al. 2011a (males presenting worthless gifts achieve similar copulation success to those with prey gifts, and significantly higher copulation success than males without gifts; males with worthless gifts achieve longer copulation duration than those without gifts, but shorter duration than those with prey gifts)
(11) *Paratrechalea ornata* (Trechaleidae); Albo et al. 2014 (males with worthless gifts achieve copulations while males without gifts do not; copulation duration—correlated with sperm transfer amount—is similar for males with worthless gifts and prey gifts)

(Hentz, 1844) females discriminate between silk of courting and non-courting males, increasing their own silk production in response to contact with the male's silk (Khan & Persons 2015). Airborne pheromones from the bodies and silk of *Scytodes* Latreille, 1804 sp. (Scytodidae) and *Evarcha culicivora* Wesolowska & Jackson, 2003 (Salticidae) males function in mate recognition and mate choice (Cross & Jackson 2009; Koh et al. 2009).

Pheromones on male silk may also be important for intrasexual communication (Table 7), including assessment of male-male competition. Airborne chemical cues from *Latrodectus hasselti* (Theridiidae) males and/or their silk provide information about the competitive environment and trigger shifts in development in other males (Kasumovic & Andrade 2006). Male *Nephila senegalensis* (Walckenaer, 1841) (Araneidae) use silk cues left behind by rival males to choose which females' webs to visit. They avoid webs previously visited by another male, irrespective of the female's quality (Schneider et al. 2011). Male courtship behavior is inhibited by a pheromone that can be extracted with methanol from the silk of *Schizocosa ocreata* (Hentz, 1844) (Lycosidae) males (Ayyagari & Tietjen 1987), and *Frontinella communis* (Hentz, 1850) (Linyphiidae) males respond to compounds on male cuticle with aggressive behavior (Suter et al. 1987).

2.3.2 Indirect effects—visual signals/cues: For spider species with well-developed vision, male silk could play a role in visual signaling, or provide cues about the state of the male that produced the silk, and thus affect female receptivity or choice.

For example, the density of silk male pisaurids and trechaleids use to wrap nuptial gifts (see section 4 below), affects the color of the gift (bright white to dark grey), and may provide information about the physiological state of the gift-giving male (Stålhandske 2002; Albo et al. 2011a; Trillo et al. 2014). White silk in itself may be highly visible, and so attract the attention of females, as has been shown in the crepuscular *Paratrechalea ornata* (Mello-Leitão, 1943) (Stålhandske 2002; Trillo et al. 2014).

2.3.3 Indirect effects—tactile cues: When silk comes in contact with females directly, or when females manipulate, touch, or move across silk laid down by males, that contact may provide information. For example, tactile cues on silk draglines allow male crab spiders to follow females, with recognition depending on mechanical characteristics of the silk (Anderson & Morse 2001).

2.3.4 Indirect effects—correlated effects of silk-laying behaviors: The behaviors associated with silk deposition may have functions independent of the silk itself. For many species, typical male abdominal movements have been described in association with silk application (see 'abdomen waggle' in Table 2), and these may produce vibrational or visual signals. In an analogous example, Vollrath (1979) showed that prey-wrapping by web-building spiders creates a characteristic pattern of vibrations that are exploited by the kleptoparasite *Argyrodes elevatus* Taczanowski, 1873. Here we focus primarily on the way in which male silk itself may affect mating outcomes, but also outline behaviors that are reliably associated with silk deposition where relevant.

2.3.5 Direct effects—structural modifications: Males of many species modify the webs or other silk structures of females, and this may involve the use of male silk in various ways, including covering or wrapping females' silk, or adding new silk lines to existing structures. Modifications to web structure are traditionally described in terms of how they affect the behavior or possible movement (mobility) of the female and/or rival males during a mating attempt. However, these structural changes may also affect the nature, directionality or efficacy of vibrational or chemical signals or cues. Thus, changes in signal transmission may be the primary mechanism by which silk use affects male fitness.

2.3.6 Direct effects—physical effects: Males produce a range of different types of silks, and comparable to the use of silk in prey-capture, male silk may be applied directly to the female in such a way that it restrains, impedes or slows the movement of females or even of rival males (physical constraints). Silken constructions may also support or adjust the posture of females in a way that facilitates genital coupling. Alternatively, silk wrapped around nuptial gifts may allow males to hide their contents when the gift is of low nutritional value (deceit).

3. SILK DEPOSITION ON FEMALES' WEBS OR OTHER SILK STRUCTURES

3.1 Overview and descriptions of behaviors.—In web-dwelling spiders, mating generally takes place on the female's web or in her retreat. During courtship, males in several families representing the full range of web architectures lay silk on the female's web, leading to modification of existing web structure (Figs. 1 & 2). Web modification with silk addition varies from the addition of a single line (a mating thread) to destruction of large areas of the female's web and replacement with male silk (web reduction). Similarly, in burrow-dwellers like some mygalomorph and lycosid spiders, silk lines the burrow and may extend from its entrance, providing the substrate on which courtship occurs. Males of these taxa may also deposit silk onto the female's silk during mating interactions, although modification of the overall architecture of the female's silk structures has not been reported. Descriptions of silk-spinning behavior of males when courting on webs or on other silk structures have many similarities, and thus we consider them together in this section.

Among the Mygalomorphae, silk deposition by males during courtship has been reported for the web-building Dipluridae and Porrhothelidae (formerly Hexathelidae) and the burrow-dwelling Theraphosidae. In the diplurid spiders *Thelechoris karschi* (Simon, 1889) and *Microhexura montigava* Crosby & Bishop, 1925, both males and females spin silk as they move about the web during courtship (Coyle 1985; Coyle & O'Shields 1990). *Porrhothele antipodiana* (Walckenaer, 1837) (Porrhothelidae) males spin silk during interactions with females on their webs (both before and after copulation), and also during interactions with other males. Silk spinning behavior in this species is accompanied by obvious lateral movements of the abdomen (Jackson & Pollard 1990). In the burrow-dwelling theraphosid spiders *Grammostola vachoni* Schiapelli & Gerschman, 1961 and *Brachypelma klaasi* (Schmidt & Krause, 1994), courting males lay down silk over the female's silk around the burrow entrance (Yáñez et al. 1999; Ferretti & Ferrero 2008).

Descriptions of silk deposition in some araneomorph spiders that build sheet webs are similar to those for the Mygalomorphae. Upon contact with the web of a virgin female, the crevice weaver *Kukulcania hibernalis* (Hentz, 1842) (Filistatidae) pulls swaths of silk threads from his spinnerets with his last pair of legs and deposits them on her web (Barrantes & Ramirez 2013). Less obvious silk deposition occurs during the courtship of the funnel weaver *Eratigena agrestis* (Walckenaer, 1802) (Agelenidae). Males deposit silk as they move around on the female's web, periodically anchoring it to the sheet (C.E. Scott, pers. obs.). Lateral 'abdomen wagging' behavior is associated with silk deposition in *E. agrestis*, and this behavior is common during the courtship of several other agelenids, most notably the genus *Agelenopsis* C.L. Koch, 1837 (Table 2; Galasso 2012). This 'wagging' that occurs as males move around the web is usually accompanied by silk emission in these agelenids (S. Riechert, pers. comm.).

In orb-weavers (family Araneidae, including subfamily Nephilinae, formerly Nephilidae), courtship is grouped into three types (A–C), two of which involve male alteration of web architecture (Robinson & Robinson 1980). Type A courtship occurs on the female's web and typically involves addition of silk near the hub. In type B courtship, the male cuts a hole in the web close to the hub and constructs a mating thread across it. Type C courtship does not involve any web cutting; the male constructs a mating thread that he attaches to the periphery of the web. In both type B and C courtship, the male engages in vibratory courtship on the mating thread (which may be multi-stranded; Table 2). Eventually the female joins the male on the mating thread, where copulation takes place. Typically, males of a given species use one type of courtship,

Table 2.—Spider taxa in which males modify the female's web or other silken structures by adding and/or removing silk (web reduction). Y = yes; N = no; P = probable; *n* = number of mating interactions observed. Where data are available, the specific behavior is described in brackets, as is the percentage of males that engage in that behavior, with a superscript indicating the reference specific to these data where necessary.

Taxon	Addition of silk	Web reduction	Citations
Agelenidae			
Agelenopsis actuosa (Gertsch & Ivie, 1936)	P (abdomen waggle)	N	Galasso 2012
Agelenopsis aperta (Gertsch, 1934)	Y (abdomen waggle)	N	Singer et al. 2000; Galasso 2012; S. Reichert pers. comm.
Agelenopsis aleenae Chamberlin & Ivie, 1935	P (abdomen waggle)	N	Galasso 2012
Agelenopsis emertoni Chamberlin & Ivie, 1935	P (abdomen waggle)	N	Galasso 2012
Agelenopsis kastoni Chamberlin & Ivie, 1941	P (abdomen waggle)	N	Galasso 2012
Agelenopsis naevia (Walckenaer, 1841)	P (abdomen waggle)	N	Galasso 2012
Agelenopsis oklahoma (Gertsch, 1936)	P (abdomen waggle)	N	Galasso 2012
Agelenopsis pennsylvanica (C. L. Koch, 1843)	P (abdomen waggle)	N	Galasso 2012
Agelenopsis potteri (Blackwall, 1846)	P (abdomen waggle)	N	Galasso 2012
Agelenopsis spatula Chamberlin & Ivie, 1935	P (abdomen waggle)	N	Galasso 2012
Agelenopsis utahana (Chamberlin & Ivie, 1933)	P (abdomen waggle)	N	Galasso 2012
Barronopsis texana (Gertsch, 1934)	P (abdomen waggle)	N	Galasso 2012
Eratigena agrestis (Walckenaer, 1802)	Y (depositing silk)	N	Vibert et al. 2014
Araneidae			
Aetrocantha falkensteini Karsch, 1879	Y (mating thread)	N	Robinson & Robinson 1980
Alpaida veniliae (Keyserling, 1865)	Y (mating thread)	N	Benamú et al. 2012, 2015
Araneus diadematus Clerck, 1757	Y (mating thread)	N	Elgar & Nash 1988
Araneus quadratus Clerck, 1757	Y (mating thread)	N	Elgar 1991
Argiope aemula (Walckenaer, 1841)	Y ('miniweb' within web & silk at hub)	N	Robinson & Robinson 1980
Argiope aetherea (Walckenaer, 1841)	Y (mating thread)	Y (small hole)	Robinson & Robinson 1980
Argiope argentata (Fabricius, 1775)	Y (dragline silk on web & female's dragline or multistranded mating thread inside or outside web)	Y (small hole) or N	Robinson & Robinson 1980
Argiope aurantia Lucas, 1833	Y (miniweb within web & silk on web)	Y (small hole)	Robinson & Robinson 1980
Argiope aurocincta Pocock, 1898	Y (mating thread & silk dep. during walkabouts)	Y (small hole)	Robinson & Robinson 1980
Argiope bruennichi (Scopoli, 1772)	Y (mating thread)	Y (small hole)	Elgar 1991
Argiope cuspidata Thorell, 1859	Y (mating thread & silk dep. during walkabouts)	Y (small hole)	Robinson & Robinson 1980
Argiope flavipalpis (Lucas, 1858)	Y (mating thread)	Y (small hole)	Robinson & Robinson 1980
Argiope florida Chamberlin & Ivie, 1944	Y (mating thread; silk dep. during walkabouts)	Y (small hole)	Robinson & Robinson 1980
Argiope keyserlingi Karsch, 1878	Y (mating thread)	Y (small hole) or N	Herberstein et al. 2002
Argiope ocyaloides L. Koch, 1871	Y (mating thread)	Y (small hole)	Robinson & Robinson 1980
Argiope picta L. Koch, 1871	Y (multistranded mating thread)	Y (large hole; male may increase size between courtship bouts)	Robinson & Robinson 1980; Elgar 1991
Argiope radon Levi, 1983	Y (mating thread)	Y (small hole)	Robinson & Robinson 1980; Wignall et al. 2014
Argiope reinwardti (Doleschall, 1859)	Y (extensive silk dep. at hub)	N	Robinson & Robinson 1980
Argiope submaronica Strand, 1916	Y (mating thread & silk dep. on web)	Y (small hole)	Robinson & Robinson 1980
Argiope submaronica Strand, 1916	Y (mating thread)	Y (small hole)	Robinson & Robinson 1980 (as *Argiope savignyi*)

Table 2.—Continued.

Taxon	Addition of silk	Web reduction	Citations
Cyclosa caroli (Hentz, 1850)	Y (mating thread)	N	Robinson & Robinson 1980
Cyclosa insulana (Costa, 1843)	Y (multistranded mating thread)	N	Robinson & Robinson 1980
Cyclosa insulana (Costa, 1843)	Y (silk laid down onto guylines of web; $n = 4$)	Y (cuts threads of rival males, web size reduced by 40%; $n = 1$)	McClintock & Dodson 1999
Cyrtophora moluccensis (Doleschall, 1857)	Y (mating thread)	N	Berry 1987
Eriophora fuliginea (C. L. Koch, 1838)	Y (mating thread)	N	Robinson & Robinson 1980
Eriophora transmarina (Keyserling, 1965)	Y (mating thread)	Y (small hole)	Elgar 1991 (as *Eriophora transmarinus*)
Gasteracantha cancriformis (Linnaeus, 1758)	Y (mating thread)	N	Robinson & Robinson 1980; Bukowski et al. 2001
Gasteracantha curvispina (Guérin, 1837)	Y (mating thread)	N	Robinson & Robinson 1980
Gea C. L. Koch, 1843 sp.	Y (mating thread)	N	Robinson & Robinson 1980
Herennia multipuncta (Doleschall, 1859)	Y (dragline silk)	N	Robinson & Robinson 1980 (as *Herennia ornatissima*)
Isoxya cicatricosa (C. L. Koch, 1844)	Y (mating thread)	N	Robinson & Robinson 1980 (as *Isoxya cicatrosa*)
Isoxya tabulata (Thorell, 1859)	Y ('treadmill'-type mating thread)	Y (cuts some web elements)	Robinson & Robinson 1980
Kapogea sexnotata (Simon, 1895)	Y (multistranded mating thread & silk dep. on web)	Y (cuts away extensive portion of lower snare)	Robinson & Robinson 1980 (as *Cyrtophora nympha*)
Leviellus thorelli (Ausserer, 1871)	Y (mating thread)	N	Kralj-Fišer et al. 2013
Mangora bimaculata (O. Pickard-Cambridge, 1889)	Y (converts radius to mating thread; $n = 3$)	Y (removes viscid spiral elements on either side of mating thread; $n = 3$)	Robinson & Robinson 1980
Mecynogea lemniscata (Walckenaer, 1841)	Y (mating thread & silk deposition on snare)	N	Robinson & Robinson 1980
Micrathena clypeata (Walckenaer, 1805)	Y (mating thread)	N	Robinson & Robinson 1980
Micrathena duodecimspinosa (O. Pickard-Cambridge, 1890)	Y (mating thread)	N	Robinson & Robinson 1980
Micrathena gracilis (Walckenaer, 1805)	Y (mating thread)	N	Bukowski & Christenson 2000
Micrathena sagittata (Walckenaer, 1841)	Y (mating thread)	N	Robinson & Robinson 1980
Micrathena schreibersi (Perty, 1833)	Y (mating thread)	N	Robinson & Robinson 1980
Micrathena sexspinosa (Hahn, 1822)	Y (converts one radius to thick, multistranded mating thread)	Y (removes viscid spiral elements on either side of mating thread radius)	Robinson & Robinson 1980
Nephila edulis (Labillardière, 1799)	Y (dragline silk)	N	Robinson & Robinson 1980
Nephila pilipes (Fabricius, 1793)	Y (dragline silk; extensive, incl. on females' dragline)	N	Robinson & Robinson 1980
Nephila pilipes (Fabricius, 1793)	Y (dragline silk)	N	Robinson & Robinson 1980 (as *Nephila maculata*)
Nephila clavipes (Linnaeus, 1767)	Y (dragline silk)	N	Robinson & Robinson 1980
Nephilengys malabarensis (Walckenaer, 1841)	Y (dragline silk)	N	Robinson & Robinson 1980

Table 2.—Continued.

Taxon	Addition of silk	Web reduction	Citations
Scoloderus cordatus (Taczanowski, 1879)	Y ('treadmill'-type mating thread)	N	Stowe 1978
Thelacantha brevispina (Doleschall, 1857)	Y (mating thread)	N	Robinson & Robinson 1980 (as *Gasterocantha brevispina*)
Zilla spp. C. L. Koch, 1834	Y (multistranded mating thread)	N	Robinson & Robinson 1980
Zygiella x-notata (Clerck, 1757)	Y (mating thread)	N	Blanke 1986 as cited by Dondale et al. 2003
Corrinidae			
Nyssus coloripes Walckenaer, 1805	Y (zigzags of silk laid down onto female's web)	N	Jackson & Poulsen 1990 (as *Supunna picta*)
Dictynidae			
Dictyna arundinacea (Linnaeus, 1758)	Y (small 'canopy')	Y (small hole)	Locket 1926; Bristowe 1958
Dictyna tridentata Bishop & Ruderman, 1946	Y	N	Jackson 1979
Dictyna volucripes Keyserling, 1881	Y	N	Starr 1988
Mallos gregalis (Simon, 1909)	Y	N	Jackson 1979
Mexitlia trivittata (Banks, 1901)	Y	N	Jackson 1979 (as *Mallos trivittatus*)
Dipluridae			
Microhexura montivaga Crosby & Bishop, 1925	Y (sometimes apply silk to female's web)	N	Coyle 1985
Thelechoris striatipes (Simon, 1889)	Y (spin silk while courting; 4%; $n = 45$)	N	Coyle & O'Shields 1990 (as *Thelechoris karschi*)
Filistatidae			
Kukulcania hibernalis (Hentz, 1842)	Y (83%; $n = 6$)	N	Barrantes & Ramirez 2013
Linyphiidae			
Florinda coccinea (Hentz, 1850)	Y	Y (part of web; 75%; $n = 20$)	Willey Robertson & Adler 1994
Lepthyphantes leprosus (Ohlert, 1865)	Y	Y (90-100% of web; 45%; $n = 29$)	van Helsdingen 1965
Linyphia triangularis (Clerck, 1757)	Y	Y (part or all of web[2]; 68%; $n = 60$[3])	[2]Rovner 1968 [3]Weldingh et al. 2011
Neriene litigiosa (Keyserling, 1886)	Y	Y (large portions of web; 28%; $n = 50$)	Watson 1986 (as *Linyphia litigiosa*)
Pityohyphantes phrygianus (C. L. Koch, 1836)	unknown	Y (web reduced to a small wad; $n = 18$)[4]	[4]Stålhandske & Gunnarsson 1996; Gunnarsson et al. 2004
Porrhomma egeria Simon, 1884	Y (adds threads to web)	N	Bourne 1978
Porrhothelidae			
Porrhothele antipodiana (Walckenaer, 1837)	Y (spins silk on web before & after copulation; 47%; $n = 186$)	N	Jackson & Pollard 1990
Psechridae			
Fecenia Simon, 1887 sp.	N	Y (most of web, leaving single thread; $n = 1$)	Robinson & Lubin 1979
Sicariidae			
Loxosceles gaucho, Gertsch, 1967	N	Y (often cut some threads of web)	Rinaldi & Stropa 1998
Tetragnathidae			
Metellina segmentata (Clerck, 1757)	Y (mating thread & wrapping silk around prey item)	Y (small section of web cut out)	Prenter et al 1994b; Bristowe 1929
Theraphosidae			
Brachypelma klaasi (Schmidt & Krause, 1994)	Y (deposits silk around female's burrow & over her silk)	N	Yáñez et al. 1999

Table 2.—Continued.

Taxon	Addition of silk	Web reduction	Citations
Grammostola vachoni Schiapelli & Gerschman, 1961	Y (lays silk over female's silk)	N	Ferretti & Ferrero 2008 (as *Grammostola schulzei*)
Theridiidae			
Argyrodes antipodianus O. Pickard-Cambridge, 1880	Y	Y	Whitehouse & Jackson 1994 (as *Argyrodes antipodiana*)
Argyrodes argyrodes (Walckenaer, 1841)	Y (web-spinning; 14%; $n = 7$)	Y	Knoflach 2004
Dipoena melanogaster (C. L. Koch, 1837)	Y (mating web)	N	Knoflach 2004
Echinotheridion gibberosum (Kulczyński, 1899)	Y (mating web)	N	Knoflach 2004
Enoplognatha afrodite Hippa & Oksala, 1983	Y (mating web; $n = 4$)	N	Knoflach 2004
Enoplognatha diversa (Blackwall, 1859)	Y (mating web; $n = 3$)	N	Knoflach 2004
Enoplognatha latimana Hippa & Oksala, 1982	Y (mating web; $n = 1$)	N	Knoflach 2004
Enoplognatha macrochelis Levy & Amitai, 1981	Y (mating web; $n = 5$)	N	Knoflach 2004
Enoplognatha ovata (Clerck, 1757)	Y (mating web; $n = 5$)	N	Knoflach 2004
Enoplognatha quadripunctata Simon, 1884	Y (mating web; $n = 2$)	N	Knoflach 2004
Enoplognatha thoracica (Hahn, 1833)	Y (mating web; $n = 1$)	N	Knoflach 2004
Kochiura aulica (C. L. Koch, 1838)	Y (mating thread; $n = 6$)	Y (hole cut for mating thread)	Knoflach 2004 (as *Anelosimus aulicus)*
Latrodectus dahli Levi, 1959	Y (50%; $n = 2$)	N	Knoflach & van Harten 2002
Latrodectus geometricus C. L. Koch, 1841	Y	Y ('less commonly')	Segoli et al. 2008
Latrodectus hasselti Thorell, 1870	Y	Y	Forster 1992, 1995
Latrodectus hesperus Chamberlin & Ivie, 1935	Y	Y (up to 50% of web; 58%; $n = 12$[1])	Ross & Smith 1979; [1]Scott et al. 2012
Latrodectus mactans (Fabricius, 1775)	Y	Y	Breene & Sweet 1985
Latrodectus pallidus O. Pickard-Cambridge, 1872	Y	Y	Harari et al. 2009
Latrodectus revivensis Shulov, 1948	Y (69% of males)	Y (up to 50% of barrier web)	Anava & Lubin 1993
Paidiscura Archer, 1950 sp.	Y (mating web)		Knoflach 2004
Paidiscura pallens (Blackwell, 1834)	Y	Y	Locket 1927 (as *Theridion pallens*)
Parasteatoda tepidarorium (C. L. Koch, 1841)	Y (web-spinning; $n = 3$)	N	Knoflach 2004 (as *Achaearanea tepidariorum*)
Parasteatoda wau (Levi, Lubin & Robinson, 1982)	Y (small mating arena)	Y (small area reduced)	Lubin 1986 (as *Achaearanea wau*)
Steatoda bipunctata (Linnaeus, 1758)	Y (mating web; $n = 3$)	Y (removed threads)	Knoflach 2004
Steatoda castanea (Clerck, 1757)	Y (mating web; $n = 1$)		Knoflach 2004
Steatoda grossa (C. L. Koch, 1838)	Y (all males added silk to female's web; $n = 23$)	Y (>50% of web; 74%; $n = 23$)	Scott et al. 2017
	Y (mating web &/or web-spinning; $n = 4$[2])	N	[2]Knoflach 2004; Gwinner-Hanke 1970 (as *Teutana grossa*)
Steatoda paykulliana (Walckenaer, 1806)	Y (silk-throwing; 66%; $n = 3$)	N	Knoflach 2004
Steatoda triangulosa (Walckenaer, 1802)	Y (mating thread; $n = 4$)	Y (removed threads; 50%; $n = 4$)	Knoflach 2004
Simitidion simile (C. L. Koch, 1836)	Y	N	Locket 1927 (as *Theridion simile*)
Theridion varians Hahn, 1833	Y	Y	Locket 1927
Tidarren argo Knoflach & van Harten, 2001	Y (mating web)	N	Knoflach 2004
Tidarren cuneolatum (Tullgren, 1910)	Y (multistranded mating thread)	N	Knoflach & van Harten 2000
Uloboridae			
Octonoba sinensis (Simon, 1880)	Y (mating thread)	N	Peaslee & Peck 1983 (as *Octonoba octonarius*)
Uloborus Latreille, 1806 sp.	Y (mating thread)	N	Bristowe 1958

Table 3.—Spider taxa in which males deposit silk 'bridal veils' onto the female during courtship.

Taxon	Context	Type of 'veil'	Reference
Agelenidae			
Eratigena agrestis (Walckenaer, 1802)	female's web	some silk on legs & carapace	S. Vibert unpublished data
Araneidae			
Argiope aemula (Walckenaer, 1841)	female's web	silk on carapace, legs & abdomen (extensive)	Robinson & Robinson 1980
Argiope aurantia Lucas, 1833	female's web	draglines attached to abdomen	Robinson & Robinson 1980
Argiope picta L. Koch, 1871	female's web	some silk on legs	Robinson & Robinson 1980
Argiope Audouin, 1826 spp.	female's web	silk on legs	Robinson & Robinson 1980
Caerostris darwini Kuntner & Agnarsson, 2010	female's web	silk on legs & body (extensive)	Gregorič et al. 2016
Herennia multipuncta (Doleschall, 1859)	female's web	silk on & around abdomen	Robinson & Robinson 1980 (as *Herennia ornatissima*)
Nephila pilipes (Fabricius, 1793)	female's web	silk between legs, between base of abdomen & dorsal surface of cephalothorax (extensive)	Robinson & Robinson 1980 (as *Nephila maculata*)
Nephila pilipes (Fabricius, 1793)	female's web	silk on carapace, legs & abdomen; connected to web (extensive)	Robinson & Robinson 1980; Kuntner et al. 2009; Zhang et al. 2011
Corrinidae			
Nyssus coloripes Walckenaer, 1805	female's web	zigzags of silk placed on female's body as male walks over her	Jackson & Poulsen 1990 (as *Supunna picta*)
Ctenidae			
Ancylometes bogotensis (Keyserling, 1877)	substrate	silk rings around front tibiae & patellae (extensive)	Merrett 1988
Ctenus longipes Keyserling, 1891	substrate	silk on forelegs, pedipalps, chelicerae, & eyes (later consumed)	Trillo 2016
Cupiennius coccineus F. O. Pickard-Cambridge, 1901	substrate	some silk on legs	Schmitt 1992
Dictynidae			
Dictyna volucripes Keyserling, 1881	female's web	some silk on female	Starr 1988
Eutichuridae			
Eutichurus ibiuna Bonaldo, 1994	substrate	legs I, II & palps tied to substrate	Laborda & Simo 2015
Homalonychidae			
Homalonychus selenopoides Marx, 1891	substrate	silk ring around legs	Alvarado-Castro & Jiménez 2011
Homalonychus theologus Chamberlin, 1924	substrate	silk ring around legs	Domínguez & Jiménez 2005
Lycosidae			
Schizocosa malitiosa (Tullgren, 1905)	substrate	legs I & II tied to substrate & silk near mouthparts	Aisenberg et al. 2008
Oxyopidae			
Oxyopes schenkeli Lessert, 1927	hanging on dragline	silk spun around legs I, II, & III	Preston-Mafham 1999
Philodromidae			
Tibellus oblongus (Walckenaer, 1802)	substrate	some silk on female	Kaston 1936; Preston-Mafham 1999
Tibellus Simon, 1875 sp.	substrate	some silk on female	Platnick 1971
Pisauridae			
Dolomedes triton (Walckenaer, 1837)	substrate	legs I & II tied to substrate	Carico 1993
Pisaurina mira (Walckenaer, 1837)	substrate or hanging on dragline	silk spun around legs I & II (extensive)	Bruce & Carico 1988; Anderson & Hebets 2016
Nilus curtus (O. Pickard-Cambridge, 1876)	female's mating web	silk ring around patellae	Sierwald 1988 (as *Thalassius spinosissimus*)
Tetragnathidae			
Metellina segmentata (Clerck, 1757)	female's web	female wrapped with fine silk	Bristowe 1929; Lopez 1987
Theridiidae			
Euryopis episinoides (Walckenaer, 1847)	female's web	some silk on female	Knoflach 2004

Table 3.—Continued.

Taxon	Context	Type of 'veil'	Reference
Latrodectus geometricus C. L. Koch, 1841	female's web	some silk on legs & body	Knoflach & van Harten 2002; Segoli et al. 2008
Latrodectus hasselti Thorell, 1870	female's web	some silk on legs & body	Forster 1992
Latrodectus hesperus Chamberlin & Ivie, 1935	female's web	some silk on legs & body	Ross & Smith 1979; Kaston 1970; Herms et al. 1935; Scott et al. 2012
Latrodectus indistinctus O. Pickard-Cambridge, 1904	female's web	some silk on legs & body	Smithers 1944
Latrodectus mactans (Fabricius, 1775)	female's web	some silk on legs & body	Breene & Sweet 1985
Latrodectus pallidus O. Pickard-Cambridge, 1872	female's web	some silk on legs & body	Shulov 1940
Latrodectus revivensis Shulov, 1948	female's web	some silk on legs & body	Anava & Lubin 1993
Latrodectus tredecimguttatus (Rossi, 1790)	female's web	some silk on legs & body	Shulov 1940
Steatoda bipunctata (Linnaeus, 1758)	female's web	some silk on female	Knoflach 2004
Steatoda grossa (C. L. Koch, 1838)	female's web	some silk on legs & body	Scott et al. 2017
Steatoda paykulliana (Walckenaer, 1806)	female's web	some silk on legs & body	Knoflach 2004
Steatoda triangulosa (Walckenaer, 1802)	female's web	some silk on female	Knoflach 2004
Thomisidae			
Bassaniana versicolor (Keyserling, 1880)	substrate	female tied to substrate	Kaston 1936 (as *Coriarachne versicolor*)
Xysticus cristatus (Clerck, 1757)	substrate	legs I & II tied to substrate	Bristowe 1931; Bristowe 1958
Xysticus lanio C. L. Koch 1835	substrate	legs I & II tied to substrate	Gerhardt 1924 as cited by Bristowe 1926
Xysticus audax (Schrank, 1803)	substrate	female tied to substrate	Thomas 1930 as cited by Kaston 1936 (as *Xysticus pini*)
Xysticus striatipes L. Koch, 1870	substrate	female tied to substrate	Sytschewskaja 1935 as cited by Kaston 1936
Xysticus triguttatus Keyserling, 1880	substrate	female tied to substrate	Kaston 1936
Xysticus tristrami (O. Pickard-Cambridge, 1872)	substrate	female tied to substrate	Gerhardt 1933 as cited by Kaston 1936
Pycnaxis krakatauensis (Bristowe, 1931)	substrate	legs I & II tied to substrate	Bristowe 1931 (as *Xysticus krakatauensis*)
Uloboridae			
Uloborus Latreille, 1806 sp.	female's web	not described	Gerhardt 1933 (as cited by Berendonck 2003)
Zoropsidae			
Tengella perfuga Dahl, 1901	female's web	some silk on legs & carapace	Mallis & Miller 2017

but in *Argiope argentata* (Fabricius, 1775), for instance, males switch types depending on context (Robinson & Robinson 1980). Some males do type A, and others type B, or the same male might do both types on different days. If another male is already courting on the web (type A or type B courtship), a second male will engage in type C courtship with a mating thread attached to the periphery of the web. Interestingly, when engaging in type B courtship, the male may add dragline silk to his mating thread after a courtship bout to which the female did not respond. Similarly, in *Argiope picta* L. Koch, 1871, males may enlarge the hole across which they spun their mating thread between bouts of unsuccessful courtship (Robinson & Robinson 1980).

In *Isoxya tabulata* (Thorell, 1859) and *Scoloderus cordatus* (Taczanowski, 1879) the mating thread is employed in a different way. The male situates himself such that the female walks onto a silk line still attached to his spinnerets, which he pays out as she tries to approach, resulting in a 'treadmill effect' (Robinson & Robinson 1980). The female attempts to walk along the line but makes no progress, rather she accumulates a bundle of the male's silk below her cephalothorax (this silk may constitute a nuptial gift; see section 5).

Male cobweb weavers (Theridiidae) also commonly construct mating threads during courtship on the female's web (Table 2). As in type C courtship of the orb-weavers, the male installs a silk line and then engages in vibratory courtship on it until the female eventually moves onto the thread, where copulation occurs (Knoflach 2004). In some species, the male reinforces the thread several times, or he constructs a larger area of threads referred to as a mating web, which is used similarly to mating threads (Knoflach 2004). In a few species, the male cuts some of the female's threads, but in general, theridiids modify the web by adding their own silk without excising sections of the female's web (Knoflach 2004). Exceptions include the widow and false widow spiders *Latrodectus* and *Steatoda* Sundevall, 1833, which engage in extensive web reduction behavior (discussed below) and males of the social theridiid spider *Parasteatoda wau* (Levi, Lubin & Robinson, 1982), which build courtship 'arenas' in their communal webs by cutting out small areas of the barrier web

Table 4.—Spider taxa in which males present females with silk-associated nuptial gifts, including silk-wrapped prey, silk alone, or silk-lined burrows.

Taxon	Type of gift	Reference
Araneidae		
Isoxya tabulata (Thorell, 1859)	mating thread silk (probably)	Robinson & Robinson 1980
Scoloderus cordatus (Taczanowski, 1879)	mating thread silk (probably)	Stowe 1978
Ctenidae		
Ctenus longipes Keyserling, 1891	bridal veil silk	Trillo 2016
Lycosidae		
Allocosa alticeps (Mello-Leitão, 1944)	silk-lined burrow	Aisenberg et al. 2010
Allocosa senex (Mello-Leitão, 1945)	silk-lined burrow	Aisenberg et al. 2007 (as *Allocosa brasiliensis*); Carballo et al. 2017
Pisauridae		
Pisaura lama Bösenberg & Strand, 1906	silk-wrapped prey	Itakura 1993 (as cited by Costa-Schmidt et al. 2008)
Pisaura mirabilis (Clerck, 1757)	silk-wrapped prey	Bristowe & Lockett 1926; Bristowe 1958
Perenethis fascigera (Bösenberg & Strand, 1906)	silk-wrapped prey	Itakura 1998
Thaumasia argenteonotata (Simon, 1898)	silk-wrapped prey	Nitzsche 1988 (as cited by Nitzsche 2011)
Tinus peregrinus (Bishop, 1924)	silk-wrapped prey	J. Carico pers. comm. in Nitzsche 2011
Tetragnathidae		
Metellina segmentata (Clerck, 1757)	silk-wrapped prey or rival male	Prenter et al. 1994a
Theridiidae		
Argyrodes elevatus Taczanowski, 1873	spider lightly wrapped in silk stolen silk-wrapped prey	Cobbold & Su 2010 Uetz et al. 2010
Theridiosomatidae		
Theridiosoma gemmosum (L. Koch, 1877)	silk	Hajer & Řeháková 2011
Trechaleidae		
Paratrechalea azul Carico, 2005	silk-wrapped prey	Costa-Schmidt et al. 2008
Paratrechalea galianoe Carico, 2005	silk-wrapped prey	Costa-Schmidt et al. 2008
Paratrechalea ornata (Mello-Leitão, 1943)	silk-wrapped prey	Costa-Schmidt et al. 2008
Trechalea amazonica F. O. Pickard-Cambridge, 1903	silk-wrapped prey	Silva & Lise 2009
Trechalea bucculenta (Simon, 1898)	silk-wrapped prey	Silva 2005 (as cited by Silva & Lise 2009)
Trechalea Thorell, 1869 sp.	silk-wrapped prey	Lapinski & Tschapka, 2009 (as cited by Nitzsche 2011)

threads and laying down one or more of their own threads (Lubin 1986). Courtship occurs on these threads and they are considered functionally equivalent to the mating threads of araneid spiders (Lubin 1986).

Variations on the theme of mating threads and webs can also be found in cribellate web-dwellers (Table 2). In *Fecenia* Simon, 1887 sp. (Psechridae), which constructs an orb-web, the courting male cuts away most of the web, leaving only a single thread on which courtship and mating proceed (Robinson & Lubin 1979). Males of the meshweaver *Dictyna arundinacea* (Linnaeus, 1758) (Dictynidae) cut a hole in the web and construct a 'canopy' of their own threads on which they mate (Locket 1926). In other dictynid spiders in the genera *Dictyna* Sundevall, 1833, *Mallos* O. Pickard-Cambridge, 1902, and *Mexitlia* Lehtinen, 1967, however, there are records of silk addition to the female's web but no mention of males cutting the female's silk (Jackson 1979).

Web reduction is a behavior involving extreme web modification with silk addition that has been recorded for sheet weavers (Linyphiidae) and some cobweb weavers (Theridiidae; Table 2). During web reduction, the male moves around the web cutting threads with his chelicerae, then he bundles dismantled sections of the web into thick ropes or balls and, in some cases, wraps them extensively with his own

Table 5.—Other behaviors involving male silk deposition during courtship and mating. Note that silk deposition on the substrate is likely widespread in cursorial spiders but is rarely explicitly mentioned in descriptions of courtship behavior.

Taxon	Behavior	Reference
Araneidae		
Manogea porracea (C. L. Koch, 1838)	Male builds web above female's & protects egg sacs from predators	Moura et al. 2017
Ctenidae		
Ctenus longipes Keyserling, 1891	Male deposits silk on the substrate prior to mounting the female (82% of males; $n = 11$ matings)	Trillo 2016
Lycosidae		
Pardosa milvina (Hentz, 1844)	Male deposits silk on substrate in response to female silk cues	Khan & Persons 2015
Salticidae		
Plexippus paykulli (Audouin, 1826)	Male spins silk as he walks around outside/near female's nest	Jackson & Macnab 1989

Table 6.—Spider taxa in which there is behavioral evidence for male-produced sex pheromones. These families are also indicated in red in Fig. 1

Taxon	Source	Type	Female response	Reference
Agelenidae				
Agelenopsis aperta (Gertsch, 1934)	body	airborne	quiescence/catalepsis	Becker et al. 2005
Coelotes terrestris (Wider, 1834)	silk	contact	orientation	Roland 1983
Tegenaria domestica (Clerck, 1757)	silk	contact	orientation	Roland 1983
Lycosidae				
Allocosa alticeps (Mello-Leitão, 1944)	body	airborne	courtship	Aisenberg et al. 2010
Allocosa brasiliensis (Petrunkevitch, 1910)	body	airborne	courtship	Aisenberg et al. 2010
Pardosa milvina (Hentz, 1844)	silk	contact	increased silk production	Khan & Persons 2015
Trochosa C. L. Koch, 1847 sp.	silk	contact	mate recognition	Engelhardt 1964 (as cited by Uhl & Elias 2011)
Pholcidae				
Pholcus beijingensis Zhu & Song, 1999	body	airborne	stimulates mating behaviour	Xiao et al. 2010
Salticidae				
Evarcha culicivora Wesolowska & Jackson, 2003	body & silk	airborne + contact	courtship & attraction/ mate recognition	Cross & Jackson 2013
Scytodidae				
Scytodes Latreille, 1804 sp.	body & silk	airborne	mate choice	Koh et al. 2009
Theridiidae				
Latrodectus hesperus Chamberlin & Ivie, 1935	silk	contact	courtship	Ross & Smith 1979
Sicariidae				
Loxosceles intermedia	body	unknown	mate recognition & avoiding cannibalism	Fischer et al. 2009

silk (first described by Van Helsdingen 1965 and later studied in detail by Watson 1986; Fig. 2b). The frequency at which this behavior occurs is variable within and among species, as is the extent to which the web is destroyed (Table 2). For instance, web reduction in *Lepthyphantes leprosus* (Ohlert, 1865) results in a web area decrease of 90% or more, but 55% of males do not engage in web reduction at all (Van Helsdingen 1965). In a field experiment, 69% of *Neriene litigiosa* (Keyserling, 1886) males reduced a large portion of the female's web, but web reduction only occurred in 28% of laboratory trials (Watson 1986). In *Latrodectus,* removal of 50% or less of the female's web is typical, with ~60–70% of males engaging in web reduction behavior (Anava & Lubin 1993; Scott et al. 2012). *Steatoda grossa* (C.L. Koch, 1838) males also engage in extensive web reduction, but unlike in *Latrodectus*, mating tends to take place on a rope or bridge-like section of the web that has been covered with male silk (Scott et al. 2017). Previous workers have described the construction of a mating web in *S. grossa* (Gwinner-Hanke 1970; Knoflach 2004), but not the removal of large sections of the female's capture web.

Behavior much like web reduction has also been reported for some araneids that build both typical and irregular orb webs. In the process of constructing their mating threads, males of *Micrathena sexspinosa* (Hahn, 1822) and *Mangora bimaculata* (O. Pickard-Cambridge, 1889) engage in extensive web modification (Robinson & Robinson 1980). They break the threads of the viscid spiral on both sides of one radius, such that the web ends up looking like the missing sector webs of *Zygiella* sp. The resulting analog to the missing sector web's signal thread is reinforced with up to 30 layers of the male's silk until it is conspicuously thickened and white in color before being used as a mating thread (Robinson & Robinson 1980). The installation of the mating thread in the irregular orb-webs of *Kapogea sexnotata* (Simon, 1895) also show

Table 7.—Spider taxa in which there is behavioral evidence for males responding to silk cues of conspecific males.

Taxon	Source	Type	Male response	Citations
Araneidae				
Nephila senegalensis (Walckenaer, 1841)	silk	contact	avoidance/mate choice	Schneider et al. 2011
Linyphiidae				
Frontinella communis (Hentz, 1850)	silk	contact	positive geotaxis	Suter & Hirscheimer 1986 (as *Frontinella pyramitela*)
	cuticle	contact	aggressive behavior	Suter et al. 1987
Lycosidae				
Pardosa amentata (Clerck, 1757)	silk	contact	increased silk production	Richter & Kraan 1970
Rabidosa rabida (Walckenaer, 1837)	body	airborne	reduces exploratory behavior	Tietjen 1978 (as *Lycosa rabida*)
Schizocosa ocreata (Hentz, 1844)	silk	airborne & contact	inhibits courtship	Ayyagari & Tietjen 1987
Theridiidae				
Latrodectus hasselti (Thorell, 1870)	body &/or silk	airborne	shift in development	Kasumovic & Andrade 2006

parallels to web reduction in the Theridiidae and Linyphiidae. Males first cut away extensive portions of the lower snare of the female's web and attach silk to the surface of the web periodically during 'walkabouts.' The male continues to cut away sections of the female's web as he installs his mating thread, which he reinforces several times (Robinson & Robinson 1980).

3.2 Proposed mechanisms and functions.—A number of hypotheses that focus on effect of the male's silk on female receptivity or aggressive behavior have been proposed, mainly for species that engage in web reduction behavior (Table 2). However, these hypotheses may also apply to mating thread production or any behavior that may allow females to come in contact with male silk. Assuming that there are chemical signals or cues associated with the male silk produced during courtship, silk addition to the female's web, retreat, or burrow entrance may function in several non-mutually exclusive ways. First, pheromones on male silk might increase or accelerate female receptivity, either by stimulating the female to mate (e.g., initiate receptive postures or behaviors), or by inducing catalepsis (which always precedes successful mating in some species) (Gering 1953; Robinson & Robinson 1973; Ross & Smith 1979, Anava & Lubin 1993). Second, silk addition could also decrease female aggression and the risk of injury to males. For example, in both *Lepthyhphantes leprosus* and *Latrodectus hesperus*, web reduction (accompanied by extensive silk deposition) is associated with fewer instances of female aggression (Van Helsdingen 1965; Scott et al. 2012). However, it is not clear whether this is because 'shy' or more receptive females tolerate web reduction while aggressive or unreceptive females prevent it, or whether chemical signals associated with male silk decrease female aggression or induce receptivity. In addition, for each of these proposed functions, if females come in contact with the male's silk, it is also possible that behavioral changes are triggered by tactile (mechanical) cues on the silk rather than by chemical cues. Finally, chemicals (e.g., anti-aphrodisiacs) associated with the male's silk may deter rival males or render the female's silk unattractive (Yañez et al. 1999).

Clearly, silk addition to the web leads to structural alterations ranging from the addition of a single line (mating threads) to the major modification of web architecture that results from web reduction behavior (Table 2). Changing web architecture via web reduction and/or silk addition may generally function to improve the transmission of vibratory courtship signals (Robinson & Robinson 1980; Berendonck 2003). By plucking or moving on an isolated mating thread rather than engaging in vibratory courtship on the female's capture web, signal attenuation and degradation may be reduced. Similarly, constructing a mating web may allow a male to produce a transmission medium with properties that minimize courtship signal attenuation or degradation; these properties may differ from those that maximize capture efficiency for a hunting female. Isolating the female from extraneous vibrations, such as those produced by prey or other males arriving at the web, is a function proposed for web reduction behavior (Rovner 1968; Lubin 1986), but it could also apply to mating threads and webs. For instance, males in several orb-weaver species cut the mating threads of simultaneously courting rivals (Robinson & Robinson 1980).

Rather than improving transmission properties of the web, vibrations associated with cutting silk lines or adding silk could themselves transmit information to the female or attract her attention; that is, silk modification activities may in themselves be courtship signals (Forster 1995; Berendonck 2003). The materials and behaviors involved in silk addition may be energetically costly and provide the female with information about male quality (Anava & Lubin 1993; Harari et al. 2009). Silk is metabolically expensive to produce (Craig 2003), and adult males of web-building spiders apparently reduce or stop foraging after maturity (Foelix 2011), so they have limited energetic resources. When males invest considerable time and large amounts of silk during courtship, this could provide honest information about male nutritional status or vigor.

Fitness benefits of structural changes to the web may be less related to communication, and more related to restricting the mobility of a potentially dangerous female (Van Helsdingen 1965; Ross & Smith 1979; Breene & Sweet 1985). For example, the male may reduce the risk of cannibalism by altering the web in a way that restricts the female's movements prior to or just after mating. For species that construct a mating thread (Table 2; Fig. 2a), a male may cut the silk line between himself and an aggressive female to remove the immediate risk of attack (Robinson & Lubin 1979; Robinson & Robinson 1980). Alternatively, the "treadmill"-type mating threads of some araneids may provide the male with some control over the female's predatory response and thus decrease the likelihood of cannibalism (Robinson & Robinson 1980).

Similarly, structural modifications may reduce the likelihood of females mating with rivals and thus reduce the risk of losing paternity due to polyandry. This effect may also arise through effects on mobility, as altering the web may allow males to control the avenue of approach for a rival male attempting to court the female. If the female is on a mating thread or if web reduction has reduced the web's surface area, then altering web structure reduces the area that must be defended from competitors (Van Helsdingen 1965; Ross & Smith 1979; Breene & Sweet 1985). Rather than affecting mobility, a similar benefit would arise if web reduction decreases the attraction of rivals in the first place by interfering with the release of the female's airborne pheromones. Cutting out portions of the female's web could reduce the surface area of pheromone-laden silk (Watson 1986), and wrapping bundles of the female's silk with a layer of the male's own silk may also block the release of pheromones (Scott et al. 2015b).

3.3 Current evidence and future directions.—Male silk deposition onto webs or other silk structures has been hypothesized to increase female receptivity and the probability of mating, decrease the likelihood of polyandry, and/or decrease the risk of cannibalism by the female. These effects may arise via indirect means (communication, in a number of modalities) or directly through the structural changes to the web, but there is scant experimental evidence supporting these ideas to date (see Table 1).

Of the numerous examples of silk deposition and web modification described above, the only experimental work to

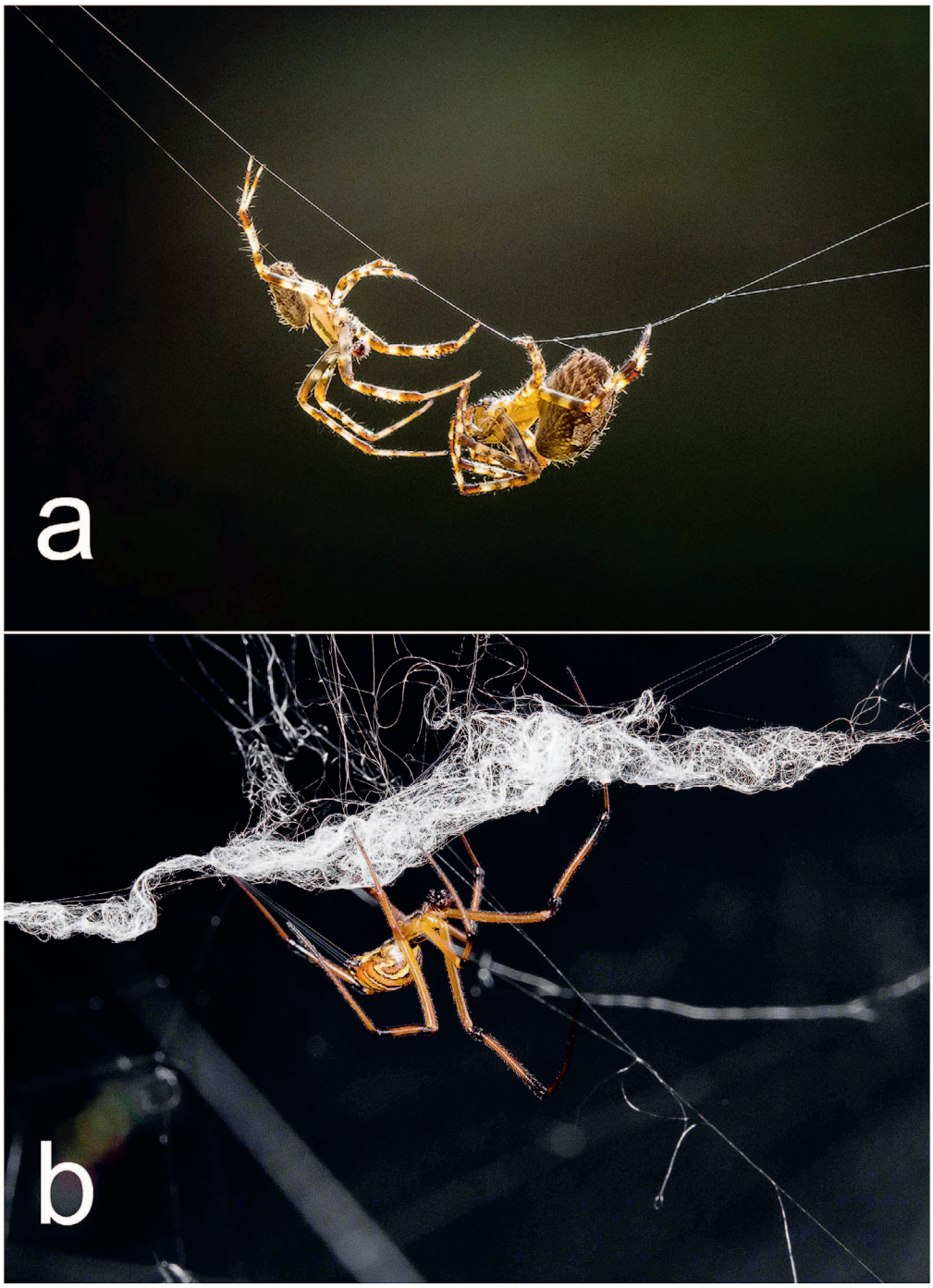

Figure 2.—Examples of silk deposition onto females' webs during courtship. (a) *Araneus diadematus* (Araneidae) male and female hanging from the male's mating thread, attached to the periphery of the female's web (photo: Maria Hiles). (b) Web reduction with silk addition by a *Latrodectus hesperus* (Theridiidae) male. The male has dismantled part of the capture web (which would have filled the lower half of the photograph before he began web reduction behavior) and is wrapping it with his own silk (photo: Sean McCann).

determine functions and mechanisms has focused on web reduction in *Neriene litigiosa* (Watson 1986) and *Latrodectus hesperus* (Scott et al. 2015b). In both species, reduced webs are less attractive to males than intact webs, indicating that males that engage in web reduction decrease the probability of their long (often several hours) courtship displays being interrupted by rival males. The effect of web reduction is presumably long lasting because mated females rebuild their webs without pheromones, so web-reducing males also benefit by decreasing the probability of sperm competition (Watson 1986). For *N. litigiosa*, Watson (1986) argued that web reduction limits female silk pheromone emission by decreasing the exposed surface area of the female's silk. Conversely, the results of a series of field experiments by Scott et al. (2015b) suggest that

physical alteration of the web and male silk addition both play roles in the function of web reduction as a mate monopolization tactic. Further work is required to determine the mechanism(s) by which web reduction decreases female attractiveness, and to what extent chemical cues affecting conspecifics (females or males) are involved.

The fitness benefits of web reduction for males are clear; decreasing female attractiveness limits sperm competition in two ways. First, it acts to quickly reduce the arrival rate of rival males, decreasing direct competition for access to females and increasing the likelihood of being first to copulate, which is important in spiders with long pre-copulatory courtship and first-male sperm precedence like *Latrodectus* and *Neriene litigiosa* (Watson 1991; Watson & Lighton 1994; Snow & Andrade 2005; MacLeod 2013). Second, mated females rebuild their webs without attractive pheromones (Watson 1986; MacLeod & Andrade 2014), decreasing the likelihood that males will face sperm competition from subsequently mating males. The fitness consequences for females, however, may be positive or negative. Females may benefit from the ability to quickly become unattractive after mating if they suffer costly harassment from subsequent males arriving at their webs. However, if females benefit from polyandry, web reduction may be costly; it may be a form of manipulation. Experimental studies are needed to explicitly test the fitness consequences to females to determine whether this is an example of cooperation or conflict between the sexes.

Other potential functions of silk addition with and without web modification remain to be experimentally investigated. A number of approaches would be valuable in future studies. First, tests of hypotheses related to vibrational signalling or signal transmission could harness Laser Doppler Vibrometry, which allows precise measurement of silk-borne vibrations with minimal loading of the web, unlike earlier methods based on accelerometers (Masters & Markl 1981; also see alternative methods in Vollrath 1979). Assessment of transmission properties of webs (e.g., Vibert et al. 2016) with and without male silk addition and the attendant web modifications (reduction and mating threads/webs) would be valuable for explicit tests of hypotheses associated with vibration transmission. For example, in recent work, Mortimer et al. (2015) combined laser vibrometry, electron microscopy, tensile testing, and behavioral assays to understand the function and biomechanical properties of the (predation-related) signal thread of *Zygiella x-notata* (Clerck, 1757). This study could be used as a model for exploring the characteristics of mating threads, and comparisons of signal threads used for predation and those used in mating may produce valuable insights. Second, once vibrations created during silk addition are characterized, synthesized vibrations can then be used in playback experiments to gauge male and female responses (e.g., see Uhl & Elias 2011; Wignall & Herberstein 2013b; Vibert et al. 2014) and how male fitness is affected. Third, behavioral experiments in the laboratory or field that focus on whether the silk itself affects female attractiveness or male mating success could utilize the experimental addition of male silk (e.g., Scott et al. 2015b), or experimental blocking of male silk production by covering the spinnerets of courting males with wax or glue (e.g., Zhang et al. 2011).

4. SILK DEPOSITION ON FEMALES

4.1 Overview and description of behaviors.—Males may deposit silk directly on the female's body during courtship or copulation—a widespread behavior reported in 16 families, including web-building and cursorial spiders (Figs. 1 & 2; Table 3). The term 'bridal veil' was coined by Bristowe (1931) as a descriptor for male silk-laying on females during mating in *Xysticus cristatus* (Clerck, 1757) and *Pycnaxis krakatauensis* (Bristowe, 1931) (Thomisidae). Other descriptions for bridal veil spinning behavior include 'tying', 'mate-binding', 'silk-binding', 'copulatory silk-wrapping', and 'trussing' (Table 3). We use 'bridal veil' and 'veil' to refer to this behavior because this is the original term and to avoid using terms that imply particular functions. There are several types of bridal veils, and species in which they have been reported vary in the context in which they are used, the part of the body on which the silk is applied, the predictability of silk-laying patterns, and the volume of silk used in the behavior (Table 3).

Extensive silk-wrapping behavior, often focused on the female's legs, is seen across a number of families of cursorial spiders and some web-builders (Table 3; Fig. 3). Males deposit silk over the female's first two pairs of legs and anchor the silk to the substrate in several crab spiders, including *Xysticus* C.L. Koch, 1835 spp., *Pycnaxis krakatauensis*, and *Bassaniana versicolor* (Keyserling, 1880) (Thomisidae; Bristowe 1931, 1958; Kaston 1936). Comparable veiling behavior has been described for the wolf spider *Schizocosa malitiosa* (Tullgren, 1905) (Lycosidae; Aisenberg et al. 2008) and the fishing spider *Dolomedes triton* (Walckenaer, 1837) (Pisauridae; Carico 1993). Similarly, males of *Ctenus longipes* Keyserling, 1891 (Ctenidae) concentrate silk deposition on the female's forelegs and also spin silk over the palps, chelicerae, and eyes (Trillo 2016). Intriguingly, the female apparently eats the veil silk after copulation in this species (discussed below in section 5). In *Oxyopes schenkeli* Lessert, 1927 (Oxyopidae; Preston-Mafham 1999) and in some cases, *Pisaurina mira* (Walckenaer, 1837) (Pisauridae; Bruce & Carico 1988; A.G. Anderson pers. obs.), both mates will hang from a dragline below a plant as the male deposits silk on the first two or three pairs of the female's legs. Males systematically deposit a ring-like veil around the female's legs as she stands on the ground in *Homalonychus selenopoides* Marx, 1891 and *H. theologus* Chamberlin, 1924 (Homalonychidae; Domínguez & Jiménez 2005; Alvarado-Castro & Jiménez 2011), or as the female hangs from her mating web in *Nilus curtus* (O. Pickard-Cambridge, 1876) (Pisauridae; Sierwald 1988). Males of *Ancylometes bogotensis* (Keyserling, 1877) (Ctenidae) wrap the distal segments of the female's legs first with an outer ring of silk, and then add a second inner ring around the patellae (Merrett 1988). Complex, extensive veiling behavior has also been described for several orb-weaver genera (Araneidae; Table 3; Fig. 3a). The diminutive males move around on the dorsum of the female, spinning silk between the bases of her legs, over her cephalothorax, and between her cephalothorax and abdomen (e.g., Robinson & Robinson 1980; Gregorič et al. 2016).

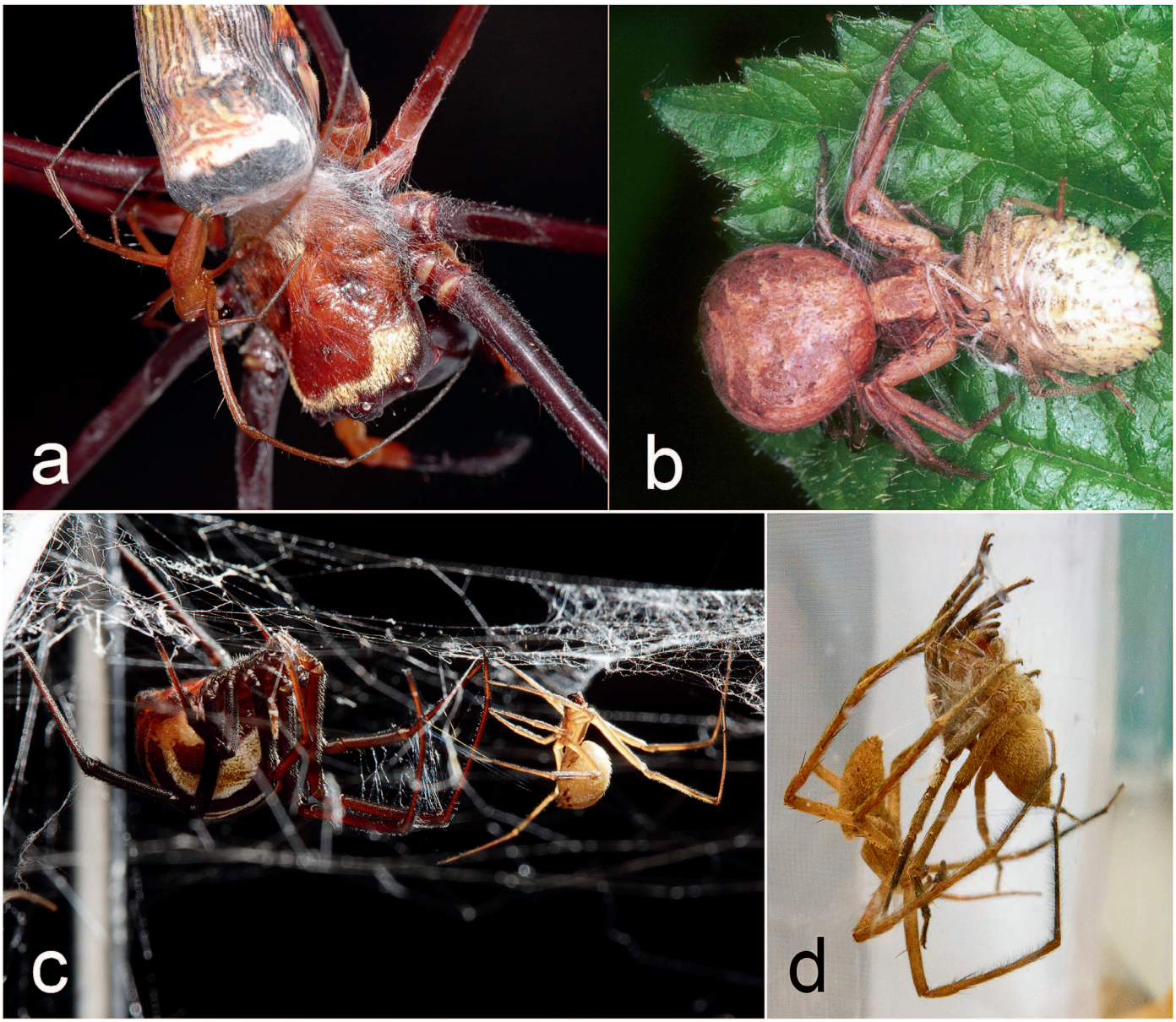

Figure 3.—Examples of silk 'bridal veils' applied to females' legs and bodies during courtship. (a) *Nephila pilipes* (Araneidae) male depositing silk onto the female's carapace, legs, and abdomen (photo: Shichang Zhang). (b) *Xysticus cristatus* (Thomisidae) female with silk on her forelegs and abdomen as she feeds on a prey item—note that the male is underneath her abdomen (photo: Ed Niewenhuys). (c) *Latrodectus hesperus* ("texanus" morph, formerly *Latrodectus mactans texanus*; Theridiidae) male depositing silk onto the female's legs (photo: Sean McCann). (d) *Pisaurina mira* (Pisauridae) male wrapping a female's legs with silk prior to sperm transfer (Photo: Alissa Anderson).

Less extensive silk deposition on females has been described for species in the Agelenidae, Corrinidae, Dictynidae, Philodromidae, Tetragnathidae, Theridiidae and Zoropsidae (see Table 3 for details and references). In these taxa veiling behavior occurs on the female's web and seems to be less ritualized or more variable than the types described above. In the Theridiidae, for example, there is variation in the occurrence of silk deposition behavior within and across species. Veiling took place in about 33% of courtship observations in *Latrodectus revivensis* Shulov, 1948 (Anava & Lubin 1993), in 50% of *Steatoda bipunctata* (Linnaeus, 1758) pairings (Knoflach 2004), and only occasionally in *Steatoda grossa* (Scott et al. 2017). Intriguingly, application of a bridal veil appears to be an obligate behavior in *Nephila pilipes* (Fabricius, 1793), as well as in *Pisaurina mira* (Bruce & Carico 1988; Kuntner et al. 2009; Anderson & Hebets 2016). Conversely, *Cupiennius coccineus* F.O. Pickard-Cambridge, 1901 (Ctenidae) males normally do not use veils in laboratory trials, but in an inter-species mating experiment, some male *C. coccineus* deposited silk on *C. salei* females, which are larger than conspecific females (Schmitt 1992).

4.2 Proposed mechanisms and functions.—Bridal veils may increase female receptivity and the probability of mating. The veil may also act as a physical restraint that increases mating success or decreases the risk of sexual cannibalism. Finally, it is also possible that application of a veil decreases the

likelihood of polyandry. Typically, silk used in veils is not placed within the female's field of view and is removed shortly after copulation, so visual cues are unlikely to play a functional role, but chemical or tactile information may be important to either the female or rival males. Below, although we focus on hypotheses that suggest mechanisms involving chemical cues, we note that all the proposed effects could also arise from female detection of tactile cues or signals, or perhaps even improved seismic signal transmission via direct contact with male silk.

Females may be more likely to mate with males that produce veils due to information in the silk itself (chemical or tactile modalities), due to mechanical stimulation of structures in the location of the veil (e.g., if silk is laid across particular sensory regions on the female's body), or due to information in the activity associated with laying silk (tactile cues/signals). Silk-laying may increase female receptivity if the veil allows females to identify males as potential mates (e.g., rather than prey), or if the veil is instrumental in female choice among conspecifics. In terms of mating with rather than attacking the male, it has been proposed that pheromones on the male's silk may lead to a general reduction in the female's predatory or aggressive behaviors (e.g., Schmitt 1992; Dominguez & Jiminez 2005). In a more extreme proposal, chemicals in the veil could inhibit movements of the female so that she remains in a cataleptic state during copulation (Ross & Smith 1979; Aisenberg et al. 2008; Preston-Mafham 1999). Silk-borne pheromones could also provide the female with information about the male's quality (Ross & Smith 1979; Anava & Lubin 1993) and thus increase her receptivity to mating with particular males. Both of these types of functional hypotheses are consistent with previous mechanistic arguments that bridal veils 'stimulate' the female or trigger physiological changes that prepare the female for mating (Robinson & Robinson 1973; Preston-Mafham 1999).

As has been proposed for web reduction (Scott et al. 2015b), the male's silk could also function to deter rival males, possibly via pheromones (Aisenberg et al. 2008) that remain on the female's body. 'Antiaphrodisiacs' (e.g., in butterflies; Estrada et al. 2011) may be particularly effective in species with first-male sperm precedence (such as many spiders), since this predicts the evolution of tactics that allow males to avoid previously-mated females (Parker 1970).

In many species, silk deposition by males seems to target the distal segments of the female's legs (usually the first two or three pairs) and sometimes the pedipalps (see Table 3) (Aisenberg et al. 2008). Spider chemoreceptors are concentrated on the distal segments of the legs and pedipalps (Trabalon 2013), thus the pattern of silk deposition supports the hypothesis of chemical information delivery to females. In a twist on this idea, Lopez (1987) argued that the female's sensory hairs might be incapacitated by direct contact with the silk. This argument suggests that reduced predatory responses could be the result of silk-mediated impairment of the female's sensory system (but see Zhang et al. 2011).

Independent of any signal function of veils, the application of silk to the female's body could directly affect female positioning or mobility during mating interactions in ways that are beneficial for the male. Silken restraints may facilitate copulation by ensuring the female's abdomen is supported in a posture that simplifies intromission. However, silk may also reduce female mobility, which could increase copulation duration and thus fertilization success (Anderson & Hebets 2017) or reduce the risk of injury or sexual cannibalism (Anderson & Hebets 2016). There has been some debate as to whether the veil is able to physically restrain the female. Most descriptions indicate that females are quickly and easily able to break free of their silken bonds (e.g., Ross & Smith 1979; Preston-Mafham 1999), making this interpretation seem unlikely for many species, but other authors argue that the brief moments of struggling free from the veil may provide the male with just enough time to escape from a potentially cannibalistic female (Breene & Sweet 1985; Bruce & Carico 1988; Anderson & Hebets 2016; Gregorič et al. 2016). The efficacy of the veil in interfering with female movement may depend on how this tactic is employed and to which body parts the veil is applied. It is worth noting that extensive binding of the female's legs, common in some species (see Table 3), is also consistent with the idea of an effective restraint.

4.3 Current evidence and future directions.—The function of the silk bridal veil has been investigated experimentally in only two studies, one with *Nephila pilipes* (Zhang et al. 2011) and another with *Pisaurina mira* (Anderson & Hebets 2016). Both studies found that the veil reduced the risk of sexual cannibalism and allowed males to obtain a second sperm transfer opportunity, and in *P. mira*, this led to higher fertilization success (Anderson & Hebets 2017). Zhang et al. (2011) ablated or occluded the female's tactile and chemical receptors, revealing that tactile cues associated with tying behavior may be critical for this effect, with chemical cues playing a secondary role. Zhang et al. (2011) conclude that the veil in *N. pilipes* reduces the risk of sexual cannibalism and allows males to overcome resistance of females to repeated copulations. While Anderson & Hebets (2016) did not directly test for chemical cues, their observations are consistent with the silk wrapping acting as a physical restraint, rather than effects mediated by chemical signals. Female *P. mira* attempt to free themselves from the silk wrapping (rather than showing reduced activity), and sexual cannibalism attempts occur whether or not the silk wrapping is present (Anderson & Hebets 2016).

For most species in which males apply silk to the female's body during mating, the fitness consequences are unclear. The varied terms used to describe this behavior in the literature suggests that authors have inferred a range of possible functions from their observations. This is a fascinating phenomenon, and we suggest a number of different approaches could be fruitful for future study.

First, the phylogenetic distribution of the behavior is broad (Fig. 1; Table 3) and may suggest more than one evolutionary origin, so comparative analysis of the behavior and underlying physiology among taxa may be informative. For example, there are many species where extensive leg wrapping is typical, and physical restraint functions should be more likely in these species than in those where wrapping concentrates on the abdomen. We predict that leg-wrapping, but not abdomen-wrapping, will be more likely in taxa with a higher occurrence of sexual cannibalism.

Second, silk wrapping in the context of mating has been proposed to have its evolutionary origin in silk wrapping of prey (Lopez 1987; Schmitt 1992). Prey-wrapping has a similar underlying function, that is, reduced risk of injury from dangerous prey (Foelix 2011). This gives rise to a mechanistic prediction that bridal veils that function as physical restraints should be constructed from aciniform silk (the toughest type of silk, also used in prey capture; Craig 2003). Testing this supporting prediction may involve comparative analysis of silk structure (e.g., Parkhe et al. 1997; Hayashi et al. 2004), or analysis of the glandular origin of bridal veil silks.

Third, careful experimental designs that manipulate the male's ability to produce the veil, or the female's ability to detect it (e.g., Zhang et al. 2011; Anderson & Hebets 2016, 2017; and see Aisenberg et al. 2015) can be combined with assessments of female aggression, mating outcomes (e.g., proxies for female choice), or the opportunity for polyandry (e.g., assessments of anti-aphrodisiac effects) to estimate effects on male fitness. Comparative approaches may be valuable here as well. If bridal veils are primarily related to female choice, then they should be more common in taxa with higher levels of inter-male competition over mates, or low overall mating rates.

Fourth, similar types of manipulations can be employed to assess which functions of the bridal veils are related to communication (rather than restraint), and which modalities are most important. Disentangling possible effects of tactile and chemical cues will be particularly interesting. For this work, examination of behavioral effects of extracts of bridal veil silk may also be informative. Moreover, given recent improvement of techniques for nerve recordings from spiders, there is the exciting potential to measure female responses to chemicals vs. tactile cues directly (Menda et al. 2014).

5. SILK ASSOCIATED WITH NUPTIAL GIFTS

5.1 Overview and descriptions of behaviors.—Nuptial gifts are material items transferred during mating that function as paternal effort (increasing male offspring number or success) or mating effort (increasing the likelihood of mating; reviewed in Vahed 1998, 2007; Gwynne 2008). Although rare in spiders, the types of gifts reported include the male's body, glandular secretions from the male's cephalothorax, and silk-wrapped prey (reviewed in Albo et al. 2013b). Here we will focus on silken nuptial gifts, in particular the wrapped-prey gifts reported in one theridiid, one tetragnathid and in several species in the closely related families Trechaleidae and Pisauridae. We also include silk produced by males and consumed by females (Theridiosomatidae, Lycosidae, and probably Araneidae provide examples of this phenomenon) and silk-lined burrows (provided by males in a sex-role reversed wolf spider) as examples of nuptial gifts. Our focus will be on the function of the silk associated with these nuptial gifts rather than the gifts themselves.

Silk-wrapped nuptial gifts have been well studied in both *Pisaura mirabilis* (Clerck, 1757) (Pisauridae; Fig. 4a) and *Paratrechalea ornata* (Mello-Leitão, 1943) (Trechaleidae). Female silk cues (probably sex pheromones) elicit courtship and gift construction in males of both *P. ornata* (Albo et al. 2009) and *P. mirabilis* (Albo et al. 2011a). However, female silk is not required to elicit gift-wrapping by *P. mirabilis* males, who sometimes prepare nuptial gifts before they encounter a female or her draglines (Lang, 1996; Albo et al. 2011a). When a *P. mirabilis* or *P. ornata* male finds a female, he presents his gift by holding it in his chelicerae and raising his front legs in a characteristic display. If the female accepts his gift, she grasps it with her chelicerae and copulation ensues while she is feeding on the gift.

Whereas nuptial gifts are the norm for *Pisaura mirabilis* and *Paratrechalea ornata,* in *Metellina segmentata* (Clerck, 1757) (Tetragnathidae) silk-wrapped prey items are used as an alternative mating tactic (Prenter et al. 1994b; reviewed in Neff & Svensson 2013; Fig. 4b). In this species, males guard females and normally wait until she has captured a prey item before initiating courtship. Once the female has captured and wrapped a prey item in silk, the male takes it from her, adds his own silk, and then incorporates the silk-wrapped prey item into his mating thread (Prenter et al. 1994a); he may also wrap the female in a light bridal veil as he does this (Bristowe 1929; Lopez 1987). Clearly, the prey in this situation is not a nuptial gift since the female captures it herself, although once the male steals it from her, he can prevent her from eating it if she does not mate with him (Schneider & Lubin 1998). In rare cases, however, when two males are present on a female's web (in the field, 7% of females are guarded by two males simultaneously) the male captures the prey item himself and waits for the female to approach it before beginning courtship (Prenter et al. 1994b). In some cases, one male kills and wraps his rival male into a package with another prey item, using this silk-wrapped package to initiate courtship with the female (Prenter et al. 1994b; Fig. 4b).

In the kleptoparasitic and araneophagic spider *Argyrodes elevatus* (Theridiidae), two anecdotal reports of nuptial gifts are available. One *A. elevatus* male used a stolen prey item as a gift, and the other used the silk-wrapped carcass of a host spider (Cobbold & Su 2010; Uetz et al. 2010). In the case of the stolen prey item, the male was observed to present the gift to a female, wait until she began feeding on it, and then copulate with her (Uetz et al. 2010). Whether this functions as an alternative mating tactic or simply represents an occasional occurrence in this species remains to be seen.

Silk-wrapped prey gifts have most commonly been reported for pisaurids in the genera *Pisaura* Simon, 1886 (*P. lama* in addition to *P. mirabilis*), *Perenethis* L. Koch, 1878, *Thaumasia* Perty, 1833, and *Tinus* F.O. Pickard-Cambridge, 1901 (Table 4). In addition to *Paratrechalea ornata,* two congeners and members of the genus *Trechalea* Thorell, 1869 also use silk-wrapped nuptial gifts (Table 4). The families Pisauridae and Trechaleidae are closely related members of the Lycosoidea (Wheeler et al. 2016; see Fig. 1) hinting at silk-wrapped nuptial gift-giving as a synapomorphy, however, spotty reports of silk-wrapped nuptial gifts in other species suggest that silk-wrapped nuptial gifts may have evolved more than once in spiders.

There a few examples of apparent nuptial gifts in which the male's silk itself, rather than a prey item, constitutes the gift. In the ray spider *Theridiosoma gemmosum* (L. Koch, 1877) (Theridiosomatidae), males feed silk directly to the female between repeated copulations (Hajer & Řeháková 2011). This silk is considered a nutrient gift, because araneoids can recycle silk proteins by consuming silk (Craig 2003). Intriguingly, in one ctenid spider species where males deposit a bridal veil, the

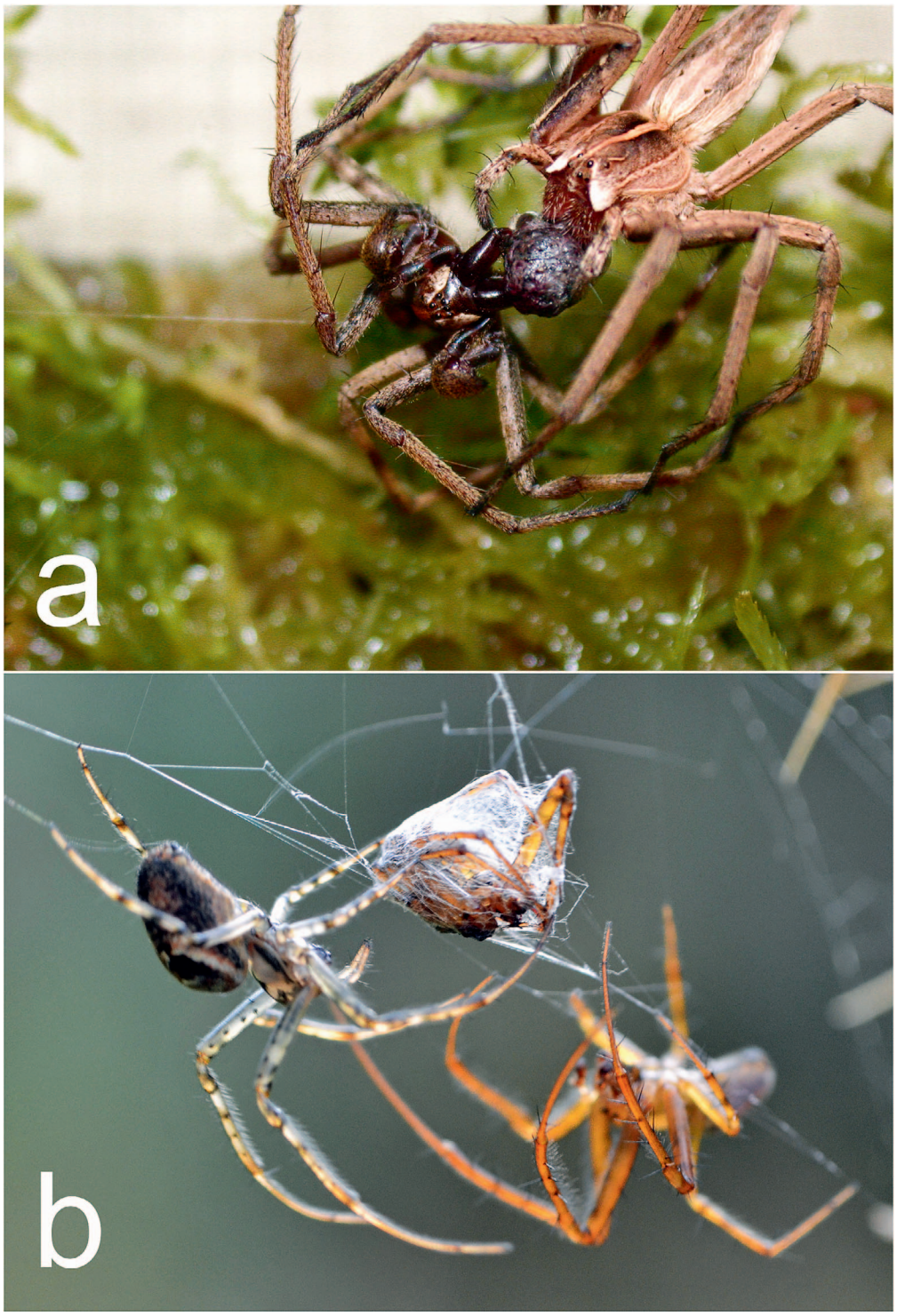

Figure 4.—Examples of silk-wrapped nuptial gifts. (a) Female (right) *Pisaura mirabilis* (Pisauridae) accepts a silk-wrapped gift from a male (photo: Alan Lau). (b) A male (right) *Metellina segmentata* (Tetragnathidae) has wrapped a rival male in silk as a nuptial gift for the female (photo: Conall McCaughey).

silk is apparently consumed after copulation. Trillo (2016) describes females of *Ctenus longipes* grooming the silk veil off of their legs and palps after mating and then bringing the silk to their mouthparts until it disappears. In the araneid spiders *Scoloderus cordatus* (Stowe 1978) and *Isoxya tabulata* (Robinson & Robinson 1980) males employ "treadmill"-type mating threads that they pay out as the female attempts to walk toward them on the thread. Robinson & Robinson (1980) note that during this process the female accumulates a conspicuous ball of silk under her cephalothorax, and though

they do not mention it being consumed, it seems probable that females eat the silk as in the examples above.

Finally, the silk-lined burrows provided by males of the sex role reversed wolf spiders in the genus *Allocosa* Sundevall, 1833 are nuptial gifts (reviewed in Aisenberg 2014). In *Allocosa senex* (Mello-Leitão, 1945) and *A. alticeps* (Mello-Leitão, 1944), males construct silk-lined burrows in which females oviposit and brood their egg sacs, providing both female and offspring with protection from predators (Aisenberg 2014). Females prefer males that provide longer burrows (Aisenberg et al. 2007) and males lengthen their burrows after experiencing rejection by a female (Carballo et al. 2017).

5.2 Proposed mechanisms and functions.—The most likely function for silk-wrapped nuptial gifts is to increase female receptivity and thus male mating success. Related to this may be a decreased risk of sexual cannibalism, which is a demonstrated function of gifts in *Pisaura mirabilis* (Toft & Albo 2016). Both of these are forms of mating effort. The silk wrapping of nuptial gifts may in general provide females with information about males via visual, tactile, or chemical cues. Proposed mechanisms for such effects in pisaurids and trechaleids generally fall into two categories. In both cases, silk wrapping may function in several non-mutually exclusive ways that either conflict or align with the female's interests. First, silk may have direct physical effects if it disguises gift contents and thus increases mating success even if prey items are insufficient (or missing). When silk is wrapped around a non-prey item, it may serve to hide the contents of a 'worthless package' (e.g., Ghislandi et al. 2017; Prokov & Semelbauer 2017), through visual obstruction and/or creating a barrier (physical or chemical) between the female and the contents. Males may thus deceive females into mating in the absence of a nutritious gift. However, recent work argues that such 'worthless' gifts may be most common in species where the nuptial gift has evolved to serve a signal function rather than a direct benefit (e.g., Albo et al. 2017; Pandulli-Alonso et al. 2017). Another possible physical effect of the silk wrapping is to allow males to maintain a firm grip on the gift to avoid it being stolen by the female (Andersen et al. 2008) or rival males (Nitzsche 2011).

Second, silk may have indirect effects through communication, whereby visual, tactile or chemical cues increase the likelihood of gift acceptance and mating by females. For example, the brightness of the silk wrapping around the gift or its chemo-tactile qualities may provide the female with information about the male's quality, since silk and/or associated pheromones may provide an honest signal of male body condition (Stålhandske 2002; Albo et al. 2011a; Trillo et al. 2014). Moreover, the amount of silk a male can spin before or during mating may also provide information about body condition (Albo et al. 2011a; Klein et al. 2014). In this context, silk wrapping around prey may also provide a method for delivery of chemicals to female chemosensory organs.

Third, rather than providing information about the male, the silk wrapping may include cues that exploit female sensory biases by mimicking egg sacs (Stålhandske 2002), which females carry in their chelicerae in pisaurids and attached to the spinnerets in trechaleids (Carico 1993).

Fourth, when silk itself is a nuptial gift, it may also function as paternal effort. When the female consumes the silk as in ray spiders (Hajer & Řeháková 2011), at least one ctenid (Trillo 2016) and possibly some araneids that use 'treadmill'-type mating threads (Stowe 1978; Robinson & Robinson 1980), it may provide additional nutrients to females that are incorporated into the male's offspring. However, the thick silk wrapping of the nuptial gift apparently does not itself provide a significant source of protein to the female in pisaurids (Nitzsche 1988 as cited by Nitzsche 2011). The silk burrows provided by *Allocosa* males clearly provide material benefits to females (safe places to oviposit and brood egg sacs) but may also represent mating effort, with males lengthening their burrows (requiring addition of costly silk) in response to rejection by females (Carballo et al. 2017).

In *Argyrodes elevatus*, silk-wrapped nuptial gifts may be an alternative mating tactic as in *Metellina segmentata*. Males of some spider species mate opportunistically with females engaged in feeding as a way to avoid sexual cannibalism (e.g., Austin & Anderson 1978; Fromhage & Schneider 2004), and the presentation of nuptial gifts may be a refinement of this mating strategy.

5.3 Current evidence and future directions.—Experimental studies of the function of nuptial gifts in spiders are restricted to a few species. There is experimental evidence for several functions of nuptial gifts in both *Paratrechalea ornata* and *Pisaura mirabilis*. Nuptial gifts in *P. mirabilis* and *P. ornata* may have evolved by sexual selection through cryptic female choice for sperm storage (Albo & Costa 2010; Albo et al. 2013a). In both species, males that provide nuptial gifts to mates have longer copulations and transfer more sperm than males who do not provide gifts (Albo & Costa 2010; Albo et al. 2013a), and nuptial gifts are also correlated with accelerated oviposition in *P. ornata* (Albo & Costa 2010). We note here the interesting functional parallel with the bridal veil in *Pisaurina mira* (Anderson & Hebets 2016, 2017).

Nuptial gift silk may provide information via visual signals or cues. *Paratrechalea ornata* females accept smaller, brighter gifts more quickly than larger gifts that are darker in color—but the mechanism is not clear (Klein et al. 2014). Brighter gifts (painted white to match egg sacs) are more quickly accepted than unmanipulated silk-wrapped gifts, which in turn are more readily accepted than gifts painted brown (*P. mirabilis*, Stålhandske 2002). In some species, visual signals alone may be insufficient to elicit gift acceptance, but ether-extractable chemical compounds specific to nuptial gift silk elicit female acceptance of filter paper 'gifts' (*Paratrechalea ornata*; Brum et al. 2012). Moreover, females more often accepted gifts wrapped by males than gifts wrapped with silk experimentally reeled from males' spinnerets, suggesting that males control the type of silk they use or the compounds they add to the silk during gift construction (Brum et al. 2012). This suggests that pheromones on male silk stimulate females to accept gifts, thereby increasing mating success of males. In no-choice tests, females responded similarly to silk extracts and prey extracts, implying that the pheromone either has chemical similarities to prey cues and exploits the female's foraging response, or comprises unrelated compounds that elicit the same response—the acceptance of and feeding on the gift (Brum et al. 2012).

The pheromone on silk-wrapped nuptial gifts may provide information about a male's quality even if the gift itself does

not necessarily honestly indicate prey capture ability (males can steal gifts from rivals or from the female herself; Prenter et al. 1994b; Nitzsche 2011). The extent of silk-wrapping during gift construction depends on male condition in *P. mirabilis*, with males in better condition adding more silk, and thus this may be an honest signal of male quality (Albo et al. 2011a). As expected if this is the case, *P. mirabilis* feed longer on gifts wrapped with more silk, and most males already carrying wrapped prey wrap it again after encountering a female (Lang 1996; Albo & Costa 2010), as do males that were previously rejected (Bilde et al. 2007), which appears to increase the attractiveness of the gift (Bilde et al. 2007; Brum et al. 2012). This suggests that visual, tactile and/or chemical cues associated with the male's silk affect female acceptance of the gift (Bilde et al. 2007).

Similarly, wrapping low-quality gifts in pheromone-laden silk may be a strategy of males that minimizes the costs of providing a gift while maintaining its attractiveness. In some species females will not copulate unless males provide a gift (*P. mirabilis*, Prokop & Maxwell 2009; Albo et al. 2011b). Such effects may be limited however, as males that present a silk-wrapped gift containing a prey carcass or plant material instead of prey may obtain a short copulation, but, in *P. mirabilis*, it ends as soon as the female detects that there is no prey inside the silk (Albo et al. 2011b; Brum et al. 2012). Consistent with this, field studies of *P. mirabilis* found no evidence for 'sham' gifts concealed in silk, instead, 40% of males carried gifts, all of these were freshly killed arthropods (Prokop & Maxwell 2009), and gift size was correlated with male body size (Prokop & Semelbauer 2017). The idea that the gift is a sensory trap exploiting female maternal care behavior (Stålhandske 2002) was not supported in this species; experimental evidence suggests that the gift exploits female foraging motivation instead (Bilde et al. 2007; Toft & Albo 2015).

In strong contrast to *P. mirabilis*, 70% of gifts carried by *Paratrechalea ornata* males are nutritionally worthless in nature. However, in *P. ornata*, female receptivity does not depend on hunger, as might be expected if females are permitting copulations with gift-bearing males because they are seeking food (Pandulli-Alonso et al. 2017). Albo et al. (2017) suggest that nuptial gifts may evolve initially due to direct benefits to females, but in some species, gifts may evolve a signal function (Bradbury & Vehrenkamp 2011). Thus *P. mirabilis* and *P. ornata* represent different points in the evolutionary ritualization of a direct benefit into a signal (Albo et al. 2017). Alternatively, the provision of worthless gifts may be maintained in a basically honest, direct-benefits system as long as the frequency of these deceptions remains sufficiently low (negative frequency dependence; Dawkins & Guilford 1991; Neff & Svensson 2013). If this is the case, then receiving deceitful gifts will be costly for females, but elevated discrimination would be even more costly than accepting worthless gifts at low frequency. Moreover, at equilibrium, the fitness of males using deceitful or honest tactics should be equal, as part of a mixed ESS (Evolutionarily Stable Strategy; Neff & Svensson 2013). Finally, a high frequency of worthless gifts may occur as a transient outcome of sexually-antagonistic coevolution (Ghislandi et al. 2014). In this case, receiving worthless gifts is costly for females, and the high frequency of male deceit would eventually lead to the evolution of increased female discrimination (Lindstedt & Mokkonen 2014).

In addition to other functions, silk-wrapping apparently affords *P. mirabilis* males greater control over their gifts by improving their grip, thus decreasing the risk of the female stealing the gift without mating. Moreover, the rounded shape of the wrapped gift facilitates access to the female's genitalia for copulation, thus increasing their mating success (Andersen et al. 2008). The gift itself may also function as a "shield" preventing cannibalism; cannibalism is six times more likely to occur when males do not provide the female with a gift (Toft & Albo 2016), although it is unclear whether silk wrapping is required for this effect.

Visual cues, chemical cues, and physical properties of the silk have all been implicated in the gift-giving systems of *P. ornata* and *P. mirabilis*. Given that the type of silk appears to be important (Brum et al. 2012), future studies could compare the chemical and biophysical properties of silk used to wrap nuptial gifts to those of other silk types. This will facilitate consideration of the origin of gifts, and the identification of putative pheromones on the silk and study of their specific function(s). Whether chemical cues are important in other species that produce silk-wrapped nuptial gifts (or when silk alone acts as a gift) remains to be investigated. In the *Allocosa* species providing burrows as nuptial gifts, the silk lining alone (i.e., in the absence of the male's body, which emits a volatile pheromone) is not sufficient to elicit female courtship behavior, but the potential role of the silk in female assessment of males has not been further tested (Aisenberg et al. 2010). Studies of the mechanisms by which nuptial gift silk influences female responses would benefit from experiments that systematically manipulate the possible cues presented in gift silk, and/or ablate the female's sensory receptors and examine the effect on mating success, cannibalism risk, and female reproductive output (e.g., in the case of species where females consume the male's silk).

Understanding the evolutionary trajectory of nuptial gift evolution in spiders will require a more explicitly comparative approach, with the addition of studies of more taxa that vary in the type of gift involved in mating. In the broadest sense, this may include males that wait until females are feeding before attempting to mate, those that steal prey from females and then present those same prey at mating, those that wrap nutritive prey to present to females, and those that frequently present non-nutritive, silk-wrapped items to females. A theoretical evolutionary sequence would predict co-occurrence of a number of features in species at different stages (e.g., Albo et al. 2017). In this case, silk wrapping may originally function to subdue prey or for easy manipulation of prey to facilitate gift giving as a direct benefit to females. Hungry females may be more likely to mate and accept these prey items, and most gifts carried by males should be nutritive. In such species, male honesty may be further augmented by the risk of cannibalism from hungry females who do not receive a gift. Later in the evolutionary sequence, silk wrapped packages may provide information to females (via visual, chemical or tactile cues), thus triggering receptive behavior regardless of female's hunger, and in the absence of a risk of cannibalism. Under this scenario, these species should show a relatively high frequency of 'worthless' gifts, but features of the silk package

itself would be correlated with male quality (e.g., Pandulli-Alonso et al. 2017). In contrast, species with a relatively high frequency of 'worthless' gifts may not be those in which the gift has evolved a signal function; rather this may be an exploitative behavior of males maintained through negative frequency dependence. If silk wrapping serves a deceptive function, it is expected that receptivity of females will be linked to hunger, and gifts should deter sexual cannibalism. This can be tested in experiments that measure the fitness payoff to males bearing worthless gifts as a function of natural or manipulated variation in the relative frequency of the tactic.

6. OTHER EXAMPLES OF MALE SILK USE DURING MATING INTERACTIONS

The three types of silk use discussed above do not include all of the ways that male spiders can use silk during courtship and mating interactions. Below we briefly discuss some other kinds of silk use related to spider mating (see Table 5).

We have not considered sperm webs in this review because their production is rarely observed and described, and, to our knowledge, there have been no suggestions or investigations of functions other than the required one of charging the palps in preparation for sperm transfer (Foelix 2011). Indeed, in many spider taxa males charge their palps with sperm before they set off in search of mates, and thus the silk involved clearly has no effect on females during courtship (Foelix 2011). However, in those species where males build sperm webs on the female's web and/or charge the palps in between mating bouts (e.g., in the Linyphiidae; Van Helsingden 1965; Watson & Lighton 1994), we cannot exclude the possibility that this silk plays some additional role.

Cursorial spiders trail dragline silk as they move around, periodically anchoring it to the substrate (Richman & Jackson 1992; Foelix 2011), and undoubtedly do so in close proximity to one another during mating interactions. In these taxa, where courtship occurs on substrates other than the female's silk, male silk function could overlap substantially with those where males deposit silk on the female's web or body. Explicit studies of male silk use in such contexts are rare, but the following example is illustrative. In the wolf spider *Pardosa milvina* (Lycosidae), the structure of male silk produced during courtship differs from typical dragline silk (e.g., in the number of attachment disks), and females respond to contact with courtship silk by spinning more of their own pheromone-laden silk (Khan & Persons 2015). Females increase their own silk production in response to males who court less intensively (i.e., males depositing less silk), suggesting that silk-bound pheromones and/or contact cues may mediate a two-way "conversation" between the sexes (Havrilak et al. 2015). Additional studies analyzing the structural and/or chemical differences between silk deposited by males during courtship and other contexts, as well as the behavioral responses of females to these different silk types (as in Khan & Persons 2015) would be very useful. Such studies may reveal that bi-directional communication mediated by silk is common across spider taxa

The orb-weaver *Manogea porracea* (Araneidae) provides a unique example of male silk use that facilitates paternal care (Moura et al. 2017). After mating, the male builds his own capture web above that of the female and remains there until the end of the reproductive season. The female then hangs her egg sacs between the two webs and the male provides parental care by protecting the egg sacs from predators. Both parents provide protection, but females frequently die before spiderlings emerge, such that egg sacs attended by males are most common at the end of the season (Moura et al. 2017). This example has clear overlap with nuptial gifts that constitute paternal effort.

7. CONCLUSIONS AND FUTURE DIRECTIONS

7.1 Summary.—Here we reviewed evidence that male silk use during courtship and mating is taxonomically widespread, diverse in possible function and mechanism (Fig. 1; Table 1), and may play an important part in the mating dynamics in many spider species (Tables 2–7). The widespread occurrence of silk deposition by male spiders during courtship and mating (Fig. 1) suggests an important, but often neglected, function of male silk in behavioral interactions between males and females, and among competing males. Moreover, the evidence for ritualized silk use in both the Mygalomorphae and Araneomorphae and its prevalence across the phylogeny (Fig. 1) presents the intriguing possibility that functional roles for male silk use are plesiomorphic among spiders. Systematic use of silk in mating by males includes the addition of silk to females' webs or other silk structures, silk deposition on females' bodies, and the use of silk associated with nuptial gifts. In the former two types of silk use, the silk is invariably deposited in close proximity to the female, often in direct contact with her chemoreceptors or proprioreceptors, and in the latter case, female manipulation and/or consumption of gifts places male silk against the sensory receptors on her palps. Thus, simply considering these patterns of silk use suggests hypotheses regarding the role of silk in intersexual communication during mating. Perhaps not surprisingly, thus far, the bulk of experimental studies have focused on the potential importance of male-produced sex pheromones in such communication (Table 1). These studies suggest that silk produced by males can play an important role in inter-sexual communication (see Gaskett 2007). However, chemical communication is just one possible mechanism by which silk use can affect the fitness of mating males (Table 1). Unfortunately, as is common in reviews of spider biology and behavior, our ability to make general inferences is limited because of the relatively narrow taxonomic range of the species that have been well-studied (Huber 2005; Schneider & Andrade 2011). Moreover, while in many spiders the role of the female's silk is clear and relatively easy to measure, the role of male silk may be more challenging to untangle from correlated activities, even in those species that are relatively well-studied. For example, since silk deposition co-occurs with courtship or nuptial gift presentation, elegant experimentation is required to make clear inferences about the independent effects of the silk itself. Nonetheless, based on the available evidence, we conclude that male silk serves a number of important functions during courtship and mating, and these may be mediated through direct or indirect mechanisms (Table 1).

7.2 Functions and mechanisms of effect.—Male silk use during mating may evolve or be maintained because it increases male success in the current mating or reduces the

risk of losing paternity through polyandry (Table 1). The (scant) current evidence suggests an interesting pattern of segregation of benefits from different types of silk use. The data show that silk addition to the female's web affects the likelihood of polyandry (and risk of paternity losses to sperm competition) but not the outcome of the mating attempt of the silk-laying male. In contrast, the data suggest that silk addition to the female's body (bridal veils) and silk associated with nuptial gifts function exclusively to increase the likelihood of favorable outcomes in the current mating, but do not affect polyandry. It seems unlikely that this is a real division, however, given the small number of experimental studies. We consider two examples in which additional work might quickly remove this pattern. First, one of the two mechanisms for which there is currently no experimental support is the hypothesis that silk use could affect female mobility. However, the creation of mating threads in orb-weaving spiders has often been described anecdotally in terms of constraints on the movement of potentially cannibalistic mates, and this makes intuitive sense. Nevertheless, this does not appear in Table 1 because, to our knowledge, there are no experimental tests of this hypothesis, nor of any other way in which male silk use might reduce female mobility (e.g., web modifications that reduce the area of the web). Second, very few studies have examined long-term effects of exposure to male silk on females. So, although in the short term, mate attraction or female receptivity to polyandry may not change, there could be longer-term effects that do confer benefits on silk-spinning males through decreased polyandry. This may be particularly likely if tactile or chemical cues trigger physiological (e.g., hormonal) changes in females that, over time, lead to changes in receptivity (e.g., in *Drosophila*; Wolfner 2002).

While it is possible that functional effects may arise through indirect effects (communication) or direct effects (physical or structural), the majority of studies to date have focused on indirect effects mediated by chemical communication (Tables 1, 5). There is experimental evidence that chemical communication is involved in all three types of silk use (web modification, veils, gifts). However, in most cases, these studies showed that chemicals are sufficient to elicit an effect but did not exclude other possible mechanisms that might also be operating simultaneously in nature. This is problematic since the hypotheses and mechanisms we suggest for male silk use may overlap, as males may acquire benefits in more than one way, context may determine which function has the strongest effect on male fitness, and more than one mechanism may operate simultaneously. Thus, it is unclear whether these results suggest the critical importance of indirect chemical information relative to other possible mechanisms of effect. Another possibility is that, since male silk is apparently pheromone-laden (Table 6), chemical communication effects may overlay other effects that also affect male fitness.

7.3 Improving our understanding of male silk use.—To better understand male silk use in courtship and communication, the functional roles of both the silk itself and the behaviors associated with its deposition must be investigated. Preventing males from depositing silk during courtship by occluding their spinnerets with wax or glue is a good technique for investigating the function of male silk (e.g., Anderson & Hebets, 2016). Ablating female chemoreceptors may also be useful in determining the function and importance of chemical signals (e.g., Zhang et al. 2011; Aisenberg et al 2015). Testing the responses of males to the silk of rival males in the context of mate-searching and mate choice (e.g., Schneider et al. 2011) will allow us to determine the function of silk in intra-sexual communication. In species where behavioral evidence indicates the presence of a male silk-borne pheromone, pheromone identification should be pursued. Comparative pheromone analyses of male and female silk may be especially fruitful in those species in which the female pheromone is already known. Recent evidence that silk gene expression and morphology of the spinning apparatus differ between males and females in *Steatoda* and *Latrodectus* (Correa-Garwhal et al. 2017) provide the opportunity to link silk structure with function in taxa for which sexual behavior and chemical communication is already well studied. Tichy et al. (2001) have obtained electrophysiological responses to volatile components from tarsal chemoreceptors in *Cupiennius salei*, and 'electrolegograms' have already been developed for whip spiders (Amblypygi; Hebets & Chapman 2000). As our knowledge of spider chemoreception improves, we should strive to develop an analog of the gas chromatographic-electroantennographic detection (GC-EAD) system previously invented for analyses of insect pheromone (Struble & Arn 1984; see Hebets & Chapman 2000). This technique would entail using a spider's chemoreceptive appendage in place of an insect antenna as a sensor to determine the volatiles that elicit sensory responses. Such a technique would allow rapid screening for potential pheromones in extracts from spider silk or cuticle. Future studies should also attempt to determine the glandular origins of silks and associated pheromones that males produce during courtship and mating behavior. We still do not know where and how spiders synthesize pheromones, but comparative morphology and careful experimentation (e.g., assaying extracts of individual silk glands or body parts) should help us begin to address this major gap in our knowledge.

An intriguing suggestion that appears frequently in the literature is that males may use silk to manipulate females; that is, to partially or completely control female behavior (*sensu* Dawkins 1978) and thus mating outcomes. Here, 'manipulation' is a useful functional concept if the induced female behaviors are beneficial to males but decrease female fitness. In the context of mating, such an outcome may arise through an evolutionary history of sexual conflict (Arnqvist & Rowe 2005). This may be contrasted with communication, which increases the likelihood of a particular female behavior because the behavior is, on average, beneficial for the female as well as the male (Bradbury & Vehrencamp 2011). Manipulation is discussed frequently for the silk-wrapping around nuptial gifts, which can, and often does, conceal 'worthless' (nutritionless) items (Ghislandi et al 2017; Pandulli-Alonso et al. 2017). In some species such 'worthless' gifts are common and they may nonetheless increase mating success (Albo et al 2017; Pandulli-Alonso et al 2017). However, these deceptive gifts should be considered manipulative only if females mating with males carrying 'worthless' gifts have reduced reproductive fitness, and this has not been examined experimentally. Particularly if 'worthless' gifts are common, it

may be that the gift itself is a ritualized representation of male quality (e.g., Albo et al. 2011a; Pandulli-Alonso et al. 2017). Studies of this aspect of male silk use may be particularly valuable, given that ritualization is thought to be the widespread basis of a wide range of signals (Bradbury & Vehrenkamp 2011), but there is very little empirical evidence for this phenomenon (e.g., Scott et al. 2010).

Another common discussion of manipulation arises in the context of silk-borne pheromones that may 'induce receptivity' in females, or otherwise change the outcome of the current mating (e.g., Becker et al. 2005). However, when chemical cues induce a behavioral change in females that increases mating success of the silk-laying male, this may also represent a normal, or necessary coordination of male and female behavior that is not maladaptive for females (e.g., Bradbury & Vehrencamp 2011). For example, a small proportion of female agelenids fail to recover from the state of catalepsis following mating (S. Riechert pers. comm.), an observation consistent with manipulation. However, Gehring (1953) suggests the complexity of the agelenid genitalia makes female immobility a necessity for copulation success. Showing a mechanism by which silk leads to negative effects on females does not necessarily demonstrate manipulation. Nevertheless, in general, the phenomena associated with male silk use during mating suggests intriguing questions regarding the role that sexual conflict plays in the evolution of male silk use during mating. Studies of fitness effects on males and females may advance our understanding of this interplay.

Unfortunately, we have insufficient data to analyze comparative patterns regarding male silk use, nor to test hypotheses about evolutionary sequences for current modes of silk use (e.g., nuptial gifts; Albo et al. 2017). We are limited because the bulk of our knowledge of spider mating behavior comes from extensive study of a small number of families including the Araneidae, Ctenidae, Linyphiidae, Lycosidae, Pholcidae, Pisauridae, Salticidae, and Theridiidae (Schneider & Andrade 2011; and see references in this review). Taxa for which we do not report male silk use are as likely to represent the absence of study as the absence of male silk use. Arguably, since males leave behind draglines when they move, and courtship and mate searching often involves extensive movement (Foelix 2011), male silk use during mating may be the rule rather than the exception, despite the limited literature now available. The more ritualized forms of silk use described here (silk deposition, bridal veils, nuptial gifts) may have arisen when more common uses that are found across spiders were coopted for mating. What is clear is that we critically need more phylogenetic coverage in studies of mating, to test these and other hypotheses (Huber 2005; Schneider & Andrade 2011).

Although there are challenges with initiating studies with new species, there may be ways to offset the risk, while maximizing the likely payoff in terms of comparative analyses that increase our understanding. Studies of new species that document the prevalence of male silk use and conduct at least preliminary examinations of the functional importance would be valuable (e.g., by comparing behaviors and mating outcomes for males with and without occluded spinnerets; Zhang et al. 2011; or females with or without ablated sensory structures; Aisenberg et al. 2015). One approach that may be particularly useful would be to focus new efforts on representative species in little-known families within taxa that already have relatively extensive records of a variety of types of male silk use. Two examples are the superfamily Araneoidea, and the Oval Calamistrum clade (Fig. 1), each of which includes records of all three categories of male silk use. Choosing new species to study within these groups would benefit from strategic thinking. Among the web-building Araneoidea, it may be more feasible to stage laboratory matings of spiders that weave irregular webs rather than orb webs since the structural requirements for appropriate web frames may be less stringent (e.g., Nesticidae: scaffold-web weavers; Cyatholipilidae: sheet-web weavers), or, among the less well-known orb-weavers, those that build small webs may be more tractable for laboratory study (e.g., Mysmenidae and Anapidae). Another approach would be to focus on studying multiple species within families in which there are already records of all categories of male silk use (e.g., Theridiidae and Tetragnathidae). Either of these approaches would move us closer to valid comparative tests for understanding the evolution of silk use.

7.4 Concluding remarks.—Overall, this review provides a functional and mechanistic framework for understanding the diversity of male silk use behaviors, and suggests fruitful approaches and taxa for study. Spiders are models for studies of sexual selection, and how choice, competition, and communication are affected by ecology, cannibalism, and sexual conflict more broadly (Herberstein et al. 2002; Schneider & Andrade 2011; Uhl & Elias, 2011; Kralj-Fiser et al. 2016). As in other fields, insight is limited by what we choose to study (Huber 2005). While technological limitations created challenges in the past, particularly to the study of silk, vibrations, or pheromones, a number of novel approaches now make these studies more feasible (e.g., Hebets & Chapman 2000; Menda et al. 2014; Mortimer et al. 2015). Harnessing these techniques and expanding the range of taxa studied may lead to big advances in understanding. The strong evidence presented here for various effects of male silk in mating suggests that we currently have only part of the picture with respect to spider mating behavior in most taxa. Understanding how male-produced silk may influence, constrain, or manipulate interactions with females and with rival males could provide significant new insights into mating behavior, the evolution of traits related to mating, and fuel new tests of a wide range of theory in sexual selection and sexual conflict.

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