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# 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.


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, & Christy, 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, Polanjnar, & Symondson, 2011; Wagner, 1996). One potentially fruitful area of investigation is facilitation of courtship arising as a consequence of social

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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 Roberts et al. (2007) and population mean courtship vigour (number of taps/min) 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 (Biobserve.com) on an iPad®) 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 $m^2$ area) constructed from 30 × 130 cm sheets of aluminium