Eavesdropping and signal matching in visual courtship displays of spiders

David L. Clark¹, J. Andrew Roberts² and George W. Uetz³,*

¹Department of Biology, Alma College, Alma, MI 48801, USA
²Department of Evolution, Ecology and Organismal Biology, The Ohio State University at Newark, Newark, OH 43055, USA
³Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221-0006, USA
*Author for correspondence (george.uezt@uc.edu).

Eavesdropping on communication is widespread among animals, e.g. bystanders observing male–male contests, female mate choice copying and predator detection of prey cues. Some animals also exhibit signal matching, e.g. overlapping of competitors’ acoustic signals in aggressive interactions. Fewer studies have examined male eavesdropping on conspecific courtship, although males could increase mating success by attending eavesdropping on conspecific courtship currently. Although, male contest call could increase mating success by attending eavesdropping on conspecific courtship current role of experience. Because our previous studies were conducted with naive spiders reared in laboratory isolation, we repeated our tests for eavesdropping with field-collected males (presumed to be exposed to male courtship and/or female cues) using video playback of male courtship.

2. MATERIAL AND METHODS
All studies were conducted with sexually mature male Schizocosa ocreata (Hentz) collected from the Cincinnati Nature Center, Rowe Woods, Clermont County, OH, USA and brought into the laboratory. 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 L:11 D cycle photoperiod. Spiders were fed two to three cricket nymphs twice weekly.

We duplicated earlier video playback studies [11] with field-collected, ‘experienced’ males (n = 24; eight males per video exemplar) and conducted trials within the first week after capture to standardize influence of the laboratory environment. Video playback stimuli were prepared from digital video of live courting male spiders as in previous studies [11,18,19]. Three different male ‘exemplars’ were used as replicate stimuli to avoid pseudoreplication [20] and were superimposed on a digital background of natural leaf litter scaled to actual size (see Uetz & Roberts [18] and Uetz et al. [19] for details). All trials took place in standard circular clear plastic playback arenas (15 cm diameter, 6.5 cm high), as in previous studies [11,18,19], with an iPod video screen (figure 1a). Each trial consisted of: (i) a 3 min period showing a video of a leaf litter background with no male present (‘pre-exposure’); followed by (ii) a 3 min exposure to video playback of a courting male stimulus against the same background (‘stimulus exposure’); and (iii) a 3 min period with the empty background again (‘post-exposure’). A second set of trials used a paired design with two iPod video screens to test male responses to courting versus walking male stimuli. Each male was tested only once to control for experience effects with a video apparatus. Trials were videotaped, and focal male test subjects were scored later for the frequency of courtship tapping displays (i.e. forelegs waved up and down and tapped against the substrate).

3. RESULTS
Field-collected males demonstrated behaviour consistent with eavesdropping on the courting male stimulus, i.e. increased interactive behaviour and courtship signalling during stimulus exposure and a subsequent increase in courtship after exposure. Males showed a significantly longer mean bout duration of interactive behaviours (approach, follow and watch) when the video male stimulus was present on the video screen (figure 1b). A two-way mixed-model ANOVA of duration of bouts of interactive behaviours, with exposure period and exemplar as main effects and focal males nested as a random factor within exemplar showed significance for exposure period (F2,22 = 5.561; p = 0.0116) but not video exemplar (F2,22 = 0.7399; p = 0.5004), or exposure period x exemplar interaction (F4,44 = 0.9293; p = 0.4659). Males showed significantly more bouts of courtship and initiating sexual displays whenever courtship is detected [11–14].

Our previous studies of eavesdropping in male Schizocosa ocreata wolf spiders using video playback of male courtship found no convincing evidence of eavesdropping behaviours [11]. However, field observations of high male density during the breeding season suggest a communication network with a high probability of signal interception, and we have frequently seen multiple males searching and courting in the vicinity of (hidden) females. Recent studies found that social experience of juvenile female Schizocosa spp. can influence subsequent mate choice behaviours as adults [15–17], raising questions about the role of experience. Because our previous studies were conducted with naive spiders reared in laboratory isolation, we repeated our tests for eavesdropping with field-collected males (presumed to be exposed to male courtship and/or female cues) using video playback of male courtship.

1. INTRODUCTION
In animal communication networks, unintended receivers may include social eavesdroppers—i.e. conspecifics that recognize and exploit the information content of signals, or interceptive eavesdroppers—i.e. predators for which signals reveal the presence of prey [1,2]. Research has examined eavesdropping in several contexts, including bystanders observing male–male contests [3–5], female mate choice copying [6,7], and predator detection of male courtship signals [8–10]. One less-studied area is social facilitation of courtship arising as a consequence of eavesdropping [11,12]. When male reproductive success is limited by costs of finding mates, selection should favor males that exploit information revealing the location of prospective mates by eavesdropping on the behaviour of nearby rivals.
activity (tapping, jerky tapping) during and after presentation of the video stimulus male (figure 1c). A two-way mixed-model ANOVA of tapping bouts, with exposure period and exemplar as main effects (and focal males nested as a random factor within exemplar) showed significance for both exposure period ($F_{2,42} = 3.277; p = 0.047$) and video exemplar ($F_{2,21} = 3.953; p = 0.0349$), but no significant exposure period × exemplar interaction ($F_{4,42} = 1.572; p = 0.199$). Although males interacted equally with courting or walking male stimuli (figure 2a; paired $t_{34} = 0.984, p = 0.3321$) the number of bouts of tapping adjacent to courting males were significantly greater (figure 2b; paired $t_{35} = 2.324, p = 0.026$). Given the significant effect of exemplar on focal male courtship rates, we reviewed the stimulus videotapes and scored rates of tapping behaviours displayed by stimulus males. Tapping rates of focal males varied positively with tapping rates of the different exemplars with which they were paired ($r = 0.534; p = 0.007$). To examine this relationship, we conducted an additional experiment in which male *S. ocreata* were exposed to exemplars from a previous study [21] that were manipulated to vary in courtship vigour ($n = 9$ exemplars; 12 focal spiders each exemplar). Focal male courtship rates varied significantly with rank order of exemplar courtship rate (Spearman $r = 0.319; p < 0.001$; figure 2c).

4. DISCUSSION

Field-experienced male *S. ocreata* attend to visual courtship displays of other males and respond by initiating courtship, possibly to attract females. Additionally,
males exhibit courtship in response to videos of courting males but not non-courting (walking) males. These findings strongly suggest eavesdropping and social facilitation. Since previous studies [11] used males collected as juveniles that matured in laboratory isolation (no exposure to other males or females), our results suggest that experience gained in the field during the breeding season may play a role in eavesdropping behaviour. Evidence for a role of experience in arthropod mating behaviour is growing [22,23], and studies have demonstrated that subadult female experience with cues from adult males influences adult female mate choice in Schizocosa spp. [15–17]. Moreover, male Schizocosa wolf spiders have demonstrated flexibility in courtship based on experience and environmental cues [24,25]. Our results show that males alter subsequent courtship display behaviour once exposed to the courtship of others, as has been shown for fiddler crabs (Uca pugnax) [12,26] and acoustic displays of bushcrickets (Elephantopus deta nobilis) and anurans [27,28]. As male S. ocreata use displays primarily in the context of courtship but not aggression [29], this observation meets criteria for social eavesdropping within a communication network [30]. The most interesting finding is that courtship rates of focal male spiders varied with tapping rates of the male exemplars to which they were exposed, suggesting signal matching or rate synchronization, which has previously been seen primarily in the acoustic communication of vertebrates, such as birds, fish, anurans and lizards [31–34], and churung insects [35].

Our findings suggest that male wolf spiders may be able to gain information about female location by eavesdropping on visual courtship displays of others and are able to adjust their subsequent performance to match that of rivals. This represents a novel finding for invertebrates, in which behavioural plasticity is limited.

Support was provided by the National Science Foundation (grants IBN 0239164/IBN 0238854 and grants IOS1026995/IOS1026817). We thank the Cincinnati Nature Center for permission to collect spiders, and graduate and undergraduate students from the University of Cincinnati and Alma College, especially Corinna Kizer.


