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Eileen Hebets

University of Nebraska - Lincoln, ehebets2@unl.edu

George W. Uetz

University of Cincinnati, Cincinnati, OH

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Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae)

Eileen A. Hebets and George W. Uetz

Department of Biology, University of Cincinnati, Cincinnati, OH 45221-0006, USA

Abstract

This study used both correlative and experimental video playback methods to test the hypothesis that the secondary sexual traits of male wolf spiders act to increase the efficacy of visual courtship displays. Direct observations of courtship of several lycosid genera and a review of the literature revealed a significant association between ornamentation and visual courtship displays. This suggests that the ornamentation may be playing the role of amplifier for a visual display. To test this hypothesis, male courtship behaviors of four *Schizocosa* species were experimentally manipulated using video-imaging techniques. Females of species with non-visually displaying, non-ornamented males (*Schizocosa duplex* and *S. uetzi*) did not increase in frequency of receptivity when tufts were added to conspecific males. In a species with a visual display and foreleg pigmentation (*S. stridulans*), the addition of foreleg tufts increased female receptivity. In a tufted species (*S. crassipes*), females tended to decrease their receptivity when male ornamentation was completely removed. In visually displaying species, ornamentation acts to increase female receptivity, supporting its role as an amplifier of a visual display.

Keywords: spiders, courtship efficacy, female choice, ornamentation, amplifier

Introduction

Although many scientists agree that sexual selection pressures lead to the evolution of elaborate male ornamentation, the mechanisms driving these ornate traits are still under debate. Among the many possible explanations for the evolution of ornaments (Andersson 1994), the idea of female choice has received the most support (Bischoff et al. 1985; Basolo 1990; Brooks and Caithness 1995; Ligon and Zwartjes 1995; Wiernasz 1995). Numerous studies have shown that females exhibit a preference among males, but the origin of these

preferences remains unclear (Bateson 1983; Andersson 1994).

Females often choose males with more conspicuous traits (Andersson 1994). These traits may reduce the time it takes a female to locate a male (Darwin 1871), they may indicate high-quality males (Trivers 1972; Zahavi 1975), they may improve species recognition (Andersson 1994), or they may take advantage of a preexisting female sensory bias (West-Eberhard 1983; Ryan 1990; Endler 1992). Conspicuous male displays may also evolve through female choice if the display acts as an amplifier of a previously recognized difference in male quality (Hasson 1989, 1990). Amplifying displays may increase resolution of other cues without themselves being attractive.

Within the context of sexual selection through female choice, male secondary sexual traits are typically involved in courtship displays. The signaling involved in courtship plays a crucial role in the reproductive success and often survival of individuals. Courtship signals may not only include species recognition components, but must successfully elicit female receptivity. Displays used in sexual interactions are typically designed for detectability, and while there are several factors that can increase the detectability of a signal (Guilford and Stamp Dawkins 1991), there are associated costs (Ryan and Rand 1990; Endler 1991, 1993). As is common throughout all aspects of animal behavior, the signaler must maximize the efficacy of the signal while minimizing its associated costs. For some animal species, the costs associated with ineffective courtship signaling may be very high. In some spiders, for example, males often lose their lives to females during courtship attempts. The pressures placed on courtship signals in potentially cannibalistic animals such as spiders are thus thought to be extremely strong (Elgar 1992).

The genus *Schizocosa*, within the wolf spider family Lycosidae, is an ideal system in which to study the role of male ornamentation in courtship displays. Courtship behavior in the family Lycosidae has been studied extensively (for a review see Stratton 1985). The signals that wolf spiders utilize consist mainly of visual, vibratory, and chemical forms. Within the genus *Schizocosa*, males possess a variety of foreleg morphologies ranging from the presence of brushes of black hair and/or pigmentation on their forelegs to males with forelegs without ornamentation. The courtship displays of males also vary, from species with extremely active leg-waving displays to species with stationary, vibration-based courtship.

Past studies have focused upon specific roles that ornamentation (specifically "tufts") may play in male courtship signaling, i.e., species recognition and female choice (McClintock and Uetz 1996; Scheffer et al. 1996). Tufts have been shown to increase the efficacy of visual courtship displays in *Schizocosa ocreata* (a tufted species), while it has been suggested that female *S. royneri* (a non-ornamented species) may have a preexisting bias for active courtship displays and/or for the presence of decorative tufts (McClintock and Uetz 1996; Scheffer et al. 1996). This study expands the examination of foreleg morphologies to include two species with varying degrees of black pigmentation and no tufts on the forelegs, another "tufted" species, and another non-ornamented species. Using four additional species within the genus, each with varying degrees of male foreleg ornamentation and visual courtship display, we examined the role of ornamentation (specifically as an amplifier) in the context of visual courtship displays. We first explored the relationship between decoration and visual displays and then used video-imaging manipulations to modify male morphologies and test female receptivity.

If ornamentation acts in conjunction with visual displays to enhance communication, male foreleg ornamentation should be correlated with other visual courtship signals. Furthermore, if decorations act to enhance a visual display, then we would predict that in a species with a visual display, female receptivity should increase with artificially enhanced decorations or decrease when ornamentation is removed. There should be an ordering effect on female preference with respect to increased ornamentation. However, in a species with no visual display, the enhancement or addition of decorations should not affect female mate choice.

Methods

Association of leg decoration and leg-waving displays

We obtained data on the presence of leg ornamentation and leg-waving displays during courtship for 39 species of lycosids from eight genera (Table 1). Data for 11 species were obtained from the literature; the remaining species were observed directly from collections made in the summers of 1993–1994 from populations throughout Alabama, north-

ern Florida, Kentucky, Louisiana, and Mississippi (USA). The numbers of individuals per species collected ranged from 1 to more than 20. The spiders were taken to the laboratory at the University of Mississippi, where they were housed individually in plastic containers in a controlled environment on a 12L:12D cycle. Two additional wolf spider species were collected from Hamilton Co., Ohio, and Cape May Co., New Jersey, in 1995. These spiders were brought back to the laboratory at the University of Cincinnati where they were housed in individual deli dishes under similar controlled conditions.

Females of each species were placed on a piece of filter paper the night prior to observation. At the time of observation, the filter paper was transferred to the 9.5-cm transparent cylindrical observation arena. The conspecific male was introduced into the arena and courtship behavior was observed and often recorded using a Panasonic HD-5000 video camera. Male courtship behavior was scored for leg-waving displays: any portion of the legs or palps that were raised, waved, or arched during courtship was scored as positive for a visual display. Visual displays typically involved leg movements not involved in normal walking or running. The preserved specimens of the males were then examined under a microscope to determine if there was any foreleg decoration—either black pigment present on the legs or tufts of black hairs. Literature describing the species and courtship displays of wolf spiders was also reviewed and analyzed.

A χ^2 -test was used to test the null hypothesis of independence of leg decorations and displays. Since the phylogenetic arrangement of the family Lycosidae is not known, it is not possible to use various recommended statistical procedures (e.g., Harvey and Pagel 1989). Instead, we conducted a second analysis in which we scored species in the same genus with the same character trait as a single value. This procedure accounted for the possibility that species within a genus that display the same character states may simply share a common ancestor and thus cannot be counted as independent data points.

Video manipulation of male foreleg morphology

Since it is impossible to add brushes of hairs to the forelegs of live male *Schizocosa*, or to delete pigmentation that is already present, video imaging was used to manipulate male foreleg morphology. Past research has shown the effectiveness of video playback experiments with spiders (Clark and Uetz 1990; McClintock and Uetz 1996).

Species

Four species of *Schizocosa* wolf spiders were used in this study.

- (1) *S. duplex* Chamberlin males are non-ornamented and have a stationary, vibrational courtship display with no visual component.
- (2) *S. uetzi* Stratton males have a "hint" of black pigmentation on the middle portion of tibia I (Stratton 1997a). The courtship display is stationary and mostly involves stridulation; however, males display a very slow foreleg arch and lift (Stratton 1997a).
- (3) *S. stridulans* Stratton males have black pigmentation on their entire tibia I and distal portion of femur I. Males display with a rapid double foreleg tap along with stationary stridulatory courtship (Stratton 1997b).
- (4) *S. crassipes* (Walckenaer) males have pigmentation on the femur, patella, and tibia of legs I along with "brushes" of black hairs on the tibia. The courtship of these males involves active walking about with extremely rapid extended leg-waving displays (description in Miller et al. 1998).

Digitized courtship manipulations

Male courtship sequences from each *Schizocosa* species were videotaped using a JVC GX-N8 camera and a Panasonic HRS-101 VHS video recorder. The camera distance from the live courting male was varied so that the image on the screen of a Sony Watchman was life size (dial calipers verified that the television image matched the average body

length of that particular species). The videotape of the courting male was then digitized onto an AMIGA 2000HD computer using a Frame Grabber-Real Time Video Image Digitizer. We used 30 images for each second of courtship display on the videotape to ensure the inclusion of all behavioral displays within a sequence and allow real-time playbacks. An animation program (Deluxe Paint IV) was then used to manipulate the morphologies of males in each frame.

Because courtship behavior and duration differed among the four *Schizocosa* species, different durations of courtship displays were digitized for each species. The digitized courtship displays for *S. duplex*, *S. uetzi*, *S. stridulans*, and *S. crassipes* were 391, 1225, 601, and 1061 frames, respectively. Each of the digitized sequences was shown to females as continuous loops.

For each of the four species, three different video courtship sequences were created: (1) a no-ornamentation video: all ornamentation (pigment and brushes) were removed from species that normally possessed them; (2) a "pigmentation" video: black pigmentation was added to species normally lacking pigment and the brush was removed, leaving pigmentation as the only ornament in species that normally possessed "brushes", and (3) a "brushes" video: brushes of black hair were added to the forelegs of males that lacked natural "brushes." When brushes were added to species normally lacking them, pigmentation was, consequently, added as well (see Figure 3D leg drawing); thus, there was never a case of brushes without

pigmentation. The resulting videos for each species included one unmanipulated video sequence and two sequences with altered foreleg morphologies.

Approximately 30 females of each species were randomly chosen for these trials, none of which had been used previously. The experimental arena consisted of a Sony Watchman micro screen television placed at one end of a clear plastic arena (Figure 1). A piece of paper was placed in front of the screen prior to each trial. Females were put in the arena on a piece of filter paper and were allowed to acclimate for exactly 2 min. The trial began when the barrier in front of the screen was removed and the female was exposed to a video playback of a previously digitized courtship sequence loop. Trials lasted 10 min and the female was scored for receptivity (i.e., a slow turn or settle; see McClintock and Uetz 1996; Stratton 1997b; Hebets and Uetz 1999). Each female was used once only. A log-likelihood ratio test (*G*-test) was used to test the null hypothesis that female receptivity was independent of stimulus shown. If female receptivity was found to be dependent upon the stimulus shown, a Fisher exact test was done on pairwise comparisons.

To test the predictions that female responses should be ordered according to increased ornamentation, we used the Jonckheere test for ordered alternatives (Siegel and Castellan 1988). Since this prediction only holds true for species in which a visual display is involved in courtship, *S. duplex* was not included in this analysis.

Table 1. An examination of wolf spiders for the presence/absence of ornamentation and leg-waving displays

Genus	Species	Ornament	Leg-waving	Source
<i>Arctosa</i>	<i>littoralis</i>	–	Yes	Present study
	<i>sanctaerosae</i>	Yes	Yes	Present study
<i>Alopecosa</i>	<i>accentuata</i>	Yes	Yes	Cordes 1988
	<i>aculeata</i>	Yes	Yes	Present study
	<i>barbipes</i>	Yes	Yes	Cordes 1988
<i>Geolycosa</i>	<i>turricola</i>	Yes	Yes	Present study
<i>Gladicosa</i>	<i>bellamyi</i>	Yes	Yes	Present study
<i>Lycosa</i>	<i>accompa</i>	–	Yes	Present study
	<i>annexa</i>	Yes	Yes	Present study
	<i>georgicola</i>	Yes	Yes	Present study
	<i>lenta</i> sp. "a"	–	–	Present study
	<i>lenta</i> sp. "b"	–	Yes	Present study
<i>Pardosa</i>	<i>amentata</i>	Yes	Yes	Vlijm and Dijkstra 1966; Hollander 1970; Cordes 1988
	<i>hortensis</i>	Yes	Yes	Vlijm and Dijkstra 1966; Locket and Millidge 1975
	<i>littoralis</i>	Yes	Yes	Present study
	<i>lugubris</i>	Yes	Yes	Vlijm and Dijkstra 1966; Locket and Millidge 1975
	<i>milvina</i>	Yes	Yes	Present study
	<i>nigriceps</i>	Yes	Yes	Vlijm and Dijkstra 1966; Locket and Millidge 1975
	<i>paludicola</i>	Yes	Yes	Cordes 1988
	<i>prativaga</i>	–	–	Hollander et al. 1973
	<i>proxima</i>	–	Yes	Hollander and Dijkstra 1974
	<i>pullata</i>	–	–	Hollander et al. 1973
<i>Rabidosa</i>	<i>saturation</i>	–	Yes	Vlijm et al. 1970; Cordes 1988
	<i>hentzi</i>	–	–	Present study
<i>Schizocosa</i>	<i>rabida</i>	Yes	Yes	Present study
	<i>aulonia</i>	Yes	Yes	Present study
	<i>avida</i>	–	Yes	Present study
	<i>crassipes</i>	Yes	Yes	Present study
	<i>duplex</i>	–	–	Present study
	<i>floridana</i>	–	Yes	Present study
	<i>mccooki</i>	–	–	Present study
	<i>ocreata</i>	Yes	Yes	Present study
	<i>retrorsa</i>	Yes	Yes	Present study
	<i>rovneri</i>	–	–	Present study
	<i>saltatrix</i>	–	–	Present study
	<i>stridulans</i>	Yes	Yes	Present study
	<i>uetzi</i>	Yes	Yes	Present study
	sp. "a"	–	–	Present study
sp. "b"	–	–	Present study	

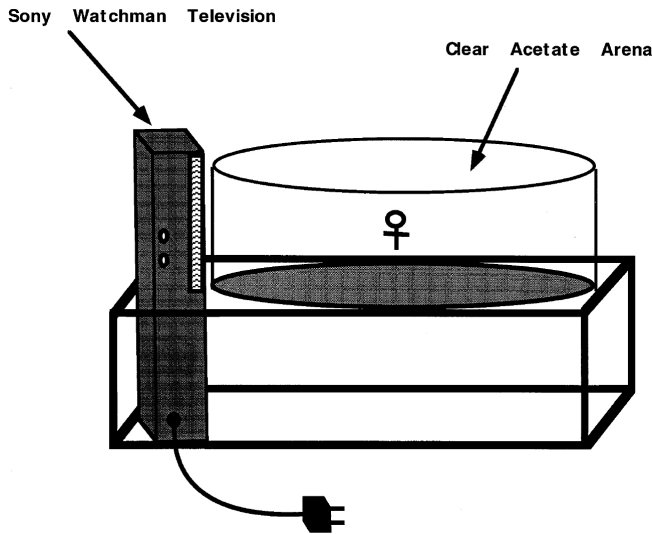


Figure 1. Video playback arena

Results

Correlation between leg decoration and visual leg-waving displays

There was interspecific variation in the presence of leg decorations and visual displays (Table 1). The Yates-corrected χ^2 2×2 contingency test showed that for all 39 species, the presence of leg decorations and visual displays were not independent ($\chi^2 = 17.4, P < 0.00001$; Figure 2A). Our analysis, which counted species in the same genus with the same character traits as a single value, yielded a total of 16 data points. A Fisher exact test revealed that the presence of leg decorations and visual displays were not independent ($P < 0.02$; Figure 2B).

Female receptivity to manipulated male morphologies

S. duplex females showed no receptivity to video stimuli and, thus, female receptivity was independent of stimulus shown ($G=0$; Figure 3A). Only a few *S. uetzi* females responded to video stimuli, and adding brushes to male forelegs did not affect female receptivity, nor did the removal of pigment. Female receptivity was thus independent of the stimulus shown ($G=0.934, P=0.627$; Figure 3B). Although there were definite trends within some of the species with respect to female receptivity to video stimuli, only one species showed statistically significant differences. *S. stridulans* female receptivity responses were dependent upon the video stimulus shown ($G=6.9763, P=0.037$; Figure 3C). Females preferred males with brushes added over males with pigment removed ($P=0.03$). With a Bonferroni correction for the overall experimentwise error rate, this trend is significant (pairwise, $P=0.017$). In *S. crassipes*, females appeared less receptive to males when ornamentation was removed from the forelegs. However, because the sample

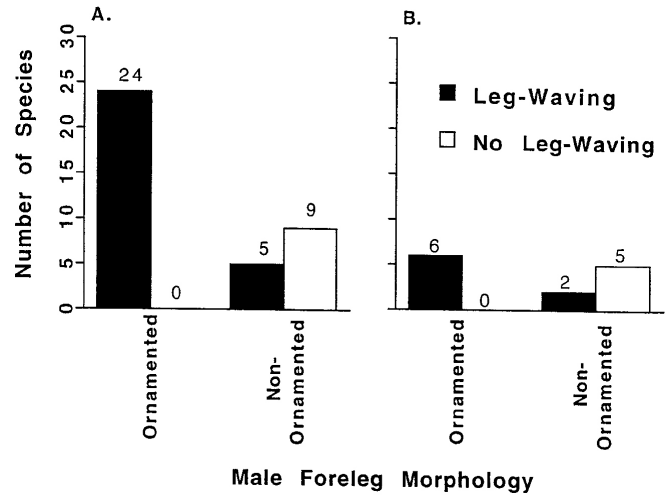


Figure 2, A, B. The frequency of co-occurrence of leg ornamentation and leg-waving displays in the family Lycosidae. A) Data from all species. B) Data in which species in the same genus with the same character traits are treated as a single value

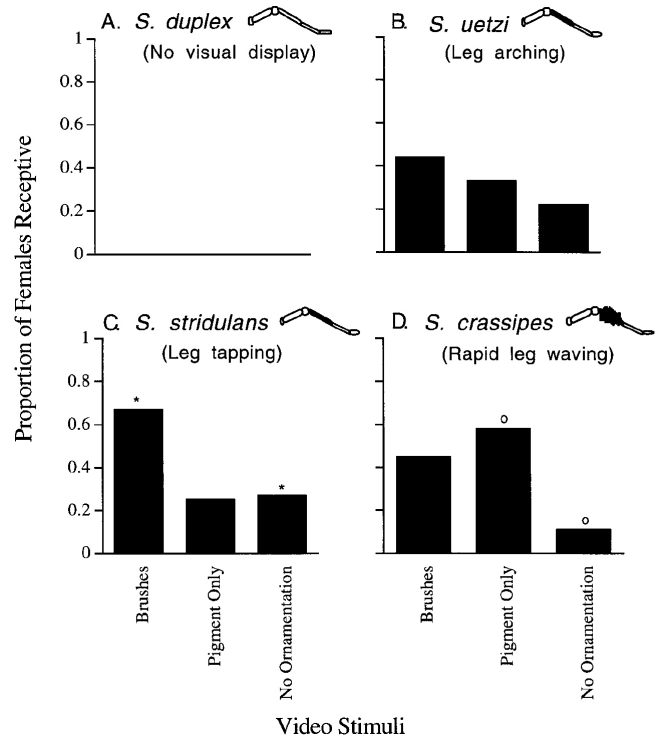


Figure 3, A–D. Female *Schizocosa* responses to video playback (* significant differences at $P < 0.05$; ° marginally significant differences at $P = 0.07$).

A) *S. duplex* (brushes $n=9$, pigment only $n=9$, no ornament $n=9$). B) *S. uetzi* (brushes $n=9$, pigment only $n=9$, no ornament $n=9$). C) *S. stridulans* (brushes $n=12$, pigment only $n=12$, no ornament $n=11$). D) *S. crassipes* (brushes $n=11$, pigment only $n=12$, no ornament $n=9$)

size was small ($n=12$), we cannot rule out independence ($G=5.14, P=0.076$; Figure 3D).

The Jonckheere test for ordered alternatives indicated that females of *S. uetzi*, *S. stridulans*, and *S. crassipes* all showed a significant increase in receptivity related to an increase in male foreleg ornamentation ($J=24, P=0.01$).

Discussion

Male leg ornamentation within the wolf spider family Lycosidae is strongly associated with the presence of leg-waving displays during courtship. All ornamented species examined possess some type of visual courtship display; we found no examples of species possessing ornamentation that lacked leg waving. However, seven species possessed an active display but were not ornamented, possibly suggesting that visual displays evolved first. A good phylogenetic history is not available for any of these spider genera or for the family itself and, thus, it is difficult to discuss the evolutionary history of courtship behavior in relation to male morphology. Better knowledge of the relationships within and between these genera would enable direct testing of the hypothesis that active leg-waving displays evolved first and ornamentation followed, playing the role of an amplifier of courtship signals in lineages with visual displays.

Our hypothesis was that ornamentation has evolved in this system to enhance visual courtship signals. According to Hasson (1991), females should not respond to the presence of an "amplifier" unless it is enhancing a previously desired male quality, such as display rate. *S. duplex* males, which lack a leg-waving display, do not possess a visual quality indicator (such as rate of display) which ornamentation might amplify. As predicted, females of this species did not respond to any male visual cue. If novel ornamentation was simply more attractive to a female in and of itself, then females should have increased their receptivity to males with added brushes. Although these data follow Hasson's predictions, there are other possible explanations that cannot be ruled out, e.g., phylogenetic constraints on the sensory system of female *S. duplex*.

In the two species with active leg-waving displays, *S. crassipes* and *S. stridulans*, the results of the playback trials also lend support to the amplifier hypothesis. Although the overall difference was only marginally significant ($P=0.07$), there was a definite trend within *S. crassipes* females to decrease receptivity from a decorated or pigmented male to a male without any ornamentation. In *S. stridulans*, females preferred males with brushes added over non-ornamented males.

Thus, in species with active visual displays, but without ornamentation, an increase in male ornamentation resulted in an increase in female receptivity. Results from *S. stridulans* females do not fit the predictions perfectly, however, since unmanipulated males were not preferred over non-ornamented males. However, the sample sizes once again were small and the female preference differences between these two treatments were negligible (i.e., 0.02 difference in proportions of receptive females). Overall, our results indicate that an increase in female receptivity is directly related to an increase in the degree to which males display visually.

Female *S. uetzi* did not respond differently to manipulated video stimuli, even when brushes were added. This lack of a significant response may be explained by the absence of an obvious quality indicator for females to assess. The courtship display of this species does not involve any quick tapping movements or leg-waving displays; it simply involves a male slowly arching the foreleg and then lowering it again. Although it is possible that the speed of both the arching and the leg raise could potentially act as quality indicators, these subtle displays may be more difficult for a female to assess. A more powerful analysis is needed to further address these issues.

These findings do not at first appear in accordance with previous studies by McClintock and Uetz (1996). They found that female *S. rovnerei* were more receptive to conspecific males with brushes added than to control conspecifics, suggesting that females prefer decorative tufts even in the absence of any leg-waving display. However, female *S. rovnerei* also responded to male *S. ocreata* with or without tufts, suggesting a pre-existing bias for active, visual courtship displays. Although *S. rovnerei* males do not exhibit leg-waving during courtship, they do exhibit a vigorous abdomen bounce. When the males bounce, their bodies come down with great force on the substratum and their legs are often lifted; much of the body vibrates immediately after each bounce. As a result, although there are no leg-waving displays, active movement occurs during courtship. Any amplification of this movement should be preferred by females and this may explain why female *S. rovnerei* prefer conspecific tufted males over controls.

If, as we propose, ornamentation amplifies a visual display, then females must be assessing something in the visual display. They may, for example, be interested in the rate of display. In several different animal species, factors most important in mate choice for females have less to do with morphology (e.g., size or coloration) than with courtship rate (Collins 1995; Karino 1995; Wagner and Sullivan 1995; Wagner et al. 1995). In a study involving another species of wolf spider (*Hygrolycosa rubrofasciata*), Parri et al. (1997) were able to show that rate and volume play an important role in male drumming during courtship. Females responded more quickly to males with higher drumming rates and volumes (Parri et al. 1997).

The importance of display rate has been shown for a variety of animal species and a variety of signaling modes, including the vibratory components of wolf spider courtship. A more recent study of male-female pairings in both *S. rovnerei* and *S. ocreata* demonstrated that males that actually mated had more active courtship (bounces per minute and taps per minute, respectively) than those that did not (K. Delaney and G. W. Uetz, unpublished data). It seems likely that rate is important in visual components of wolf spider courtship. Future studies, involving more species, that focus upon the effect

that different rates of leg waving may have on female choice could lend more support to the notion that ornamentation acts as an amplifier.

Our results suggest that a correlation exists between male foreleg ornamentation and visual leg-waving displays in wolf spiders. Thus, it seems reasonable to assume that in all species with these traits, females are using visual courtship components to assess males. However, Scheffer et al. (1996) previously showed that not all species may have this female visual bias. Hebets and Uetz (1999) found that among six species of *Schizocosa* females, three exhibited a vibrational bias during courtship assessment. The proportion of females receptive to isolated visual cues of a courting conspecific male increases in more ornamented, visually courting species (Hebets and Uetz 1999). The differences in female communication biases may help explain the variation with respect to male foreleg morphology and courtship communication seen in this genus.

This study controlled for conspecific male courtship display while experimentally manipulating morphology. Future studies should directly address issues of female receptivity in response to varying degrees of visual courtship displays. By experimentally altering both morphology and behavior in opposite directions, we may be able to gain insight into the relative importance of both ornamental and visual cues used during courtship communication.

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