Title: The role of social experience in eavesdropping by male wolf spiders (Lycosidae).

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When reproductive success is limited by mate search costs, males can reduce costs by eavesdropping and initiating displays if conspecific courtship is detected. Here, we examine eavesdropping by male *Schizocosa ocreata* wolf spiders, with field studies, lab studies using video playback and live exposure studies. In field enclosure experiments, introduced males responded with increased courtship signaling behavior in the presence of a courting male. In the lab, field-collected males showed a longer duration of interaction behaviors and more bouts of courtship activity in response to a courting video male stimulus than did lab-reared males, suggesting that eavesdropping might arise as a consequence of field experience. To explore this further, we conducted associative learning studies on naïve, lab-reared males pairing video playback of male courtship with sensory cues indicating female presence. Results showed that males with no prior exposure learned to associate courtship of other males with cues indicating the presence of females. In subsequent video playback experiments, field-collected males recognized differences in male behavior, responding with courtship more often and for a longer time to video stimuli of courting male spiders than to walking males or an empty leaf litter background (no spider). Additional studies showed that males exhibited significantly more time in courtship displays when presented with two to three live or video male stimuli simultaneously. Together, these findings confirm that male wolf spiders meet assumptions of eavesdropping behavior, and suggest that social experience arising from exposure to courtship interactions of conspecifics may impact male eavesdropping and subsequent courtship behavior.

Introduction

Much evidence suggests that courtship signals of males are selected to be conspicuous to females against a complex background of environmental noise (Candolin 2003; Partan & Marler 2005; Hebets & Papaj 2005; Rosenthal 2007). Unfortunately, these signals may also be detected by others in the communication network encompassed by signal active space (Brenowitz 1982; McGregor & Dabelsteen 1996; McGregor & Peake 2000; Shier 2002; McGregor 2005; Searcy & Nowicki 2005; Roberts, Taylor & Uetz 2007; Roberts & Uetz 2008; Uetz, Clark, Roberts, et al. 2013). In communication networks, unintended receivers may include social eavesdroppers - i.e., conspecifics that recognize and exploit the information content of signals (Peake 2005; Dabelsteen 2005; Searcy & Nowicki 2005), or interceptive eavesdroppers - i.e., predators for which signals reveal the presence of potential prey (Zuk & Kolluru 1998; Haynes & Yeargan 1999; Rosenthal et al. 2001; McGregor 2005; Rosenthal 2007). Much research on communication networks has examined eavesdropping in several highly specific contexts (see McGregor 2005 and chapters within), including: bystanders observing male-male contests (Oliviera, McGregor & Latruffe 1998; Johnstone 2001; Peake, Terry, McGregor & Dabelsteen 2001; Earley & Dugatkin 2002, 2005), female mate choice copying (Dugatkin 1992; Dugatkin & Godin 1993), and predator detection of male courtship signals (Wagner 1996; Kotiaho, Alatalo, & Mappes, et al. 1998; Koga, Backwell & Christy et al. 2001; Macedonia, Brandt & Clark 2002; Peake 2005; Page & Ryan 2005; Bernal, Page, Rand & Ryan 2007; Roberts et al. 2007; Roberts et al. 2008; Virant-Doberlet, King, Polanjanar & Symondson 2011). One potentially fruitful area of

investigation is facilitation of courtship arising as a consequence of social eavesdropping, which may indicate a form of mate competition (Zajonc 1965; Farr 1976; Waas 1988; Galef 1988; Doutrelant and McGregor 2000).

When male reproductive success is limited by costs of finding mates, selection would favor males that take advantage of any available information revealing the location of prospective mates. Under these circumstances, males might reduce costs by eavesdropping on the behavior of nearby rivals and initiating sexual displays whenever courtship is detected, as it indicates the presence of a female (i.e., social facilitation of displays). In two previous studies (Roberts, Galbraith, Milliser, et al. 2006; Clark, Roberts & Uetz 2012), we examined the possibility that males of the brush-legged wolf spider, *Schizocosa ocreata* (Hentz), exhibit eavesdropping and social facilitation of courtship behaviors. Results of the first study (Roberts et al., 2006) were inconclusive, as we found no convincing evidence of eavesdropping, social facilitation of courtship, or increased exploratory behaviors by male *S. ocreata*. However, our field observations of high male density during the breeding season suggested the possibility of a communication network (*sensu* McGregor 2005) as well as a high probability of signal interception. In addition, we frequently saw multiple males searching and courting in the vicinity of other males that we presumed were courting visually hidden females. Roberts et al. (2006) conducted experiments exclusively in the laboratory with spiders reared in isolation, so we consequently repeated our tests for eavesdropping and social facilitation using field-collected (presumably socially experienced) males (Clark et al. 2012). Results of that follow-up study were dramatically different, as field-collected males clearly exhibited eavesdropping, courtship and signal matching behaviors (Clark

et al. 2012), leading to the hypothesis that eavesdropping may be acquired as the result of experience with other males during the breeding season in the field.

Despite evidence suggesting that previous experience affects mating decisions in female *Schizocosa* spp. (Hebets 2003; Hebets & Vink 2007; Rutledge, Miller & Uetz 2010), we know little about the effects of social experience in males and how it may impact their courtship behaviors. Male courtship behavior in *S. ocreata*, is usually seen in response to chemotactile cues from adult females (Roberts & Uetz 2004, 2005), involves conspicuous displays, including tapping, waving and arching of the first pair of legs (Stratton & Uetz 1986; Delaney et al. 2007). In this study, we examine further the phenomenon of social eavesdropping in male wolf spiders, with a series of experimental studies in the field and lab. In field experiments, we examined responses of males to the presence of courting males, while in the lab, we used video playback to eliminate the possibility of male-male interaction, and compare responses of lab-reared vs. field-collected males to male video stimuli representing courting and non-courting behaviors. To examine the role of experience, we tested the hypothesis that male eavesdropping behavior is learned by association of male courtship behavior with sensory cues indicating female presence. Lastly, to confirm that wolf spider behaviors were consistent with eavesdropping, we also compared responses of field-collected focal males to different stimulus male behaviors, and examined the role of male density in social facilitation of courtship behavior.

Methods

All lab studies were conducted in May and June of 2011-2013, with either: (a) sexually mature male *Schizocosa ocreata* (Hentz) collected from the Cincinnati Nature Center, Rowe Woods, Clermont County, OH, and brought into the lab, or (b) lab-reared spiders from the same population raised in the lab from the early juvenile stage. Spiders were housed individually and visually isolated from others, provided water *ad libitum*, and maintained at room temperature (22-25°C) with stable humidity and a 13:11h light:dark photoperiod. Spiders were fed a diet of 2-3 cricket nymphs twice weekly. Field studies were conducted in a forest habitat on private land near New Richmond, Clermont County, OH, in spring 2014. Male spiders used in field experiments were collected from leaf litter on the two days prior to the experiments, and housed as above.

Video playback studies

Video playback stimuli of spider courtship were identical to those prepared for and used in numerous earlier studies (for a detailed description of video capture and manipulation, see Uetz 2000; Uetz & Roberts 2002), with male images superimposed on a digital photo background of natural leaf litter (see Uetz, Clark, Roberts, et al. 2011). In all video playback trials, spiders were presented with identical, standardized courting or walking male stimuli (derived from different exemplars). The male stimuli were standardized by video animation rendering with a mean body size and average leg tuft size based on the population average from Roberts et al. (2007) and population mean courtship vigor (number of taps per minute) from Delaney et al (2007). We used a Canon XL1 digital video recorder fitted with a macro lens to capture a representative

digital still photo of the background of the natural microhabitat of *S. ocreata*, i.e., leaf-litter taken at ground level. The male video exemplars were superimposed against the digital background of leaf litter using Final Cut Pro® (v 7) software. Both the background and male video stimuli were appropriately scaled to life-size for presentation on the iPod® LCD video screens used in our experiments.

Video playback trials were conducted within the first week after field-collected males were captured, or one week after lab-reared males reached sexual maturity.

Video playback trials were conducted in standard circular clear plastic playback arenas (15 cm diameter, 6.5 cm high) as in previous studies (McClintock & Uetz 1996; Hebets & Uetz 2000; Uetz & Norton 2007; Uetz et al. 2011; Moskalik & Uetz 2011), but modified for up to three iPod® video screens (Fig. 1 a,b,c). Focal male subjects were gently released from a vial placed below the arena and introduced to the video playback arenas through a small hole in the arena floor (to mimic natural movement within the complex leaf litter of the forest floor). Each male was tested only once to control for experience effects with the video apparatus. Focal males were video recorded from above and video files were scored later with an event recorder (Spectator Go!® software [Biobase.com] on an iPad®) for how much a male invests in courtship, indicated by an increase in the frequency and duration of leg tapping and other behaviors (Table 1).

Field tests for eavesdropping

Although it is possible that field conditions absent from the laboratory environment (e.g., environmental enrichment – see Carducci & Jakob 2000) might affect

the tendency of males to exhibit higher rates of courtship behavior overall, our field observations suggest this behavior often occurs in response to the courtship of other males. Consequently, we first tested the hypothesis that males collected directly from the field are more likely to exhibit eavesdropping in response to courtship of other males. If males exhibited increased courtship activity during and after exposure to male courtship, this would indicate eavesdropping and social facilitation.

We used small circular field enclosures (40 cm dia., approx. 0.5 m² area) constructed from 30 cm x 130 cm sheets of aluminum placed in natural leaf litter. Males were introduced first to an empty arena for five minutes, and then introduced to an arena in which a courting male was present for a second five minute trial. Focal males were handled gently using plastic vials and allowed to acclimate for one minute prior to recording. Courting males were enclosed in a clear plastic chamber affixed to a maple leaf upon which a female *S. ocreata* had laid silk (and courtship-inducing pheromones) for 12 hrs. Females used to provide silk stimuli were unmated females 2-3 weeks post-maturity that were collected in the field as sub-adults and allowed to mature in isolation in the lab. This protocol allowed the focal male to perceive both visual and seismic/vibratory signals of the courting male, but without contacting female cues. Each trial was video recorded for later analysis where focal male subjects were scored for the frequency and duration of tapping (Table 1).

Eavesdropping in lab-reared vs. field-collected males

We conducted a set of laboratory experiments to confirm earlier observations about male eavesdropping and courtship behavior in lab-reared vs. field-collected males

(Roberts et al. 2006; Clark et al. 2012). We tested the hypothesis that field-collected males are more likely than lab-reared males to exhibit courtship in the presence of a courting male, by examining responses to video playback of either a courting male or a male engaged in non-courtship activity (walking). We presented lab-reared and field-collected males with video playback on a single iPod screen, using video playback arenas as above (Fig. 1a). Male spiders were presented with either a courting male or a non-courting (i.e. walking) male. Each trial was videotaped and test subjects were scored with an event recorder (Spectator® software on an iPad®) for the frequency and duration of tapping displays (Table 1).

Associative learning studies

Observed differences between field-collected and lab-reared lab males might be attributable to experience gained during the breeding season. We tested the hypothesis that these differences reflect a conditioned response, i.e., association of male courtship with the presence of females, and consequent response to courtship of other males with increased courtship display. Courtship behavior of male *S. ocreata* is innate and displayed in response to female silk cues without prior experience (Stratton & Uetz 1981; Roberts & Uetz 2004). We therefore predicted that naïve males (no experience with mature males or females in the field) would learn to associate male courtship (conditioned stimulus) with female presence if exposed to a male courtship stimulus paired with female cues (unconditioned stimulus). Over a three day period, males were placed in an arena (Fig. 2) and exposed once a day for five minutes to either (a) a video of a courting male in combination with female silk cues and a nearby, but inaccessible

female (Fig. 2a), or (b) a male video alone (Fig 2b). On day four, after three days of conditioning trials, responses of males to the courting male video were assessed from video recordings. As a control we also included and tested a group of naïve males (with no exposure to either male courtship or female cues).

Verifying eavesdropping in lab studies with video playback

We tested field-collected males in a choice paradigm – i.e., between video playback of a male engaged in courtship behavior (against a leaf litter background) vs. either a control leaf litter background (no male present), or a male engaged in non-courtship activity (walking in front of leaf litter background). Males responding to the courtship of other males with increased courtship signaling behavior, but not responding with courtship to an empty background or to walking male stimuli, would indicate recognition of conspecific courtship behavior (and eavesdropping).

We presented field-collected males with video playback on two iPod screens simultaneously, using modified video playback arenas (Fig. 1b). Male spiders were given choice tests where they were presented with the following pairs of stimuli: a) courting male vs. control leaf litter background; b) non-courting (i.e. walking) male vs. control leaf litter background; c) courting male vs. walking male. Each trial was video recorded and scored later for the frequency and duration of tapping (Table 1).

Effects of male density on social facilitation and eavesdropping

In social eavesdropping, males attend to the courtship displays of other males

and respond by courting (presumably to pre-empt competitors and attract females away from them). Social density of courting males might affect the tendency to eavesdrop and exhibit courtship (social facilitation), as multiple courting males are a stronger indication of the presence of a female. We varied the number of courting stimulus males perceived by a focal male in order to explore whether social facilitation of courtship is related to social density (density of competitors). We conducted experiments using both video playback and live male stimuli for several reasons. Video playback presented only visual cues, but served as a control for potential competitive interactions with other males. Live male courtship is multimodal, providing both visual and vibratory/seismic signals (Scheffer, Uetz & Stratton 1996; Uetz 2000).

Video playback trials were conducted in video playback arenas (described above), modified to accommodate three iPod® monitors (Fig. 1 c). Sexually mature male *S. ocreata* were presented with the same courting male video stimuli as in other experiments above or a control (an empty leaf litter background as in other video stimuli) on the three screens in the following treatments to represent varied densities of courting conspecifics: a) one courting male + two control; b) two courting males + one control; c) three courting males; and d) three control screens. Male behaviors (Table 1) were video recorded for later scoring and analysis as above.

The live male treatments were conducted in a modified arena (Fig. 1d) with a focal male in a 15 cm diam. circular center arena, surrounded by a 25 cm outer ring of three 26 cm (outside length) x 16 cm (inside length) x 5 cm (width) chambers. The space between the two rings was divided into three equal chambers into which stimulus males could be placed, along with filter paper containing silk and chemical cues

collected overnight from a single adult female. Treatments consisted of either: a) one courting male + two control (empty) chambers; b) two courting males + one empty chamber; c) three courting males; or d) three empty chambers. Male behaviors were video recorded for scoring and analysis as above.

Ethical Note

To our knowledge, no animal welfare laws or regulations in the USA or the State of Ohio govern the use of invertebrates such as spiders in research. Wherever possible, we adhered to the “Guidelines for the treatment of animals in behavioural research and teaching” (Animal Behaviour 85 (2013) 287–295) of the Animal Behavior Society. At the end of this study, spiders were either transferred to another researcher in the lab for further study, or ultimately humanely euthanized with CO₂ and freezing.

Results

Field tests for eavesdropping

Males collected directly from the field and introduced to an experimental field arena - with and without the presence of a courting male - demonstrated behavior consistent with eavesdropping, i.e. increased following and courtship behavior during and after exposure to a live courting male (Fig. 3 a, b). Introduced males were significantly more likely to exhibit courtship with a courting male present (McNemar’s test, $p = 0.0003$, $df = 17$), and had higher rates of tapping in the presence of a courting male (paired $t = 4.409$; $p = 0.0003$; $df = 17$).

Eavesdropping in lab-reared vs. field-collected males

Field-collected males interacted with video males more than did naïve lab-reared males, indicating (likely) conspecific recognition and/or increased responsiveness (Fig. 4). A two-way ANOVA of the number of interaction bouts (approach, watch, follow) showed significance overall ($F_{3,146} = 5.1527$; $p = 0.002$), with a significant effect of rearing environment (lab vs. field: $F_{1,146} = 13.8219$; $p = 0.0003$). Neither group showed a significant difference between the video stimuli (courting vs. walking males: $F_{1,146} = 0.8574$; $p = 0.356$), and the rearing environment x video stimulus interaction was not significant ($F_{1,146} = 0.6788$; $p = 0.4133$). Field-collected males showed significantly more interaction bouts with male video stimuli, regardless of behavioral activity (Fig. 4).

In contrast, the number of bouts of tapping behaviors exhibited in response to male video stimuli (Fig. 5) showed significance overall ($F_{3,132} = 5.5431$; $p = 0.0013$), as well as a significant effect of rearing environment (lab vs. field: $F_{1,132} = 10.8403$; $p = 0.0013$) and video stimulus (courting vs. walking males: $F_{1,132} = 4.817$; $p = 0.0295$). The rearing environment x video stimulus interaction was not significant ($F_{1,132} = 0.9328$; $p = 0.3359$). While field-collected males showed a greater number of tapping bouts than lab-reared males, they also showed a two-fold increase in number of bouts in response to observation of the courtship of other males (Fig. 5), indicating both conspecific recognition and discrimination of courtship behavior from non-courtship activities (walking).

The length of individual tapping bouts varied with both rearing environment and video stimulus as well (Fig. 6), with significance overall ($F_{3,51} = 31.4654$; $p < 0.0001$), a

significant effect of rearing environment (lab vs. field: $F_{1,51} = 82.6028$; $p < 0.0001$) as well as video stimulus (courting vs. walking males: $F_{1,51} = 5.213$; $p = 0.0256$). The source x video stimulus interaction was not significant ($F_{1,51} = 1.4825$; $p = 0.2290$). Field-collected males exhibited longer bouts of tapping behaviors in the presence of video males compared to lab-reared males (Fig. 6). They also had longer tapping bouts with courting males than with walking males, suggesting increased investment in courtship activity.

Overall, the amount of time spent in courtship tapping behavior varied with both rearing environment and video stimulus (Fig. 7), with significance overall ($F_{3,129} = 7.7061$; $p < 0.0001$), a significant effect of rearing environment (lab vs. field: $F_{1,129} = 17.5954$; $p < 0.0001$) as well as video stimulus (courting vs. walking males: $F_{1,129} = 4.0786$; $p = 0.0455$). The source x video stimulus interaction was not significant ($F_{1,129} = 1.6907$; $p = 0.1958$). Field-collected males spent more time courting in the presence of courting males than walking males, while lab-reared males did not (Fig. 7), indicating the potential for eavesdropping, recognition, and social facilitation to arise from field experience.

Associative learning studies

Males conditioned with female cues and male video exhibited higher levels of courtship, indicating that eavesdropping is influenced by experience (Fig. 8). Males that were exposed to conditioning with both female cues and male courtship showed significantly higher numbers of signaling bouts when presented with male courtship signals alone after their training period ($F_{2,26} = 5.024$; $p = 0.0143$) than those exposed to

male courtship alone or with no exposure (naïve males). These results suggest that males learn to associate male courtship behavior (conditioned stimulus) with cues indicating the presence of females (unconditioned stimulus).

Verifying eavesdropping in lab studies with video playback

Choice tests with live focal males presented with two video screens simultaneously showed that males respond to video stimuli of walking and courting male wolf spiders with interaction behaviors (approach, watch, follow) but responded far less to an empty leaf litter background. Males exhibited a significantly greater number of interaction bouts, significantly longer bouts of interaction behavior, and a greater total amount of time interacting with both walking and courting male stimuli vs. a blank screen (Table 2). Studies also showed that when presented with two male video stimuli simultaneously, males interacted equally with courting males and walking males (Table 2). However, results from choice tests (Fig. 9) show that males display significantly more tapping bouts (paired $t_{33} = 2.252$, $p = 0.0311$) and more time in tapping displays (paired $t_{33} = 2.328$, $p = 0.0262$) in the presence of a courting male vs. a walking male stimulus, although there was no difference in the length of tapping bouts (paired $t_{33} = 1.0465$, $p = 0.3029$).

Effects of male density on social facilitation and eavesdropping

Studies manipulating social density (number of courting male stimuli) found that duration of male courtship (total time in tapping displays) was significantly longer in the presence of additional males (Fig. 10). A two way ANOVA of the log-transformed total

duration of time spent in courtship display behaviors showed significance for the number of courting males ($F_{3,63} = 6.3664$; $p = 0.0008$), but no difference between live and video male stimuli ($F_{1,63} = 2.6729$; $p = 0.1071$). The interaction of number of courting males x male stimulus type (video/live) was also not significant ($F_{3,63} = 0.3718$; $p = 0.7736$).

Discussion

Results of this study suggest that male *Schizocosa ocreata* wolf spiders recognize conspecific males, are attentive to their behavior, and respond to male courtship displays by initiating courtship (presumably exploiting signals to intercept a female), which is consistent with common definitions of eavesdropping behavior (McGregor 2005). While most examples of eavesdropping have come from vertebrate animals (see McGregor 2005), it appears that some invertebrates also exhibit this ability (Bailey & Field 2000; Pope 2005; Aquiloni, Buřić & Gherardi, 2008; Aquiloni & Gherardi 2010; Milner, Jennions, M., & Backwell 2010, 2012; Fitzsimmons & Bertram 2013). A number of previous studies have demonstrated that eavesdropping has fitness benefits, particularly when mate location and/or assessment costs limit reproductive success. Under such conditions, individuals can reduce costs by observing the behavior of others (Peake 2005; Dabelsteen 2005; Searcy & Nowicki 2005). For example, females may reduce time invested in mate assessment by eavesdropping on male contests, and/or copying mate choices of others (Dugatkin 1992; Dugatkin & Godin 1993; Peake et al. 2001; Earley & Dugatkin 2005; Aquiloni & Gherardi 2010). Males, on the other hand,

might reduce costs of mate searching and compete more effectively by eavesdropping and initiating displays whenever courtship is detected, although there is less empirical support (Zajonc 1965; Farr 1976; Waas 1988; Galef 1988; Doutrelant and McGregor 2000; Milner & Jennions 2012). Results of our studies suggest eavesdropping may be a form of competitive interference, i.e., males use information gained from eavesdropping to determine mate location, and thereby increase success in mate competition.

The results of this study contrast significantly with a previous study, which concluded that male *S. ocreata* did not exhibit eavesdropping or social facilitation of courtship behavior (Roberts et al. 2006). Males used in that study were collected as juveniles or subadults prior to the emergence of adults in the field, matured in isolation in the lab, had little or no opportunity for exposure to the behavior or cues of adult conspecifics, and were thus socially naïve. Along with results of a subsequent study done with field-collected males (Clark et al. 2012), results from this study suggest experience gained in the field during the breeding season may play a role in eavesdropping behavior. Several previous studies have demonstrated that wolf spider behavior is influenced by experience, and that subadult female exposure to adult male courtship cues can affect adult female mating behavior in wolf spiders (Hebets 2003; Hebets & Vink 2007; Rutledge et al 2010). In comparison with lab-reared males, field-collected males showed a longer duration of interaction behaviors and more bouts of courtship activity in response to a courting video male stimulus, suggesting that eavesdropping might arise as a consequence of field experience.

To test whether experience in the field could explain these differences, we conducted associative learning studies pairing video playback of male courtship with sensory cues indicating female presence. Results showed that males with no prior exposure learned to associate courtship of other males with cues indicating the presence of females. This latter finding not only explains differences seen between previous studies (Roberts et al 2006; Clark et al 2012), but suggests that male spiders learn quickly (5 min exposures over three days), potentially gaining a great deal from social experience in the fairly short breeding season (3-5 weeks). Other evidence suggests that previous experience affects mating decisions of female *Schizocosa* spp. (Hebets 2003; Hebets & Vink 2007; Rutledge et al. 2010), but this study is the first to show males learn to associate presence of females from behavior of other males. It is important to note that courtship behavior of male *S. ocreata* is innate and displayed in response to female silk cues without prior experience (Stratton & Uetz 1981; Roberts & Uetz 2004, 2005). However in this study, naïve males with no prior experience with either mature males, females or silk cues learned to associate male courtship with female presence only when a male courtship stimulus was paired with female cues.

Information gained from eavesdropping could be advantageous to courting male *S. ocreata* in several possible ways. Female *S. ocreata* are essentially monogamous and mate only once, so information on location of females allows eavesdropping males to increase probability of mating by acting as “interlopers”, pre-empting the courtship efforts of others. Gaining information by eavesdropping might also reduce the high energetic costs of mate search and courtship (Cady, Delaney & Uetz 2011), as information on location of females could reduce time spent searching, which could in

turn decrease predation risk. In communication networks, unintended receivers may also include interceptive eavesdroppers - i.e., predators for which signals reveal the presence of potential prey (Zuk & Kolluru 1998; Haynes & Yeargan 1999; Rosenthal 2007). Courtship display of male *S. ocreata* is conspicuous, and clearly detectable by predators (Pruden & Uetz 2005; Roberts et al. 2007; Roberts & Uetz 2008), and males have been shown to cease courting in the presence of predator cues (Lohrey, Clark, Gordon, & Uetz 2009; Fowler-Finn & Hebets 2011). In this context – i.e., courting when behavior of others indicates female presence nearby - eavesdropping might be seen as tipping the balance of the trade-off between mating success vs. mate competition and predation risk.

This study suggests that field-collected (and presumed experienced) male wolf spiders can recognize male conspecifics and discriminate between behaviors, evidenced in field enclosure experiments where males responded with increased courtship signaling behavior to the presence of a courting male. In video playback experiments, males responded to video stimuli of courting male wolf spiders with courtship far more often and for a longer time than to walking males or an empty leaf litter background (no spider). Video playback data suggest that live focal males recognize conspecific males on video, and approach and follow them. Moreover, focal males exhibit greater amounts of courtship signaling in front of screens with courting males, which supports the hypothesis of eavesdropping and exploiting the courtship behavior of others. Additional studies with both live males and video playback showed that males exhibited significantly more time in courtship displays when presented with two to three additional males or video stimuli simultaneously, suggesting a form of

social facilitation of courtship. These data provide evidence for context-dependent social facilitation of courtship by eavesdropping males, and confirm that wolf spiders meet common assumptions of social eavesdropping behavior.

Taken together, results presented here provide strong evidence that male *S. ocreata* wolf spiders exhibit behaviors consistent with social eavesdropping. These findings are potentially significant, considering that this is an invertebrate animal, for which behavioral plasticity is assumed to be limited (Gordon & Uetz 2011). At very least, this finding suggests that variables such as field exposure to conspecific behaviors and competitor density may impact male behavior and suggests that experience arising from exposure to courtship interactions of other conspecifics allows them to exploit the information gained.

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Table 1. Behaviors of male *S. ocreata* wolf spiders in response to video and live male stimuli. See Roberts & Uetz (2005) and Delaney, Roberts & Uetz (2007) for a more detailed description.

Behavior	Description
Orient	Male swivels and aligns main axis of body to face screen
Locomotion	Spider moves about arena at a walking pace
Approach	Male moves toward screen
Watch	Having oriented initially, male follows stimulus from stationary position, swiveling back and forth
Follow	Male actively moves with stimulus
Interaction	Sum of Approach, Watch and Follow behaviors
Tapping	Courtship behavior, consisting of leg tapping and “jerky tap” displays

Table 2. Number of bouts of interaction behaviors (approach, follow, watch) shown by focal male *S. ocreata* in response to paired video playback of walking vs. courting male stimuli. Results of paired t-tests comparing means are shown.

Focal Male Behavior	Video stimulus	Mean $\pm$ S.E.	Paired t	P	df
No. of interaction bouts	Walking male	2.405 $\pm$ 0.581	8.465	< 0.0001	72
	Blank screen	7.864 $\pm$ 0.581			
	Courting male	19.019 $\pm$ 6.562	7.467	< 0.0001	80
	Blank screen	1.883 $\pm$ 6.56			
	Courting male	7.171 $\pm$ 1.185	0.0482	0.9618	34
	Walking male	7.228 $\pm$ 1.185			
Interaction bout length	Walking male	53.983 $\pm$ 4.538	7.107	< 0.0001	71
	Blank screen	8.048 $\pm$ 4.601			
	Courting male	52.578 $\pm$ 7.613	4.231	< 0.0001	80
	Blank screen	6.186 $\pm$ 7.706			
	Courting male	31.710 $\pm$ 7.493	0.134	0.894	33
	Walking male	40.121 $\pm$ 8.570			
Total time interacting	Walking male	175.310 $\pm$ 10.81	9.995	< 0.0001	72
	Blank screen	22.572 $\pm$ 10.85			
	Courting male	167.608 $\pm$ 11.647	8.980	< 0.0001	80
	Blank screen	16.960 $\pm$ 11.788			
	Courting male	89.943 $\pm$ 13.65	0.427	0.672	33
	Walking male	99.519 $\pm$ 13.844			

FIGURE CAPTIONS

Figure 1. Arenas for male eavesdropping studies: (a) standard video playback arena; (b) modified video playback arena with two iPod screens; (c) modified video playback arena with three iPod screens; (d) live male arena with a focal male and three stimulus males.

Figure 2. Arenas for conditioning study: (a) arena with male video iPod, female silk cues and live female (behind barrier); (b) male video only.

Figure 3. Courtship behaviors (tapping) of field-collected males ($N = 18$) in response to an empty field arena (control) vs. a field arena containing a courting male enclosed on leaf w/female silk cues (experimental): (a) percent of males that exhibited courtship after introduction to an arena; (b) mean number of tapping bouts exhibited by males after introduction.

Figure 4. Mean number of bouts of interaction behaviors (orient, approach, follow, watch) exhibited by field-collected vs. naïve lab-reared males in response to video playback of courting or walking male stimuli.

Figure 5. Mean number of bouts of courtship tapping behavior displayed by field-collected vs. lab-reared males in response to courting or walking male video stimuli.

Figure 6. Mean length (secs) of tapping bouts for field-collected vs. lab-reared males with courting or walking male video stimuli.

Figure 7. Total time (secs) spent in courtship display behaviors for field-collected vs. lab-reared males with video stimuli of courting or walking males.

Figure 8. Responses to male video courtship by naïve lab-reared males exposed in conditioning trials to either: male video courtship paired with female cues, male video courtship only, or no cues (male raised in isolation).

Figure 9. Courtship behaviors (tapping) of male *S. ocreata* in response to video playback of courting vs. walking males: (a) number of tapping bouts; (b) total time spent in tapping displays.

Figure 10. Mean total time spent in courtship tapping displays by focal male *S. ocreata* exposed to increasing numbers of live or video courting male stimuli.

Figure 1.

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Fig. 2

Fig. 3.

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Fig. 8.

Fig. 9.

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