

## **Assessment of Potential Predation Costs of Male Decoration and Courtship Display in Wolf Spiders Using Video Digitization and Playback**

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*Accepted September 18, 2003; revised October 14, 2003*

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*We used video digitization and playback techniques to examine the potential predation risk of leg decorations and visual displays of male wolf spiders, which vary across the genus *Schizocosa* (Araneae: Lycosidae). Video images of courting males of four *Schizocosa* species were modified by adding or removing tufts and presented on LCD minitelevisions to the wolf spider *Hogna helluo*, a common predator of *Schizocosa*. Predatory responses of *H. helluo* varied significantly among stimuli and were highest for *S. ocreata* (which has decorative tufts and leg-waving displays) and lower for *S. rovneri*, *S. duplex*, and *S. uetzi* (which lack decorations and visual displays). Removal of tufts from *S. ocreata* significantly reduced predatory responses of *H. helluo*, but addition of tufts to other species had no effect. Results suggest that leg decorations may increase detection of active leg-waving displays and thereby increase predation risk.*

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**KEY WORDS:** predation; video playback; male decorations; wolf spiders; Lycosidae.

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## INTRODUCTION

While it is generally accepted that male traits favored by sexual selection are often counteracted by natural selection from predation (Endler, 1980, 1983; Thornhill and Alcock, 1983; Ryan, 1985; Andersson, 1994; Møller and De Lope, 1994), the role of predation as a constraint on the evolution of male secondary traits and signals has only been investigated more recently (Endler, 1987, 1991, 1992, 2000; Sakaluk, 1990; Zuk and Kolluru, 1998; Haynes and Yeargan, 1999). While numerous studies indicate that male signals acting to increase conspicuousness to females also attract the attention of predators (Moodie, 1972; Endler, 1978, 1980; Reznick and Endler, 1982; Sakaluk and Belwood, 1984; Petrie, 1992; Koga *et al.*, 2001), there are fewer empirical or mechanistic studies (Endler, 1987, 1991; Gotmark, 1997; Kotiaho *et al.*, 1998; Rosenthal *et al.*, 2001) on aspects of predator detection.

The wolf spider genus *Schizocosa* (Araneae: Lycosidae) is an excellent model system for evaluating the influence of sexual selection and predation on sexual signaling (see reviews by Uetz, 2000; Uetz and Roberts, 2002). Members of this genus are wandering, non-web-building wolf spiders that inhabit most of the deciduous forest region of eastern North America (Dondale and Redner, 1978, 1990). The *S. ocreata* clade contains at least six closely related species that appear to have recently speciated as a consequence of behavioral reproductive isolation (Stratton and Uetz, 1986; Miller *et al.*, 1998). Females are nearly indistinguishable morphologically, while males are distinguishable by the presence or absence of decorative tufts or pigments on the forelegs and species-specific courtship behaviors. Females of *Schizocosa* spp. usually mate only with conspecific males, whose courtship signals involve various combinations of visual and vibratory displays.

In this study, we examine how variation in male visual courtship displays and decorations of wolf spiders influence the risk of detection by predatory spiders. Previous studies of several species have shown that sexual receptivity of female *Schizocosa* varies with the presence/absence and/or size of male tufts (Uetz, 2000; Hebets and Uetz, 2001). We tested the hypothesis that decorative leg tufts and visual courtship displays in the genus *Schizocosa* incur a potential predation risk, by comparing responses of a predator to variation in leg tufts and visual displays among four species in this genus, using digital video image manipulation and playback.

## MATERIALS AND METHODS

### Study Species

We used the large wolf spider *Hogna* [*Lycosa*] *helluo* (Walkenaer) as the predator in this study. *H. helluo* is common in the deciduous forests and

edge habitats of eastern North America and is sympatric with all species of *Schizocosa* wolf spiders in this study (Kaston, 1948; Uetz, 1976; Cady *et al.*, 1980; Dondale and Redner, 1990). This species was chosen because *Hogna* (1) hunt prey using visual cues (Marshall *et al.*, 2000, personal observation), (2) have been observed to eat *Schizocosa* both in the lab and in the field (Wise and Chen 1999a, b; personal observation), and (3) respond to video playback of wolf spiders with orientation and prey-capture behavior (Roberts, 2003, personal observation). Because of its abundance and large mass (ca. 200 mg), *H. helluo* is thought to be an important intraguild predator (Marshall and Rypstra, 1999; Marshall *et al.*, 2000; Persons *et al.*, 2001). We collected *H. helluo* in September 1996 from a deciduous forest edge microhabitat adjacent to an open grass field in Mount Airy Forest, Cincinnati, Hamilton County, Ohio. We used only mature females in the experimental studies, since they are generally more rapacious than males or juveniles.

We used male courtship of four representative species from the genus *Schizocosa* as stimuli for video playback. These four species were chosen because they vary in the degree of decoration and pigmentation of the forelegs and the use of visual and vibratory signaling during courtship (Hebets and Uetz, 1999, 2000).

(1) *Schizocosa ocreata* (Hentz) has decorative tufts of dark bristles on the forelegs as well as a highly visual and locomotive courtship display, which involves conspicuous tapping of the tufted forelegs and stridulation with the pedipalps (Uetz and Denterlein, 1970; Stratton and Uetz, 1981, 1983, 1986). Females of this species exhibit receptivity with equal frequency to isolated visual and vibratory courtship signals from conspecific males (Scheffer *et al.*, 1996). There is some evidence from studies with live males and video playback that female spiders prefer males with larger tufts when presented with only visual courtship cues (McClintock and Uetz, 1996; Uetz, 2000; Uetz and Roberts, 2002).

(2) *Schizocosa rovneri* Uetz and Dondale, a sibling species to *S. ocreata* (G. E. Stratton, unpubl.), lacks decorative foreleg tufts and the conspicuous leg-tapping display involved in the courtship of its congener. It does, however, exhibit a body “bounce,” in which it thrusts the abdomen and cephalothorax against the substratum and simultaneously produces a vibratory signal via palpal stridulation (Uetz and Denterlein, 1979; Stratton and Uetz, 1981, 1983, 1986). Female *S. rovneri* respond receptively more often to conspecific male vibration signals than visual cues. However, when presented with only visual courtship cues (in a video playback study), *S. rovneri* females prefer conspecific males that have had tufts artificially added to the forelegs over typical male *S. rovneri* (McClintock and Uetz, 1996).

(3) *Schizocosa uetzi* Stratton exhibits a mostly stationary courtship sequence, with intermittent slow foreleg arch displays (Stratton, 1997). There are no decorative tufts on the forelegs, but there is a slight “hint” of

pigmentation (Stratton, 1997; Hebets and Uetz, 2000). Female *S. uetzi* respond receptively more often to conspecific male vibration cues than to visual signals (Hebets and Uetz, 1999, 2000), but in the presence of both visual and vibratory cues, female *S. uetzi* prefer video playback of conspecific males that have had tufts digitally added (Hebets, unpubl.).

(4) *Schizocosa duplex* Chamberlin has no decorative tufts on the forelegs, and exhibits a stationary courtship with no visual display (Hebets and Uetz, 1999, 2000). There is, however, locomotion between courtship bouts (Hebets and Uetz, 2000). Females of this species respond only to vibratory cues from males and do not respond to video playback of male courtship (Hebets and Uetz, 2000).

### Spider Maintenance

All spiders were maintained in individual opaque plastic containers (12-cm diameter, 4-cm height) and provided water *ad libitum*, under controlled environmental conditions: a temperature of 25–27°C and a 13:11-h light:dark cycle. Spiders were fed one medium-size (8- to 10-mm) cricket immediately after spiders were field-captured and then maintained without food until after each experimental trial. Trials began 14 days after capture of the spider. The feeding regime was maintained thereafter as one cricket every 14 days, immediately after each set of trials was completed.

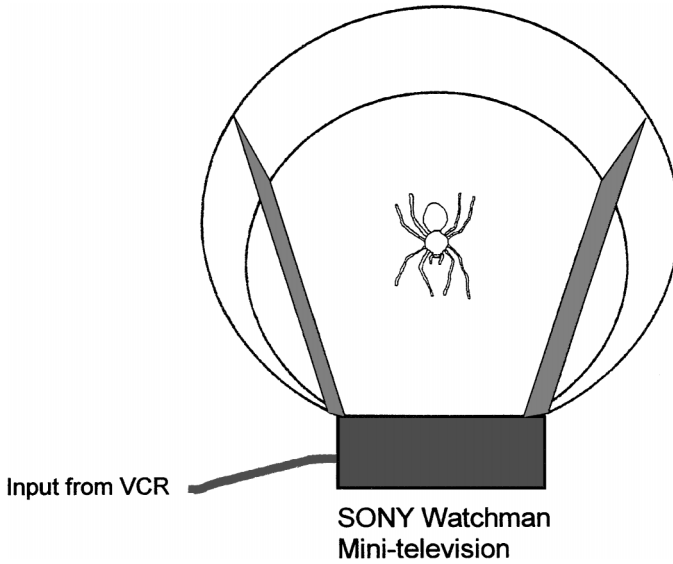
### Experimental Stimuli

Digitized courtship sequences of *Schizocosa* spp. from previous studies were used as video playback stimuli in this research (McClintock and Uetz, 1996; Hebets and Uetz, 2000). Male courtship sequences of each *Schizocosa* species were previously videotaped, and samples were captured, digitized, rendered frame-by-frame to a standardized background, and reanimated as described by Clark and Uetz (1990, 1992, 1993), McClintock and Uetz (1996), and Hebets and Uetz (2000). Courting male *Schizocosa* were videotaped using a JVC GX-N8 camera and a Panasonic HRS-101 VHS video recorder. Samples of 10–30 s of live courtship of each species were digitized using an AMIGA 2000HD computer and Frame Grabber-Real Time Video Image Digitizer software. Spider images were rendered frame-by-frame and standardized to a light gray background, adding or deleting tufts using the Deluxe Paint IV animation program, then reanimated into continuous loops for playback. Video images were played back through a SONY Model SLV-720 VCR and presented to *Hogna* on a SONY Watchman Model FDL-310

liquid crystal display (LCD) microtelevision. As a stimulus, we used a representative male video exemplar of each species, which had been previously been shown to elicit receptivity in conspecific females (Hebets and Uetz, 2000). The same stimulus exemplar of each species was presented to predatory *Hogna*, both as a control (unmodified video) and as a manipulated treatment (with decorative tufts digitally added or deleted, depending on the species), to control for possible variation among courting males (McGregor, 2000; Wiley, 2003).

The experimental design was a repeated-measures design with species and treatment (tufts/no tufts) as factors. Nine video playback stimuli were presented to each of 25 female spiders in random sequence in experimental trials. The video playback treatment groups consisted of stimuli from each *Schizocosa* species (*S. ocreata*, *S. rovneri*, *S. uetzi*, and *S. duplex*) either with or without decorative tufts on the forelegs. Additionally, a blank screen control with the same color background as the other treatments was used to control for the effects of lunging at reflection, heat generated from the screen, and screen flicker. Trials were conducted at 14-day intervals from late September to early November 1996. Each spider was run every 13th and 14th day. This was done because previous studies (McClintock and Uetz, 1996; Persons and Uetz, 1997) have shown that wolf spiders do not habituate to video stimuli presented at daily intervals up to 4 days but can go without food for several weeks. Thus trials were conducted for 2 days at 2-week intervals both to standardize hunger level as closely as possible and to reduce the possibility of habituation to video playback. Spiders were fed a cricket immediately after the 2-day set of trials, then fasted 13–15 days prior to their next testing. After the ninth set of trials, each spider had seen each treatment only once, with at least 24 h rest between.

Video playback trials were conducted in a video playback arena modified from one used in previous studies (McClintock and Uetz, 1996). The arena was amphitheater shaped, with a lengthwise dimension of 15 cm, 11.5 cm across at the widest point, and 8.5 cm across at the narrowest point by the screen (Fig. 1). The minitelevision was placed 1 cm from a clear acetate barrier comprising one end of the arena, with a fan circulating air to control for effects of a possible temperature gradient in the arena. Filter paper was placed on the bottom of the arena for each trial and was changed between trials to control for possible buildup of silk, which may alter the behavior of spiders for subsequent trials. Arenas were also wiped with a cotton swab moistened with 70% alcohol in an attempt to remove any traces of pheromones. The individual spider was placed in the center of the arena facing the screen under a vial and rested for 5 min. Each trial commenced with removal of the vial and raising of an opaque barrier to reveal the screen. Trials lasted for 10 min. Trials were scored for the presence of predatory

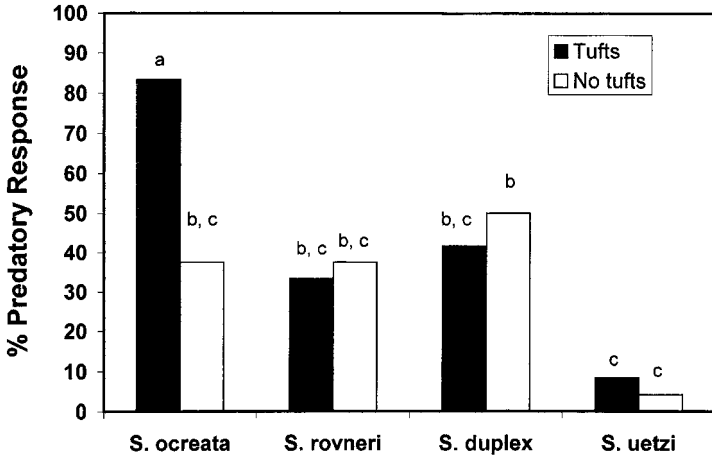


**Fig. 1.** Video playback arena; view from above.

behaviour toward the screen image, i.e., a sudden turn and orientation toward the image on the video screen, followed by a “lunge” (a rapid approach and grabbing at the image with the forelegs). Latency to attack was measured as the time elapsed (seconds) prior to the occurrence of a lunge event.

### Statistical Analysis

Because this experiment involved measurements of responses from the same individuals to all treatments (stimuli), we used statistical tests appropriate for a repeated measures design. To test the null hypothesis of independence, i.e., spider predatory response is independent of stimulus treatment group, we used a Cochran’s  $Q$  test and appropriate post hoc multiple contrast test (Zar, 1999). Two analyses were done, including and excluding the series of trials with the blank screen control. This was done to establish that lunging was elicited by the image on the screen and not the screen itself and to identify if there was a significant difference in lunging frequency considering only the experimental groups. Subsequent to Cochran’s  $Q$  test, we used a multiple-comparison test (Marasciullo and McSweeney, 1967) and McNemar’s  $\chi^2$  tests (Zar, 1999) on each of the four pairwise comparisons (treatments within species). Latency (seconds) to attack was analyzed several ways: (1) a repeated-measures ANOVA, (2) a survival analysis with



**Fig. 2.** Proportion of *Hogna helluo* responding to video stimuli of male *Schizocosa* spp. with predatory behavior (orient, approach, lunge). Letters indicate statistically significant differences between groups, based on *post hoc* tests.

nonparametric Wilcoxon test, and (3) a Wilcoxon signed-rank test for pairwise comparisons of treatments within species.

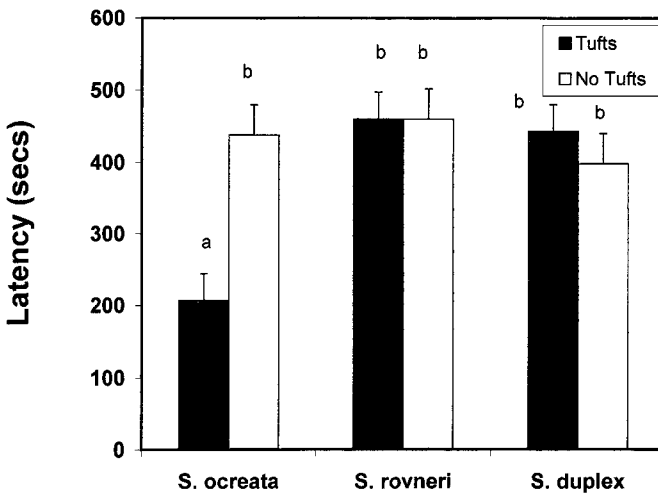
## RESULTS

Predatory *Hogna* responded with typical prey attack behavior (orient, rapid approach, lunge) in response to videos of courting male *Schizocosa* (with varying frequency depending on stimulus) but not to the blank screen. We found a significant difference in *H. helluo* response across all groups using Cochran’s *Q* test; i.e., predatory response was not independent of stimulus (Fig. 2). This result was significant whether or not the blank screen control was included or excluded from the analysis (including the blank screen,  $\chi^2 = 59.6363$ , 8 df,  $P < 0.001$ ; excluding the blank screen,  $\chi^2 = 44.3829$ , 7 df,  $P < 0.001$ ). As no predation attempts were made by *H. helluo* at a blank screen, this control was excluded from further analyses.

Predatory responses of *Hogna* varied significantly among the *Schizocosa* species stimuli (Fig. 2) and appear to be related to the degree of active courtship; i.e., the highest frequency of predation response was observed with *S. ocreata* (19/25 trials = 76%) and the lowest predation response was with *S. uetzi* (1/25 trials = 4%). An intermediate rate of lunge responses was observed with both *S. rovneri* (9/25 trials = 36%) and *S. duplex* (12/25 trials = 48%). Subsequent *post hoc* multiple-comparison tests, using the method of

Marasciullo and McSweeney (1967; cited in Zar, 1999) revealed significant differences among species and tuft treatments. Responses were significantly higher for control *S. ocreata*, intermediate for *S. rovneri* (control, with tufts), *S. duplex* (control, with tufts), and *S. ocreata* (tufts removed), and lowest for *S. uetzi* (control, with tufts). A significant effect of the presence/absence of decorative tufts on the frequency of *H. helluo* lunge response was found only with *S. ocreata* (McNemar's test,  $\chi^2 = 8.1$ ,  $P < 0.005$ ). For each of the three species that naturally lack tufts (*S. rovneri*, *S. duplex*, and *S. uetzi*), the addition of tufts made no significant difference on *Hogna* predation response (*S. rovneri*  $\chi^2 = 0$ ; *S. duplex*  $\chi^2 = 0$ ; *S. uetzi*  $\chi^2 = 0$ ). Because there were so few attacks observed for *S. uetzi*, subsequent analyses excluded this species.

Latency of predatory lunge responses of *Hogna* to video stimuli varied among species and treatments (Fig. 3). Repeated-measures ANOVA (Table I) revealed significance for species and the species  $\times$  tufts interaction but not tuft treatment or individual. Post hoc tests revealed that significance was due entirely to the difference in latency of attack between the lower value for the control *S. ocreata* treatment and all others (Tukey's HSD,  $P < 0.05$ ). However, since the trial was truncated at 10 min, nonresponding individuals might have biased variance in the outcome, and the



**Fig. 3.** Mean latency (seconds) to predatory response for *H. helluo* presented with video stimuli of male *Schizocosa* courtship. Letters indicate statistically significant differences between groups, based on *post hoc* tests.



**Table I.** Repeated-Measures Analysis of Variance Table for Latency to Attack

Source	df	MS	F	P
Species	3	569,562	12.03	<0.0001
Tufts	1	107,277	3.059	0.0835
Species × tufts	3	195,359	5.57	0.0014
Individual (species)	96	47,319.9	1.34	0.072

appropriateness of parametric analyses of this sort may be questionable. We therefore also used a nonparametric product-limit survival analysis with a Wilcoxon test to determine between-group differences. Results indicate significance ( $\chi^2 = 31.965$ , 5 df,  $P < 0.0001$ ), which similarly appears due entirely to the lower latency for the *S. ocreata* control treatment vs. all others. Additionally, a nonparametric Wilcoxon signed-rank test of the predicted directionality of the response latency difference between stimuli (with and without tufts) revealed significance only for *S. ocreata* ( $P < 0.0001$ ); addition of tufts to *S. rovneri* and *S. duplex* made no significant difference in attack lunge latency.

**DISCUSSION**

The results of this study indicate that male decorations and active courtship displays incur costs from visual detection by potential predators and that the probability of detection varies for wolf spider species with different levels of activity in courtship. The courtship of *S. ocreata*, which includes active visual foreleg displays and locomotion, elicited the highest predatory response, while *S. rovneri* and *S. duplex*, whose courtship behavior did not include foreleg tapping but did include locomotion between display bouts, elicited intermediate responses. The courtship of *S. uetzi*, which exhibits a stationary display, elicited the lowest response. Apparently, the slow, controlled vertical leg-waving display employed by *S. uetzi* does not incur high risk of detection by *Hogna* predators.

The results also suggest that decorative tufts only increase the likelihood of predator response in species that use visual leg-tapping displays. This is seen in that the *removal* of tufts significantly decreases the likelihood of predatory attack in *S. ocreata*, while the *addition* of tufts had no effect on predatory responses to the other three *Schizocosa* spp. It is apparently the combination of tufts and foreleg tapping that attracts predator attention. This supports earlier hypotheses that decorative tufts on the forelegs of *S. ocreata* function as amplifiers or attention signals (Hasson, 1991, 1997) increasing the efficacy of the leg-tapping display (McClintock and Uetz, 1996;

Scheffer *et al.*, 1996; Hebets and Uetz, 2000). Hebets and Uetz (2000) found a correlation between the presence of decorations and pigmentation on the forelegs of *Schizocosa* species males and the level of visual display they exhibited. A correlation was also found between the presence of decoration and display in a species and the tendency of females of that species to respond to visual vs. vibratory signals during courtship (Hebets and Uetz, 1999, 2000). Results of this study suggest that the same mechanisms that attract conspecific female attention during courtship can also act as visual cues to predators.

Several studies have suggested that the presence/absence and size of tufts in *S. ocreata* influence the responses of females and may be subject to sexual selection via female mate choice. Scheffer *et al.* (1996) found that in the absence of vibratory cues in courtship, the presence of tufts on courting male *S. ocreata* significantly increased female receptivity. The size of male tufts, in both live males (McClintock and Uetz, 1996) and video playback experiments (Uetz, 2000), may also influence female receptivity. However, in species that do not have male leg decorations, video playback studies with the addition of tufts produce varying results. The addition of tufts to *S. duplex* and *S. uetzi* does not affect female receptivity when presented with video images of courting conspecifics (Hebets and Uetz, 2000). For *S. rovneri*, however, the addition of tufts to video images of courting males did increase female receptivity (McClintock and Uetz, 1996). All of this suggests that there are trade-offs between sexual selection and predation pressure within *Schizocosa* wolf spiders.

The role of predation as a selection pressure in shaping the evolution of male traits and displays in the genus *Schizocosa* is far from clear. A recent study by Rosenthal *et al.* (2001) has suggested that some male visual traits, which evolve in response to preexisting female sensory biases, may also exploit sensory biases shared with predators. If the apparent preference of female *S. rovneri* for male tufts demonstrated by McClintock and Uetz (1996) represents a preexisting female bias (as originally suggested), results of this study could be used to test this hypothesis. Since predatory *Hogna* do not respond with increased frequency to the addition of tufts to species without visual displays, a shared preexisting bias for this trait by predators and females is not indicated. However, phylogenetic analyses of the *S. ocreata* clade (which includes *S. ocreata*, *S. rovneri*, and *S. uetzi*) are at the moment equivocal, and tufts may have either (a) arisen independently in several taxa (e.g., *S. ocreata*, *S. crassipes*) or (b) been secondarily lost in *S. rovneri* and *S. uetzi* (McClintock and Uetz, 1996; Hebets and Uetz, 1999). As a consequence, questions regarding preexisting biases of female *Schizocosa* wolf spiders and/or *Hogna* predators remain unresolved.

Environmental constraints on communication often play a role in the evolution of elaborate male traits and displays (Endler, 1992, 2000), and evolution of signals used in communication between male and female *Schizocosa*, as well as their detection by predators, may be influenced by these constraints. Microhabitats of *Schizocosa* spp. differ in structure and effectiveness in transmitting visual or vibratory cues in courtship and may also influence signaling (Uetz, 1991; Scheffer *et al.*, 1996). For example, *S. rovneri* is often found in the flattened leaf litter of flood plains, which has been shown to transmit vibrations at greater distances than the complex leaf litter habitat of *S. ocreata* (Scheffer *et al.*, 1996). It is possible that *S. rovneri* does not have a well-developed visual component to its courtship because that might increase predation risk in this relatively open microhabitat. On the other hand, it is also possible that *S. ocreata* males must bear the burden of predation costs of their conspicuous decorations and display because their microhabitat places constraints on vibratory communication.

Verrell (1991) proposed that predation pressure on male decoration and signaling behaviors may also play a role in the speciation process, e.g., if different signaling mechanisms were subject to selection via predator detection, and ancestral populations were exposed to different suites of predators. In such a case, sexual signaling mechanisms might be expected to diverge. The genus *Schizocosa*, and the *S. ocreata* clade in particular, has been suggested as an example of rapid speciation in response to sexual selection for male courtship displays and decorations (Miller *et al.*, 1998; Uetz, 2000). Verrell's model therefore has interesting implications for the genus *Schizocosa*, considering that these species are behaviorally isolated by male sexual signaling behavior and that these sexual signaling behaviors may be subject to different predation pressures. Despite the many unanswered questions raised by this study, results strongly suggest that the possible role of predation pressure in the speciation process of *Schizocosa* wolf spiders merits further investigation.

#### ACKNOWLEDGMENTS

This research was supported in part by National Science Foundation Grants IBN-9414239 and IBN-9906446 (to G.W.U.) and a Research Experiences for Undergraduates supplement to IBN-9414239. We are grateful to E. Hebets for use of the digitized spider courtship sequences and to M. Persons, M. Orr, K. Delaney, A. DeLay, D. Kroeger, and B. Kilinc for collecting and maintaining spiders for this research project. We also appreciate statistical consulting by B. Jayne and P. Taylor and comments

on the manuscript from J. A. Roberts, C. M. Harris, and two anonymous reviewers.

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