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Enigmatic multimodal courtship signals and mating in *Schizocosa saltatrix* (Hentz, 1844)

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Abstract. Wolf spiders (Araneae: Lycosidae) in the genus *Schizocosa* Chamberlin, 1904 show a diverse array of male courtship behaviors, signaling modes and morphological traits, and have been the subject of extensive study. Although *S. saltatrix* (Hentz, 1844) is not as well-studied as some of its congeners, this species occupies a phylogenetic position basal to the well-studied *ocreata* clade within the genus. Here, we present a detailed analyses of its courtship and provide some insights about multimodal signals in the genus *Schizocosa*. Male and female *S. saltatrix* were collected from the field and raised to maturity in the lab, then paired randomly for mating trials, in which courtship and mating behaviors were recorded. Male courtship displays consist of vibratory signals coupled with leg-raising visual signals, suggesting that males apparently use complex (multimodal) signals in courtship despite assumptions from other studies. While the overall amplitude of vibratory signals is not related to mating success, rates and amplitude of some individual components (leg strikes) appear to play a role. Female responses show that variation in visual and vibratory signals is associated with receptivity and mating success, although signal information content (e.g., body condition) is unclear. Although visual displays may serve as attention-altering signals and attract female attention, vibratory signals are more important to receptivity. Recent phylogenies suggest that while leg decorations, extensive leg pigmentation and visual signals have likely been secondarily lost, visual displays are retained in *S. saltatrix*, perhaps as attention-altering signals.

Keywords: Visual signals, vibratory/seismic signals, power spectrum, stridulation, percussion

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Multimodal communication, used in many animal species as well as in some spiders, is defined by signal production and reception in more than one sensory mode—e.g., visual, acoustic, chemical, tactile, vibratory (Higham & Hebets 2013). The use of two or more sensory modes in communication is common, and examples may be found in most animal groups (Hebets & Papaj 2005; Partan & Marler 2005), including spiders. While many spider species are known to produce unimodal visual, vibratory and/or chemical signals in courtship and aggressive behavior (see chapters in Robinson 1982; Witt & Rovner 1982; Uetz & Stratton 1983), some species of Lycosidae and Salticidae are known to use multimodal signals combining visual and vibratory modes (Jackson 1977; Richman & Jackson 1992; Uetz 2000; Elias et al. 2005, 2012; Uetz et al. 2015, 2017; Bollatti et al. 2023).

Wolf spiders (family Lycosidae) in the genus *Schizocosa* Chamberlin, 1904 are an emerging model for studying the evolution of animal communication (Hebets et al. 2013; Uetz et al. 2016; Starrett et al. 2022). Common in deciduous forests of the Eastern and Midwestern U.S., *Schizocosa saltatrix* (Hentz, 1844) is not as well-studied as some of its congeners and less is known about its courtship behavior (Rovner 1974). Mature males of *S. saltatrix* show no leg ornamentation and limited leg pigmentation (Starret et el. 2022), although they do exhibit visual displays (leg raising/lowering) in courtship, suggesting potential multimodal communication (Stratton 2005). Despite this, responses of females to isolated visual male courtship signals are greatly reduced (Hebets et al. 2013). This is of interest because in both earlier morphology-based phylogenies (Stratton 2005) and more recent phylogenomic analyses (Hebets et al. 2013; Starrett et al. 2022), this species has been shown to occupy a phylogenetic position basal to the well-studied *ocreata* clade within the genus *Schizocosa*. The main objective of this research was to gain a better understanding of courtship and mating behavior of this lesser known, but phylogenetically important species. We also sought to determine whether aspects of male courtship behavior (vibratory and visual signals) are related to mating success, so we recorded and analyzed visual and vibratory courtship signals of *S. saltatrix* during mating trials.

METHODS

We collected *S. saltatrix* from the Cincinnati Nature Center Rowe Woods site in Milford, OH (39°07′31.2″N 84°15′04.3″W), in 2005 ($n = 50$) and 2020/2021 ($n = 24$). Spiders were collected as juveniles and raised to maturity in the lab to assure lack of exposure to males and to prevent bias from experience (Stoffer & Uetz 2015). All spiders were housed in opaque, plastic deli dish containers (10 cm diameter) and maintained at room temperature (22–25°C) with stable humidity and a 13:11 hour light/dark cycle to approximate late spring/early summer lighting conditions. Spiders were supplied water *ad libitum* and fed 2–3 0.5–1.0 cm crickets twice/week.

Once mature, male and female spiders were paired in an arena in mating trials. The mating arena was constructed using a 20 cm diameter cylinder with a circular piece of filter paper lining the bottom as in previous studies (Meyer & Uetz 2019). Females were allowed to explore the arena for 15 minutes and lay silk prior to trial start, then corralled into an inverted vial. A male was introduced into the arena and given a two-minute acclimation period before the female was released. During these two minutes, males typically detected the female presence and began courting. After two minutes, the female was released, and the pair were allowed to interact for up to 1-hour. Trials ended when successful mating occurred or after 1-hour of interaction, allowing for variable trial lengths if mating was the outcome. Trials were video recorded and later scored for behaviors.

Male courtship was recorded from parchment paper, a close facsimile of leaves with respect to vibration transmission (Uetz, unpubl. data), lining the floor of the arena. Male vibratory/seismic signals were recorded from below (through a hole in the arena) using a Polytec PDV-100 laser Doppler vibrometer

Table 1.—Ethogram of mating behaviors of *S. saltatrix*.

A. Male Behaviors	Behavior Description
Chemoexploration	Male rubs pedipalps on substrate to sense chemical cues from female.
Orient	Male turns to face female.
Slow Approach	Male slowly moves directly toward female from stationary position and stops in front of her.
Fast Approach	Male quickly moves toward female from stationary position and attempts to mount female.
Leg Raise/Lower	Male raises one or both forelegs past a position parallel to the ground at the beginning of its rattle vibration. Once foreleg(s) reaches its peak, it is slowly lowered until it is just off the ground. At this point, male performs a strike vibration, which is followed by slowly lowering the foreleg(s) all the way to the ground and performing one or two more strikes before it reaches the ground. Typically, three strikes total are performed while the male lowers the foreleg(s).
Stationary Pose	Male stops moving, raises his body and makes vibratory signals.
Mount	Male raises forelegs higher than female's forelegs, then male climbs on dorsum of female (in settle position).

B. Female Behaviors	Behavior Description
Orient	Female turns to face male.
Approach	Female quickly moves toward male from stationary position.
Lunge/Attack	Female quickly lunges at male with legs arched, usually after male approaches female, and then retreats.
Slow Pivot	Female pivots 90° to 180° toward male.
Tandem Leg Extension	Female extends both forelegs fully and parallel to the ground to allow male to mount.
Settle	Female lays body on the ground, performs tandem leg extension, and rotates abdomen to allow male to mount.

(125 mm/s/V sensitivity, 100 mm/s max, 96 mm standoff distance). The laser Doppler vibrometer (LDV) was connected to an external sound card (Roland QuadCapture) and calibrated with a 1 kHz tone (50% FS). The LDV was used to record male vibratory courtship signals for 15 minutes, when the female was released and allowed to mate. Vibratory signals and behaviors were recorded simultaneously using a SONYvideo camera (Model: HDR-XR260V).

LDV recordings of male vibration signals were analyzed using the software packages Raven Pro® ver 1.6 (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology) and SpectraPlus® (Pioneer Hill Software). The processing of male vibratory signals was conducted in SpectraPLUS-SC (24 kHz sampling rate, 2048 FFT, Hanning window) to calculate the frequency (Hz) and amplitude (root mean square in dB) of each percussive element. Spectrograms of male vibratory signals were generated in Raven Pro®. Patterns and components of vibrations were analyzed for differences between mated and non-mated males, and different leaf substrates. Behaviors were observed on video recordings and scored using BORIS® (Behavior Observation Research Interactive Software), a freeware package for event recording (online at http://www.boris.unito.it/), then output to spreadsheets for statistical analyses.

An ethogram for male and female behaviors during mating trials was developed (Table 1A, B). Male courtship behaviors and vibratory signals (amplitude in mm/s) occur as events and were recorded up to the time of mating, allowing for a rate or mean to be calculated. Female *S. saltatrix* pre-copulatory behaviors include receptivity displays (slow pivot, tandem leg extend and settle) similar to other species in this genus, and a sum of displays was calculated as a receptivity score. We used this ethogram when scoring selected male *S. saltatrix* courtship behaviors (number of leg raises, number of vibratory signals) as well as female receptivity displays from recordings of mating trials.

We conducted an additional experiment in 2005 to examine the receptivity responses of females to isolated visual and vibratory/seismic cues, similar to the approach used in previous studies of *S. ocreata* (Hentz, 1844) (Hebets & Uetz 1999; 2000; Uetz et al. 2009). Males and females were placed in adjacent, bottomless plastic corrals (12 cm × 6 cm × 6 cm) made of clear acetate

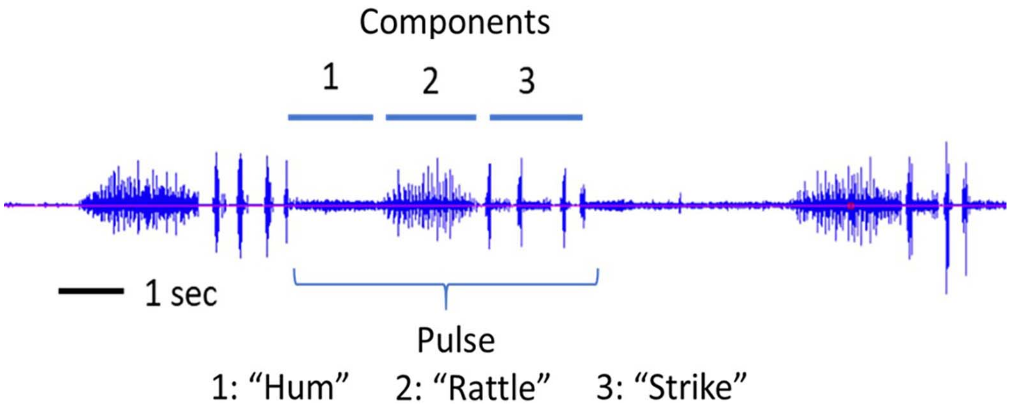


Figure 1.—Oscillogram of representative recording of vibratory/seismic signal of *S. saltatrix* (shown as amplitude/time in secs).

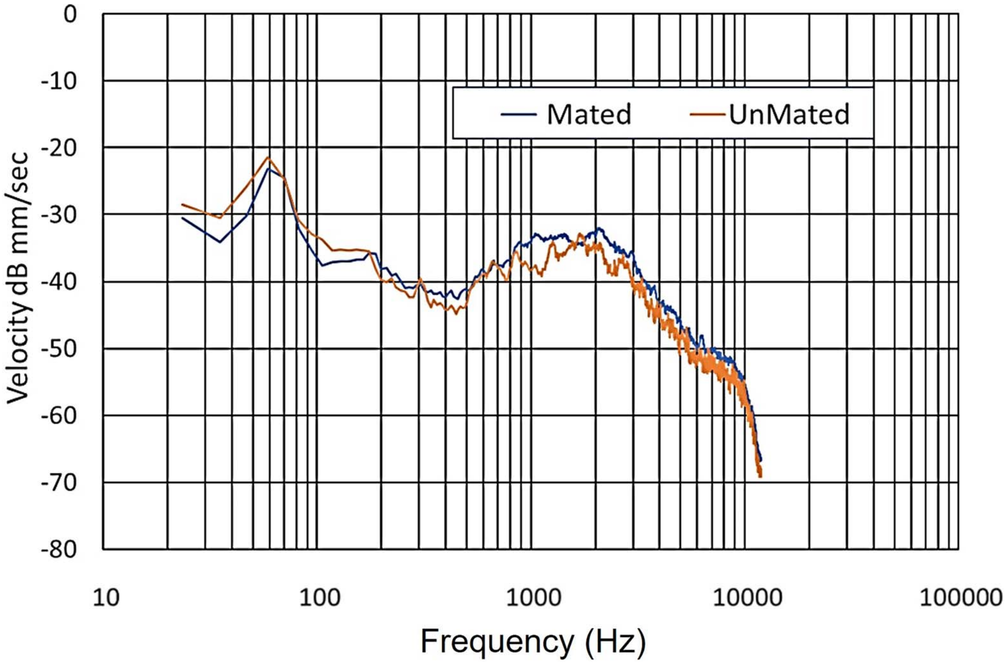


Figure 2.—Power spectrum of male *S. saltatrix* vibratory/seismic signals.

plastic as follows: vibratory/seismic cues alone (males and females on a common paper-covered posterboard substratum with a visual barrier between containers); visual cues alone (males and females separated with a clear barrier on adjacent 2.8 × 10 × 20 cm granite blocks that eliminated vibration); or multimodal cues (both vibratory/seismic and visual cues available to males and females behind a clear partition on a common paper and paperboard substratum). The substrata were tested for successful vibration conduction or elimination before the experiment using the LDV as above. As males exhibit courtship behaviors in response to the presence of conspecific adult female silk and chemical cues (Roberts & Uetz 2004), females were placed on the paper substratum of male containers to deposit silk for 12 h before each trial to ensure deposition of cues. Trials lasted 1 hr and were videorecorded with a Sony camcorder (Model: HDR-XR260V) with input from the LDV for later analysis.

Statistical analyses were performed using JMP® (JMP Statistical Discovery LLC, Cary, NC). Data on rates and amplitudes were tested for fit to a normal distribution and subsequently analyzed with parametric or non-parametric tests. We determined whether male and/or female behaviors influenced mating success using both logistic regression of mating vs. continuous variables or one-way ANOVA as well as two sample tests (or non-parametric equivalents).

We adhered to the ASAB/ABS Guidelines for the Use of Animals in Research (available online at https://doi.org/10.1016/j.anbehav.2019.11.002). All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. There are no institutional, local, state or federal government rules regarding animal care for invertebrates (spiders). At the end of our experimental studies, all spiders were humanely euthanized with CO_2 anesthesia and freezing. Voucher specimens have been deposited at the Museum of Natural History & Science at Cincinnati Museum Center, 1301 Western Avenue, Cincinnati, OH 45203 (https://www.cincymuseum.org/geier-research-center).

RESULTS

Recordings show male vibratory/seismic signals are complex in structure, with three distinct components—called Hum, Rattle and Strike—in each pulse, each having a different temporal profile (Fig. 1). Power spectra of vibration signals for mated vs. unmated males (Fig. 2) show considerable overlap, although mated males have slightly higher peaks in some intermediate

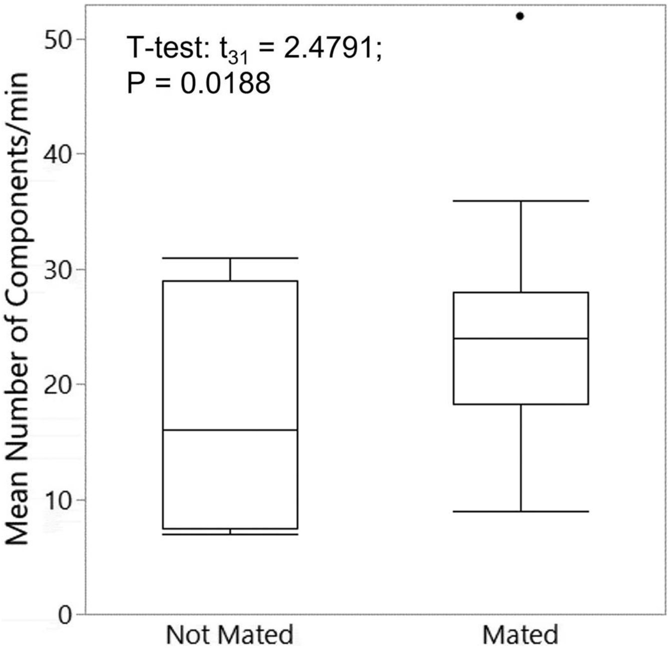


Figure 3.—Signal Complexity (expressed as mean number of courtship components)/min.

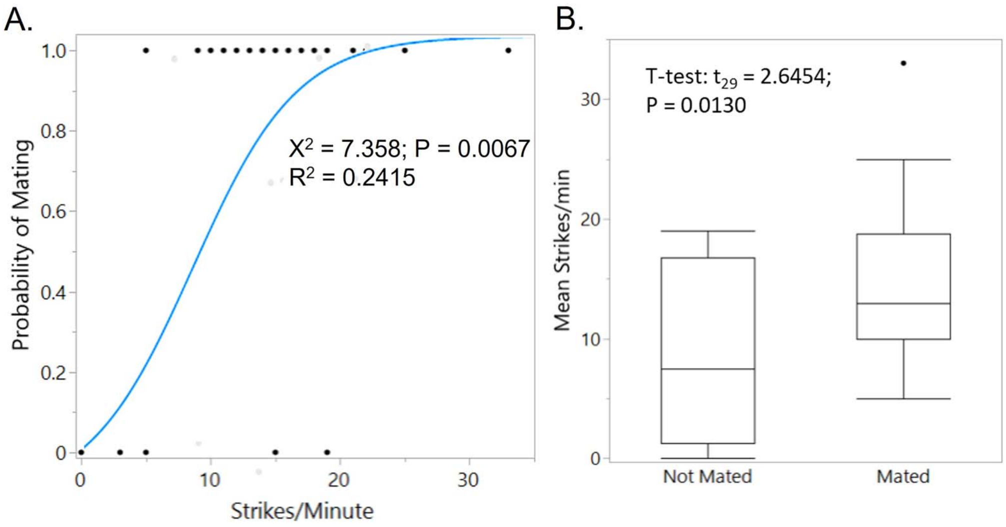


Figure 4.—Male courtship signal components—vibratory/seismic strikes—and mating success. A. Logistic regression of mating probability vs. strike rate; B. Two-sample test of mean rates for mated/unmated males.

frequencies (800–3000 Hz). Differences (with varying degrees of statistical significance) between mated and unmated males were seen for: Hums (t = 1.986; *P* = 0.0533), Rattles (t = 2.394; *P* = 0.0226) and Strikes (t = 4.175; *P* = 0.0002). In almost all cases, males that mated successfully had higher signal component rates. Signal complexity, measured as the mean number of components within signal pulses (Fig. 3), varied significantly between mated and unmated males. Males with more complex signals were more likely to mate. While there were no significant differences in mating probability for rattles and hums, there was a significant difference based on signal rate of one component (strike) (Fig. 4a). Males that mated had a higher strike rate (Fig. 4b). Amplitude of strike signals also showed significant differences in mating probability (Fig. 5a); males that mated had higher amplitude strikes (Fig. 5b).

Our observations confirm that the complex courtship displays of *S. saltatrix* consist of vibratory/seismic signals coupled with leg-raising visual signals (Stratton 2005; Table 1A). Logistic regression showed that the probability of mating was significantly predicted by rates of visual leg raises (Fig. 6a); males that mated successfully had higher visual signaling rates (Fig. 6b). A comparison of rates of vibratory/seismic signals (strikes) and visual signals (leg raises) shows a significant correlation (Fig. 7). These results support the hypothesis that courtship signal production in *S. saltatrix* is multimodal.

Information content of signals (e.g., mate quality) was unclear, as we found no correlation between male size measured as carapace width (CW) with signal rates in either mode, or in the amplitude of vibratory signals. Measured aspects of signals were not correlated with male size (strike rate x male CW: $R^2 = 0.037$, $P = 0.4413$; strike amplitude x male CW: $R^2 = 0.0293$, $P = 0.5111$; leg raise rate x male CW: $R^2 = 0.049$, $P = 0.406$).

Behavior responses of females to isolated courtship signal modes reveal a different pattern (Fig. 8). The number of orientations (Fig. 8a) and approaches (Fig. 8b) are equal for both isolated visual signals and multimodal signals, but almost nonexistent for isolated

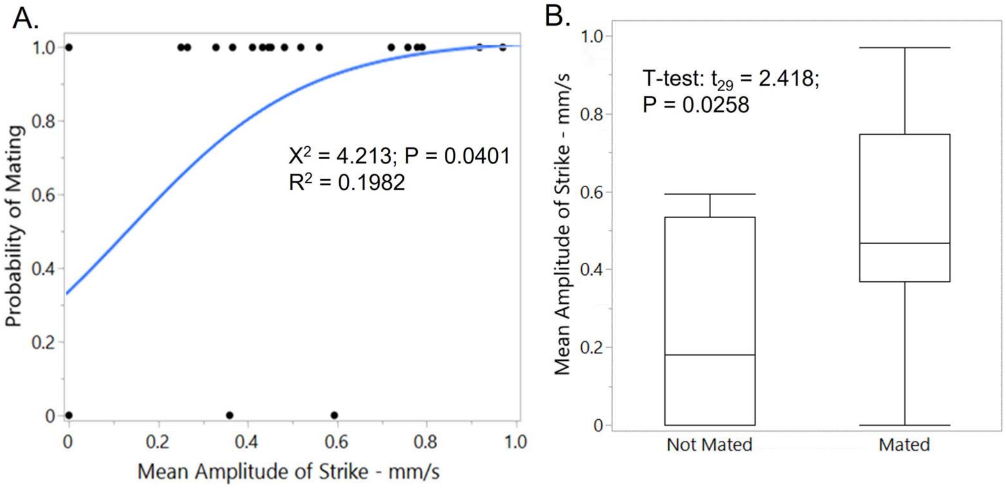


Figure 5.—Male courtship signal components—vibratory/seismic strike amplitude—and mating success. A. Logistic regression of mating probability vs. strike amplitude; B. Two-sample test of mean strike amplitude for mated/unmated males.

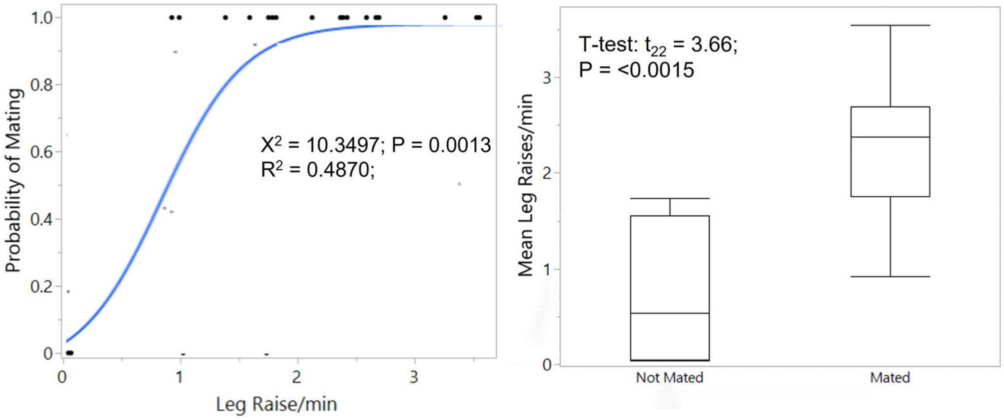


Figure 6.—Male courtship signal components and mating success – mean visual leg raise displays.

vibratory/seismic signals. In contrast, female receptivity displays (Fig. 8c), were equal for isolated vibratory/seismic and multimodal signals, and barely present for isolated visual signals.

DISCUSSION

Many animals exhibit complex, multimodal signals that contain two or more signaling modes that occur synchronously (simultaneously) and that are perceived by multiple sensory systems (Hebets & Papaj 2005; Partan & Marler 2005; Higham & Hebets 2013; Hebets et al. 2016). Lycosidae are known for using multiple modes of communication in courtship, although not all modes are produced simultaneously or synchronously. For example, *Rabidosa rabida* (Walckenaer, 1837), produce visual and vibratory signals both simultaneously and separately (asynchronously) at different times during pre-copulatory behavior, while others, e.g., *Schizocosa ocreata* (Hentz, 1844), use simultaneous vibratory and visual signals throughout courtship (Uetz & Stratton 1982; Rovner 1996; Wilgers & Hebets 2011; Uetz et al. 2016). Consequently, it is necessary to examine both rates of production of signals and female responses to multimodal vs. vibratory and visual signals.

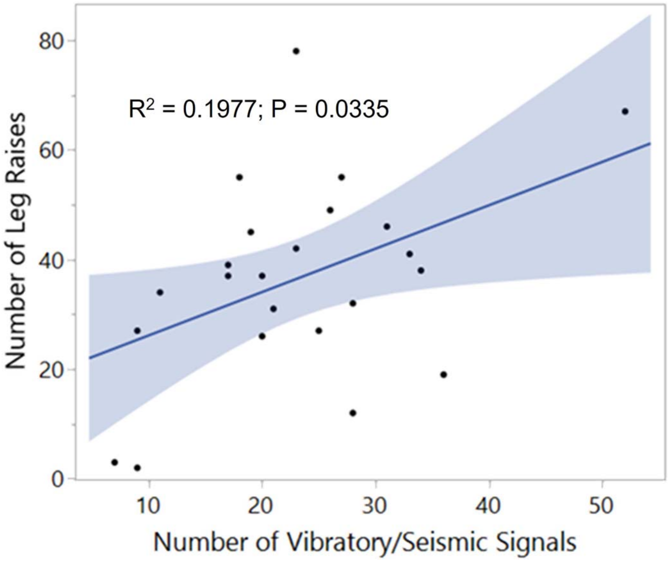
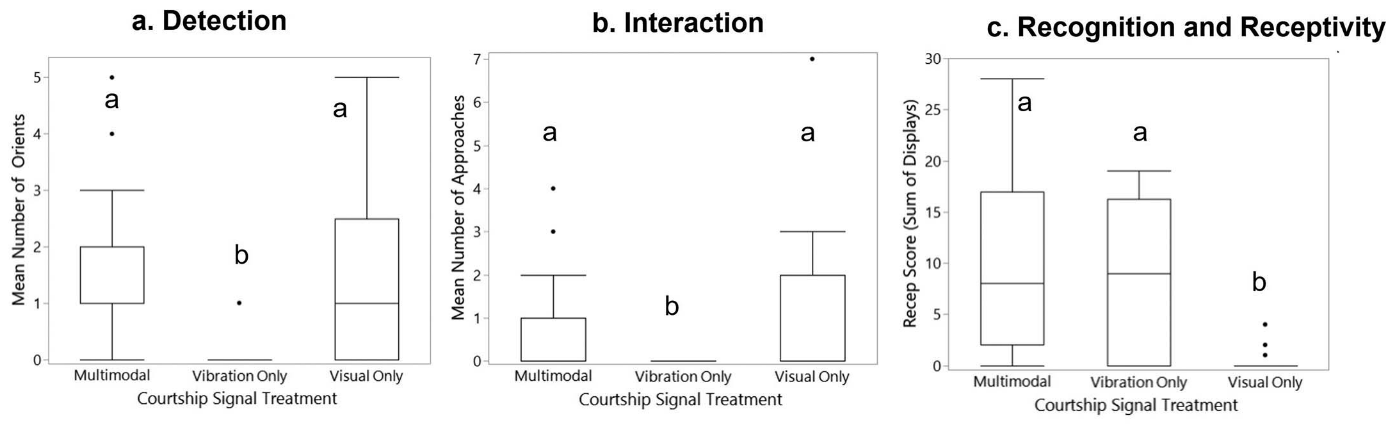


Figure 7.—Correlation of number of male *S. saltatrix* visual signals (leg raises) and vibratory/seismic signals.

Male *Schizocosa saltatrix* produce complex multimodal signals in courtship, as courtship displays consist of vibratory/seismic signals coupled with leg-raising visual signals. Mating responses of female receivers show that variation in both modes is associated with sexual receptivity displays and mating success. Results of our studies suggest that mating success varies with parameters of structurally complex male vibration signals of *S. saltatrix*, as well as signal rates in both vibratory and visual modes. Mated male *S. saltatrix* signals exhibited higher pulse rates and greater complexity, suggesting potential for mate preference. However, subtle differences in power spectra might also suggest that females assess signal structure as well as overall rate of male courtship signals in choosing mates.

While male *S. saltatrix* produce complex multimodal signals in courtship, and female receivers' responses show that variation in both male signal modes is associated with mating success, isolated visual displays do not elicit female sexual receptivity displays. Cue isolation studies confirm earlier findings (Hebets et al. 2013) that females respond primarily to vibratory and multimodal signals, but not visual displays. In our cue isolation experiments, females oriented and approached visual signals and multimodal signals equally but they barely responded to isolated vibration signals (Fig. 8a,b). However, female sexual receptivity displays were more frequent with isolated vibratory and multimodal signals (Fig. 8c). This finding supports the idea that leg-raising visual displays coupled with vibratory/seismic signals more likely serve to attract female attention and/or serve as attention-altering displays. Given the nature of the leaf litter environment, with visual background complexity and discontinuity of vibration-conducting surfaces, attention-getting visual displays can enhance detection of signals (Hebets 2005; Wilgers & Hebets 2011; Uetz et al. 2013).

Phylogenetic analyses of the genus *Schizocosa* (Stratton 2005; Hebets et al. 2013, 2020; Starrett et al. 2022) suggest that extensive leg pigmentation, leg decorations and reliance on visual signals have likely been secondarily lost in a number of species within or related to the well-studied *ocreata* clade, including *S. saltatrix*. However, visual displays are retained in *S. saltatrix*. Information content of these signals regarding mate quality, condition and feeding history is unclear, as there was no correlation



One-way ANOVA: F = 7.3561 ; P = 0.0017 One-way ANOVA: F = 3.684 ; P = 0.0326 One-way ANOVA: F = 8.9182; P = 0.0005

Figure 8.—Mean number of responses by female *S. saltatrix* to male courtship signal modes.

between male size with signal rates in either mode, or in the amplitude of vibratory signals (other measures were not available). Based on the information at hand, we conclude that even though visual signals are coupled with production of vibration, and resulting multimodal signals are associated with mating, visual displays serve to attract female attention while vibratory/seismic signals are more important to eliciting female receptivity. Future studies on male signal information content and female mate preference and choice may allow better understanding of the evolution of these signals.

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LITERATURE CITED

Bollatti F, Aisenberg A, Toscano-Gadea CA, Peretti AV, González M. 2023. Updates and perspectives on reproductive behavior of South American wolf spiders. *Journal of Arachnology* 51:63–79.

Elias DO, Hebets EA, Hoy RR, Mason AC. 2005. Seismic signals are crucial for male mating success in a visual specialist jumping spider (Araneae: Salticidae). *Animal Behaviour* 69:931–938.

Elias DO, Maddison WP, Peckmezian C, Girard MB, Mason AC. 2012. Orchestrating the score: complex multimodal courtship in the *Habronattus coecatus* group of *Habronattus* jumping spiders (Araneae: Salticidae). *Biological Journal of the Linnean Society* 105:522–547.

Hebets EA. 2005. Attention-altering signal interactions in the multimodal courtship display of the wolf spider *Schizocosa uetzi*. *Behavioral Ecology* 16:75–82.

Hebets EA, Papaj DR. 2005. Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology* 57:197–214.

Hebets EA, Uetz GW. 1999. Female responses to isolated signals from multi-modal male courtship displays in the wolf spider genus *Schizocosa* (Araneae: Lycosidae). *Animal Behaviour* 57:865–872.

Hebets EA, Uetz GW. 2000. Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). *Behavioral Ecology and Sociobiology* 47:280–286.

Hebets EA, Barron AB, Balakrishnan CN, Hauber ME, Mason PH, Hoke KL. 2016. A systems approach to animal communication. *Proceedings of the Royal Society B* 283: 20152889.

Hebets EA, Bern M, McGinley RH, Roberts A, Kershenbaum A, Starrett J, et al. 2020. Sister species diverge in modality-specific courtship signal form and function. *Ecology and Evolution* 11:852–871.

Hebets EA, Vink CJ, Sullivan-Beckers L, Rosenthal MF. 2013. The dominance of seismic signaling and selection for signal complexity in *Schizocosa* multimodal courtship displays. *Behavioral Ecology and Sociobiology* 67:1483–1498.

Hentz, NM. 1844. Descriptions and figures of the Araneides of the United States. *Boston Journal of Natural History* 4:386–396.

Higham JP, Hebets EA. 2013. An introduction to multimodal communication. *Behavioral Ecology and Sociobiology* 67:1381–1388.

Jackson RR. 1977. Courtship versatility in the jumping spider, *Phidippus johnsoni* (Araneae: Salticidae). *Animal Behaviour* 25:953–957.

Meyer TB, Uetz GW. 2019. Complex male mate choice in the brush-legged wolf spider. *Behavioral Ecology* 30:27–38.

Partan SR, Marler P. 2005. Issues in the classification of multimodal communication signals. *The American Naturalist* 166:231–245.

Richman DB, Jackson RR. 1992. A review of the ethology of jumping spiders (Araneae, Salticidae). *Bulletin of the British Arachnological Society* 9:33–37.

Roberts JA, Uetz GW. 2004. Chemical signaling in a wolf spider: A test of ethospecies discrimination. *Journal of Chemical Ecology* 30:1271–1284.

Robinson MH. 1982. Courtship and mating behavior in spiders. *Annual Review of Entomology* 27:1–20.

Rovner JS. 1974. Copulation in the lycosid spider *Schizocosa saltatrix* (Hentz): an analysis of palpal insertion patterns. *Animal Behaviour* 22:94–99.

Rovner JS. 1996. Conspecific interactions in the lycosid spider *Rabidosa rabida*: the roles of different senses. *Journal of Arachnology* 24:16–23.

Starrett J, McGinley RH, Hebets EA, Bond JE. 2022. Phylogeny and secondary sexual trait evolution in *Schizocosa* wolf spiders (Araneae, Lycosidae) shows evidence for multiple gains and losses of ornamentation and species delimitation uncertainty. *Molecular Phylogenetics and Evolution* 169:107397.

Stoffer B, Uetz GW. 2015. The effects of social experience with varying male availability on female preference in a wolf spider. *Behavioral Ecology and Sociobiology* 69:927–937.

Stratton GE. 2005. Evolution of ornamentation and courtship behavior in *Schizocosa*: insights from a phylogeny based on morphology (Araneae, Lycosidae). *Journal of Arachnology* 33:347–376.

Uetz GW. 2000. Signals and multi-modal signalling in spider communication. Pp. 387–405. *In* Animal Signals: Signalling and Signal Design in Animal Communication. Proc. Fifth Int. Kongsvoll Symp. (Espmark Y, Amundsen T, Rosenqvist G, Eds.) Tapir Publishers, Trondheim, Norway.

Uetz GW, Stratton GE. 1982. Acoustic communication in spiders. Pp. 123–159. *In* Spider Communication: Mechanisms and Ecological Significance. (Witt PN, Rovner JS, Eds.) Princeton University Press, Princeton, NJ.

Uetz GW, Stratton GE. 1983. Communication via substratum-coupled stridulation and reproductive isolation in wolf spiders (Araneae: Lycosidae). *Animal Behaviour* 31:164–172.

Uetz GW, Clark DL, Roberts JA. 2016. Multimodal communication in wolf spiders (Lycosidae) – an emerging model for study. *Advances in the Study of Behavior* 48:117–159. (Naguib M, Mitani JC, Simmons LW, Barrett L, Healy S, Zuk M, Eds.). DOI:10.1016/bs.asb.2016.03.003

Uetz GW, Clark DL, Roberts JA, Gibson JS, Gordon SD. 2013. Active space of multimodal signals of wolf spiders in a complex litter environment. *Behavioral Ecology and Sociobiology* 67:1471–1482.

Uetz GW, Clark DL, Stoffer B, Kozak EC, Lallo M, Kane H. 2015. Multimodal communication in wolf spiders: playback studies with visual and vibratory signals. *Journal of the Acoustical Society of America* 137: 2395–2395.

Uetz GW, Roberts JA, Taylor PW. 2009. Multimodal communication and mate choice in wolf spiders: Female responses to multimodal vs. unimodal male signals in two sibling wolf spider species. *Animal Behaviour* 78:299–305.

Uetz GW, Stoffer B, Lallo M, Clark DL. 2017. Complex signals and comparative mate assessment in wolf spiders: results from multimodal playback studies. *Animal Behaviour* 134:283–299.

Wilgers DJ, Hebets EA 2011. Complex courtship displays facilitate male reproductive success and plasticity in signaling across variable environments. *Current Zoology* 57:175–186.

Witt PW, Rovner JS. 1982. Spider Communication: Mechanisms and Ecological Significance. Princeton University Press, Princeton, NJ.

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