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Web Vibrations in Intraspecific Contests of Female Black Widow Spiders, *Latrodectus hesperus*

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Abstract

Female black widow spiders, *Latrodectus hesperus* Chamberlin and Ivie (Araneae: Theridiidae), are solitary predators of arthropods with no tolerance for intruders on the webs. In California, *L. hesperus* are found in urban and agricultural settings and can be a phytosanitary pest in fresh produce. Spatial separation of *L. hesperus* webs could be determined by seasonal population densities, with territorial competition expected under high densities in the environment. However, little is known about female-female communication behaviors in this species. In 1-hr laboratory observations, displays of female-female rivalry included production of vibrational signals in a majority (20 of 30) of trials. The number of signals produced by both females was highest during the initial 10 min of trials, with signaling rate (time interval between signals) peaking during the 40–50 min observation period. The overall ratio of signals produced by the resident female and the introduced female was about 5:1, with the number of signals produced by the resident female higher than the number of signals produced by the introduced female. Analysis of rivalry signals showed a peak in magnitude (about 0.4 m/s) ranging from 6 to 23 Hz and smaller peaks at about 29, 38, and 47 Hz. Collectively, these results demonstrate that female *L. hesperus* exhibit territorial rivalry and that female-female rivalry is mediated by emission of vibrational signals through the web. Understanding the mechanisms of intraspecific competition in *L. hesperus* is required for elucidating interspecific interactions in the environment and may lead to development of novel methods to prevent spiders from colonizing crops.

Key words: vibrational communication, Theridiidae, territorial rivalry

Western black widow spiders, *Latrodectus hesperus* Chamberlin and Ivie (Araneae: Theridiidae), are a concern because of their abundance in human-inhabited areas and the extreme neurotoxicity of their venom (α-latrotoxin) (Garb and Hayashi 2013), which is highly lethal to small mammals, amphibians, and reptiles (Gendreau et al. 2017, Nyffeler and Vetter 2018). In California, *L. hesperus* is abundant in agricultural settings (Nyffeler and Vetter 2018) and can be a phytosanitary problem in table grape vineyards due to trade barriers imposed to fruit destined for international markets (Walse et al. 2017). Spiders are generalist predators of arthropods with intraspecific competition predicted to be strong due to resource overlap, which results in many spider species being territorial, and potentially cannibalistic (Marshall and Rypstra 1999). Competition for resources has been described in spiders (Jackson 1988; Elias et al. 2008, 2010; Kasumovic et al. 2009), with interactions typically starting with noncontact displays that can escalate to touching and physical combat (Elwood and Prenter 2013). For example, female feather-legged spiders, *Uloborus plumipes* Lucas (Araneae: Uloboridae), compete for webs by interacting at a distance through vibrational signaling on the web, and if contests are not resolved through communication, interactions can escalate to physical combat (Joel et al. 2017).

Female *L. hesperus* are solitary predators with little to no tolerance for intruders on the webs, which consist of a three-dimensional silk structure that radiates out from a retreat and is suspended by threads (Benjamin and Zschokke 2003). The matrix of silk threads physically isolates individuals from potential predators and allows early warnings of attacks from vibratory cues transmitted through the silk (Blackledge et al. 2003). In California, *L. hesperus* is common in or near human dwellings such as garages, garden sheds, barns, and farm equipment and exhibit a preference for locations close to the ground (Vetter et al. 2012). Wires used in vineyard trellis serve as anchor points that allow *L. hesperus* to build webs extending from the ground into the grapevine canopy. The closest spatial separation between two female *L. hesperus* webs observed in a natural setting was about 0.5 m at the ground level and no spiders have been found to vertically share their hunting grounds (i.e., one female occupying the top and on the bottom of the same structure) (Krugner, personal observation). Horizontal and vertical separation of *L. hesperus* webs are likely determined by seasonal population densities, with inter- and intraspecific territorial competition expected under relatively high densities in the environment.

Mating communication in *L. hesperus* is mediated by chemical and vibrational signals (Vibert et al. 2014, 2016). Males use pheromones from female webs to localize mates (Ross and Smith 1979) and, upon arriving on female webs, males initiate courtship behaviors characterized by the production of web-transmitted vibrations (Vibert et al. 2014). During mating communication, males display three distinct types of signals (abdominal tremulation, bounce, and web plucks) (Sivalinghem and Mason 2021), that differ from vibrations produced by prey (Vibert et al. 2014). While male and female *L. hesperus* are known to use vibrational signals in mating communication, little is known about female-female communication behaviors in this species. Using high-speed video vibrometry and stereo vision combined with laser vibrometry, Justus et al. (2022) applied a three-dimensional vibration analysis to extract vibrational information from an *L. hesperus* web during female-female displays of rivalry. Bounce signals produced by *L. hesperus* females peak at about 40-mm displacement and travel on the web with average wave speeds of 19.5 m/s.

One potential approach for developing a novel *L. hesperus* control method in vineyards is through the exploitation of natural competition and cannibalism. The brown widow spider, *L. geometricus* Koch (Araneae: Theridiidae), was first reported from southern California in 2003 (Vincent et al. 2008) and has since spread to many regions of California. Surveys showed that *L. geometricus* now greatly outnumbers *L. hesperus* in urban settings, but are very rare or nonexistent in agricultural crops compared to *L. hesperus*. Although *L. geometricus* and *L. hesperus* prefer sites close to the ground (<1 m), findings of *L. geometricus* up to 3 m above ground suggest that *L. geometricus* might be taking the high ground (Vetter et al. 2012). Understanding the mechanism of inter- and intraspecific female competition may help elucidate native × invasive spider interactions in the environment and lead to development of novel methods to prevent *L. hesperus* from colonizing a grapevine canopy. In this study, the hypotheses that 1) female *L. hesperus* exhibit intraspecific territorial rivalry and 2) displays of female-female rivalry are mediated by the emission of vibrational were tested.

Materials and Methods

Male and female spiders collected from the field in Spring 2019–2022 were kept individually in cubic cages (30 × 30 × 30 cm) made of 0.5-cm thick acrylic walls with meshed ventilation holes and an access door (15 × 15 cm) on top. Spiders were kept in a laboratory room at 24–27°C, 22–25% RH, and 10:14 (L:D) hr for 2–3 wk and fed with commercially available crickets (Bassetts Cricket Ranch Inc., Visalia, CA) until used in the experiments described below. Experiments were conducted in a chamber that provided a uniform background and reduced both airborne noise and observer interference. The acrylic cubic cages described above were centered inside the chamber, which was formed by 86 × 86 × 98 cm high blackout fabric and sound isolating walls (Studiofoam Pyramids, Auralex Acoustic, Indianapolis, IN). The arena and chamber were placed on an active vibration isolation table (Model 20-561, Technical Manufacturing Corporation, Peabody, MA). Spider behaviors were monitored via video surveillance (Panasonic Lumix GH4). Vibrational signals produced by individuals were recorded using a laser Doppler vibrometer (PDV-100, Polytec, Inc., Irvine, CA), a data acquisition system (Polytec, Inc.), and Adobe Audition C26 (Adobe Systems, Inc., San Jose, CA) at a 44.1 kHz sample rate, 32 bits resolution, and fixed settings for computer and software audio input across recordings.

For the recordings, a square piece of foam (0.5 × 0.5 × 0.5 cm) wrapped in reflective tape (Polytec, Inc.) was placed on the center of the web to facilitate contactless recordings by the laser, keeping the recording within approximately 15 cm of all locations of the web. About 0.1 cm of the edge of the reflective tape was left unfolded to expose the adhesive side to provide a secure coupling to the web. *Latrodectus hesperus* females are primarily nocturnal spiders, but preliminary observations of spiders maintained in captivity in the laboratory indicated that behaviors such as hunting, mating, and rivalry occurred during the day. Therefore, trials were conducted between 0800 and 1700 hr at room temperature. Before testing, spiders were allowed 15 min to acclimatize to ambient conditions in the respective cubic cages placed within the chamber. In each trial (n = 30), a female spider was collected into a glass vial and gently placed on the bottom of another cage containing a female on her web. As controls, female-female trials were alternated with trials conducted using a male spider (n = 5) or a prey item (cricket) (n = 5) placed on a female cage to allow differentiation between potential rivalry signals produced by females and other signals (e.g., male and female courtship signals, vibrations produced by prey). Trials consisted of 1-hr recordings. Individuals were used only once in the experiments. Video recordings did not accurately reveal which spider produced signals. Therefore, to quantify separately the number of signals produced by the resident, and by the introduced female, 10 trials were conducted as described above, except two observers recorded the occurrences of vibrational signals.

Temporal parameters of recorded signals were analyzed with Raven Pro 1.6 (The Cornell Lab of Ornithology, Ithaca, NY) and Adobe Audition. Signals shown in figures below were modified for illustrative purposes using the noise reduction process in Adobe Audition. The signaling rate, measured as the time period between the onset of two consecutive elements, was recorded. Signal velocity (m/s) was analyzed from the initial 1-s section of 10 randomly selected signals recorded from female-female trials (n = 10) and a female-male trial using the Fast Fourier Transform function in SigPro (Polytec, Inc.), with Hanning type window. Temporal characteristics of signals recorded from female-female trials were compared using ANOVA followed by Tukey's post hoc test, whereas t-test was used to compare the number of signals produced by the resident and the introduced female. For the analysis described above, the 1-hr recording was divided into six 10-min periods.

Results

Female vibrational signals were never recorded from the prey-only trials, whereas vibrational signaling was recorded from a majority (20 of 30) of trials with two female spiders. Vibrational signals produced by male-female pairs were similar to those reported by Sivalinghem and Mason (2021) and mating occurred in only one of the five 1-hr trials. Female signals recorded from male-female communication were limited to abdominal vibrations with relatively low intensity when compared to the high-intensity bounce signals recorded from female-female interactions (Fig. 1). In the latter, signals were produced by a rapid dorso-ventral movement of the female body.

In most trials where female-female vibrational communication occurred (16 of 20), the introduced female perceived vibrational signals produced by the resident females and moved away from it, thereby avoiding physical or signaling combat. Production of relatively stronger vibrational signals was recorded when the introduced female continued to move on the web or produced signals. In four (of 20) trials, the resident and introduced females moved to close range physical contact and with the exception of one trial, all trials ended with both spiders alive and positioned away from each other in the cage. During close range contacts, females initially touched each other using the frontal legs, followed by bursts of grappling-like movements. Lethal combat between females was observed once (1 of 20 trials), where the introduced female did not retreat after perceiving bounce signals and was able to immobilize the resident female by spinning webs around its legs during the grappling-like movements.

In female-female pairs, the number of signals produced by both spiders was higher ($F = 3.385$; df = 5, 114; $P = 0.007$) during the first 10 min of the trial than during the last 20 min of the trial, with the time interval between the onset of individual signals peaking during the 40–50 min time period compared to the earlier time periods ($F = 4.802$; df = 5, 1311; $P < 0.0001$) (Fig. 2). Short sequences (groups) of bounce signals were recorded (Fig. 3B, C), but most signals were produced individually (Fig. 3A). In cases where signals were produced in groups with short intervals (<3 s) between the onset of signals within the sequence, the average (±SEM) number of signals per group was 11.16 ± 2.26 (range = 5–34 signals) with an interval between signals of 1.71 ± 0.14 s (range = 0.70–2.50 s). There was no evidence for temporal structuring in signaling as females were observed to produce individual and groups of signals throughout the 1-hr recording of female-female communication. In trials where both spiders were closely monitored by two observers, female-female vibrational communication occurred in seven (of 10) trials and initiated with bounces produced by the resident spider. In the first 10 min of the observation period, the ratio of signals produced by the resident and introduced spiders was about 12:1, with an overall ratio of about 5:1 across the observation periods. The number of signals produced by the resident spider was higher than the number of signals produced by the introduced spider ($t = 3.239$; df = 41; $P = 0.002$) (Fig. 2C). On average (±SEM), the resident spider produced 9.05 ± 2.46 signals whereas the introduced spider produced 1.88 ± 0.82 signals across the six observation periods.

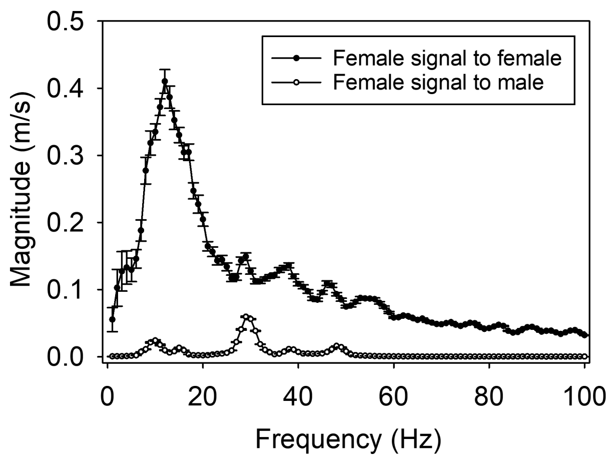

Fig. 1. Mean (±SEM) magnitude of female *Latrodectus hesperus* signals produced during intraspecific contests and courtship communication. The initial 1-s section of vibrational signals recorded in time domain from webs was analyzed using the Fast Fourier Transform function. Female rivalry signals showed a peak in magnitude from 6 to 23 Hz and smaller peaks at about 29, 38, and 47 Hz.

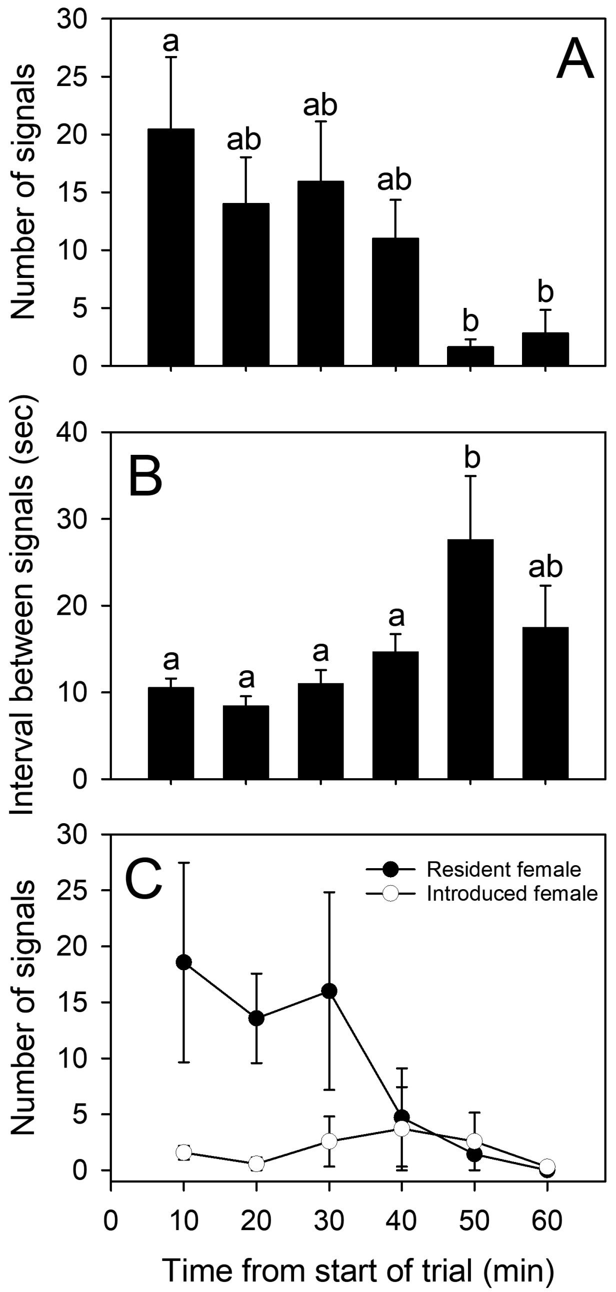

Fig. 2. Mean (±SEM) number of signals produced by both *Latrodectus hesperus* females during a 1-hr observation period (A), signaling rate, measured as the interval between the onset of two consecutive signals (B), and number of signals produced by the resident and the introduced females (C). Occurrence of rivalry signals was highest in the initial 10 min of the interaction between the resident and the introduced female with a respective ratio of 12:1.

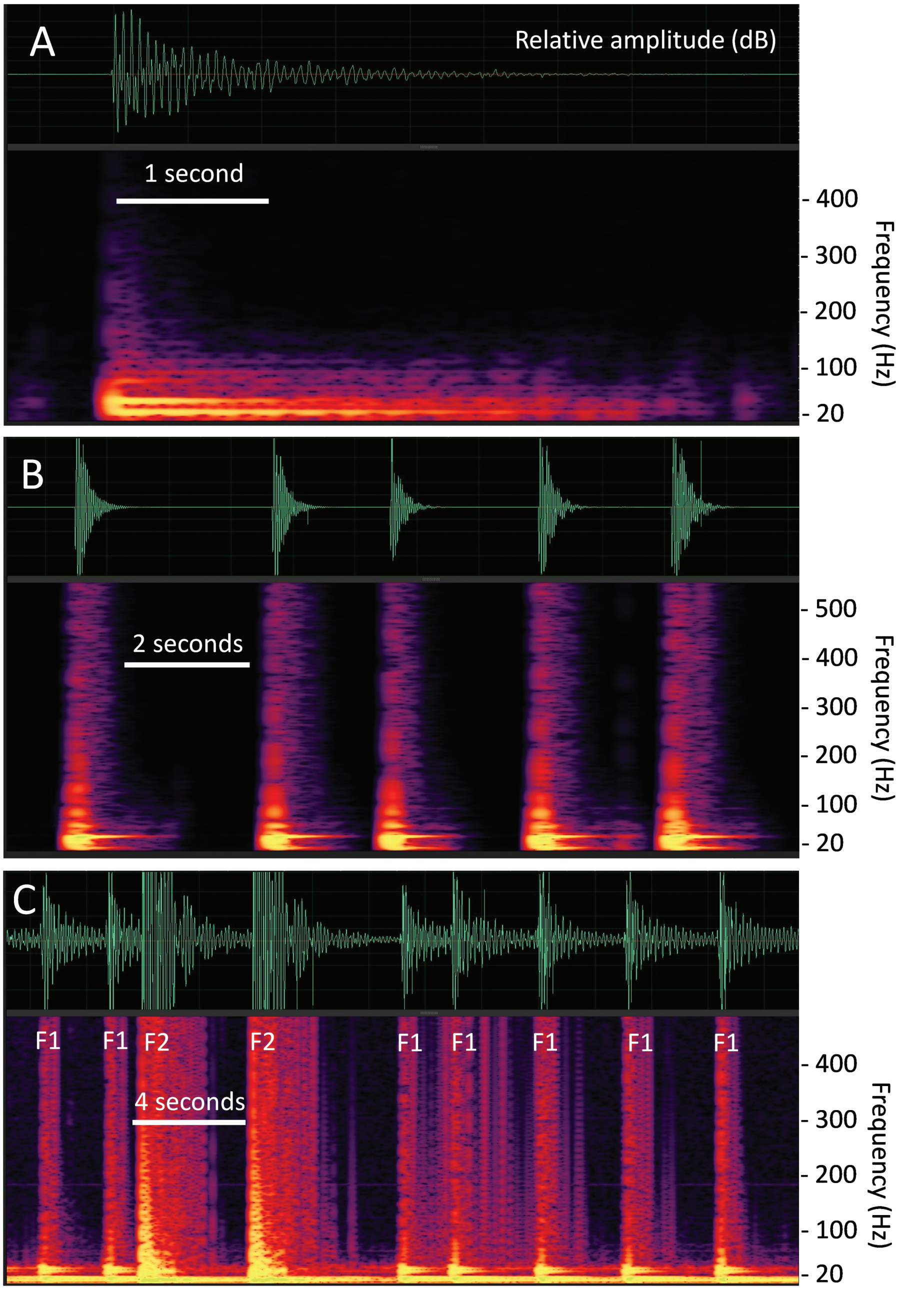

Fig. 3. Oscillogram (top of each figure) showing relative amplitude of female *Latrodectus hesperus* signals and spectrogram (bottom of each figure) showing the most intense part of signals in yellow. In female-female contests for a web, vibrational signals were produced as single (A) or groups (B) of bounces on the web. Interactions between the resident (F1) and the introduced spider (F2) were mediated by exchange of vibrational signals transmitted through the web (C).

Durations of individual bounce signals measured from the beginning and end of oscillograms ranged from 0.55 to 27.46 s (average 4.54 ± 0.21 s, n = 354). Variable signal durations are presumably a result of web characteristics such as tension that affect resonance on the web. Analysis of the initial 1-s section of bounce signals showed a peak in velocity (m/s) ranging from 6 to 23 Hz and smaller peaks at about 29, 38, and 47 Hz (Fig. 1).

Discussion

Here, we present evidence that female *L. hesperus* exhibit territorial rivalry behaviors when the web is invaded by a conspecific and that displays of female-female contests are mediated by the production of vibrational signals from the resident and introduced females. In contrast to the haphazard spectral characteristics of web vibrations produced by prey, a female *L. hesperus* intruder moved smoothly when exploring another female's web. Vibrations produced by movement or signaling by the introduced female were rapidly identified by the resident female as those of another spider, as indicated by the production of rivalry-specific vibrational signals. Similarly, vibrational signals produced by the resident female were perceived by the introduced female, which either replied to the warning signals or moved away from the occupant.

We further demonstrated that female-female vibrational communication was more frequent in the early stages of the interaction (<10 min) and physical combat was not common, indicating that potential disputes for a web are more likely resolved at a distance instead of engaging in physical combat. Although vibrational signaling was observed until the end of the 1-hr recording period, this could be an artifact of the experimental arena that didn't allow females to move away from the web environment. In the only case when lethal combat was recorded during the observation period, the 'winner' was the introduced spider. Given that *L. hesperus* prefers to avoid physical combat, it is predicted that mortality under natural field conditions due to intraspecific contests is low. Collectively, data support that web cohabitation by adult *L. hesperus* females is unlikely to occur.

In most cases, the introduced female moved away from the resident female. Because *L. hesperus* are well familiar with the architecture of their own webs and can navigate on the web using path integration (e.g., short cuts) (Sergi et al. 2021), it is possible that the advantage of being a resident female in this scenario affected behaviors of the introduced spider, which in turn adopted the optimal strategy of avoiding the risk of injury or death. In contrast with observations of female-female interactions in *Phidippus clarus* Keyserling (Salticidae) where 59% of pairs arrived at close range contact and 16% of contacts resulted in death (Elias et al. 2010), and in *U. plumipes* (Uloboridae) where 73% of interactions escalated to physical contact that included a fight between contestants (Joel et al. 2017), in this study close range contact and death occurred in only 13% and 3% of the cases, respectively. Results support that the outcome in *L. hesperus* female competition is often determined before physical combat, which makes this species potentially sensitive to artificial behavioral manipulation such as vibrational playback of female rivalry signals or even a pheromone-based approach.

Pheromones can be used by spiders for long- and short-range communication, without necessarily involving contact between the emitter and the receiver (Gaskett 2007). Therefore, future studies are needed to determine whether *L. hesperus* females perceive pheromones from other females and use such compounds as a web spacing mechanism that can be exploited as a control tactic to keep them away from the crop. Similarly, past and current research on transmission of disruptive vibrational signals for the glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae), through trellised grapevines showed that signal characteristics are affected by distance from the signal source, but transmission is feasible in commercial operations and could be economically viable as a novel method to suppress pest populations in vineyards (Krugner and Gordon 2018). Further playback studies of female rivalry signals are needed for the identification of vibrational signals that can potentially interfere with spider behaviors on grapevines.

Vibrational signals recorded from reflective cubes placed on the web revealed that most of the energy in female rivalry signals occurs in the low-frequency range, albeit it is expected that the reflective foam block used to record vibrations acts as a filter that reduces high-frequency signals more than low-frequency signals due to the difference in mass between the foam cube and a spider. Because both females were fairly mobile on the web during the trials, it was impossible to compare the relative amplitude of signals produced by one versus the other female. For example, in contrast with leafhoppers (Krugner and Gordon 2021) and sharpshooters (Nieri et al. 2017) where females (and often males) remain stationary on the plant allowing comparisons of signal amplitude, attempts to compare signal amplitude from mobile spiders would be highly inaccurate due to constant changes in the distance between the source of vibrations and the recording location on the web. Recently, Justus et al. (2022) developed a method of three-dimensional vibration analysis from an *L. hesperus* web that combines video vibrometry with stereo vision. Stereo video vibrometry is a promising method to accurately analyze web vibrations in the context of characteristics such as intensity that may be involved in establishing dominance in this and other web-building species.

Female *L. hesperus* are deeply misunderstood predators that presumably serve a role in urban and agroecosystems by helping suppress populations of herbivorous arthropods. Surveys in Californian vineyards showed that up to 95% of the arthropod predators in vineyards were spiders, but population density of *L. hesperus* was relatively low among the 27 species of spiders recorded (Costello and Daane 1995). Understanding the ecological factors driving the high abundance of *L. hesperus* in grape clusters can help the development of management strategies to mitigate the postharvest impact on the table grape industry. To our knowledge, this study is the first to provide insights to vibrational communication of female *L. hesperus* in the context of territorial rivalry. Knowledge of female *L. hesperus* intraspecific communication is required for designing further studies of interactions with other species in the environment such as *L. geometricus* and *Pholcus phalangioides* Füssli (Araneae: Pholcidae), which are known to outnumber or even prey on *L. hesperus*, respectively.

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References Cited

Benjamin, S. P., and S. Zschokke. 2003. Webs of theridiid spiders: construction, structure and evolution. *Biol. J. Linn. Soc*. 78: 293e305.

Blackledge, T. A., J. A. Coddington, and R. G. Gillespie. 2003. Are three-dimensional spider webs defensive adaptations? *Ecol. Lett*. 6: 13e18.

Costello, M. J., and K. M. Daane. 1995. Spider (Araneae) species composition and seasonal abundance in San Joaquin Valley grape vineyards. *Environ. Entomol*. 24: 823–831.

Elias, D. O., C. A. Botero, M. C. B. Andrade, A. C. Mason, and M. M. Kasumovicc. 2010. High resource valuation fuels '"desperado"' fighting tactics in female jumping spiders. *Behav. Ecol*. 21: 868–875.

Elias, D. O., M. M. Kasumovic, D. Punzalan, M. C. B. Andrade, and A. C. Mason. 2008. Assessment during aggressive contests between male jumping spiders. *Anim. Behav*. 76: 901–910.

Elwood, R., and J. Prenter. 2013. Aggression in spiders, pp. 113–133. *In* I. Hardy and M. Briffa (eds.), *Animal contests*. Cambridge University Press, Cambridge.

Garb, J. E., and C. Y. Hayashi. 2013. Molecular evolution of a-latrotoxin, the exceptionally potent vertebrate neurotoxin in black widow spider venom. *Mol. Biol. Evol*. 30: 999–1014. doi: 10.1093/molbev/mst011

Gaskett, A. C. 2007. Spider sex pheromones: emission, reception, structures, and functions. *Biol. Rev*. 82: 27–48. doi: 10.1111/j.1469-185x.2006.00002.x

Gendreau, K. L., R. A. Haney, E. E. Schwager, T. Wierschin, M. Stanke, S. Richards, and J. E. Garb. 2017. House spider genome uncovers evolutionary shifts in the diversity and expression of black widow venom proteins associated with extreme toxicity. *BMC Genomics*. 18: 178.

Jackson, R. R. 1988. The biology of *Jacksonoides queenslandica*, a jumping spider (Araneae: Salticidae) from Queensland: intraspecific interactions, web-invasion, predators, and prey. *N.Z. J. Zool*. 15: 1–37. doi: 10.1080/03014223.1988.10422606

Joel, A. C., A. Habedank, J. Hausen, and J. Mey. 2017. Fighting for the web: competition between female feather-legged spiders (*Uloborus plumipes*). *Zoology*. 121: 10–17. doi: 10.1016/j.zool.2016.12.002

Justus, N., R. Krugner, and R. L. Hatton. 2022. Validation of a novel stereo vibrometry technique for spiderweb signal analysis. *Insects*. 13: 310. doi: 10.3390/insects13040310

Kasumovic, M. M., D. O. Elias, D. Punzalan, A. C. Mason, and M. C. B. Andrade. 2009. Experience affects the outcome of agonistic contests without affecting the selective advantage of size. *Anim. Behav*. 77: 1533–1538.

Krugner, R., and S. D. Gordon. 2018. Mating disruption of *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae) by playback of vibrational signals in vineyard trellis. *Pest Manag. Sci*. 74: 2013–2019. doi: 10.1002/ps.4930

Krugner, R., and S. D. Gordon. 2021. Mating communication of the variegated leafhopper, *Erasmoneura variabilis*, with notes on vibrational signaling of other grapevine cicadellids in California. *Ann. Entomol. Soc. Am*. 114: 528–537. doi: 10.1093/aesa/saab024

Marshall, S. D., and A. L. Rypstra. 1999. Spider competition in structurally simple ecosystems. *J. Arachnol*. 27: 343–350.

Nieri, R., V. Mazzoni, S. D. Gordon, and R. Krugner. 2017. Mating behavior and vibrational mimicry in the glassy-winged sharpshooter, *Homalodisca vitripennis*. *J. Pest Sci*. 90: 887–899. doi: 10.1007/s10340-017-0840-5

Nyffeler, M., and R. S. Vetter. 2018. Black widow spiders, *Latrodectus* spp. (Araneae: Theridiidae), and other spiders feeding on mammals. *J. Arachnol*. 46: 541–548.

Ross, K., and R. L. Smith. 1979. Aspects of the courtship behavior of the black widow spider, *Latrodectus hesperus* (Araneae: Theridiidae), with evidence for the existence of a contact sex pheromone. *J. Arachnol*. 7: 69–77.

Sergi, C. M., T. Antonopoulos, and R. L.Rodríguez. 2021. Black widow spiders use path integration on their webs. *Behav. Ecol. Sociobiol*. 75: 73.

Sivalinghem, S., and A. C. Mason. 2021. Vibratory communication in a black widow spider (*Latrodectus hesperus*): signal structure and signalling mechanisms. *Anim. Behav*. 174: 217–235. doi: 10.1016/j.anbehav.2021.01.016

Vetter, R. S., L. S. Vincent, D. W. R. Danielsen, K. I. Reinker, D. E. Clarke, A. A. Itnyre, J. N. Kabashima, and M. K. Rust. 2012. The prevalence of brown widow and black widow spiders (Araneae: Theridiidae) in urban southern California. *J. Med. Entomol*. 49: 947–951. doi: 10.1603/me11285

Vibert, S., C. Scott, and G. Gries. 2014. A meal or a male: The 'whispers' of black widow males do not trigger a predatory response in females. *Front. Zool*. 11: 4. doi: 10.1186/1742-9994-11-4

Vibert, S., C. Scott, and G. Gries. 2016. Vibration transmission through sheet webs of hobo spiders (*Eratigena agrestis*) and tangle webs of western black widow spiders (*Latrodectus hesperus*). *J. Comp. Physiol. A Sens. Neural Behav. Physiol*. 202: 749–758.

Vincent, L. S., R. S. Vetter, W. J. Wrenn, J. K. Kempf, and J. E. Berrian. 2008. The brown widow spider *Latrodectus geometricus* C. L. Koch, 1841, in southern California. *Pan-Pac. Entomol*. 84: 344–349.

Walse, S. S., J. S. Tebbets, and J. Leesch. 2017. Postharvest fumigation of California table grapes with ozone to control Western black widow spider (Araneae: Theridiidae). *Postharvest Biol. Technol*. 134: 1–4.