Courtship and mating behavior of the wolf spider *Schizocosa bilineata* (Araneae: Lycosidae)

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Abstract.   Of all the wolf spiders (Araneae: Lycosidae), the genus *Schizocosa* Chamberlin 1904 is probably the most widely studied, and has become an established model in studies of behavior, sexual selection, and speciation. Much of the work to date involves the complex, often multimodal courtship behaviors and secondary sexual traits used by males to elicit receptivity from potential mates. *Schizocosa bilineata* (Emerton 1885) is one of those species where males possess decorative tufts of bristles on the forelegs that likely play a role in sexual selection, but little is known of male courtship behavior or its role in mate choice. In the present study, we provide the first description of visual and seismic behaviors performed by males in response to female silk and chemical cues, and examine male-female behavioral interactions in live mating trials. Males clearly recognized and responded to female chemical cues by displaying several species-specific visual signaling behaviors accompanied by seismic signals from stridulation. As these behaviors rarely occurred in the absence of female cues, we suggest they function primarily in a courtship context. In live mating trials, females typically responded to male courtship with visual receptivity behaviors, which were seen prior to mounting and copulation. While both visual and seismic signals of males are clearly implicated in courtship and mate choice, future work will be necessary to fully understand the interaction between modalities in this species. The description of behavior provided here should help resolve the relationship between male ornamentation and courtship behavior in the genus *Schizocosa*.

Keywords: Chemical signaling, multimodal communication, sexual selection

Probably the most widely studied of all the wolf spiders (Lycosidae), are members of the genus *Schizocosa* Chamberlin 1904. The genus has become an established model for exploring many aspects of evolution and speciation, multimodal communication, and sexual selection (reviewed in Uetz 2000; Uetz & Roberts 2002; Hebets & Papaj 2005; Framenau & Hebets 2007), for which studies of members of the *S. ocreata* clade (Stratton 2005) have been especially informative. The importance and utility of this genus for scientific study is due not only to the fact that most *Schizocosa* species are relatively easy to collect and maintain in the laboratory, but more importantly because males of many species possess complex, sexually selected courtship elements and secondary sexual characteristics (decorative tufts and/or pigmentation) that can be manipulated in a number of ways for study (reviews in Uetz & Roberts 2002; Hebets & Papaj 2005; Stratton 2005; Framenau & Hebets 2007). In the most recent comprehensive morphological phylogeny of the North American *Schizocosa*, Stratton (2005) divided the genus into three major clades: Clade A, containing most of the species from eastern North America as well as the well-studied *S. ocreata* clade, and the much smaller Clades B and C, containing many western and southern species. Despite extensive work on several members of this genus, there remain a number of described species for which little or no behavioral data have been collected (Stratton 2005). This is unfortunate as it prevents definitive conclusions about any correlation between male ornamentation and courtship behavior in *Schizocosa* (Stratton 2005).

Currently, courtship and mating behavior has been described for all but three of the 17 species contained within Clade A [*S. bilineata* (Emerton 1885), *S. humilis* (Banks 1892),

and *S. segregata* Gertsch & Wallace 1937]. *Schizocosa bilineata* is the focus of the present study. Stratton (2005) placed *S. bilineata* as a sister taxon to *S. crassipalpata* Roewer 1951 within Clade A, but outside the *S. ocreata* clade. This placement is consistent with the more recent molecular phylogeny by Hebets and Vink (2007). While specimens of *S. bilineata* have turned up periodically in collections, species descriptions, and taxonomic studies (Montgomery 1902, 1904; Chamberlin 1908; Comstock 1912, 1940; Kaston 1948; Dondale & Redner 1978, 1990; Sierwald et al. 2005; Stratton 2005; Finkes et al. 2006; Framenau & Hebets 2007; Hebets & Vink 2007), they have otherwise received little attention. A unique opportunity to address this lack of information arose when we discovered a sizable population of *S. bilineata* on and around the campus of The Ohio State University at Newark in Newark, Ohio, USA in May 2006.

Schizocosa bilineata is a Nearctic species, thought to be widely distributed throughout the eastern part of North America, from Canada south to Georgia and Texas, and from the East coast to as far west as Kansas and Nebraska (Comstock 1940; Kaston 1948; Dondale & Redner 1990; Sierwald et al. 2005; Stratton 2005). Females of this species are light brown to yellow and cryptically colored. Males are also light brown to pale yellow (often lighter than females) but, as in several other *Schizocosa* species, have dark tufts of bristles on the tibia of their forelegs at maturity which may play a role in courtship and mate attraction. Montgomery (1903) provided the only known description of courtship and mating behavior for this species based on direct observation, in which he specified that he could find no evidence of visual courtship from males prior to mounting and copulation. Based on this finding, Kaston (1936) included *S. bilineata* in his comparative analysis of courtship behavior as an example of a species possessing secondary sexual traits but lacking visual displays (without confirming by direct observation), and this has likely

hindered further work on the species. In the present study, we first describe visual display behaviors performed by the males during mate searching and courtship, challenging the original assessment of male courtship by Montgomery (1903). We then provide evidence of seismic communication by males, confirm several male visual behaviors that occur primarily in a courtship context in response to female chemical and multimodal cues, and describe visual receptivity behaviors shown by females in live mating trials.

METHODS

Animal collection and maintenance.—*Schizocosa bilineata* were collected in open grassy habitats along riparian zones on the campus of The Ohio State University at Newark (OSUN) (40°04.155′N, 82°26.743′W). Spiders were returned to the laboratory and housed individually in opaque, square plastic containers (150 mm × 150 mm × 50 mm, 740 ml), each with a clear lid and containing a short piece of garden hose (250 mm) for shelter. Individuals were fed two or three 10-day old crickets (*Acheta domesticus*) twice a week, and provided ad libitum access to 10 ml of fully hydrated, high molecular weight polyacrylamide gel (Watersorb®, medium crystal polymer) for water and humidity. Spiders were maintained at 24 ± 1° C with a 13:11 h light: dark photoperiod. At the conclusion of each set of experiments, spiders were euthanized by freezing and preserved in 70% ethanol. Voucher specimens are available in the collections of the corresponding author (JAR) and the Denver Museum of Nature and Science.

Male *Schizocosa* are known to respond to silk and chemical cues with courtship behavior (reviewed in Uetz & Roberts 2002; Roberts & Uetz 2004a, b; Roberts & Uetz 2005), and we followed the methods outlined in Roberts & Uetz (2005) to elicit male courtship. Specifically, cues were collected from females by placing the female on a piece of filter paper (Fisherbrand® 90 mm diam) inside a clean, glass Petri dish. Females were allowed to deposit silk, chemical cues, and excreta on the filter paper for a period of 24 h, at which time they were returned to their individual containers. Filter paper disks were then used to elicit male behavioral responses.

Experiment 1: Observation and description of male behaviors.—We collected 38 *S. bilineata* (16 males & 22 females) at OSUN on 25 May–1 June 2006 for use in the description of male behaviors. All individuals were collected as adults, and therefore we had no definitive way to determine mating status or previous experience with conspecifics before starting the experiment. We assumed, therefore, that all individuals had experience with adult conspecifics and that all had likely already mated. Mating status of males was of little concern because male *Schizocosa* are likely to mate multiply (Norton & Uetz 2005), and will display in response to silk of mated females, though at considerably reduced frequency, rate, and total duration (Norton & Uetz 2005; Roberts & Uetz 2005). We therefore felt confident that we could elicit behaviorally appropriate responses from males, even using the silk of mated females. Females were maintained until they produced (and hatched) egg sacs and/or died naturally, at which time they were preserved in 70% ethanol. Spiderlings from each egg sac were counted to obtain an average number of offspring per egg sac.

Females (*n* = 16) were selected randomly (here and throughout using a random digits table: Rohlf & Sokal 1969) from the 19 collected without egg sacs and were used to collect silk and chemical cues to elicit male behavior. Filter paper disks containing female cues were transferred to clear plastic containers (100 × 100 × 250 mm), and males (*n* = 16) were gently deposited on these disks from above. Each male was filmed for 20 min using a digital video camera (Sony, Model # DCR-HC42) for later analysis. Observations of male behavior were used only to describe basic behavioral elements for the construction of an ethogram (Table 1), and we made no attempt to determine frequency, rate, and/or duration of male display elements in this experiment. Plastic containers were cleaned between trials using lens paper and 70% ethanol to remove all chemical and silk cues from previous trials, and then allowed to air dry.

To explore seismic signals of male *S. bilineata*, we followed the recording methods of Gibson & Uetz (2008), using a randomly selected set of five males and five females from the laboratory population. Females were confined to a small area (130 × 70 mm) on a poster board substrate for 24 h to deposit cues, after which they were returned to their containers. In each recording trial, we placed the poster board substrate on a non-conductive block of carpet foam on top of a heavy table within a sound isolation chamber. An acetate ring (100 mm diam) was placed over the area containing female cues, and a male was gently placed into the apparatus from above. We utilized acetate because it is transparent, allowing direct observation of male behavior, and light enough to reduce detrimental surface loading that might interfere with seismic signal transmission. Males that began courting in response to female cues were recorded for 30 s blocks using a laser Doppler vibrometer (Polytech PI, Model # PDV-100) set to a sampling rate of 12.5 kHz, a four-channel analyzer and software set to 48 dB gain (Oros Inc., Dulles, VA, USA, Model # OR24), and a laptop computer (Dell Inspiron 4100).

Experiment 2: Male response to conspecific cues.—*Schizocosa bilineata* were hand collected as juveniles in late March and early April 2007 at OSUN to ensure that all experimental individuals were virgin at the time of the study and to control for any experience with adult conspecifics that might influence behavior (Hebets 2003). Spiders were returned to the laboratory and maintained as in Experiment 1, except that individuals were checked daily for molts to obtain an exact date of maturity. All spiders used in this experiment were between one and three weeks of maturity to maximize courtship response (Roberts & Uetz 2005).

We randomly selected male spiders from the laboratory population and placed them into one of four cue treatments (resulting in slightly unequal sample sizes) as follows: "no-cue control" where males were exposed to blank filter paper (*n* = 10), "male silk-cues" where males were exposed to male silk and chemical cues on filter paper (*n* = 8), "female silk-cues" where males were exposed to female silk and chemical cues (*n* = 10), or "female multi-cues" where males were exposed to female silk and chemical cues as well as any potential visual and/or seismic cues from live females corralled in the same apparatus (*n* = 10). Additional males and females were selected randomly from the laboratory population to serve as stimulus individuals. We collected silk, chemical cues, and excreta from stimulus individuals as in Experiment 1. In each

Table 1.—Ethogram of behaviors performed by *Schizocosa bilineata*.

Behavior	Description
Male behaviors	
Chemoexplore	Active exploratory behavior where anterior, lateral surfaces of pedipalps are brushed on the substrate in rapid succession (adapted from Tietjen 1977; Stratton & Uetz 1986)
Quick Tap	One or (rarely) both extended forelegs, is/are very quickly dropped toward the substrate from an above parallel position (in live observation often perceived as a flicker of motion), often striking the substrate; simultaneous downward motion of the distal abdomen; generally performed while Stationary, but may be produced in combination with Incremental Leg Descend or Slow Jerky Walk
Incremental Leg Descend	One or (rarely) both forelegs is/are partially or fully flexed, extended vertical to the substrate, then slowly lowered (while extended) in a series of slow, short, incremental movements; generally from a stationary position, sometimes interrupted by, or culminating in, one or more Quick Taps
Slow Jerky Walk	Slow forward locomotion characterized by short, jerky, forward leg movements; may be produced independently or in combination with chemoexploratory behavior
Female behaviors	
Settle	Female lowers body to the substrate, often with forelegs extended anteriorly
Slow Turn	Generally from a stationary position, female slowly turns body either clockwise or anticlockwise one-third to almost one full turn (also called Pivot, see Miller et al. 1998)
Shared behaviors	
Approach	Directed locomotion toward the stimulus
Groom	Legs (or pedipalps) are drawn through the chelicerae (both sexes) and/or legs are brushed together rapidly (males)
Leg Raise	One or more legs are raised above parallel with the cephalothorax and then lowered without striking the ground
Locomotion	Walking with no other behaviors expressed
Orient	Turning the body to direct the posterior median eyes toward the stimulus
Retreat	Directed movement away from the stimulus
Stationary	Motionless with no other behaviors expressed
Threat Display	Both forelegs are raised above parallel with the cephalothorax in the direction of a stimulus; often culminates in approach or lunge
Wave	One foreleg (or the first pair of legs), fully extended, raised above the cephalothorax and then lowered back to the substrate; in females this sometimes precedes Settle or Slow Turn

"female multi-cues" trial, the live stimulus female was the same individual from which the silk and chemical cues were collected, and the female was corralled within a transparent acetate ring (25 mm dia.) on the filter paper containing her own silk and chemical cues. This prevented direct contact between the male and female, but specifically allowed transmission of all other multimodal signals/cues that might play a role in courtship.

Using the same clear plastic containers ($10 \times 100 \times 250$ mm) from Experiment 1, we gently deposited males onto filter paper disks from above and filmed for 5 min using a digital video camera (Sony DCR-HC42) for later analysis. Male behavior was scored according to the ethogram developed in Experiment 1 (see Table 1). We determined the frequency (total number of bouts per 300 s trial) and total duration of male behaviors described in Table 1 using JWatcher (Version 1.0), a behavioral analysis software package freely available for download from the University of California, Los Angeles. One behavior (Quick Tap – see Table 1) was scored only for frequency, as it occurs too quickly to establish a precise duration for each bout and often occurs during bouts of other behaviors. Frequency results were square root transformed, and total duration results were log transformed for analysis using the statistical software JMP version 7 (SAS Institute, Cary, North Carolina). We analyzed results by ANOVA using the Bonferroni-adjusted critical value ($\alpha = 0.005$) in all significance tests to account for multiple comparisons (Shaffer 1995). Post hoc comparisons among treatments were conducted using Tukey-Kramer HSD tests (Zar 1999).

Experiment 3: Female receptivity and mating behavior.— Following the completion of Experiment 2, we selected males ($n = 12$) and females ($n = 12$) randomly from the laboratory population and paired them arbitrarily for mating trials. Males all had prior experience with female silk and chemical cues, but not with live females. Females had no previous (adult) experience with conspecifics. Individuals used in this experiment were between 2 and 6 wk of maturity. The translucent plastic arenas ($140 \times 130 \times 100$ mm) used in this experiment were filled to a depth of 20 mm with white sand (Quikrete, #1113) to provide a semi-natural substrate with high contrast for filming. Males and females were fed two 10-day old crickets (*Acheta domesticus*) 48 h prior to the start of experiments to standardize hunger levels, and females were then placed into the apparatus 24 h before introduction of a male to deposit silk and chemical cues. At the start of a trial, males were gently deposited into the arena in the corner most nearly opposite the location of the female. We filmed pairs from above for one hour using a video camera (Watec, model # 902H2) wired to a remote recording device (Sony Digital Videocassette Recorder, model # DSR-11) for later analysis. At the end of the recording period all individuals not in copula (or cannibalized) were returned to their individual containers. Mating pairs were allowed to separate naturally and (survivors) were then returned to individual containers.
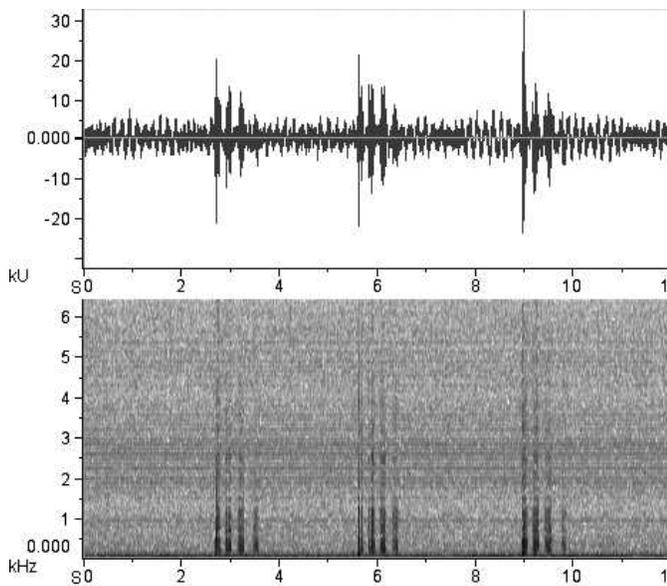
Figure 1.—Waveform and spectrogram of male *Schizocosa bilineata* seismic signaling.

RESULTS

Experiment 1: Observation and description of male behaviors.—Basic behaviors performed by male *S. bilineata* in response to female cues are similar to behaviors seen in other *Schizocosa* species (e.g., chemoexplore), but three behaviors are described which we propose as species-specific visual courtship behaviors (Incremental Leg Descend, Slow Jerky Walk, and Quick Tap). Table 1 contains a full description of all male and female behavioral elements. Further, based on recordings of seismic signals, males of this species produce distinct vibratory signals (Fig. 1). Seismic signaling bouts by male *S. bilineata* occur as short bursts of vibration, approximately one second in duration, at regular 3–5 s intervals. Each individual burst is a pulse train consisting of four pulses of stridulation, and a pulse lasts approximately 0.1 s. Though stridulatory pulses represent a sound spectrum of 1–3 kHz (with harmonics to 6 kHz), most sound energy appears to be below 1200 Hz. Unfortunately, we were only able to record brief signaling bouts of two males, so we make no attempt to further analyze aspects of the signal. Of the 22 females collected for this experiment, 20 produced (or were collected with) egg sacs. Of these twenty, 12 egg sacs (60%) successfully hatched with the number of spiderlings per egg sac ranging from two to 63 (mean = 23 ± 5.51 SE).

Experiment 2: Male response to conspecific cues.—ANOVA results for frequency and total duration of male behaviors performed in response to conspecific cues are summarized in Table 2. We did not observe some behaviors described in Experiment 1 in this experiment (Leg Raise and Retreat: Table 1), and we excluded these from analysis. Grooming and threat display did not vary significantly across treatment categories for either frequency or total duration (Table 2). Frequency and total duration of male behavior varied significantly by treatment across most other behaviors (Table 2). Orient and approach behaviors occurred only in the presence of a live female (female multi-cues), and wave

Table 2.—ANOVA results for behaviors of male *Schizocosa bilineata* in response to conspecific cues in experiment 2. Key behaviors in bold.

Behavior	Frequency		Total duration	
	$F_{3,34}$	P	$F_{3,34}$	P
Approach	7.4749	0.0006[*]	7.0919	0.0008[*]
Chemoexplore	**15.7700**	**< 0.0001[*]**	**21.2598**	**< 0.0001[*]**
Groom	0.9787	0.4142	1.9706	0.1369
Locomotion	6.4839	0.0014[*]	7.7682	0.0004[*]
Orient	8.3509	0.0003[*]	6.7151	0.0011[*]
Quick Tap	**10.5033**	**< 0.0001[*]**	-	-
Incremental Leg Descend	**6.0274**	**0.0021[*]**	**10.6720**	**< 0.0001[*]**
Slow Jerky Walk	**11.2184**	**< 0.0001[*]**	**20.9891**	**< 0.0001[*]**
Stationary	2.3067	0.0941	5.5349	0.0033[*]
Threat Display	0.7645	0.5219	0.7393	0.5360
Wave	6.2188	0.0017[*]	8.5837	0.0002[*]

[*] Indicates significance using Bonferroni correction (α = 0.005)

occurred only in the absence of all conspecific cues (Table 2). The frequency of bouts of stationary behavior was not significantly different by treatment; however, there were significant differences by treatment for total duration (Table 2). Locomotion varied significantly across treatment categories for both frequency and total duration of behavior (Table 2), and chemoexploratory behavior was also significantly different across treatment categories with bouts occurring at higher frequency and longer duration in response to female silk cues (Table 2, Fig. 2).

The behaviors proposed as species-specific courtship behaviors all varied significantly by treatment for both frequency and total duration (as appropriate) of bouts (Table 2). Quick Tap was only observed in the presence of conspecific cues, but very rarely in response to male silk cues (Fig. 3). Quick Tap was considerably more frequent in response to female silk and multimodal cues, and frequency was not different between these treatments (Fig. 3). Incremental Leg Descend and Slow Jerky Walk both varied significantly by treatment for frequency and total duration of behavioral bouts (Table 2). We observed Incremental Leg Descend across all treatments, but it occurred most frequently in the presence of female cues (Fig. 4a). Bouts of Incremental Leg Descend behavior were of significantly longer duration in the female multi-cues treatment, and not significantly different across the other treatment categories (Fig. 4b). We never observed Slow Jerky Walk in response to male cues and only very rarely in the no-cue control treatment (Fig. 5a). Neither frequency nor total duration of Slow Jerky Walk was different between the female silk-cues or multi-cues treatments (Fig. 5), but both frequency and total duration were significantly higher than in the no-cue control or male silk-cue treatments (Fig. 5).

Experiment 3: Female receptivity and mating behavior.—Males exhibited chemoexploratory and courtship behaviors in all but one trial, which was excluded from further analysis, since both the male and the female remained stationary for the entire 1 h trial period. Mean latency to begin chemoexploratory behavior in the remaining trials was 7.2 s (± 2.84 SE, n = 11), and mean latency to begin courtship (defined as first instance of Quick Tap, Incremental Leg Descend, or Slow Jerky Walk) was 34.5 s (± 5.00 SE, n = 11). Female receptivity
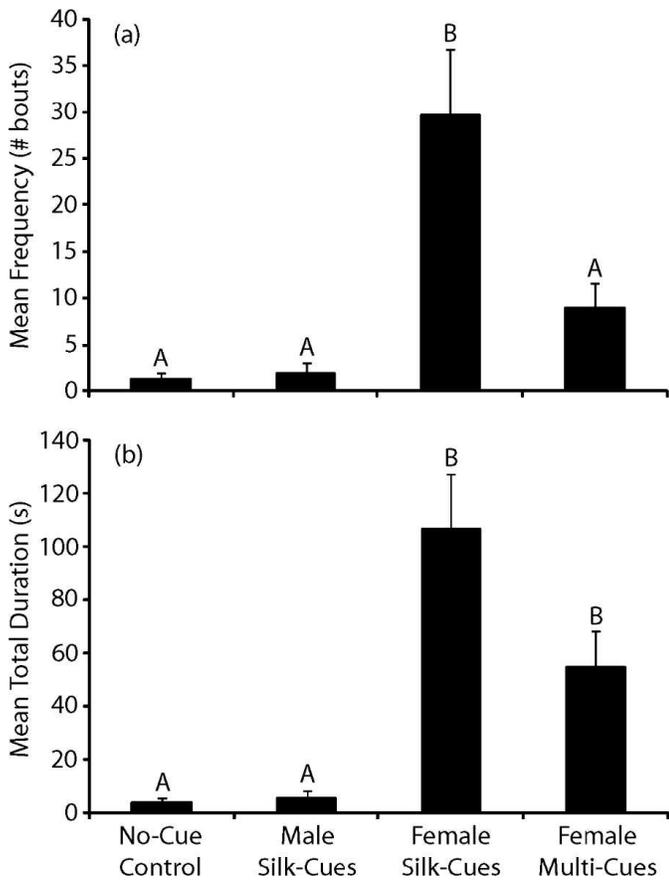
Figure 2.—Mean + SE a) frequency and b) total duration of bouts of Chemoexplore behavior for male *Schizocosa bilineata* exposed to blank control, conspecific silk cues, or multimodal female cues. Shared letters above the bars indicate no significant difference between treatment categories by Tukey-Kramer post-hoc analysis ($\alpha = 0.05$).
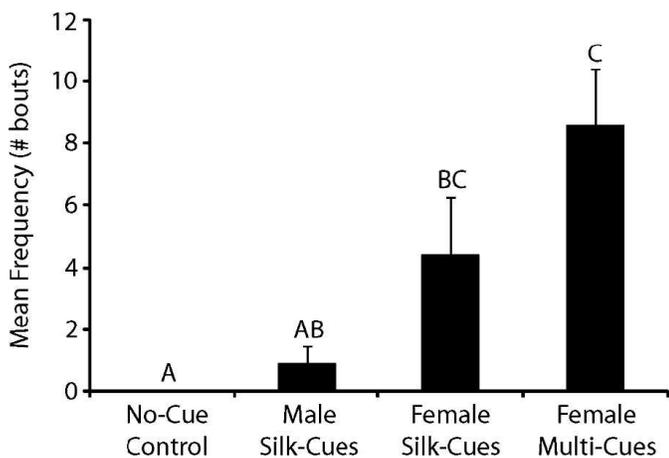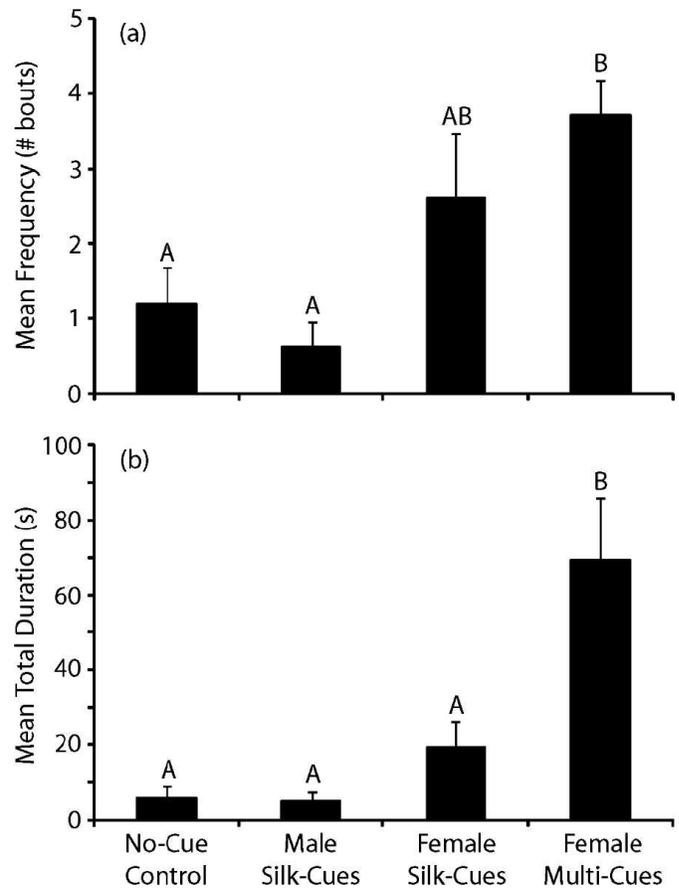

Figure 4.—Mean + SE a) frequency and b) total duration of bouts of Incremental Leg Descend behavior for male *Schizocosa bilineata* exposed to blank control, conspecific silk cues, or multimodal female cues. Significant differences for post-hoc analysis indicated as in Fig. 2.

Figure 3.—Mean + SE frequency of bouts of Quick Tap behavior for male *Schizocosa bilineata* exposed to blank control, conspecific silk cues, or multimodal female cues. Significant differences for post-hoc analysis indicated as in Fig. 2.

behaviors were typical of other *Schizocosa* (summarized in Table 1) and were observed in 8 of 11 trials (72.7%). We observed mounting and copulation in 5 of 11 trials (45.5%) and mean latency to copulate in these trials was 1402.8 s ($\pm$ 559.2 SE, $n = 5$). In all cases, males initiated courtship prior to attempting to mount, and females adopted a Settle position prior to mounting by the male. Four of the five females performed at least one Slow Turn prior to Settle. Males mounted females from the anterior or anterior lateral position, and copulation position was of the normal type for Lycosidae with male above on the female dorsum and facing the female posterior (Foelix 1996). We observed two instances of sexual cannibalism by females out of 11 mating trials (18.2%), one pre-copulatory and one post-copulatory.

DISCUSSION

In the Lycosidae, ornamentation of male forelegs (e.g., tufts of bristles, pigmentation) is generally associated with active leg-waving displays that play a role in visual communication. This seems especially true within the genus *Schizocosa* (Hebets & Uetz 2000; Stratton 2005; Framenau & Hebets 2007), but a few species remain within the genus for which little or no behavioral data exist (Stratton 2005). Unfortunately,
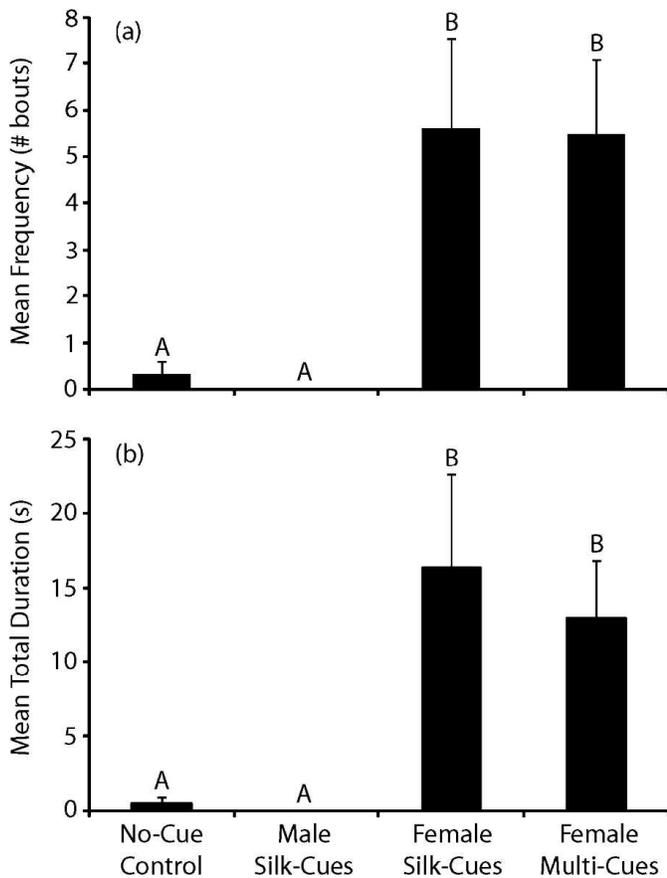
Figure 5.—Mean + SE a) frequency and b) total duration of bouts of Slow Jerky Walk behavior for male *Schizocosa bilineata* exposed to blank control, conspecific silk cues, or multimodal female cues. Significant differences for post-hoc analysis indicated as in Fig. 2.

this 'missing data' has hindered any thorough phylogeny-based exploration of the correlation between leg decoration/ornamentation and visual display behavior (Stratton 2005). The work presented here represents the first comprehensive analysis of courtship and mating behavior for *Schizocosa bilineata*, a species whose males possess leg decoration but for which little behavioral work has been done. Results clearly indicate the presence of visual display elements during male mate searching and courtship (Table 1), and refute earlier assertions by Montgomery (1903) that males of this species do not exhibit discernable visual courtship. This is not entirely surprising, as a careful review of methods reveals that the assertion is based on a single, successful male/female pairing (Montgomery 1903). In fact, three visual display behaviors (Quick Tap, Incremental Leg Descend, and Slow Jerky Walk) are described here for *S. bilineata* males and, as all three were expressed predominantly in the presence of conspecific female cues and prior to copulation in mating trials, any or all could play a role in mate choice.

Of the three male visual display behaviors, Quick Tap seems least likely to play a role in visual communication. During the real-time video analysis of male behaviors, we observed Quick Taps only as a 'flicker' of motion. This probably corresponds to the "quiver" of leg motion described by Montgomery (1903). Frame-by-frame analysis of bouts of this behavior

demonstrate that each bout is conducted within three video frames at the NTSC video standard of 29.97 frames per second (corresponding to an approximate bout length of 0.1 s). Considering the visual system characteristics of wolf spiders, which have flicker fusion rates similar to humans (Land 1985; Uetz 2000), at this speed it seems likely that the behavior would serve as an attention signal or driver of seismic signals, but not function effectively as a courtship signal in and of itself.

The other two display behaviors, Incremental Leg Descend and Slow Jerky Walk, seem more promising for a role in mate choice. These behaviors are similar to behaviors in other *Schizocosa* species that have been demonstrated to be important in female mate choice. In particular, Incremental Leg Descend resembles the "Extension" behavior described for *S. crassipes* (Miller et al. 1998) and Slow Jerky Walk, the "Jerky Walk" behavior described for *S. ocreata* (Stratton & Uetz 1983, 1986). We stress, however, that the behaviors seen in *S. bilineata* are distinctly different from these other behaviors. In Incremental Leg Descend, the extended leg is slowly and incrementally lowered (in a series of pauses) to the substrate (never quickly tapped). Slow Jerky Walk is not only slower than Jerky Walk, but also lacks the distinctive cheliceral strikes and leg taps characteristic of bouts of *S. ocreata* courtship.

The assertion of a role for these behaviors in sexual selection, however, is speculative at present, despite the coincidental production of these behaviors immediately prior to copulation and in response to female cues. Additional work will be necessary to explore the actual function of the display traits in conspecific interactions. Kaston (1936) raised an important point concerning sexual traits and display behaviors (even if it was based on the faulty assumption of no visual display in *S. bilineata*). He emphasized that possession of such traits and behaviors does not necessarily mean that said characteristics are actually important for or directly involved in mate choice. This point is especially important concerning the recent work by Hebets (2008) where she demonstrates that although male *S. stridulans* Stratton 1991 produce a visual signal, only simultaneously produced seismic signals are important for female choice. We made no attempt to isolate signaling modalities (visual/seismic) in mating trials and as such, we are not able to determine whether visual or seismic cues are of greater or equal importance in this species.

We can, however, draw some important conclusions for males of this species. Clearly, as in other *Schizocosa* species, females signal to males using chemical signals associated with silk (reviewed in Roberts & Uetz 2004a, b; Roberts & Uetz 2005), and signals from chemical cues are lacking in males (Figs. 2–5). Although only rarely performed in the absence of silk and chemical cues, Slow Jerky Walk was never performed in the presence of male silk cues (Fig. 5), and thus may offer evidence for a male inhibitory chemical as suggested by Ayyagari &Tietjen (1987). Male *S. bilineata* recognize and respond to chemical cues alone with species-specific courtship behavior (Figs. 3–5), and perform bouts of one behavior (Incremental Leg Descend) for a significantly longer duration in response to live females (Fig. 4b). This suggests that males alter their behavior in response to some behavioral feedback from females, though aside from visual receptivity behavior

and chemical signals, we did not find evidence of other signaling by females. The significant increase in frequency of Quick Taps in response to female multimodal cues further supports this suggestion. Females, whether responding to visual, seismic, of multimodal male cues, do respond to male courtship with typical receptivity behaviors. These behaviors precede mounting and copulation, and males must recognize female receptivity behaviors and respond accordingly.

It is unfortunate that we were unable to fully describe male seismic signals in our study. There is a good chance that these signals play a critical role in courtship and mate choice in this species (Stratton 2005), maybe more so than visual signals alone (Hebets 2008). Future work will be necessary to fully understand the interaction between visual and seismic modalities, but both are likely important and our description of behavior in this species should help resolve the relationship between male ornamentation and courtship behavior in the genus *Schizocosa*.

ACKNOWLEDGMENTS

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