2015. Journal of Arachnology 43:168–173

Female *Pardosa milvina* wolf spiders increase silk advertisements when in the presence of silk from courting males

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Abstract. Female wolf spider silk is known to elicit searching and courtship behavior among adult males, however variation in the types of silk females deposit, the context in which it occurs, and the role of male silk in courtship displays and female responses has rarely been examined. We measured male *Pardosa milvina* (Hentz 1844) silk deposition while performing courtship displays. We then examined whether female silk deposition changes when encountering silk produced from a courting rather than a non-courting male and compared these conditions to female silk deposition in the absence of male silk. We measured the quantity of three different types of silk (draglines, cord silk, and attachment disks) deposited by females across substrates previously occupied by a courting male, a non-courting male, or no male. Females significantly increased attachment disk deposition in the presence of silk from a courting rather than a non-courting male. Females also showed elevated dragline deposition in the presence of male silk but whether or not the male was courting had no effect on dragline deposition. Female cord silk deposition did not vary across treatments. Courting males produced significantly fewer attachment disks than non-courting males while dragline and cord silk deposition did not vary. We conclude that females can discriminate between silk from courting and non-courting males and increase attachment disk deposition in the presence of courting males. The number of male attachment disks deposited may be one mechanism by which females can discriminate between silk produced by courting rather than non-courting males.

Keywords: Courtship, dragline silk, cord silk, attachment disks, Lycosidae, pheromone

Silk is an important medium for chemical communication among spiders. Females of many species use silk either as a direct sexual advertisement toward males or as a medium to convey sex pheromones (reviewed in Schulz 2004; Gaskett 2007; Uhl & Elias 2011). Although the function of female silk in eliciting male courtship has been established for over one hundred years (reviewed in Montgomery 1903; Kaston 1936), the role of male silk or pheromones in sexual communication has received comparatively little attention (Ross & Smith 1979; Roland 1984; Becker et al. 2004; Aisenberg et al. 2010; Plunkett 2010). Further, despite the fact that female silk is used to convey information about mating status and receptivity to males, it is often assumed to be a passively deposited material detected by males rather than an active and context-specific component of a female chemical courtship display (Roland 1984; Havrilak et al. 2015).

Conspicuous courtship displays and secondary sexual ornaments of male wolf spiders have been well studied in the context of female mate choice (Stratton & Uetz 1986; McClintock & Uetz 1996; Scheffer et al. 1996; Parri et al. 1997; Hebets & Uetz 1999, 2000; Deng et al. 2014), while the possible presence or function of concurrent male silk deposition during these displays remains relatively understudied (Richter & Van der Kraan 1970; Aisenberg et al. 2010; Plunkett 2010). Male silk deposition may well be an integral part of multi-modal courtship displays and convey important information to females about body condition, genetic quality, or the motivation to mate. Given that females of the wolf spider, *Pardosa milvina* (Hentz 1844) are capable of evaluating predation risk using information in heterospecific lycosid silk (Persons & Rypstra 2001; Persons et al. 2001, 2002; Barnes et al. 2002; Lehmann et al. 2004), it seems likely that females may be equally adept at evaluating male conspecifics using silk information as well.

Female wolf spider silk, like that in many spiders, is an important component of sexual communication and frequently serves as an advertisement to males (Kaston 1936; Hegdekar & Dondale 1969; Richter et al. 1971; Hebets & Uetz 1999; Rypstra et al. 2003; Schultz 2004; Gaskett 2007; Havrilak et al. 2015). Males can determine female location, body condition, species identity, and mating status through information in silk alone (Rypstra et al. 2003; Roberts & Uetz 2004a, 2004b, 2005; Hoefler et al. 2009). The information that females glean from male silk remains unknown, but such information could potentially change the type or quantity of silk advertisements produced by the female. Females could indirectly assess males using cues in male silk and modify the investments in their own silk advertisements based on this information. Female behavior, in turn, may then influence the prevalence or intensity of male displays.

Silk is not a homogeneous material but rather varies in its chemical and tactile properties depending on the gland that produced it as well as the method of extrusion (Foelix 1996; Vollrath 1999). It also varies intra-specifically and intra-individually (Madsen et al. 1999). *Pardosa milvina* produces at least three types of silk while moving through the environment: dragline silk, attachment disks, and cord silk. The most widely studied, dragline silk, is produced from the major ampullate glands and is likely the most important for eliciting male attention (Bristowe & Locket 1926; Richter 1970; Tietjen 1977). These strands are typically very thin, as little as 0.25 µm in diameter in *P. milvina* (Havrilak et al. 2015). Draglines appear white or translucent under light magnification and are deposited in straight lines on the substrate. Attachment disks are another silk type deposited by female and male wolf spiders. These are produced from the piriform silk glands and are often used to anchor dragline silk to the substrate but they can be deposited independently of other silk types as well (Richter 1970; Havrilak et al. 2015). Dijkstra (1976) showed

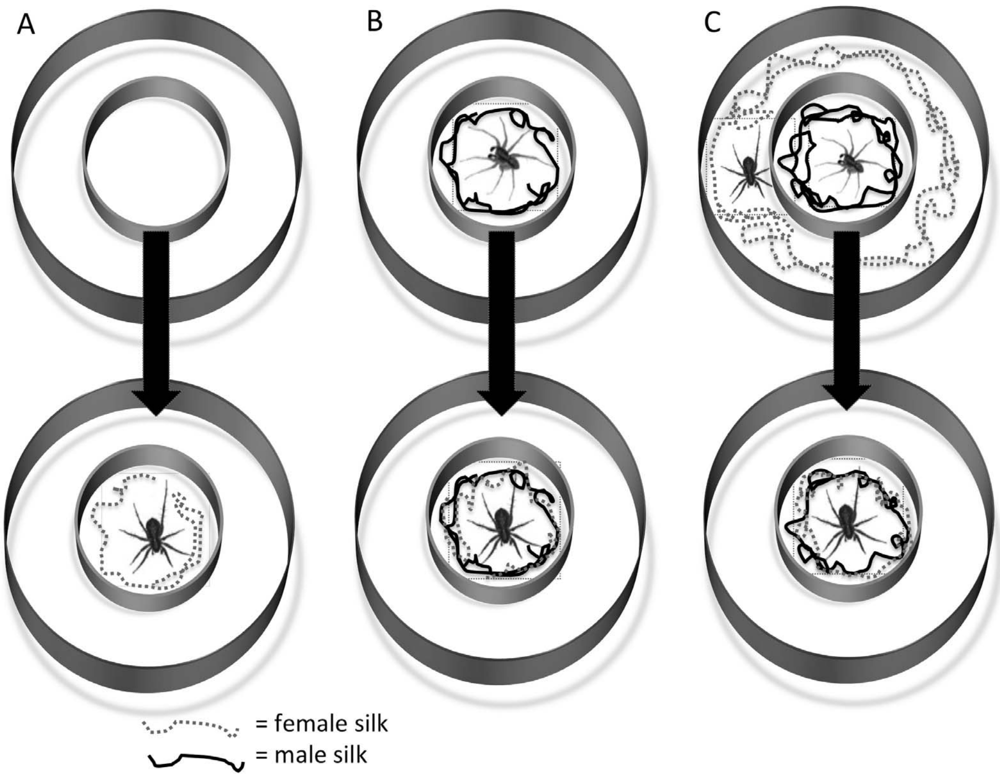

Figure 1.—Female *Pardosa milvina* silk deposition behavior was measured across three different stimulus treatments. The stimuli were produced as shown in the top row and females' responses, as measured by silk deposition, are shown in the bottom row. The three treatments were: (A) female silk deposition in the absence of male silk (control); (B) female silk deposition on silk cues from a male without access to a female (non-courting male); and (C) female silk deposition on silk cues from a courting male that viewed a female at the time of his silk deposition (courting male). Dotted gray lines represent female silk. Black lines represent male silk.

that males of *Pardosa amentata*, use attachment disks to identify the appropriate direction to follow females. Thus both of these silk types may provide important information to males and may be used differently by females to attract males. Cord silk is a third structurally distinct silk often found in association with draglines and attachment disks in *P. milvina*. It is thick, approximately 20 µm or more in diameter and may be amber or tan in color (Havrilak et al. 2015). Cord silk is also generally short and appears sinuous when deposited on the substrate. The glandular source of this silk type as well as its function are currently unknown but Richter & Van der Kraan (1970) mention "broad trails" produced by males of *Pardosa* species that are produced by the piriform glands. Qualitative or quantitative differences in the deposition of these silk types may be important in the context of sexual communication.

We tested whether courting males produce significantly different quantities and types of silk than non-courting males, which would suggest a sexual communication function for male silk deposition. We also used females' own silk deposition behavior to determine whether female *P. milvina* could discriminate between silk from a courting versus non-courting male. If female silk is part of an active chemical courtship display, we expect females to significantly vary the type and amount of silk deposited when encountering silk from courting vs. non-courting males. A sexually receptive female may benefit by discriminating between silk from a courting or non-courting male since this may serve as a signal that the male has received a previously deposited silk advertisement from the female. If silk deposition is energetically expensive, females may conserve energy by modifying investment in silk advertisements when signaling is redundant.

METHODS

Spider collection.—One hundred twenty subadult female and 80 subadult male *P. milvina* were collected in agricultural fields near and on the campus of Susquehanna University in Selinsgrove, Snyder County, Pennsylvania, USA. All spiders were allowed to mature in the laboratory to ensure the virginity of test spiders. Spiders were maintained in 74 ml translucent containers (8 cm diameter 5 cm high) with a 2-cm substrate of moistened peat moss. Each spider was given water *ad libitum* and fed a diet of 2–3 early instar domestic house cricket nymphs (*Acheta domesticus* Linnaeus) every four days and then fed to satiety 1–2 hours before testing to minimize the effects of body condition and hunger level on silk production and male courtship. Only spiders that had finished feeding at the time of testing were used.

Experimental protocols.—We exposed females to one of three substrate treatments ($n = 40$ for each group for a total of 120 trials) (Fig. 1). In one treatment, females were exposed to a blank paper substrate (control). In a second treatment, females were exposed to paper previously occupied by an unmated adult conspecific male for 30 minutes (non-courting male). In a third treatment, females were also exposed to paper previously occupied by a male, but in this case, the male had the opportunity to observe an adult unmated female behind a transparent barrier during the entire 30 minutes (courting male). All 120 female subjects were randomized with respect to treatment designation and each female was tested only once. All trial data were alternately collected across treatments to minimize possible sequence effects. For each experimental trial, individual females were placed on the designated experimental treatment for a 30-minute period and their silk deposition behavior was recorded. The test female had no access to a live spider during trials.

All substrate treatments were prepared by placing an 8 cm diam, gridded black disk of copy paper within a 9 cm diam, 19 mm high transparent plastic petri dish. This small petri dish was then concentrically arranged within a larger 14.5 cm diam transparent plastic petri dish (Fig. 1). For the non-courting male treatment, the male was placed in the center of the smaller inside petri dish. For the courting male treatment, the male was also placed inside the smaller petri dish and allowed to deposit silk but a virgin female was placed in the outer petri dish. A 30-minute trial for each of the male stimulus treatments was conducted to measure male courtship intensity and silk deposition. Each of the 80 males used as stimuli were tested only once and randomly assigned to either the courting or non-courting treatments ($n = 40$ for courting and non-courting treatments). Prior to testing, all petri dishes used for this study were rinsed with 95% ethyl alcohol and left to dry to remove any extraneous chemical residues.

Quantifying silk deposition.—To measure silk deposition, each testing arena contained the gridded black sheet of paper. Each gridded sheet contained 840 squares with each square containing an area of 6.25 mm^2. Spiders were placed on each of these gridded substrates for a 30-minute period. We then removed the spider and three different types of silk were counted: dragline silk, cord silk, and attachment disks (see Havrilak et al. (2015) for a detailed description of similar methods and photos of silk types). The total number of cord silk segments and attachment disks on the gridded paper were counted. For dragline silk, we counted the number of times a dragline thread completely crossed each of the 840 squares.

After quantifying the silk produced by a stimulus male for 30 minutes, a subject female was released onto the same gridded sheet inside the petri dish. For 30 minutes the female was left to deposit her own silk. At the end of 30 minutes, the total silk produced by both spiders was scored again. Male silk was subtracted from that deposited by both spiders to determine the quantity of female silk present. For the control treatment, a subject female deposited her silk on a clean gridded sheet of paper for 30 minutes ($n = 40$).

Quantifying male courtship behavior.—We quantified male courtship to insure that the courting and non-courting treatments were significantly different. Courtship in *P. milvina* was operationally defined as a combination of two separate and distinct behaviors, leg raises and body shakes. A leg raise is lifting of the first pair of legs in unison above the cephalothorax and bringing them down abruptly. A body shake is rapid oscillations of the abdomen and cephalothorax, often in conjunction with a leg raise. These behaviors have been described elsewhere and are known to influence female mate choice (Montgomery 1903; Kaston 1936; Brautigam & Persons 2003; Rypstra et al. 2003). To confirm that the non-courting and courting males were indeed different in their courtship displays, we quantified differences in courtship elements between the courting male and non-courting male treatments (mean ± S.E.). Total courtship (number of body shakes and leg raises within 10 minutes) was significantly different between treatments (unpaired $t = -5.860$, $P = <$ 0.0001). In a 10-minute period, non-courting males on average displayed 1.70 ± 0.67 leg raises and 0.53 ± 0.13 body shakes. In contrast, males in the courting male treatment displayed on average 19.48 ± 3.04 leg raises and 8.78 ± 1.44 body shakes over ten minutes.

We analyzed silk deposition behavior using one-way ANOVAs with total silk as the dependent variable and non-courting male, courting male, and control as independent categorical variables. An additional three ANOVAs were conducted separately on the three measured silk types: dragline silk, attachment disks, and cord silk respectively to determine how or whether these different silks differed across treatments.

RESULTS

Female silk deposition.—We found a significant difference in total female silk deposition across treatments (one-way ANOVA $F_{2,117} = 3.332$; $P = 0.0392$; Fig. 2A). Based on a Fisher's PLSD post-hoc comparison of means test, females deposited more total silk when exposed to courting male silk compared to a blank control, while deposition on non-courting males was intermediate between courting males and the control substrate. We also found a significant difference in female dragline deposition across treatments (one-way ANOVA $F_{2,117} = 3.392$; $P = 0.037$; Fig. 2B), and it followed the same pattern as total dragline silk (Fig. 2A). Female attachment disk deposition varied across treatments (one-way ANOVA $F_{2,117} = 5.451$; $P = 0.0055$) , with significantly more attachment disks being deposited when exposed to courting male silk compared to the control or non-courting male silk (Fig. 2C); however, female cord silk deposition did not vary across treatments (One-way ANOVA $\mathrm{F}_{2,117} = 0.476$; $P =$ 0.6226; Fig. 2D).

Male silk deposition.—There was no significant difference in dragline silk deposition or cord silk deposition between non-courting males and courting males; however, courting males did deposit significantly fewer attachment disks compared to non-courting males (Table 1).

DISCUSSION

Female *P. milvina* distinguish between the silk of courting and non-courting males. Females deposited significantly more attachment disks when encountering silk from a courting rather than a non-courting male and deposited significantly more dragline silk in the presence of silk from a courting male compared to the control. Females did not differ in their cord silk deposition based on the type of male silk however. Given that male *Pardosa* species can extract directional information from attachment disks (Dijkstra 1976), our data suggest that females may be enhancing directional signals for a male motivated to mate. The fact that female silk deposition may be modulated in part by male silk as well as silk from courting and non-courting males suggests that male silk may be used for sexual communication.

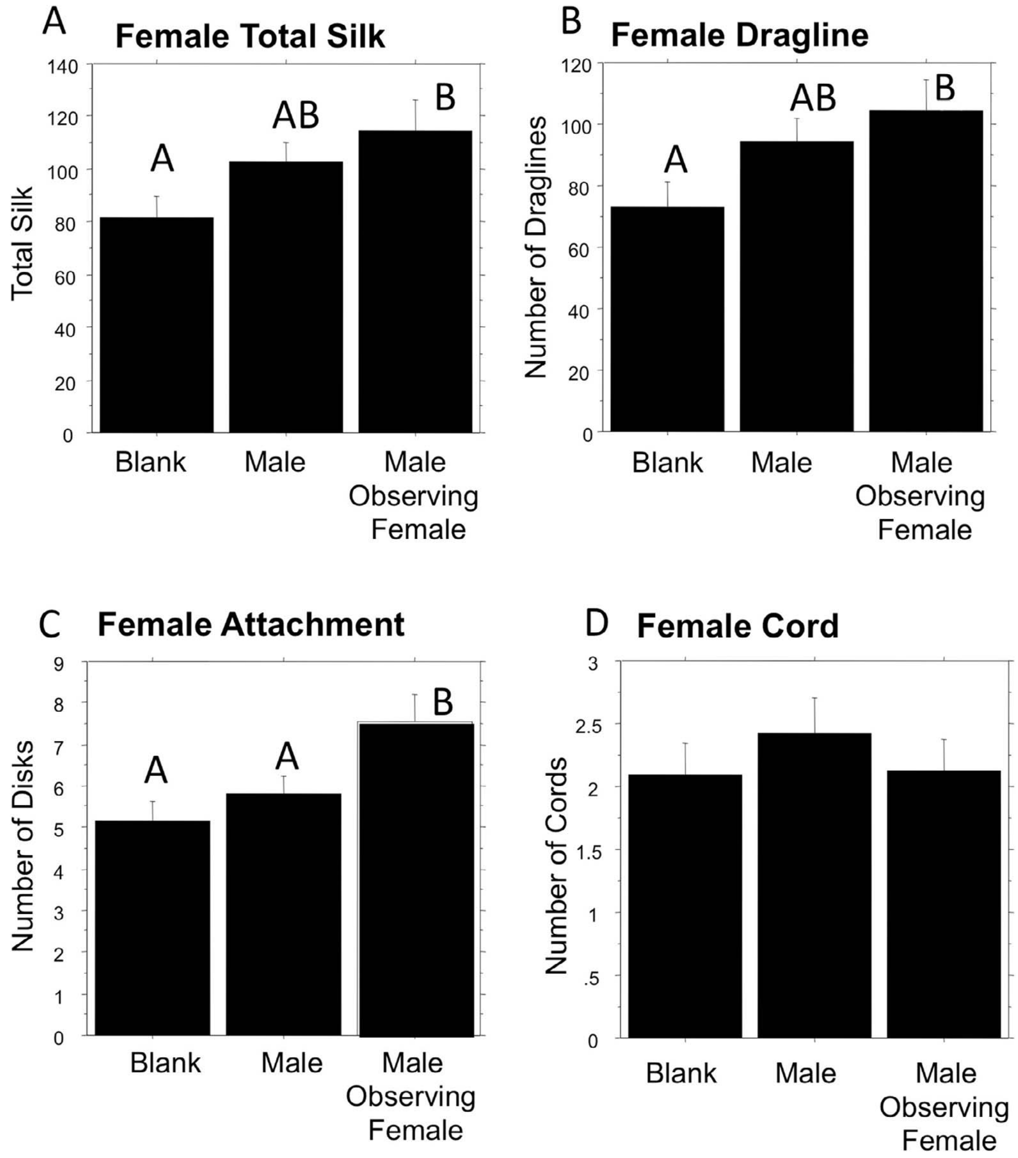

Figure 2.—Female silk deposition behavior on a blank sheet of paper (Blank), paper previously occupied by a male for 30 minutes (Male), or paper previously occupied by a male that had been observing a female for 30 minutes. Silk types measured include (A) female total silk deposition, (B) female dragline silk deposition, (C) female attachment disk silk deposition, and (D) female cord silk deposition Different letters indicate significant differences between treatments based on a Fisher's PLSD post-hoc comparison of means test ($n = 40$ for all treatments, $N = 120$).

The mechanism by which females discriminate between courting and non-courting males via silk remains unknown. Courting males did deposit significantly fewer attachment disks compared to non-courting males. This quantitative difference may provide one means of assessment by females either through different encounter rates with attachment disks or possibly through detection of a ratio of attachment disks to dragline silk. Given that males were in visual range of females at the time of deposition, directional cues provided by attachment disks may not have been necessary. It remains

Table 1.—Total silk deposition, and dragline, attachment disk, and cord silk deposition among courting and non-courting males of *Pardosa milvina*. Deposition measures are expressed as Mean + S.E.

Silk type	Courting male (n = 40)	Non-courting male (n = 40)	t	P
Total	167.95 ± 14.05	183.66 ± 17.73	0.692	0.4907
Attachment	5.28 ± 0.39	7.78 ± 0.91	2.517	0.0139
Cord	2.18 ± 0.27	2.15 ± 0.32	0.060	0.9527
Dragline	160.50 ± 13.91	178.33 ± 17.09	0.809	0.4210

possible that males produce a substratum-borne pheromone attached to silk and it may also be possible that the quantity of this cue could be produced independently of the amount of silk, allowing discrimination by females. Different silk types may also show considerable variation in thickness and texture which could conceivably be a source of discrimination beyond simply the quantity of different silk types (Havrilak et al. 2015). Female wolf spiders are known to produce substratum-borne pheromones along with silk (Tietjen & Rovner 1982; Schulz 2004; Gaskett 2007) as well as volatiles that may be associated with silk or independently produced (Searcy et al. 1999). Pheromones among male wolf spiders are largely unknown (but see Ayygari & Tietjen 1986) and no male sex pheromones have been characterized among lycosids to date. Male activity level generally increased during courtship while silk deposition remained the same or dropped among courting males. This suggests that male silk deposition doesn't increase with activity. The fact that attachment disks, but not other silk types changed among courting and non-courting males suggests different functions for these silk types. Fixing attachment disks to the substrates involves periodic dropping of the opisthosoma. It is possible that this behavior interferes with the seismic and visual components of the male display, resulting in fewer attachment disks.

Our study shows that female *P. milvina* deposit greater quantities of dragline silk and attachment disks when detecting silk from a courting rather than a non-courting male. Cord silk did not differ across treatments for either males or females, which suggests that cord silk may have a different function than other types of depositional silk. Collectively, these results indicate that both sexes can exchange considerable chemical information regarding the willingness to mate even when not directly interacting, but this must be confirmed by chemical analyses of the silk that is deposited. It also remains unknown whether information is transmitted primarily through physical variation in the silk itself or is mediated primarily through pheromones that may be added to it. Our results support other studies showing that female *P. milvina* silk deposition is not passive (Havrilak et al. 2015) but rather contingent on the presence and quality of male silk in the area. These chemical courtship signals among males and females likely are mediated in a complex way during searching and pre-mating interactions in *P. milvina* and should be investigated more widely in other spider species as well.

ACKNOWLEDGMENTS

We would like to thank Michael Platt, Megan Marchetti and Michael O'Donovan for their help collecting and maintaining spiders used for this study. Additional thanks go to two anonymous reviewers for their insightful comments that helped improve this manuscript.

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Manuscript received 17 December 2014, revised 25 March 2015.