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Female responses to isolated signals from multimodal male courtship displays in the wolf spider genus *Schizocosa* (Araneae: Lycosidae)

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Abstract

Male wolf spiders within the genus *Schizocosa* display considerable variation in foreleg ornamentation as well as in courtship communication. Multiple modes of male signaling have evolved in a number of species. Divergence in courtship signals among species within this genus may be directly associated with variation in the sensory sensitivities of conspecific females. We isolated the visual and vibratory courtship cues of four species of *Schizocosa* and recorded conspecific female receptivity to each isolated cue. We also examined female receptivity to complete multimodal courtship signals. We found that the sensory sensitivities of conspecific females were associated with the predominant modes of male courtship communication. Species in which females use mostly stridulatory cues in assessing conspecific males tended to have stridulation-based male courtship displays (*S. duplex* and *S. uetzi*) while the opposite was true for species in which females used more visual cues in male assessment (*S. stridulans* and *S. crassipes*). This study suggests coevolution between male signal design and female sensory design. We discuss possible scenarios that could be driving this coevolution, including hypotheses of sensory bias and environmental constraints.

The signals involved in communication between individuals can employ several different channels, which are dependent, in part, upon the available sensory systems of both the signaler and the receiver. For a signal to be effective, it must not only travel through a given environment successfully, but must also stimulate the receiver in the appropriate way; it must play into the sensory system of the receiver. Thus, it is presumed that both the design of the signal and the “psychology” of the receiver must evolve in concert (Lande 1981; Guilford & Stamp Dawkins 1991; Endler 1992, 1993).

Signals used in intra- and interspecific interactions are often selected, at some level, for detectability (Guilford & Stamp Dawkins 1991). However, due to the potential for cannibalism in certain animal groups, immediate detectability may not be beneficial. In these potentially cannibalistic species, such as some spiders, the efficacy of courtship signals is presumed to be subject to high selection pressures, thus making spiders ideal organisms for studies of sexual selection. The importance of specific species recognition signals in spider courtship displays has been demonstrated by several studies (Stratton & Uetz 1981, 1983, 1986; Uetz & Stratton 1982), while

others have shown the importance of female choice (Jackson 1977; Watson 1991, 1993; Clark & Uetz 1992; Scheffer et al. 1996; McClintock & Uetz 1996). However, the selective pressures acting upon the evolution of these signals are not necessarily mutually exclusive.

The use of multiple male ornaments or signals is seen in many animal species, but only recently have scientists begun asking what factors may have led to the evolution of these multiple male advertisements (Omland 1996). Wolf spiders (Family Lycosidae) are known to use signals involving visual, stridulatory and chemical modes of communication during courtship interactions. *Schizocosa* is one of two wolf spider genera that possesses a stridulatory organ located at the tarsal joint of the male palp, which is capable of producing sounds during courtship (Rovner 1975). A variety of courtship displays within the genus *Schizocosa* are multimodal: that is, they use both visual and vibratory (produced through stridulation) signals simultaneously. However, while only some species possess decorations or display visual signals, all species stridulate. There is tremendous variation within this genus with regard to male morphology and the use of visual signals.

Males of some species have no ornamentation on their forelegs; in others, males have black pigmentation only on certain foreleg segments; and in others, males have black pigmentation and black tufts of hair on portions of their forelegs (Dondale & Redner 1978).

To understand fully the diversity of both signaler behavior and morphology within the genus *Schizocosa*, we approached the issue from the receiver's perspective. Do females vary in their responses to male signals and what is the nature of cues required to elicit receptivity from females? By isolating visual and vibratory courtship communication cues and assessing female responses, we examine variation in the relative importance of each communication mode in four species of *Schizocosa*. We also compare female detection of cues to male courtship displays to explore the possibility of coevolution of signal design and female response. Data on two additional species, *S. ocreata* and *S. royneri* (Stratton & Uetz 1983; Scheffer et al. 1996), are included in the analysis to give a more comprehensive overview of the genus.

METHODS

Species

(1) Mature *S. duplex* Chamberlin males are nonpigmented/undecorated and have a stationary courtship display consisting entirely of stridulation accompanied by abdomen vibrations. (2) Mature *S. uetzi* Stratton males have black pigmentation on a small portion of the tibiae of their forelegs. The courtship of these males is mostly stationary stridulation, however, there is a slow foreleg arch displayed intermittently. These males have a slight ornamentation pattern accompanied by an intermediate visual display. (3) Mature *S. stridulans* Stratton males have pigmentation on their forelegs, consisting of black pigment on the distal portion of the femur and the entire tibia. *Schizocosa stridulans* males display with a rapid double leg tap of the forelegs, along with stationary stridulatory courtship (Stratton 1997). (4) *Schizocosa crassipes* (Walckenaer) males have black pigmentation on the distal portion of the femur and the entire tibia, along with "brushes" of black hairs on the tibia. The courtship of these males involves walking with extremely rapid extended leg waving displays (description in Miller et al. 1998).

Published data on two additional species are included in our Results and Discussion. *Schizocosa ocreata* (Hentz) males resemble males of *S. crassipes*. The courtship involves "in-unison leg tapping, waves and leg arches" and "substratum-coupled vibrations" (Stratton & Uetz 1981, 1983; Scheffer et al. 1996). This species is found in areas of complex leaf litter. Male *S. royneri* are nonpigmented/undecorated and possess a courtship that consists mostly of "stationary body pulses" (Uetz & Denterlein 1979; Scheffer et al. 1996). In the mid-west portion of its range, this species tends to be found in areas of flood plains with compact leaf litter.

Habitats

We collected *S. crassipes* and *S. duplex* from the same sites in three counties in the panhandle of Florida between March 20 and March 23, 1995: Bay County, Pine Log State Forest; Santa Rosa County, Krul Recreation Area Campground, Blackwater State Forest; and Hancock County, Mcleod State Park. These habitats consist of fairly open and exposed forest edges. The ground litter is primarily made up of pine needles and a scattered layer of thin leaf litter.

We collected *S. stridulans* and *S. uetzi* from the same site in Mississippi. Mature females of both species were collected at night from three sites in Lafayette and Marshall Counties in northern Mississippi between July 4 and 5, 1996: Lafayette County at Clear Creek Recreation Area; Marshall County, 2.5 miles south of Waterford; and Wall Doxey State Park, Marshall County. These habitats consist of a deciduous/pine mix. We collected the spiders from the surface of dense layers of leaf litter.

Housing

We brought all of the specimens to the laboratory and housed them individually in opaque deli dishes (15 cm in diameter). We placed each deli dish inside another translucent deli dish filled with approximately 1 cm of water. We drilled a hole in the top dish and placed a cotton wick through the opening so that it rested in a reservoir of water beneath, which provided a constant source of moisture. We fed the spiders three to five crickets once a week and kept them at approximately 25°C, under a 13:11 h light:dark cycle.

Because the females of *S. uetzi* and *S. stridulans* were mature when collected, their species identity and sexual history were unknown and thus could not be used in receptivity trials. However, once these individuals were brought to the laboratory, 29 produced egg sacs. These egg sacs hatched between August 16 and September 24, 1995. We removed the spiderlings from their mother's containers after dispersal; we labeled them by egg sac with individual numbers and placed them into individual deli dishes. We fed the spiderlings pinhead crickets once a week and placed them under the same environmental conditions as described above. We checked all specimens at least every third day for moults and recorded the date of maturation. Once males matured, we confirmed species identity by examination of secondary sexual traits.

Experimental Design

We selected 8–12 virgin mature females and presented each female in random order with three stimuli which included a randomly chosen, live conspecific male with (1) visual cues only (courting with no shared substratum), (2) vibration (stridulation) cues only (females shared the substratum with the male yet could not see him), and (3) visual and vibration cues (one which she could both see and sense through substratum-bound vibrations). The different arenas built for each of

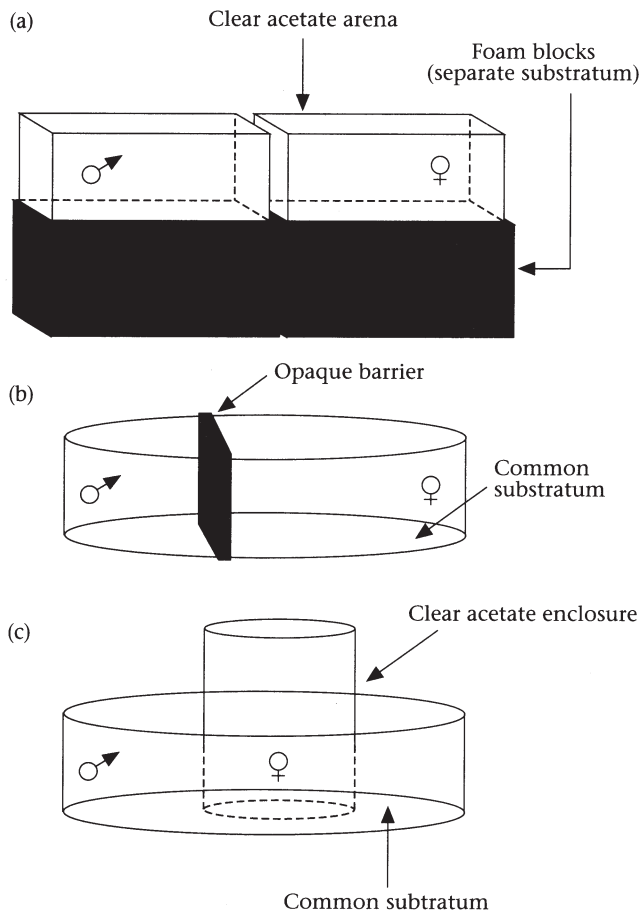


Figure 1. Experimental arenas. (a) visual cues only, (b) vibration cues only, and (c) visual and vibration cues together.

these three stimuli are shown in Figure 1. We did not choose females from the same egg sac and there were no brother/sister pairings.

Presentation of visual cues

The visual cues-only arena consisted of two rectangular, clear plastic arenas placed end to end (Figure 1a). Each container was raised off the table on individual foam blocks, preventing any vibrational communication between the test subjects (Scheffer et al. 1996). Prior to testing, we placed a piece of paper between the arenas to prevent visual communication. We then placed the female into her arena. We placed the male into his arena, on a piece of filter paper that a female had rested upon the prior night (to accumulate pheromones). As soon as male courtship began, we lifted the visual barrier and started the stopwatch. Trials lasted 10 min and the female was scored for receptivity (see below).

Presentation of vibration cues

The vibration cues-only arena was a clear plastic arena (15.5 cm in diameter, 6.5 cm tall) with a piece of opaque foam board placed across the diameter at approximately one-third the length of the arena (Figure 1b). The foam board acted as a

visual barrier and spanned the diameter of the container. However, it did not rest upon the bottom of the container, and thus vibration could travel between a male and female in contact with the same substratum. We introduced the female into the larger section of the arena and then placed the male into the smaller one. Once male courtship began, we started the stopwatch and scored female receptivity (see below) during the 10-min trial.

Presentation of visual and vibration cues together

The trials with visual and vibration cues together used the same clear plastic arenas, but without the visual barrier. Females were held within a small clear acetate enclosure in the centre of the arena (Figure 1c), where they could see the male and were in contact with the same substratum as the male. Placing the female behind the barrier eliminated any tactile stimuli and also eliminated the possibility of losing the male to sexual cannibalism. Once again, we placed males on pheromone-laden filter paper, and began the trial once the male initiated courtship. Trials lasted 10 min, during which time we scored females for receptivity (see below).

Measuring female receptivity

We scored females for the presence or absence of two behaviors of receptivity responses: (1) slow turns, 90–180° towards or away from the male, and (2) settling behavior (assuming position for copulation). Past research with *Schizocosa* females has shown these behaviors to be indicative of a female's readiness and willingness to mate (Stratton & Uetz 1981, 1983; McClintock & Uetz 1996; Scheffer et al. 1996). If the female showed at least one slow turn or settle during her 10-min trial, she was scored as positive, if not, she was scored as negative.

Statistical Analysis

The null hypothesis was that the frequency of females showing receptivity would be independent of stimulus. Because we used females more than once, we used a repeated measures Cochran's Q test to analyze this as a randomized block experimental design with dichotomous variables (receptive/unreceptive). When the null hypothesis was rejected, we used a McNemar's test of a two-by-two contingency table with dichotomous data to determine the location of the differences.

RESULTS

Schizocosa duplex

Female receptivity for *S. duplex* was not independent of the stimulus shown ($Q_4 = 14.3$, $P < 0.05$). Female receptivity to visual cues alone was significantly lower than receptivity to vibration alone and visual and vibration cues together (Figure 2a). None of the *S. duplex* females showed any response to the live male visual cues alone (Figure 2a). Female receptivity to vibration cues alone was very high and not significantly

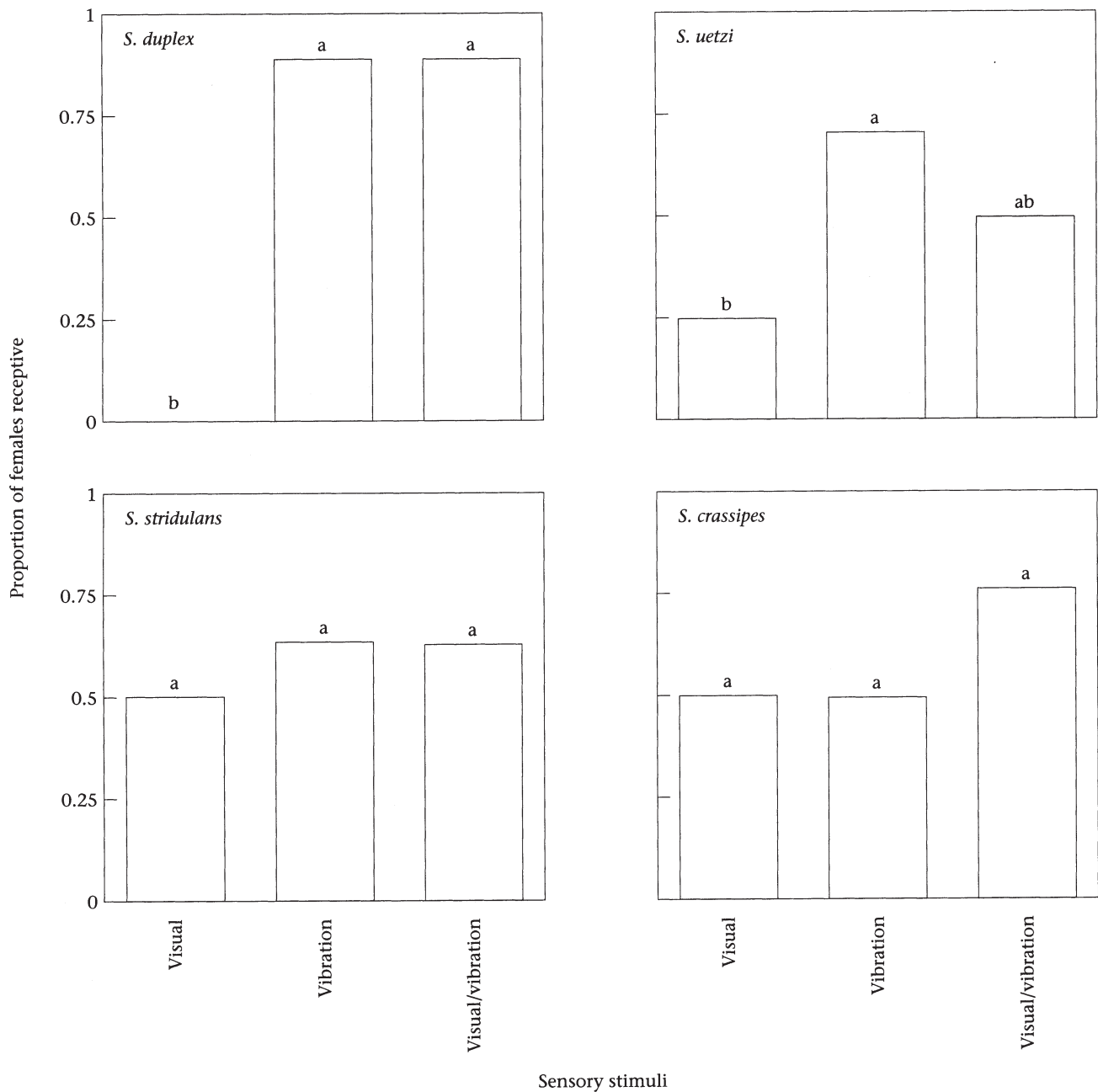


Figure 2. Female *Schizocosa* responses to sensory stimuli: *S. duplex* ($N = 9$), purely vibrational courtship, *S. uetzi* ($N = 10$), vibration plus a slight leg arch, *S. stridulans* ($N = 8$), vibration plus leg tapping and *S. crassipes* ($N = 12$), vibration plus rapid leg waving. Shared letters indicate no significant difference between sensory stimuli.

different from visual and vibration cues together (Figure 2a). Vibration cues therefore are both necessary and sufficient to elicit female receptivity in this species.

Schizocosa uetzi


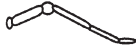
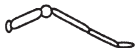



Female *S. uetzi* showed receptivity to all stimuli but not equally (Figure 2b); female receptivity was not independent of the stimulus shown ($Q_2 = 21.28$, $P < 0.05$). Vibration cues alone were significantly more effective at eliciting female receptivity than visual cues alone (Figure 2b), however, both stimuli together were not significantly more effective than vi-

sual cues alone. Visual cues alone were enough to elicit female receptivity in three of the females. Thus, both sensory cues are sufficient to elicit female receptivity in *S. uetzi*, but vibration appears to play a larger role.

Schizocosa stridulans and *S. crassipes*

For both of these species, females responded to all stimuli (Figure 2c, d) but female response was independent of the stimulus shown ($Q_2 = 6.588$, $P > 0.05$; $Q_2 = 5.25$, $P > 0.05$). While either visual or vibration cues alone were sufficient to elicit female receptivity in both species, female receptivity to

Table 1. Male foreleg morphologies and female responses in six species of *Schizocosa*

<i>Schizocosa</i> species	Male foreleg	Proportion of females receptive		Data source
		Visual cue	Vibration cue	
<i>S. ocreata</i>		0.64	0.69	Scheffer et al. (1996)
<i>S. rovneri</i>		0.37	0.79	Scheffer et al. (1996)
<i>S. duplex</i>		0	0.89*	Present study
<i>S. uetzi</i>		0.25	0.71*	Present study
<i>S. stridulans</i>		0.5	0.63	Present study
<i>S. crassipes</i>		0.5	0.5	Present study

*Indicates a significant difference between female responses to visual cues versus vibration cues ($P < 0.05$).

isolated visual and vibration cues from live males was low, and very similar (Figure 2d).

DISCUSSION

While male spiders within the genus *Schizocosa* use vibrational and/or visual signals during courtship, females show differences in receptivity to isolated modes of conspecific male courtship displays. Differential responses of females to communication modes of males, and the apparent matching of modes and responses, support the hypothesis that male courtship modes and female responses have co-evolved. The four species examined in this study differ in their degree of male leg morphology, vary greatly in their modes of courtship signaling, and differ in female responses to isolated conspecific courtship cues. Throughout all six *Schizocosa* species examined to date, there appears to be concordance between the importance of visual sensory cues in female assessment of courtship and the degree to which conspecific males display visually. Those species that have more visually oriented displays also have the most decorated males. *Schizocosa duplex* and *S. rovneri*, both lacking ornamentation, do not have leg-waving displays and show significantly higher female receptivity to vibration cues than to visual cues (Table 1).

Although we analyzed the male visual courtship signals simply by their presence/absence, the species can be ranked in order of visual display from the least visual to the most visual in the following manner: *S. duplex*, *S. rovneri*, *S. uetzi*, *S. stridulans*, and a tied rank for *S. crassipes* and *S. ocreata*. The first three species in the above ranking show greater female responses to stridulatory signals over visual signals. Thus, as one moves up the ranking, visual displays increase as do female receptivities to visual displays. Further research along

these lines could generate correlations between the degree to which females use different sensory modes and the degree to which the males incorporate these modes into their courtship signaling. Interestingly, the degree to which males are ornamented also increases with increasing visual displays. This supports the idea that the secondary sexual traits of males within this genus act to increase the efficacy of visual displays (Hebets & Uetz, in press).

The results of this study demonstrate a correlation between male signal and female detection within species, and show the expected patterns arising across species. However, the selective pressures that are guiding these apparently coevolved patterns remain uncertain. There are several possible scenarios that could lead to this association between signal design and receiver sensitivities. Sexual selection theory predicts a close association between male display traits and female attraction through one of two different routes: (1) through a positive feedback loop between the increase in male ornament or display and the increase in female receptivity or attraction (Fisher’s run-away and good-genes models, for review see Andersson 1994); or (2) through the evolution of male signals in response to pre-existing biases in the sensory system of the female (West-Eberhard 1979; Kirkpatrick 1987; Ryan 1990; Ryan & Rand 1993).

The first scenario of coevolution, involving a feedback loop between male traits and female attraction, is difficult to test experimentally. Although *S. ocreata* females show receptivity more often to males with larger tufts, the variability in male body size and female preference for male body size confounds these results (McClintock & Uetz 1996). In video playback trials where male body size and behavior are held constant, and only tuft size is altered, females do not significantly increase in receptivity to males with enlarged tufts (McClintock & Uetz 1996). Thus, a feedback loop between male traits and female attraction remains questionable in this genus.

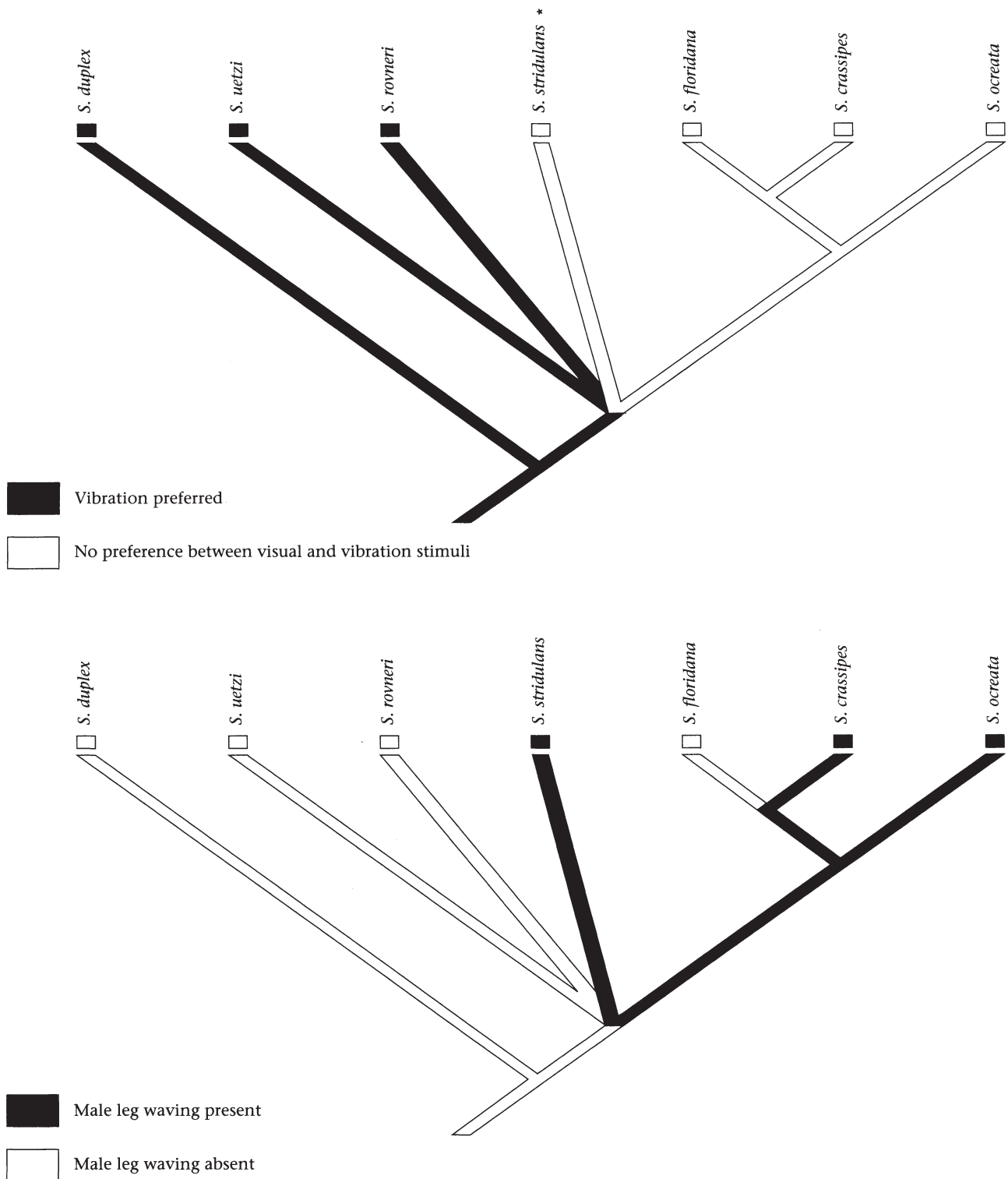


Figure 3. Combined cladogram from McClintock & Uetz (1996) and Stratton et al. (1996) showing phylogenetic relationships between selected species of *Schizocosa*. *Indicates that the presence or absence of a vibration bias is not known for *S. floridana*.

The evolution of male traits in response to female biases has recently received a great deal of attention and may play an active role in the evolution of secondary sexual traits of *Schizocosa* (West-Eberhard 1979; Ryan 1985, 1990; Endler 1993). Female *S. rovneri*, *S. uetzi*, and *S. duplex* all respond

to vibration cues significantly more than visual cues and male courtship in these species is primarily vibrational. However, because males of these species show little, if any, visual displays during courtship, it may not be surprising that females do not show receptivity to a conspecific male that can only be

seen and not felt. According to Basolo (1996), in order to provide evidence for female sensory bias, three criteria must be met: (1) females must prefer a conspecific male trait; (2) the absence of this male trait must be ancestral; and (3) females of the ancestral group must prefer the male trait even though it is not present in conspecifics. In this system, it is difficult to place these results into the context of sensory bias because a phylogeny encompassing all of the relevant species is not available. Although a phylogeny has been reconstructed for a small portion of this genus, the *S. ocreata* clade (McClintock & Uetz 1996), it does not include all of the species used in this study. None the less, using this phylogeny, we will briefly discuss the issue of female sensory bias.

According to McClintock & Uetz (1996), *S. uetzi*, *S. stridulans*, and *S. rovneri* form a polytomy basal to *S. ocreata* and *S. crassipes* (Figure 3). This phylogeny suggests that visual-based courtship displays are absent in the basal groups of *Schizocosa* and thus, the second of Basolo's (1996) criteria is present in this system. McClintock & Uetz (1996) also discovered that female *S. rovneri* responded to video playback of the visual courtship display of heterospecific *S. ocreata* males. Male *S. ocreata* have a very active signaling display involving leg waving and cheliceral strikes. Because female *S. rovneri* (a non-leg-waving species) show a heterospecific preference, it was suggested that they may have a pre-existing sensory bias for visual displays (McClintock & Uetz 1996). These results provide evidence of criterion number three (Basolo 1996). However, according to Basolo's (1996) first criteria, females must prefer a conspecific male trait. In this case, the male trait is a visual signal. Although females of visually displaying species prefer conspecific males, there is no evidence yet of a female preference for conspecific males with more visual displays. Future studies should include manipulations of visual displays (adding and deleting visual signals) by conspecifics to test the hypothesis that females prefer males with more visual displays.

The preferences that we see in females regarding different sensory cues could also result from differences in microhabitat structure (Uetz 1991; Scheffer et al. 1996). The variation in the ways in which specific modes of communication travel through a given environment may have influenced the evolution of male signal design and female receptivity. For example, when a weight was dropped on the compact leaf litter in the flood plains where *S. rovneri* is mainly found, the vibrations could be detected up to 100 cm away (Scheffer et al. 1996). However, when the same weight was dropped onto complex deciduous leaf litter, such as that found in the microhabitat of *S. ocreata*, the vibrations only traveled half as far (Scheffer et al. 1996). The stridulatory cues produced by *S. rovneri* also travel a much greater distance upon the compact leaf litter than do the vibrations produced by *S. ocreata* courting males. Scheffer et al. (1996) suggested that in an environment in which sound could not travel far (i.e. complex leaf litter), it would be advantageous to use a visual signal as well as a vibration signal. The differences seen in both female response preferences and male courtship modes may be

due solely to microhabitat differences. It may also be that the environmental constraints have led to female sensory biases, thus incorporating the mechanisms underlying both hypotheses. Unfortunately, the substrata upon which we collected the four species used in this study were not quantitatively analyzed and thus, hypotheses of environmental constraints are purely speculative.

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