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SHORT COMMUNICATION

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Flexibility in the multi-modal courtship of a wolf spider, *Schizocosa ocreata*

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Abstract Male *Schizocosa ocreata* wolf spiders court females with synchronous visual and seismic displays. We tested whether male *S. ocreata* modify their courtship in relation to light environment, and associated utility of the visual components. Males were generally more active and more likely to perform the major courtship element ("jerky tapping") when in the light. One courtship element ("arching") was only observed in the light while another ("vertical leg-extend") was only observed in the dark. Courtship in the dark retained "visual" components, suggesting spiders cannot disengage these components of multi-modal display even when superfluous. Once initiated, there was no evidence that performance rate or time spent in each courtship element differed in the light and in the dark.

Key words Behavioral flexibility · Courtship · Multi-modal · *Schizocosa ocreata* · Wolf spider

Introduction

Animal communication systems often span several sensory modes ("multi-modality") and contain a variety of signals within each sensory mode. For example, birds may produce a variety of visual and acoustic signals during begging (Price and Ydenberg 1995) and courtship (Höglund et al. 1997); tephritid flies may use simultaneous visual, olfactory, and acoustic signals during courtship (Alonso-Pimental et al. 2000); snapping shrimp combine visual and chemical signals during sexual and agonistic interactions (Hughes 1996); humans routinely use complex combinations of visual and acoustic signals when communicating (Alibali et al. 2001; Iverson and Goldin-Meadow 2001; Rooney et al. 2001). Questions of how and why animals use multiple signals and sensory modes when communicating are currently a major focus in communication research (Møller and Pomiankowski 1993; Johnstone 1995, 1996; Brooks and Couldridge 1999; Partan and Marler 1999).

Schizocosa wolf spiders (Lycosidae) have provided one of the most fruitful model systems for studies of multimodal communication (Uetz 2000; Uetz and Roberts 2002). This genus includes representatives with various degrees of reliance on visual and vibratory ("seismic") modes for communication (McClintock and Uetz 1996; Miller et al. 1998; Hebets and Uetz 1999, 2000). *Schizocosa ocreata* has been one of the most thoroughly studied representatives of this spider genus. During courtship, males of *S. ocreata* rely on elaborate displays that involve jerky up-and-down body motion and several distinct categories of foreleg motion (Table 1). Males have dark forelegs bearing tufts of hairs that have been interpreted as amplifiers (see Hasson 1997; Taylor et al. 2000; Moya-Laraño et al. 2003) of leg displays both in *S. ocreata* and in congenors (McClintock and Uetz 1996; Scheffer et al. 1996; Hebets and Uetz 1999, 2000). Tuft size may reflect developmental nutrition, and so may also be a quality indicator (Uetz et al. 2002); females show greater receptivity toward males with large tufts (McClintock and Uetz 1996; Scheffer et al. 1996; Uetz 2000; Persons and Uetz 2004).

Each display element used by courting *S. ocreata* males includes physical motions of forelegs and/or body, many of which are known to function as visual displays. Synchronous seismic components accompany each visual display component (Table 1). These visual and seismic components have been interpreted together as multi-modal displays when used in the light (Uetz and Denterlein 1979; Stratton and Uetz 1981, 1983, 1986): up-and-down body motion produces percussion as the body strikes the substrate and leg motions occur in close synchrony with powerful and distinctive bursts of stridulation (produced by specialized organs in the pedipalps). Stridulation is also occasionally emitted during courtship while males are standing still or walking slowly, but the vibrations produced in this context are weak and lack the characteristic pulses that accompany leg and body motions.

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Table 1. Courtship elements of *Schizocosa ocreata* males

Behavior	Description
Stationary	Standing still, palps still
Locomotion	Walking
Groom	While standing still, the spider draws legs through its chelicerae, rubs legs together and rubs legs over the soma
Chemoexplore	Spider slides its palps back and forth against the substrate
Vertical leg extend	Legs raised slowly 70–90° up, usually while walking, then lowered to the substratum. Stridulation evident during leg movement
Wave	One or both forelegs raised and lowered slowly while all joints close to full extension. Stridulation evident during leg movement
Tap	One or both forelegs raised and lowered rapidly so that they struck the substrate. Stridulation evident during leg movement
Jerky tap	Prosoma rapidly lowered so that it forcefully strikes the substrate emitting a percussive "thump". Forelegs raised and lowered immediately before and after prosoma movement. Stridulation evident during leg movement
Arch	One leg raised slowly in several steps with distal joints flexed. Stridulation evident during leg movement

While considerable attention has been paid to *S. ocreata* female decisions of which males to accept as mates, and the role of multi-modal displays in these decisions, far less attention has been paid to male decisions of whether and how to display. Are males able to tailor their courtship activities to suit local sensory conditions or are they instead automaton-like with rigid, inflexible responses to courtship-eliciting stimuli? In nature, males may court females in well-lit open situations where visual and seismic display components can be equally useful, or may instead court females in darkness below the surface layers of the dense vegetation and leaf litter that forms their typical habitat. We consider two potential types of signal flexibility that might be expected in spiders matching their courtship activity to local sensory conditions. First, we consider whether male *S. ocreata* have different tendencies to use each courtship element (Table 1) in the light and in the dark. Condition-dependence would be consistent with the idea that utility of affected courtship elements is limited under the conditions where they are less used and that the spiders are matching display choice to suit. Second, we consider whether the elaborate body and foreleg motions that characterize each display element are omitted when rendered superfluous by darkness. That is, do spiders in the dark use the powerful pulses of seismic components alone, without the leg and body movements usually interpreted as visual display components?

Materials and methods

Sub-adult males and females of *S. ocreata* were collected from dense leaf litter at Cincinnati Nature Center, Rowe Woods (Clermont County, Ohio, USA), during March, April, May and September 2001. We kept the spiders visually isolated from each other in cylindrical white plastic containers (11 cm diameter; 8.5 cm high) under laboratory conditions of 13 : 11 L : D photoperiod, c.23°C and c.65% RH. Spiders were fed 2–3 pinhead crickets twice weekly and had continual access to water by way of a soaked cotton wick inserted through a hole in the cage floor into a reservoir below. Spiders matured in the laboratory and were used in experiments between 7 and 50 days after maturing. All spiders were virgins when tested.

We investigated whether males of *S. ocreata* modify their courtship behavior depending on sensory environment (light vs dark) and the associated efficacy of visual and seismic signal components. Twenty virgin females were confined for 12 h on sheets of card (100 × 150 mm) by restraining each female in an upturned plexiglas box (50 mm wide, 100 mm long, 50 mm high). Cues associated with silk on areas recently occupied by conspecific females are effective in releasing courtship in *S. ocreata* males (Stratton and Uetz 1981, 1983, 1986). After the silk-collecting period, females were returned to their cages and the silk-covered cards were used in courtship trials within the following 8 h. When not being used in trials, the silk-covered cards were set aside on a shelf in the laboratory. A male *S. ocreata* was assigned to each of the 20 silk-covered cards and his courtship behavior was recorded on the same card both in the light and in the dark. Trials in the light and in the dark were carried out at least 4 h apart on the same day (ten males light first, ten males dark first).

All trials were carried out in a photographic darkroom. For trials in the light, illumination was provided by two 25-W fluorescent lights suspended 0.5 m above the arena. For trials in the dark, illumination was provided by an Infra-Red (IR) light source (Sony HVL-IRC). Wolf spider eyes are not sensitive to IR light (Yamashita 1985) and so this set-up is equivalent to total darkness for the spiders. All trials were videorecorded using an IR-sensitive camera (Watec WAT-902C) positioned above the testing arena, connected to the video input of a Sony DA Pro 4 Head VHS VCR.

Seismic courtship components were recorded using an accelerometer (PCB Piezoelectronics model 352C65) connected to a signal conditioner (PCB Piezoelectronics model 480E09) that was, in turn, connected to the audio input of the VCR used to videorecord spider activity. By recording spider seismic signals on the video soundtrack, we could easily confirm the temporal association between visual and seismic components reported in previous studies (Uetz and Denterlein 1979; Stratton and Uetz 1981, 1983, 1986) and that these associations were evident both in the light and in the dark.

To set up a trial, a clear plexiglas "corral" with open top (50 mm wide, 100 mm long, 50 mm high) was placed over the 50 × 100 mm patch of silk where the female had been. The male was released onto this patch of silk-covered card by transferring him from his maintenance cage in a 10-ml plastic vial and lowering him in from above. After the male exited the vial and was standing on the silk-covered card, his behavior was videorecorded for the following 5 min. An ethogram containing nine distinct courtship elements (derived from descriptions of previous studies and an initial review of our own recordings) was used to compare each male's performance in the light and in the dark (Table 1). Videorecordings of male courtship activity were assessed using The Observer 3.1 software (Noldus).

We tested whether each courtship element was more likely to be observed in the light or in the dark using McNemar's test for significance of changes with Williams' correction (Sokal and Rohlf 1981). As the same male was used under each of the two light regimes, the number of times each courtship element was performed and the total amount of time spent in each behavior were compared by paired *t*-test. Only cases in which a courtship element was performed by a male at least once in each light regime were considered, thereby excluding all zero counts. In this way, we separated the question of whether a courtship element was performed at all from the questions of how often and for how much time a courtship element was performed by an individual male.

Results

Performance probability

Some courtship elements (locomotion, stationary, chemoexplore, wave and tap) were as likely to be performed by a spider in the light as in the dark (Table 2). However, other courtship elements were more likely to be performed in one of the two light regimes. Most spiders (75%) performed jerky tapping (the major courtship element; Stratton and Uetz 1981, 1983, 1986) both in the light and in the dark. However, whereas some spiders performed jerky tap only in the light, there were no spiders that performed jerky tap only in the dark. Also, more spiders groomed in the dark than in the light (Table 2). Two courtship elements were observed in only one of the light regimes. Arching, in which one foreleg is raised with distal joints flexed while stridulating, was only observed in the light. Vertical leg-extend, in which one or both forelegs were held up 70–90° above horizontal and then lowered while stridulating, was only observed in the dark (Table 2). Strongly pulsed stridulation that characterizes display was not observed in the absence of up-and-down leg-movement, despite these leg movements being undetectable by females in the dark.

Table 2. Number of the 20 tested *Schizocosa ocreata* males that displayed each courtship element in the light and in the dark (under IR light), and results of McNemar tests for significance of changes (Sokal and Rohlf 1981)

	Light only	Dark only	Both	Neither	*G*	*P*
Stationary	0	0	20	0	–	–
Locomotion	0	0	20	0	–	–
Groom	0	5	4	11	6.301	<0.025
Chemoexplore	2	2	16	0	<0.001	>0.9
Vertical leg extend	0	12	0	8	15.970	<0.001
Wave	3	5	4	8	0.476	>0.25
Tap	3	2	15	0	0.183	>0.5
Jerky tap	4	0	15	1	4.929	<0.05
Arch	5	0	0	15	6.301	<0.025

Performance frequency

Among individual spiders that performed a given courtship element under both light regimes, no courtship elements were performed significantly more often in one of the two light regimes (Table 3). There was a suggestive trend of more waving in the dark than in the light (Table 3), but this analysis is limited by small sample size for this infrequent element. Only four spiders waved in both light regimes, but in each case the spider waved more often in the dark.

Performance total duration

Although performed equally often in the light and in the dark, significantly more time was spent walking in the light and significantly more time was spent standing still in the dark (Table 4). There were no significant differences in the amount of time spent tapping, jerky tapping, grooming and chemoexploring under the two different light regimes (Table 4). The suggestive trend of spiders waving more often in the dark (Table 3) translated into a similarly suggestive trend for amount of time spent waving in the two light regimes (Table 4).

Discussion

Males of *S. ocreata* were less likely to perform the major courtship display element of jerky tapping in the dark than in the light (Table 2). This may be best interpreted as reluctance to enter into full courtship when in the dark. Such reluctance may stem from diminished ability to detect imminent attacks from potentially aggressive females. If

Table 3. Average number of bouts of each courtship element performed by males in the light and in the dark (under IR light). Only spiders that performed a courtship element at least once in both light regimes are included. Comparison is by paired *t*-test

	n	Light	Dark	|*t*|	*P*
Stationary	20	35.05	38.00	0.665	0.514
Locomotion	20	27.20	22.60	1.255	0.225
Groom	4	12.00	9.00	0.516	0.642
Chemoexplore	16	21.19	22.75	0.574	0.574
Wave	4	1.50	4.50	2.777	0.069
Tap	15	10.93	8.87	0.783	0.447
Jerky tap	15	27.73	27.40	0.074	0.942
Vertical leg extend	12	–		4.17	
Arch	5	3.00		–	
Total displays[a]	20	32.95	31.75	0.315	0.756

[a] Wave + Tap + Jerky tap + Leg extend + Arch

Table 4. Average amount of time (seconds) spent in each courtship element by males in the light and in the dark (under IR light). Only spiders that performed a courtship element at least once in both light regimes are included. Comparison is by paired *t*-test

	n	Light	Dark	$\|t\|$	*P*
Stationary	20	88.46	119.43	2.163	0.044
Locomotion	20	83.91	47.36	3.289	0.004
Grooming	4	54.80	40.58	0.586	0.599
Chemoexplore	16	62.21	65.44	0.409	0.689
Wave	4	0.73	3.60	2.585	0.082
Tap	15	6.30	5.77	0.242	0.812
Jerky tap	15	69.31	69.99	0.048	0.962
Vertical leg extend	12	–		4.03	
Arch	5	6.54	–		
Total displays[a]	20	62.62	60.66	0.182	0.858

[a] Wave + Tap + Jerky tap + Leg extend + Arch

released at all, the major courtship element of jerky tapping was performed similarly often and for a similar total time in the light and in the dark (Tables 2, 3, 4). Interestingly, some minor elements of male courtship were only observed in the light (arch) or in the dark (vertical leg extend) (Table 2), indicating a degree of light-dependent flexibility in the courtship repertoire used by male *S. ocreata*. An ability to tailor courtship repertoire in relation to sensory environment is common in jumping spiders (Jackson 1992; Taylor and Jackson 1999), but has not previously been reported in a *Schizocosa* wolf spider. Although arching was only observed in the light, it does contain a seismic component (stridulation) that could potentially function also in the dark. It may be that the seismic component of arching is not functional when isolated from the visual component (e.g., the seismic component of arching may be a "modifier" sensu Partan and Marler 1999).

Each of the courtship display elements observed in the dark was performed in full, including both the seismic components and the leg and body motion components that function as visual displays in the light (see Uetz and Roberts 2002). Even vertical leg extend, which was only observed in the dark, contains distinctive and elaborate leg movements that would not be perceptible by females under these conditions. Strong seismic pulses of stridulation were only noted in association with the defined courtship elements (i.e. along with up-and-down leg motions). Performance of leg motions in a context where they would be superfluous as visual displays requires some explanation. It is no surprise that jerky up-and-down body motions are retained in the dark; these motions are the direct means by which percussive seismic components are produced. Could a similar explanation underlie the persistence of leg motions in the dark? It could be that the leg motion is more than a visual display component; these leg motions may, like body motion, be integral to the production of pulsed seismic components. For example, leg motion might provide a hydraulic impetus that helps to drive the powerful bursts of stridulation, and leg movements that accompany jerky tapping may help to counterbalance the powerful up-and-down body motion. Another possibility is that the spiders are simply "wired" in an inflexible fashion that prohibits disengaging of the two modal components of courtship displays that involve leg motion. These speculative possibilities are consistent with the high degree of synchrony between visual and pulsed seismic signals.

The close synchrony of visual and seismic components means that performance rates in the visual and seismic modes are highly coincident in the light and that information from the seismic mode alone in the dark is a reliable predictor of visually undetectable leg and body movements. If performance rate is a key male attribute of interest to females, as has been reported in some other wolf spiders (Kotiaho et al. 1996; Parri et al. 1997) and many more distant taxa (see Ryan and Keddy-Hector 1992), then the two signalling modes may provide similar information to females. The two modal components of each display element may be largely "redundant" and "equivalent" (sensu Partan and Marler 1999); all the necessary information about male display rate may be evident to females assessing males in the seismic mode alone when in the dark.

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