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, laboratory studies using video playback and live exposure studies. In field enclosure experiments, introduced males responded with increased courtship signalling behaviour in the presence of a courting male. In the laboratory, field-collected males spent more time engaged in interaction behaviours and performed more bouts of courtship activity in response to a courting video male stimulus than did laboratory-reared males, suggesting that eavesdropping might arise as a consequence of field experience. To explore this further, we conducted associative learning studies on naïve, laboratory-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 behaviour, responding with courtship more often and for longer periods to video stimuli of courting male spiders than to walking males or an empty leaf litter background (no spider). Additional studies showed that males spent 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 behaviour, and suggest that social experience arising from exposure to courtship interactions of conspecifics may impact male eavesdropping and subsequent courtship behaviour.

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Much evidence suggests that courtship signals of males are selected to be conspicuous to females against a complex background of environmental noise (Candolin, 2003; Hebets & Papaj, 2005; Partan & Marler, 2005; Rosenthal, 2007). Unfortunately, these signals may also be detected by others in the communication network encompassed by signal active space (Brenowitz, 1982; McGregor, 2005; McGregor & Dabelsteen, 1996; McGregor & Peake, 2000; Roberts, Taylor, & Uetz, 2007; Roberts & Uetz, 2008; Searcy & Nowicki, 2005; Shier, 2002; Uetz, Clark, Roberts, Gibson, & Gordon, 2013). In communication networks, unintended receivers may include social eavesdroppers (i.e. conspecifics that recognize and exploit the information content of signals; Dabelsteen, 2005; Peake, 2005; Searcy & Nowicki, 2005), or interceptive eavesdroppers (i.e. predators for which signals reveal the presence of potential prey; Haynes & Yeargan, 1999; McGregor, 2005; Rosenthal, 2007; Rosenthal, Flores Martinez, García de León, & Ryan, 2001; Zuk & Kolluru, 1998). 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 (Earley & Dugatkin, 2002, 2005; Johnstone, 2001; Oliveira, McGregor & Latruffe, 1998; Peake, Terry, McGregor, & Dabelsteen, 2001), female mate choice copying (Dugatkin, 1992; Dugatkin & Godin, 1993) and predator detection of male courtship signals (Bernal, Page, Rand, & Ryan, 2007; Koga, Backwell, & Chisty, et al., 2001; Kotiaho, Alatalo, & Mappes, et al., 1998; Macedonia, Brandt, & Clark, 2002; Page & Ryan, 2005; Peake, 2005; Roberts et al., 2007; Virant-Doberlet, King, Polanjanar, & Symondson, 2011; Wagner, 1996). 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 (Doutrelant & McGregor, 2000; Farr, 1976; Galef, 1988; Waas, 1988; Zajonc, 1965).

When male reproductive success is limited by costs of finding mates, selection would favour 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 behaviour 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 (Clark, Roberts, & Uetz, 2012; Roberts, Galbraith, Milliser, Taylor, & Uetz, 2006), we examined the possibility that males of the brush-legged wolf spider, Schizocosa ocreata (Hentz), show eavesdropping and social facilitation of courtship behaviours. Results of the earlier study (Roberts et al., 2006) were inconclusive, as we found no convincing evidence of eavesdropping, social facilitation of courtship or increased exploratory behaviours 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 showed eavesdropping, courtship and signal-matching behaviours (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 behaviours. Male courtship behaviour 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 (Delaney, Roberts, & Uetz, 2007; Stratton & Uetz, 1986). 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 laboratory. In field experiments, we examined responses of males to the presence of courting males, while in the laboratory, we used video playback to eliminate the possibility of male–male interaction, and compared responses of laboratory-reared versus field-collected males to male video stimuli representing courting and noncourting behaviours. To examine the role of experience, we tested the hypothesis that male eavesdropping behaviour is learned by association of male courtship behaviour with sensory cues indicating female presence. Lastly, to confirm that wolf spider behaviours were consistent with eavesdropping, we also compared responses of field-collected focal males to different stimulus male behaviours and examined the role of male density in social facilitation of courtship behaviour.

METHODS

All laboratory studies were conducted in May and June of 2011–2013, with either: (1) sexually mature male Schizocosa ocreata (Hentz) collected from the Cincinnati Nature Center, Rowe Woods, Clermont County, OH, U.S.A., and brought into the laboratory, or (2) laboratory-reared spiders from the same population raised in the laboratory 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 13:11 h light:dark photoperiod. Spiders were fed a diet of two to three 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 2 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, & Rector, 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 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 1 week after laboratory-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 (Hebets & Uetz, 2000; McClintock & Uetz, 1996; Moskalik & Uetz, 2011; Uetz et al., 2011; Uetz & Norton, 2007), but modified for up to three iPod® video screens (Fig. 1). 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 videorecorded from above and video files were scored later with an event recorder (Spectator Go!® software (Biobeserve.com) on an iPod®) to determine how much a male invests in courtship, indicated by an increase in the frequency and duration of leg tapping and other behaviours (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 express higher rates of courtship behaviour overall, our field observations suggest this behaviour 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 showed 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 diameter, ca. 0.5 m² area) constructed from 30 × 130 cm sheets of aluminium
placed in natural leaf litter. Males were introduced first to an empty arena for 5 min, and then introduced to an arena in which a courting male was present for a second 5 min trial. Focal males were handled gently using plastic vials and allowed to acclimate for 1 min 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 h. Females used to provide silk stimuli were unmated females 2–3 weeks post-maturity that were collected in the field as subadults and allowed to mature in isolation in the laboratory. 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 videorecorded for later analysis where focal male subjects were scored for the frequency and duration of tapping (Table 1).

**Eavesdropping in Laboratory-reared versus Field-collected Males**

We conducted a set of laboratory experiments to confirm earlier observations about male eavesdropping and courtship behaviour in laboratory-reared versus field-collected males (Clark et al., 2012; Roberts et al., 2006). We tested the hypothesis that field-collected males are more likely than laboratory-reared males to show courtship in the presence of a courting male, by examining responses to video playback of either a courting male or a male engaged in noncourtship activity (walking). We presented laboratory-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 noncourting (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 laboratory-reared laboratory 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 behaviour of male *S. ocreata* is innate and displayed in response to female silk cues without prior experience (Roberts & Uetz, 2004; Stratton & Uetz, 1981). We therefore predicted that naive 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 3-day period, males were placed in an arena (Fig. 2) and exposed once a day for 5 min to either (1) a video of a courting male in combination with female silk cues and a nearby, but inaccessible, female (Fig. 2a), or (2) a male video alone (Fig. 2b). On day 4, after 3 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 Laboratory Studies with Video Playback**

We tested field-collected males in a choice paradigm: between video playback of a male engaged in courtship behaviour (against a leaf litter background) and either a control leaf litter background (no male present), or a male engaged in noncourtship activity (walking in front of leaf litter background). Males responding to the

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**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.
courtship of other males with increased courtship signalling behaviour, but not responding with courtship to an empty background or to walking male stimuli, would indicate recognition of conspecific courtship behaviour (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: (1) courting male versus control leaf litter background; (2) noncourting (i.e. walking) male versus control leaf litter background; (3) courting male versus walking male. Each trial was videorecorded 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 preempt competitors and attract females away from them). Social density of courting males might affect the tendency to eavesdrop and show 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. 1c). 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 conspecífics: (1) one courting male + two control; (2) two courting males + one control; (3) three courting males; and (4) three control screens. Male behaviours (Table 1) were videorecorded for later scoring and analysis as above.

The live male treatments were conducted in a modified arena (Fig. 1d) with a focal male in the centre of a 15 cm diameter arena, surrounded by a 25 cm outer ring of three 26 cm (outside length) × 16 cm (inside length) × 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 (1) one courting male + two control (empty) chambers, (2) two courting males + one empty chamber; (3) three courting males; or (4) three empty chambers. Male behaviours were videorecorded for scoring and analysis as above.

Ethical Note

To our knowledge, no animal welfare laws or regulations in the U.S.A. or the state of Ohio govern the use of invertebrates such as spiders in research. Wherever possible, we adhered to the ASAB/ABS (2013) Guidelines for the treatment of animals in behavioural

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Behaviours of male S. ocreata wolf spiders in response to video and live male stimuli</th>
</tr>
</thead>
<tbody>
<tr>
<td>Behaviour</td>
<td>Description</td>
</tr>
<tr>
<td>Orient</td>
<td>Male swivels and aligns main axis of body to face screen</td>
</tr>
<tr>
<td>Locomotion</td>
<td>Spider moves about arena at a walking pace</td>
</tr>
<tr>
<td>Approach</td>
<td>Male moves towards screen</td>
</tr>
<tr>
<td>Watch</td>
<td>Having oriented initially, male follows stimulus from stationary position, swiveling back and forth</td>
</tr>
<tr>
<td>Follow</td>
<td>Male actively moves with stimulus</td>
</tr>
<tr>
<td>Interaction</td>
<td>Sum of approach, watch and follow behaviours</td>
</tr>
<tr>
<td>Tapping</td>
<td>Courtship behaviour, consisting of leg tapping and ‘jerky tap’ displays</td>
</tr>
</tbody>
</table>

For a more detailed description, see Delaney et al. (2007) and Roberts and Uetz (2005).

Figure 2. Arenas for conditioning study: (a) arena with male video iPod, female silk cues and live female (behind barrier); (b) male video only.
research and teaching. At the end of this study, spiders were either transferred to another researcher in the laboratory 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 behaviour consistent with eavesdropping (i.e. increased following and courtship behaviour during and after exposure to a live courting male; Fig. 3). Introduced males were significantly more likely to show courtship ($\chi^2_1 = 10.833, P = 0.002$; Fig. 3a) and higher rates of tapping ($t_{17} = 4.409, P = 0.001$; Fig. 3b) in the presence of a courting male.

Eavesdropping in Laboratory-reared versus Field-collected Males

Field-collected males interacted with video males more than did naive laboratory-reared males, indicating (likely) conspecific recognition and/or increased responsiveness (Fig. 4). A two-way ANOVA of the number of interaction bouts (orient, approach, follow, watch) showed significance overall ($F_{3,146} = 5.1527, P = 0.002$), with a significant effect of rearing environment (laboratory versus field: $F_{1,146} = 13.8219, P = 0.001$). Neither group showed a significant difference between the video stimuli (courting versus walking males: $F_{1,146} = 0.8574, P = 0.356$), and the rearing environment*video stimulus interaction was not significant ($F_{1,146} = 0.6788, P = 0.413$). Field-collected males showed significantly more interaction bouts with male video stimuli, regardless of behavioural activity (Fig. 4).

In contrast, the number of bouts of tapping behaviours performed in response to male video stimuli (Fig. 5) showed significance overall ($F_{3,132} = 5.5431, P = 0.001$), as well as a significant effect of rearing environment (laboratory versus field: $F_{1,132} = 10.8403, P = 0.001$) and video stimulus (courting versus walking males: $F_{1,132} = 4.817, P = 0.03$). The rearing environment*video stimulus interaction was not significant ($F_{1,132} = 0.9328, P = 0.336$). While field-collected males performed more bouts of tapping than laboratory-reared males, they also showed a two-fold increase in the number of bouts in response to observation of the courtship of other males (Fig. 5), indicating both conspecific recognition and discrimination of courtship behaviour from non-courtship activities (walking).

Individual tapping bout duration varied with both rearing environment and video stimulus (Fig. 6), with significance overall ($F_{3,51} = 31.4654, P < 0.0001$), and a significant effect of rearing environment*video stimulus ($F_{3,51} = 4.768, P = 0.007$). The duration of tapping in response to courting males was longer than that in response to walking males ($F_{1,51} = 7.649, P = 0.007$).

Figure 3. Courtship behaviours (tapping) of field-collected males ($N = 18$) in response to an empty field arena (control) versus a field arena containing a courting male enclosed on leaf with female silk cues (experimental): (a) percentage of males that showed courtship after introduction to an arena; (b) mean number of tapping bouts performed by males after introduction.

Figure 4. Mean number of bouts of interaction behaviours (orient, approach, follow, watch) shown by field-collected versus naive laboratory-reared males in response to video playback of courting or walking male stimuli.

Figure 5. Mean number of bouts of courtship tapping behaviour displayed by field-collected versus laboratory-reared males in response to courting or walking male video stimuli.
environment (laboratory versus field: \( F_{1,51} = 82.6028, P < 0.0001 \)) as well as video stimulus (courting versus walking males: \( F_{1,51} = 5.213, P = 0.0256 \)). The source × video stimulus interaction was not significant (\( F_{1,51} = 1.4825, P = 0.229 \)). Field-collected males performed longer bouts of tapping in the presence of video males compared to laboratory-reared males (Fig. 6). They also performed longer tapping bouts in response to courting males than in response to walking males, suggesting increased investment in courtship activity.

Overall, the amount of time engaged in courtship tapping varied with both rearing environment and video stimulus (Fig. 7), with significance overall (\( F_{1,129} = 7.7061, P < 0.0001 \)), and a significant effect of rearing environment (laboratory versus field: \( F_{1,129} = 17.5954, P < 0.0001 \)) as well as video stimulus (courting versus walking males: \( F_{1,129} = 4.0786, P = 0.046 \)). The source × video stimulus interaction was not significant (\( F_{1,129} = 1.6907, P = 0.196 \)). Field-collected males spent more time courting in the presence of courting males than in the presence of walking males, while laboratory-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 showed 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 performed significantly more signalling bouts when presented with male courtship signals alone after their training period (\( F_{2,26} = 5.024, P = 0.014 \)) than those exposed to male courtship alone or with no exposure (naïve males). These results suggest that males learn to associate male courtship behaviour (conditioned stimulus) with cues indicating the presence of females (unconditioned stimulus).

**Verifying Eavesdropping in Laboratory Studies with Video Playback**

In choice tests with videos of two live male wolf spiders presented simultaneously, males responded to courting and walking male stimuli with interaction behaviours (approach, watch, follow) but responded far less to an empty leaf litter background. Males performed significantly more interaction bouts and significantly longer bouts of interaction behaviour, and spent more time interacting with walking and courting male stimuli than with a blank screen (Table 2). 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) showed that males performed significantly more tapping bouts (paired t test: \( t_{13} = 2.252, P = 0.031 \)) and spent more time tapping (\( t_{13} = 2.328, P = 0.026 \)) in the presence of a courting male versus a walking male stimulus, although there was no difference in tapping bout duration (\( t_{13} = 1.0465, P = 0.303 \)).

**Effects of Male Density on Social Facilitation and Eavesdropping**

Studies manipulating social density (number of courting male stimuli) revealed that duration of male courtship (total time performing 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 behaviours showed significance for the number of courting males (\( F_{3,63} = 6.3664, P = 0.001 \)), but no difference between live and video male stimuli (\( F_{1,63} = 2.6729, P = 0.107 \)). The interaction of number of courting males × male stimulus type (video/live) was also not significant (\( F_{3,63} = 0.3718, P = 0.774 \)).

**DISCUSSION**

Results of this study suggest that male *S. ocreata* wolf spiders recognize conspecific males, are attentive to their behaviour, and...
respond to male courtship displays by initiating courtship (presumably exploiting signals to intercept a female), which is consistent with common definitions of eavesdropping behaviour (McGregor, 2005). While most examples of eavesdropping have come from vertebrate animals (see McGregor, 2005), it appears that some invertebrates also show this ability (Aquiloni, Burić, & Gherardi, 2008; Aquiloni & Gherardi, 2010; Bailey & Field, 2000; Fitzsimmons & Bertram, 2013; Milner, Jennions, & Backwell, 2010, 2012; Pope, 2005). 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 behaviour of others (Dabelsteen, 2005; Peake, 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 (Aquiloni & Gherardi, 2010; Dugatkin, 1992; Dugatkin & Godin, 1993; Earley & Dugatkin, 2005; Peake et al., 2001). 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 (Doutrelant & McGregor, 2000; Farr, 1976; Galef, 1988; Milner et al., 2010; Waas, 1988; Zajonc, 1965). 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 do not show

### Table 2
Number of bouts of interaction behaviours (approach, follow, watch) shown by focal male S. ocreata in response to paired video playback of walking versus courting male stimuli

<table>
<thead>
<tr>
<th>Focal male behaviour</th>
<th>Video stimulus</th>
<th>Mean±SE</th>
<th>Paired t</th>
<th>P</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of interaction bouts</td>
<td>Walking male</td>
<td>2.405±0.581</td>
<td>8.465</td>
<td>&lt;0.0001</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>Blank screen</td>
<td>7.864±0.581</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Courting male</td>
<td>19.019±6.562</td>
<td>7.467</td>
<td>&lt;0.0001</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>Blank screen</td>
<td>1.883±6.562</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Courting male</td>
<td>7.171±1.185</td>
<td>0.0482</td>
<td>0.9618</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>Walking male</td>
<td>7.228±1.185</td>
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<td></td>
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<tr>
<td>Interaction bout length</td>
<td>Walking male</td>
<td>53.983±4.538</td>
<td>7.107</td>
<td>&lt;0.0001</td>
<td>71</td>
</tr>
<tr>
<td></td>
<td>Blank screen</td>
<td>8.048±6.601</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Courting male</td>
<td>52.578±7.613</td>
<td>4.231</td>
<td>&lt;0.0001</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>Blank screen</td>
<td>6.186±7.706</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Courting male</td>
<td>31.710±7.493</td>
<td>0.134</td>
<td>0.894</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>Walking male</td>
<td>40.121±5.570</td>
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<td></td>
</tr>
<tr>
<td>Total time interacting</td>
<td>Walking male</td>
<td>175.310±10.81</td>
<td>9.995</td>
<td>&lt;0.0001</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>Blank screen</td>
<td>22.572±10.85</td>
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<td></td>
<td></td>
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<tr>
<td></td>
<td>Courting male</td>
<td>167.608±11.647</td>
<td>8.980</td>
<td>&lt;0.0001</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>Blank screen</td>
<td>16.960±11.788</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Courting male</td>
<td>89.943±13.605</td>
<td>0.427</td>
<td>0.672</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>Walking male</td>
<td>99.519±13.644</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Results of paired t tests comparing means are shown. Significant outcomes are indicated in bold.

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

**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.
eavesdropping or social facilitation of courtship behaviour (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 laboratory, had little or no opportunity for exposure to the behaviour 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 behaviour. Several previous studies have demonstrated that wolf spider behaviour is influenced by experience and that subadult female exposure to adult male courtship cues can affect adult female mating behaviour in wolf spiders (Hebets, 2003; Hebets & Vink, 2007; Rutledge et al., 2010). In comparison with laboratory-reared males, field-collected males spent more time engaged in interaction behaviours and performed 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 (Clark et al., 2012; Roberts et al., 2006), but suggests that male spiders learn quickly (5 min exposures over 3 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 that males learn to associate the presence of females from the behaviour of other males. It is important to note that courtship behaviour of male S. ocreata is innate and displayed in response to female silk cues without prior experience (Roberts & Uetz, 2004, 2005; Stratton & Uetz, 1981). 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 ways. Female S. ocreata are essentially monogamous and mate only once, so information on location of females allows eavesdropping males to increase the 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; Haynes & Yeqorgan, 1999; Rosenthal, 2007; Zuk & Kolluru, 1998). Courtship display of male S. ocreata is conspicuous and clearly detectable by predators (Pruden & Uetz, 2004; Roberts et al., 2007; Roberts & Uetz, 2008), and males have been shown to cease courting in the presence of predator cues (Fowler-Finn & Hebets, 2011; Lohrey, Clark, Gordon, & Uetz, 2005). In this context, that is, courting when behaviour of others indicates female presence nearby, eavesdropping might be seen as tipping the balance of the trade-off between mating success versus mate competition and predation risk.

This study suggests that field-collected (and presumably experienced) male wolf spiders can recognize male conspecifics and discriminate between behaviours, evidenced in field enclosure experiments where males responded with increased courtship signalling behaviour 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 they did 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 show greater amounts of courtship signalling in front of screens with courting males, which supports the hypothesis of eavesdropping and exploiting the courtship behaviour of others. Additional studies with both live males and video playback showed that males spent significantly more time engaged 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 behaviour.

Taken together, results presented here provide strong evidence that male S. ocreata wolf spiders show behaviours consistent with social eavesdropping. These findings are potentially significant, considering that this is an invertebrate animal, for which behavioural plasticity is assumed to be limited (Gordon & Uetz, 2011). At the very least, this finding suggests that variables such as field experience in the fairly short breeding season may play a role in eavesdropping behaviour. Several previous studies (Hebets, 2003; Hebets & Vink, 2007; Rutledge et al., 2010) supports the hypothesis of eavesdropping and exploiting the courtship behaviour of others. Additional studies with both live males and video playback showed that males spent significantly more time engaged 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 behaviour.

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References
