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Exploring a novel substrate-borne vibratory signal in the wolf spider *Schizocosa floridana*

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Abstract

Animals communicate using a diversity of signals produced by a wide array of physical structures. Determining how a signal is produced provides key insights into signal evolution. Here, we examine a complex vibratory mating display produced by male *Schizocosa floridana* wolf spiders. This display contains three discrete substrate-borne acoustic components (known as “thumps”, “taps”, and “chirps”), each of which is anecdotally associated with the movement of a different body part (the pedipalps, legs, and abdomen respectively). In order to determine the method of production, we employ a combination of high-speed video/audio recordings and SEM imaging of possible sound-producing structures. Previous work has suggested that the “chirp” component is tonal, a signal trait that would be potentially unique in the genus. We measured signal tonality for all courtship components, as well as for courtship components from sixteen other *Schizocosa* wolf spiders. Our results suggest that *S. floridana* produces courtship song using a combination of shared (palpal stridulation and foreleg percussion) and novel (abdominal movement) sound production mechanisms. Of particular interest, the “chirp”, which is produced using a novel abdominal production mechanism, is the only known tonal signal with acoustic properties that are unique within the genus. We argue that the potential evolution of a novel sound production mechanism has opened up a new axis of signaling trait space in this species, with important implications for how this signal is likely to function and evolve.

KEYWORDS

communication, spider, vibratory

1 | INTRODUCTION

Animals produce a wide array of signals intended to modify the behavior of other individuals to their benefit. The forms of these signals, which may be used to communicate in contexts ranging from mate choice to predator avoidance, are famously diverse. Often, this variation is extensive even between closely related species. Yet, while the roles of signaler, receiver, and environment in driving the divergence and evolution of new animal signals have received considerable attention (e.g., Endler, 1992; Endler & Basolo, 1998;

Hebets & Papaj, 2005; Pfennig & Pfennig, 2012), less work has focused on how the physical mechanisms that produce these signals might drive their evolution (but see Elias et al., 2006). Understanding the physical mechanisms of signal production is critical, however, as the nature of these mechanisms can both constrain and direct signal evolution (e.g., Derryberry et al., 2012; Montealegre-Z, 2009; Podos, 2001).

Specifically, whether new signals arise through new production mechanisms or through modifications of pre-existing mechanisms is of particular interest, as this distinction dictates the constraints and limitations under which these signals may evolve. Many, perhaps most,

of the most commonly studied acoustic signals have arisen through the modification of existing signal-producing structures (e.g., Ewing, 1989; Fitch, 2006). For example, the great diversity of birdsong derives from modifications in the use and form of a shared mechanism: the syrinx (Catchpole & Slater, 1995; Kingsley et al., 2018; Read & Weary, 1992; Searcy & Andersson, 1986). And because the physical structure of the avian vocal tract attenuates harmonic overtones, many bird songs share a similar pure-tone musical sound (Nowicki & Marler, 1988). These similarities are also potentially evidence of constraints, and the shared physical bases of the syrinx and of its associated neuromuscular structures limit the trait space through which many bird songs are able to evolve (Podos et al., 2004). Likewise, for complex signals containing multiple components, variation between signal components produced by the same structure might be limited (e.g., Reichert, 2013), constrained by shared neuromuscular architecture (Arnold, 1992). Alternatively, novel signals, or signal components, produced by different production mechanisms may be more able to vary independently.

Arthropod systems are well suited to the study of acoustic signal evolution (including both air- and substrate-borne acoustics; Ewing, 1989; Hill, 2008). Arthropods produce sound using a number of unique structures (Ewing, 1989; Uhl & Elias, 2011; Virant-Doberlet & Čokl, 2004), and their rigid exoskeleton means that new sound production structures can evolve anywhere on the body (e.g., Jocqué, 2005; Virant-Doberlet & Čokl, 2004). Additionally, many arthropods produce complex vibratory songs that utilize the synchronous deployment of multiple distinct sound production mechanisms (Virant-Doberlet & Čokl, 2004). We suggest that investigating how individuals produce distinct signal components within a complex song, whether signal components are produced using the same, different, new, or pre-existing production mechanisms, and how members of one species differ from others in their sound production mechanisms are all key to understanding how complex signals evolve and function.

Here, we investigate the acoustic properties and production mechanisms of the song of a common North American forest floor arthropod—the wolf spider *Schizocosa floridana* (Bryant, 1934). Courting individuals in the wolf spider genus *Schizocosa* generate substrate-borne songs to attract mates, with each species producing a unique song. But though these songs are often distinguished in their temporal patterning (see Hebets et al., 2013; Stratton, 2005), the underlying production mechanisms are mostly common to wolf spiders in general (e.g., Hallander, 1967; Rovner, 1967). These mechanisms include percussion of the pedipalps and the front pair of legs, and stridulation via specialized structures on the tibio-cymbial joint of the pedipalp (Rovner, 1975). *Schizocosa floridana* song includes repeated production of three acoustic elements. Two of these (the “thump” and the “tap”) are broadband and atonal and are hypothesized to be produced using stridulatory and percussive mechanisms common to the genus (Rosenthal & Hebets, 2012; Rundus et al., 2011). The third component, the “chirp”, appears to be pure tone, and it has not yet been determined what the mechanism of production is.

Broadband acoustic signals can vary in their amplitude, or in temporal characteristics such as production rate, duration, or rhythm.

However, they cannot vary significantly in pitch, or perceived frequency. Tonal signals thus have the potential to vary along three independent axes (amplitude, temporal patterning, and pitch) whereas broadband signals vary along only two. Tonal variation can provide information to receivers. For example, pitch differences between individuals commonly reflect differences in body size (e.g., Gingras et al., 2012; Hauser, 1993). Likewise, variations in pitch within individuals can indicate signaler quality (Christie et al., 2004). Tonal signals can also respond differently to changes in the environment. For example, narrow-bandwidth signals may respond differently to noise than other signals (Raboin & Elias, 2019) and may take advantage of unique spectral transmission properties of their environment (e.g., McNett & Coccoft, 2008). A truly tonal chirp would thus open up the possibility of *S. floridana* song varying in an axis that is known to be important in many non-spider species, and that is not available to its congeners.

In this study, we explore the spectral properties of the three major sounds produced by *S. floridana*. In particular, we focus on measurements of tonality, as pure-tone signals are unknown in this genus. To establish the presumptive acoustic novelty of the chirp, we also compare its tonality with measurements made on courtship signals from 16 of the 24 described North American species in the genus (Stratton, 2005). Additionally, we explore the potential mechanisms by which these courtship sounds are produced. We use high-speed video recordings and SEM imaging of putative sound-producing areas to begin assessing whether novelty in signal acoustic properties is associated with modifications of pre-existing signal-producing mechanisms or the evolution of new structures/mechanisms.

2 | METHODS

2.1 | Animal collection and care

We collected immature *S. floridana* at night in Alachua County, Florida, over two collection trips. Spiders used in courtship tonality measurements and for scanning electron microscopy were collected in February 2017. Spiders used in high-speed courtship recording were collected in January 2019. In both cases, we transported spiders to UC Berkeley and individually housed them in 6 cm × 6 cm × 8 cm clear plastic containers (Amac Plastic Products). The rearing room in which they were housed was maintained on a 12 hr:12 hr light/dark schedule at an ambient temperature of 25°C. We fed spiders one body-size-matched cricket twice per week and provided them with ad libitum water.

2.2 | Courtship tonality and genus-wide comparison

To measure courtship tonality, we recorded the songs of ten mature males (identified by the unique palpal morphology associated with sperm transfer) who were induced to court on a stretched nylon

substrate impregnated with female silk. Pheromones in female silk elicit spontaneous courtship in male *Schizocosa* on contact (Kaston, 1936; Roberts & Uetz, 2005; Rovner, 1968). We recorded these songs using a scanning laser vibrometer (Polytec PSV-400, Waldbronn, Germany). We situated the laser point on the nylon surface within 1 millimeter of the spider's body and recorded the output from the vibrometer as a 24-bit WAV file using Audacity (audacity.sourceforge.net).

Using these recordings, we separately measured the tonality of each courtship component within the *S. floridana* song. For each male, we extracted three exemplars of each component (thumps, taps, chirps; see also Figure 1 from Rosenthal et al., 2018 or Figure 1 from Rosenthal & Elias, 2019). We quantified the spectral entropy from a power spectral density of each isolated component exemplar in MATLAB (see Chivers et al., 2017; Giannakopoulos & Pikrakis, 2014; Sueur et al., 2008; Supplemental file S1). Lower entropy values indicate more pure tones, and higher values indicate more "noisy", broadband signals. Spectral entropy has been assessed for numerous taxa (e.g.; Chivers et al., 2017; da Silva et al., 2000; Suzuki et al., 2006) including as a measure of spectral purity (Chivers et al., 2017). To assess differences in tonality across signal components, we conducted a linear mixed-effects model with component tonality as the dependent variable and component type (i.e., thump, tap, or chirp) as a fixed effect. Given the inclusion of multiple recordings per male, we included individual identity as a random factor in this model. We performed post hoc *t* tests comparing the estimated marginal means obtained from the mixed model using the "emmeans" R package.

We also compared the measurements of *S. floridana* tonality to the tonality of courtship components from sixteen other species in the genus from previously made recordings (Table S1). These sixteen species represent more than two thirds of all North American *Schizocosa* species (Stratton, 2005). Quantification of tonality was performed in the same manner as above, but the number of exemplar components within an individual, and the number of individuals within each species varied as a result of differences in recording techniques, locations, and times (Table S1). Because these recordings were made in three different laboratories using different laser vibrometers and potentially different recording substrates, we chose not to analyze the differences statistically. We present the differences for qualitative assessment.

2.3 | Movement during sound production

We recorded synchronized high-speed video and audio of courting males in order to match acoustic courtship component production (i.e. sound) with body movements. We recorded high-speed camera footage with a Photron Fastcam SA3 (Tokyo, Japan) at 2000 frames per second, paired with recording substrate-borne vibrations using a scanning laser vibrometer (Polytec PSV-400, Waldbronn, Germany). Males were induced to court using the methods described above, and laser recordings were made directly off the stretched nylon substrate in the same fashion. We digitized the vibrometer signal (National Instruments USB-6251; Austin, TX, USA) and synchronized it with the

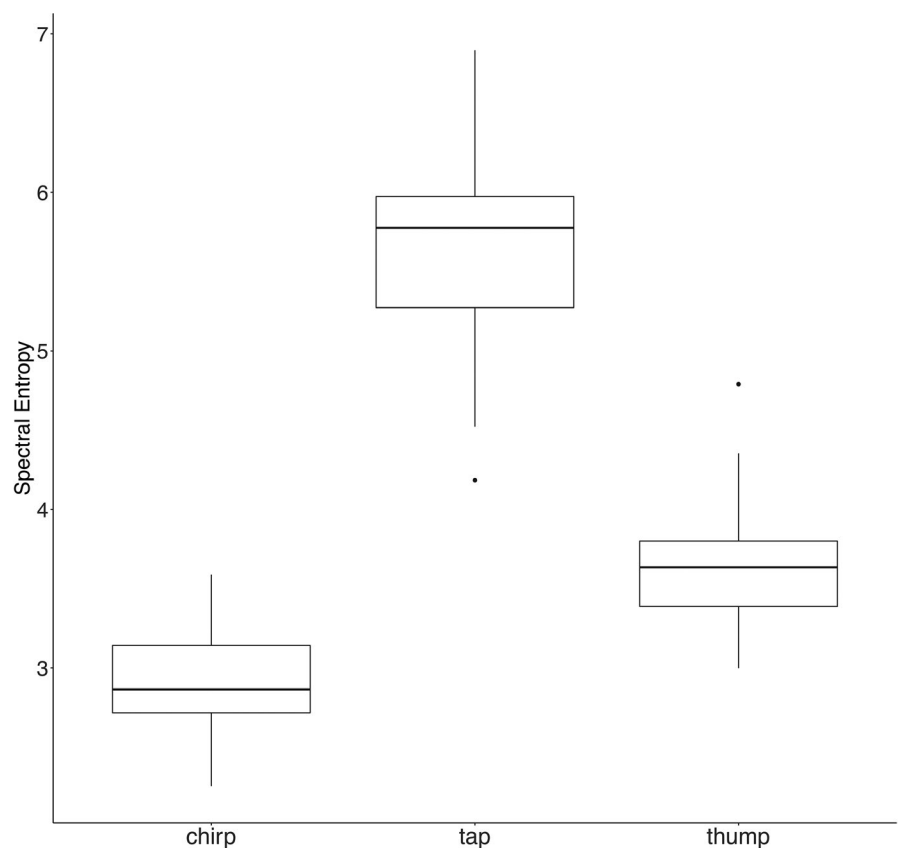


FIGURE 1 Spectral entropy (tonality) for the three *S. floridana* courtship components

simultaneously recorded high-speed footage using Midas software (v.2.0; Xcitex, Inc.). We made combined video/audio recordings of all three courtship components for four individual males, with recordings made from both the side-on view (both palps and opisthosoma in focus) and the front view (palps and forelegs in focus) when possible. We replicated observations across multiple individuals to ensure that all potential angles had been filmed when needed. For selected courtship videos, we exported individual frames as .tiff files and identified landmarks on each spider (e.g., tip of foreleg and tip of opisthosoma). The initial xy coordinates are the 0 position. We then tracked the positions of the identified landmarks through the course of a particular signaling behavior using Adobe Photoshop. We modified the number of frames we measured based on the speed of observed movements (chirps—every 0.005 s, taps—every 0.005 s, thumps—every 0.03 s).

2.4 | Scanning electron microscopy

We used scanning electron microscopy in order to search for potential morphological structures associated with sound production. We dissected adult male *S. floridana* specimens under a light microscope. Samples were fixed in 2% glutaraldehyde in 0.1 M sodium cacodylate buffer, post-fixed in 1% osmium tetroxide in 0.1 M sodium cacodylate

buffer, dehydrated in a series of ethanol baths, critical point dried, and stored in a desiccator cabinet overnight. Samples were mounted on a stub using carbon tape and imaged with a Hitachi TM-1000 SEM at the UC Berkeley Electron Microscope Laboratory.

We imaged the tibio-cymbial joint of the pedipalp, which is known to be the location of stridulatory structures in related species (Rovner, 1975), and which we observed to be in motion during some phases of courtship (i.e., during bouts of thumping). Imaging was done on both intact and dissected joints. We imaged pedipalps in two ways. First, pedipalps were dissected away from the body at the coxa and mounted whole. Second, we dissected the palpal cymbium (which is the modified tarsus, or last segment) away from the tibia. We mounted both joints for imaging of the dorsal surface of the cymbium and of the ventral surface of the tibia. Our high-speed videos demonstrated vigorous opisthosomal movement during some phases of courtship (i.e., during chirps) and so we also imaged the posterior surface of the cephalothorax and the anterior surface of the opisthosoma, because these surfaces appeared the most likely to come into contact during opisthosomal movement and are also known to be the location of sound-producing structures in other spider species (e.g., *Habronattus* opisthosomal stridulation, Maddison & Stratton, 1988). Vibration-producing structures at that location in *Schizocosa*, however, would be

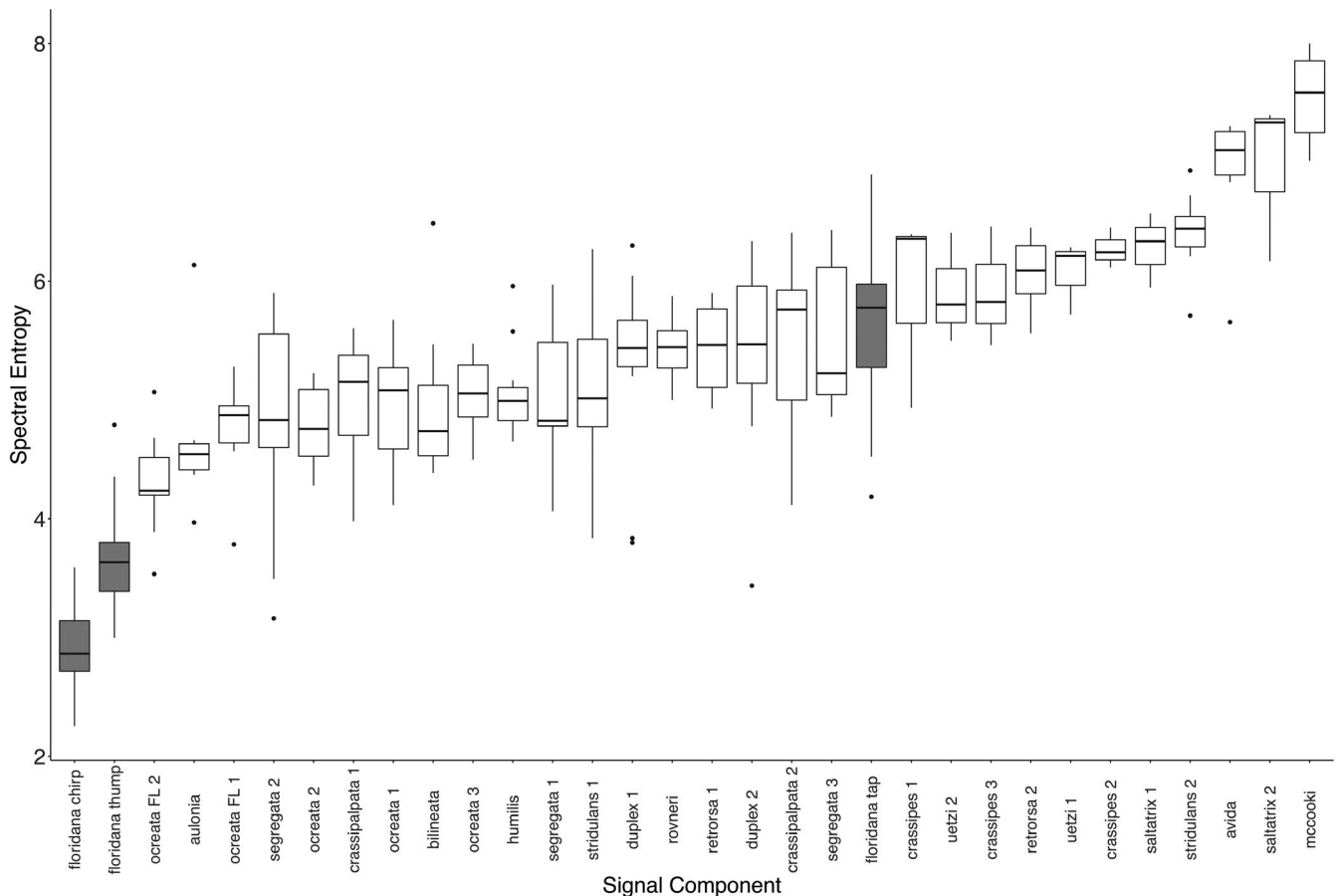


FIGURE 2 Spectral entropy (tonality) for courtship components from seventeen *Schizocosa* species, including *S. floridana*, ordered from most to least tonal. Numbers at the end of species names indicate different song components. *S. floridana* components are shaded in gray

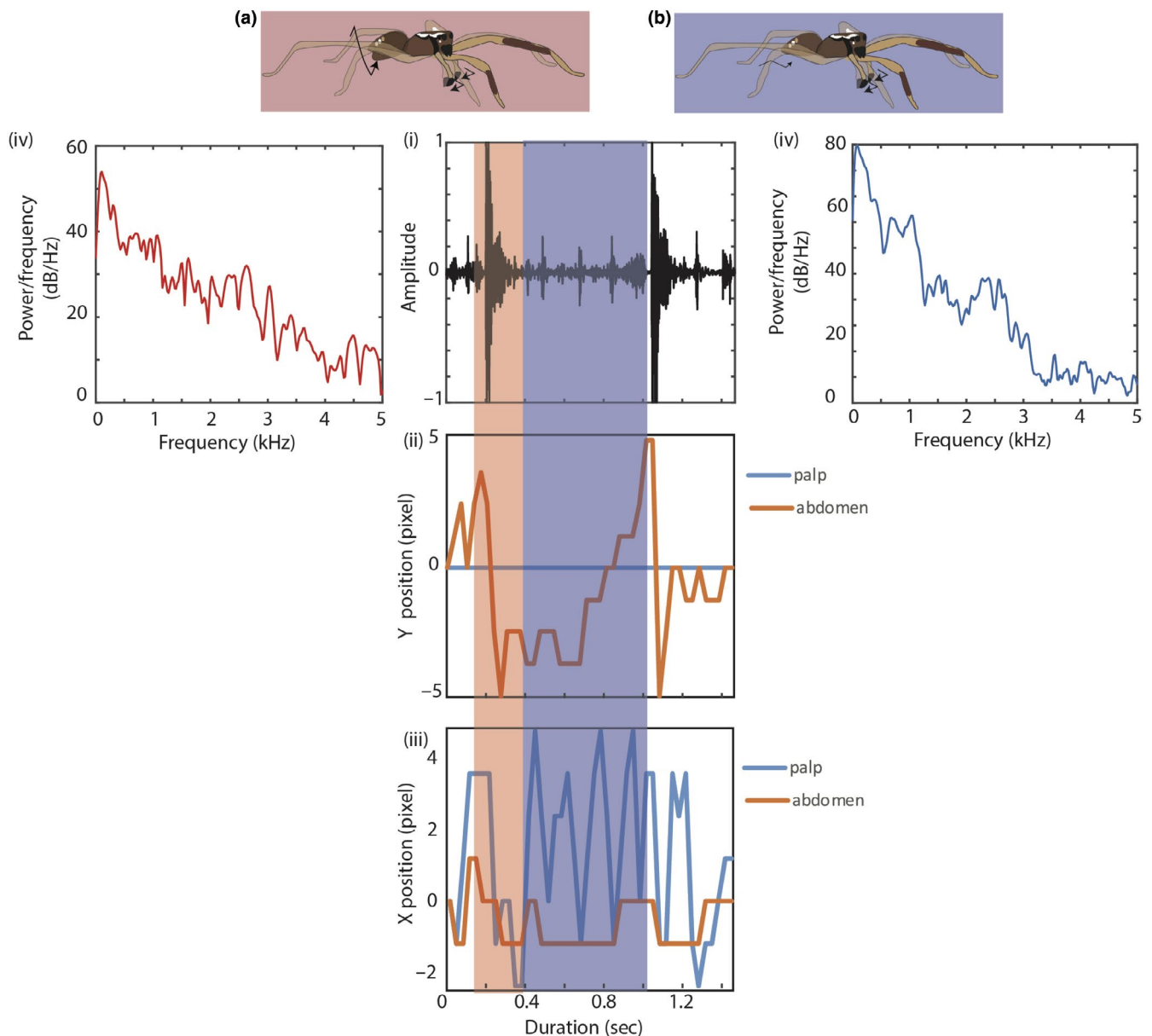


FIGURE 3 The coordinated body movements and sounds of a thump, which contains two components: (a) a pronounced vertical movement of the opisthosoma, and horizontal flexion of the pedipalps, followed by (b) small opisthosomal movements and continuing flexion of the pedipalps. Also shown are (i.) changes in signal amplitude, (ii.) vertical movement of palps and opisthosoma, and (iii.) horizontal movement of palps and opisthosoma over the duration of the signal. The frequency spectrum of these two thump components is also shown (iv.)

unique. These two body parts were separated through severing of the connecting pedicel. All legs were removed from the cephalothorax prior to positioning for imaging.

3 | RESULTS

3.1 | Tonality of courtship components

All three courtship components differ significantly from each other in tonality (measured as their degree of spectral entropy; $F_{2,78} = 351.86$, $p < .0001$; pairwise tests: chirp–tap, $t = -25.659$, $p < .0001$; chirp–thump, $t = -6.998$, $p < .0001$, tap–thump, $t = 18.661$, $p < .0001$),

with leg taps being the least tonal, and opisthosomal chirps the most tonal (Figure 1). Opisthosomal chirps are also the most tonal of any *Schizocosa* signal component measured to date (Figure 2). Thumps were the second most tonal of any *Schizocosa* component, and leg taps were around average tonality for those *Schizocosa* species for which we had available recordings.

3.2 | Movement during sound production

Thumps are composed of two distinct acoustic components (Figure 3, red and blue regions), (a) a high-amplitude pulse, which is primarily associated with vertical movement of the opisthosoma and

a significant horizontal flexion of the pedipalps, and (b) an underlying rumble, which is associated with constant horizontal movements of the pedipalp. Both of these components are atonal, comprising a broad bandwidth of frequencies (Figure 1), similar to songs of other previously described *Schizocosa* species. Taps are also broadband, associated with rapid percussion of the forelegs on the substrate. Neither the pedipalps nor the opisthosoma appears to move during leg taps (Figure 4).

Chirps commonly contain one to three repeated pulses. Each pulse is associated with a single dorsoventral movement of the opisthosoma. Neither the legs nor the palps appear to move during chirp production. The downward stroke is swift (0.035 s) and smooth (Figure 5, red region), producing a narrow-bandwidth tone (~350 Hz) corresponding to a ~8 Hz opisthosomal movement. The upward stroke is less smooth, with some vibration of the opisthosoma (~12 Hz opisthosomal movement). Both the downward and

upward movements are fast, taking less than a combined tenth of a second spanning an angle of deflection of around 66.6° (range 61.5° to 71.6°). Importantly, the opisthosoma is not observed to be shaking at the frequency of the chirp itself (8–12 Hz vs. 350 Hz), which rules out tremulation as a production mechanism.

3.3 | Sound production morphology

SEM images of the tibio-cymbial joint of the pedipalp revealed the presence of stridulatory structures, with a file on the dorsal surface of the cymbium (Figure 6a,b) and a plectrum on the ventral base of the tibia (Figure 6a,b). This structure is similar in placement and morphology to the palpal stridulatory organs of other lycosids (Rovner, 1975). Imaging of the posterior surface of the opisthosoma and the anterior surface of the opisthosoma revealed no structures

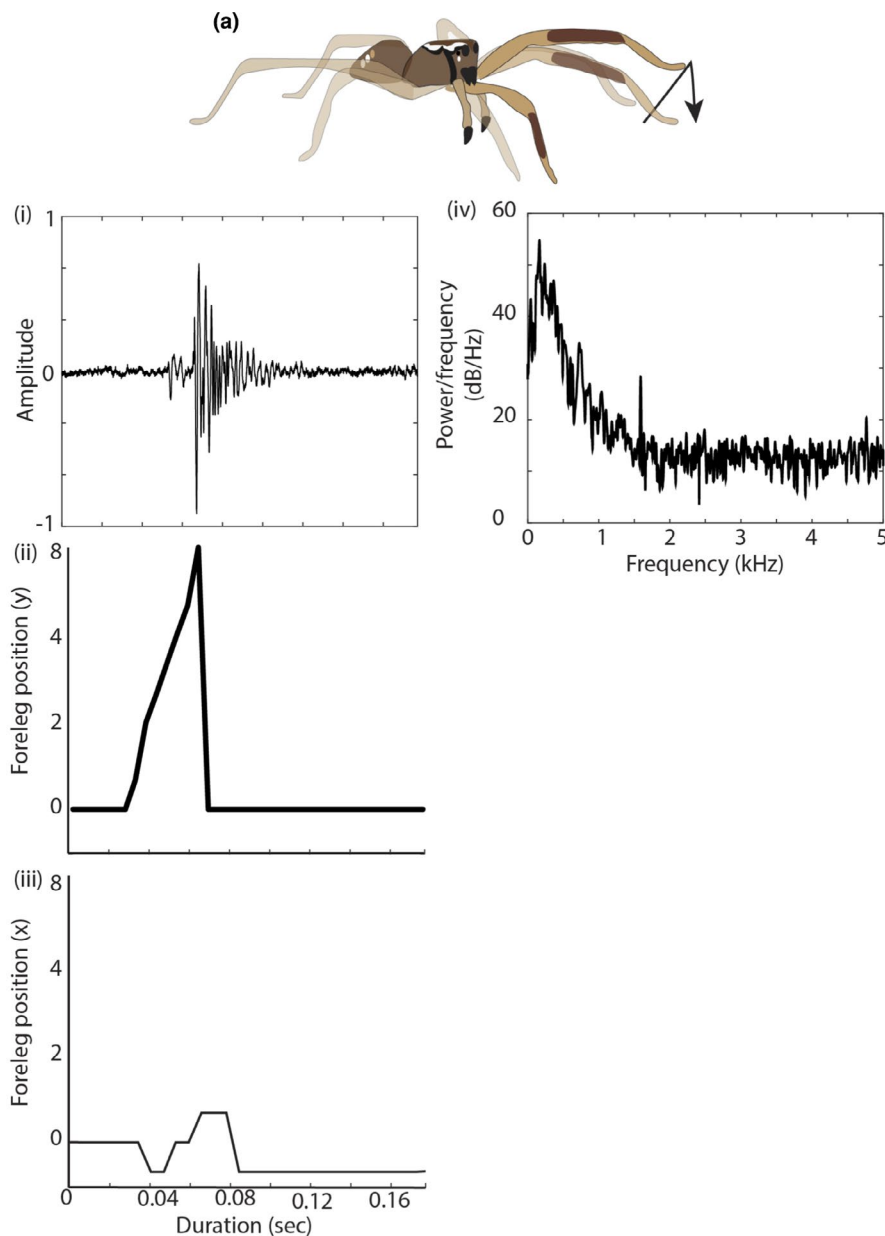
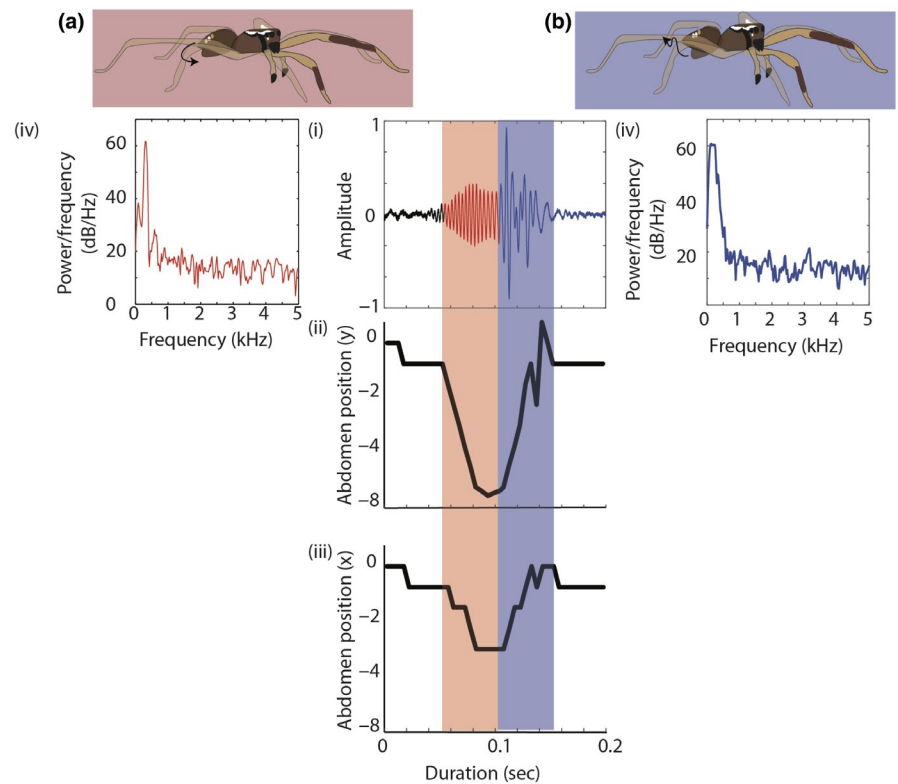


FIGURE 4 The coordinated body movements and sounds of a tap, which contains one component: (a) the percussion of a single foreleg against the substrate. (i.) Signal amplitude, and the (ii.) vertical and (iii.) horizontal positions of the foreleg across the duration of the tap are also shown, as is (iv.) the frequency spectrum of the tap

FIGURE 5 The coordinated body movements and sounds of a chirp, which contain two components: (a) the smooth downward movement of the second body part (opisthosoma), and (b) the slower, shaky upward movement of the opisthosoma. (i.) Signal amplitude, and the (ii.) vertical and (iii.) horizontal positions of the opisthosoma over the duration of the chirp are also shown, as is (iv.) the frequency spectrum of both the first and second component



known to be associated with sound production, which commonly requires two interacting sclerotized surfaces. The opisthosomal surface is entirely soft cuticle, with no evidence of sclerotization, and the cephalothorax is also smooth (Figure 7).

4 | DISCUSSION

Schizocosa floridana produces multicomponent courtship songs using the coordinated movements of three body parts. The thumps are associated with flexion of the pedipalps, which is consistent with stridulation, as well as significant opisthosomal movement. We also uncovered stridulatory structures on the pedipalps that are likely the mechanism responsible for the production of thumps. The taps are associated with vigorous striking of the forelegs on the substrate and are therefore most likely purely percussive. No other body parts are in motion during the production of the taps. Chirp production is associated only with the rapid movement of the opisthosoma. However, it is not clear how this movement is generating the chirp sound. SEM imaging turned up no structures on the prosoma or opisthosoma that are clearly related to sound production. Additionally, the chirp is truly pure tone, a signal type that no documented *Schizocosa* signal production mechanism is known to produce. In fact, the chirp is as pure tone as some bird song (Silva et al., 2000), and potentially more tonal than the calls of some crickets (e.g., Chivers et al., 2017).

It is noteworthy that *Schizocosa floridana* males produce sounds through a variety of production mechanisms (e.g. stridulation, percussion, novel opisthosomal movement). We suggest that the lack of shared production mechanisms across courtship signals may allow

the different components of *S. floridana* song to vary independently. In support of this idea, previous work has found that the structure of *S. floridana* song varies significantly across signaling environments, with the chirps often responding independently of thumps and taps. For example, chirp rate and duration are correlated with thump and tap rate in some, but not all, light environments (Rosenthal et al., 2018). Likewise, *S. floridana* courtship changes across temperatures, but chirps change in a pattern opposite to the other courtship components. Specifically, chirp duration and the number of pulses within a chirp decrease with increasing temperature, whereas all other components increase in rate or duration with increasing temperature (Rosenthal & Elias, 2019). This finding suggests interesting future avenues of research in the study of complex signal function, which is often concerned with the relationships between multiple signal components. In particular, we suggest that the functional relationships between components of a complex signal may be driven (or constrained) by the structural relationships underlying signal component production.

The chirp component of *S. floridana* male courtship is obviously of particular interest. Not only is it acoustically unlike any described *Schizocosa* courtship component, its method of production remains a mystery. Our findings rule out three of the most commonly used methods for sound production in spiders including the genus *Schizocosa*: stridulation, percussion, and tremulation (Uhl & Elias, 2011). Stridulation is produced using specialized cuticular structures. Although we found evidence for these on the pedipalps, which are associated with thump production, our high-speed recordings revealed that the palps are not moved during chirping, and no structures or sclerotized tissue of any kind were found on the

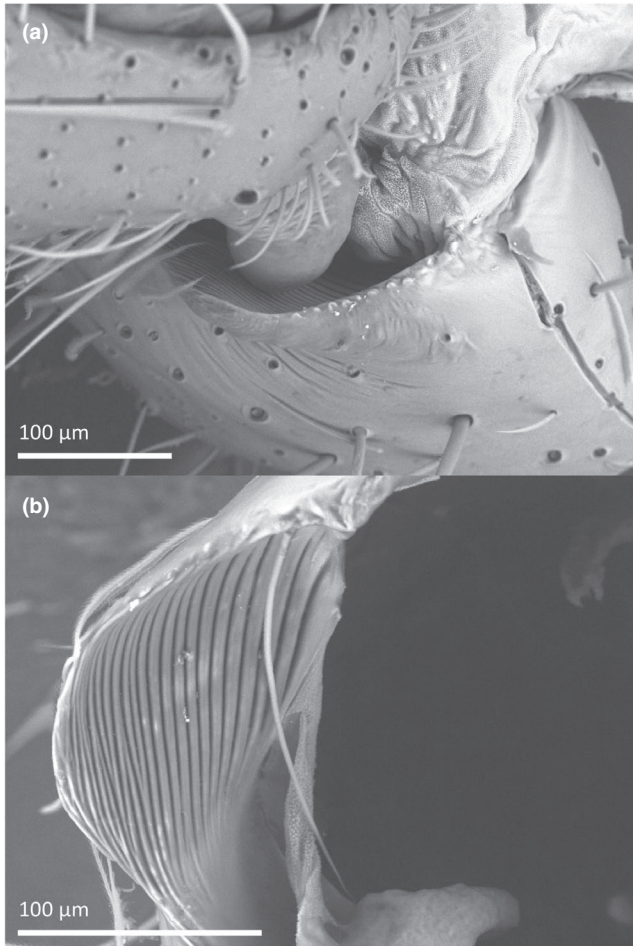


FIGURE 6 Electron micrographs of (a) the tybio-cymbial joint, with both plectrum and file visible, and (b) the dissected cymbium, with magnified view of the file structure

opisthosoma. Neither percussion (striking of one body part against another, or against the substrate) nor tremulation (rapid shaking of a body part that produces vibrations) require specific morphology. However, high-speed video reveals no percussive component to the opisthosomal movement observed during chirps (i.e., the opisthosoma does not strike the substrate). Additionally, unlike the observed frequency spectrum of chirps, percussive signals are inherently broadband (Elias & Mason, 2014). Likewise, the chirp is not tremulatory, as the opisthosoma is not oscillating at the frequency of the chirp.

Although the current study is able to rule out several potential mechanisms for chirp production, it does not definitively point toward any other specific mechanism. Because the single down-up opisthosomal movement of the chirp produces a vibration at a much higher frequency, the structures that produce it must involve some type of frequency multiplier. One example of such a multiplier would be a stridulatory file and scraper, with each sweep of the opisthosoma drawing a scraper across a file with numerous ridges. However, no such structure was observed in this case. Likewise, because the chirp is pure tone, we might expect the presence of resonant structures. In crickets, for example, stridulatory chirps are amplified and

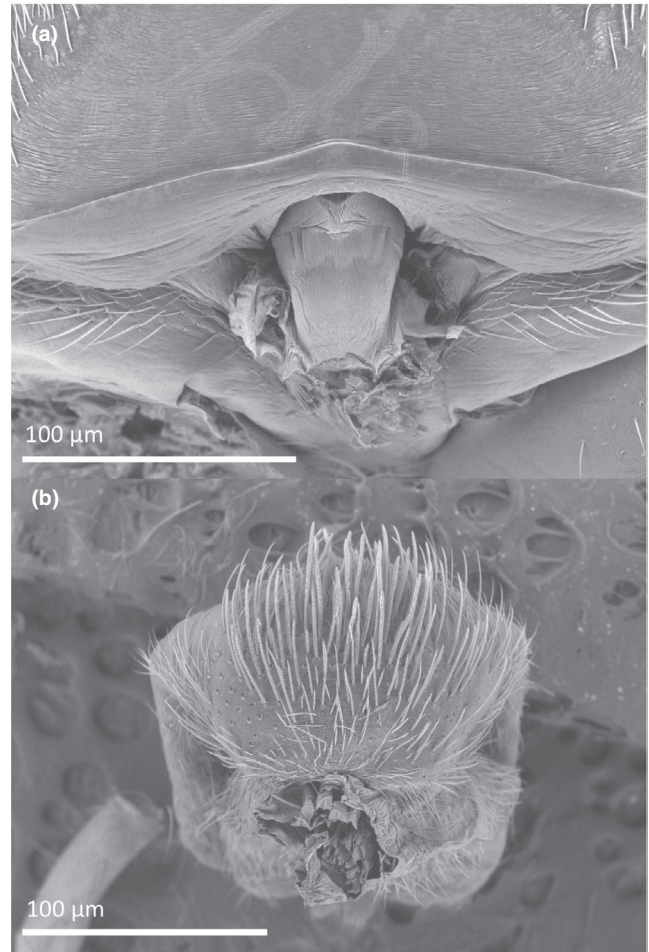


FIGURE 7 Electron micrographs of (a) the posterior-most surface of the prosoma and (b) the anterior-most surface of the opisthosoma. There are no apparent sound-producing structures on either body part

filtered through resonating areas present on the wings (e.g., Bennet-Clark, 2003). It is not yet clear what this could be in *S. floridana*. Possibly the opisthosoma itself, or some structure within the opisthosoma, is being excited to resonate at the frequency of the chirp. Alternatively, it is possible that the chirps of *S. floridana* are produced via a “stick and slip” mechanism, which involves the frictional rubbing of soft tissues, similar to the sound produced by pulling a bow across a violin string (Patek, 2001). Supporting this, the opisthosoma of *S. floridana* appears to be completely unsclerotized soft tissue, as is common in wolf spiders, and the high frequency chirp is produced via a single, down-up movement of the opisthosoma. Future work will include ultra-high-speed imaging of the opisthosoma-prosoma joint to look for evidence of body parts resonating or interacting frictionally. We also intend to compare prosomal and opisthosomal morphology of *S. floridana* with related species to identify potentially novel external structures, and to perform microCT scans for potential internal structures. It is also worth noting that there is significant opisthosomal movement during thumps, which are also more tonal than most *Schizocosa* courtship components. Future experimental work is necessary to tease apart the potentially interacting

contributions of palpal stridulation and opisthosomal movement on this signal component.

While the findings of this study suggest that the chirps may offer a novel axis of signal phenotypic variation (i.e., frequency), it is not yet clear whether frequency information is important in *S. floridana* communication. One possibility is that it may encode information on signaler size or body condition, as is the case in many non-spider species (e.g., *Anurans*: Gingras et al., 2012; *Insects*: Bennet-Clark, 1998; *Birds*: Ryan & Brenowitz, 1985; *Primates*: Hauser, 1993). The production rate of thumps, taps, and chirps are known to affect mate choice (Rosenthal & Elias, 2019; Rosenthal & Hebets, 2012; Rosenthal et al., 2018; Rundus et al., 2011), but do not reflect male size or condition (Rosenthal & Hebets, 2012). It is possible that *S. floridana* body size is encoded in chirp frequency rather than in rate, and we are currently engaged in work testing this idea as well as exploring other potential roles of this novel acoustic component.

5 | CONCLUSIONS

The investigation of new animal signals is, like the signals themselves, multicomponent. How do novel signals evolve, how are they produced, and how do they function? We suggest that whether novel signals arise through the modification of an existing signal-producing structure or through the evolution of a new signal-producing structure sets the stage for two different evolutionary trajectories. First, signal trait space can stretch along existing axes of variation through the modification of existing structures. This kind of change may be consistent with reinforcement, character displacement, or even simply directional receiver preferences, all of which select for extreme values along currently existing signaling axes. However, new signals will likely inherit some or all of the constraints of the previously existing signals, and the ability of these signals to evolve will be likewise constrained. Second, with the evolution of new structures, trait space can expand to new axes of variation, potentially releasing signal form from previous evolutionary constraints. Thus, new signals derived in this way may be unique, bearing little similarity to the phenotypic characteristics of older signals. This single study does not have the scope to address such broad evolutionary claims, but we consider it intriguing that the only known tonal signal in *Schizocosa* wolf spiders appears to be produced by a novel mechanism, rather than a modification of a pre-existing one. We suggest that the study of signal evolution needs a broader understanding of how signals are produced, whether signals are made through the modification of pre-existing structures or the evolution of completely new structures, and how mate choice operates on these different categories of “novel” signals. By exploring the details of the mechanisms of sound production, we can examine sexual selection and signal evolution in new and valuable ways.

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REFERENCES

- Arnold, S. J. (1992). Constraints on phenotypic evolution. *American Naturalist*, 140, S85–S107. <https://doi.org/10.1086/285398>
- Bennet-Clark, H. C. (1998). Size and scale effects as constraints in insect sound communication. *Philosophical Transactions of the Royal Society B*, 353, 407–419. <https://doi.org/10.1098/rstb.1998.0219>
- Bennet-Clark, H. C. (2003). Wing resonances in the Australian field cricket *Teleogryllus oceanicus*. *Journal of Experimental Biology*, 206, 1479–1496. <https://doi.org/10.1242/jeb.00281>
- Bryant, E. B. (1934). New Lycosidae from Florida. *Psyche*, 41, 38–41. <https://doi.org/10.1155/1934/40858>
- Catchpole, C. K., & Slater, P. J. B. (1995). *Bird Song. Biological Themes and Variations*. Cambridge University Press. <https://doi.org/10.1017/cbo9780511754791.009>
- Chivers, B. D., Jonsson, T., Soulsbury, C. D., & Montealegre-Z, F. (2017). Structural biomechanics determine spectral purity of bush-cricket calls. *Biology Letters*, 13, <https://doi.org/10.1098/rsbl.2017.0573>
- Christie, P. J., Mennill, D. J., & Ratcliffe, L. M. (2004). Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees. *Behavioral Ecology and Sociobiology*, 55, 341–348. <https://doi.org/10.1007/s00265-003-0711-3>
- da Silva, M. I., Piqueira, J. R. C., & Vielliard, J. M. E. (2000). Using Shannon entropy on measuring the individual variability in the Rufous-bellied thrush *Turdus rufiventris* vocal communication. *Journal of Theoretical Biology*, 207, 57–64.
- Derryberry, E. P., Seddon, N., Claramunt, S., Tobias, J. A., Baker, A., Alexio, A., & Brumfield, R. T. (2012). Correlated evolution of beak morphology and song in the neotropical woodcreeper radiation. *Evolution*, 66, 2784–2797. <https://doi.org/10.1111/j.1558-5646.2012.01642.x>
- Elias, D. O., Lee, N., Hebets, E. A., & Mason, A. C. (2006). Seismic signal production in a wolf spider: Parallel versus serial multi-component signals. *Journal of Experimental Biology*, 209, 1074–1084. <https://doi.org/10.1242/jeb.02104>
- Elias, D. O., & Mason, A. C. (2014). The role of wave and substrate heterogeneity in vibratory communication: Practical issues in studying the effect of vibratory environments in communication. In *Studying vibrational communication* (pp. 215–247). Springer. https://doi.org/10.1007/978-3-662-43607-3_12
- Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *American Naturalist*, 139, s125–s153. <https://doi.org/10.1086/285308>
- Endler, J. A., & Basolo, A. L. (1998). Sensory ecology, receiver biases and sexual selection. *Trends in Ecology and Evolution*, 13, 415–420. [https://doi.org/10.1016/s0169-5347\(98\)01471-2](https://doi.org/10.1016/s0169-5347(98)01471-2)
- Ewing, A. W. (1989). *Arthropod bioacoustics: Neurobiology and behaviour*. Cornell University Press. <https://doi.org/10.5860/choice.28-0285>
- Fitch, W. T. (2006). Production of vocalizations in mammals. *Visual Communication*, 3, 145. <https://doi.org/10.1016/b0-08-044854-2/00821-x>
- Giannakopoulos, T., & Pikrakis, A. (2014). *Introduction to audio analysis: A MATLAB® approach*. Academic Press. <https://doi.org/10.1016/b978-0-08-099388-1.00010-8>

- Gingras, B., Boeckle, M., Herbst, C. T., & Fitch, W. T. (2012). Call acoustic reflect body size across four clades of anurans. *Journal of Zoology*, 289, 143–150. <https://doi.org/10.1111/j.1469-7998.2012.00973.x>
- Hallander, H., & Hallander, H. (1967). Courtship display and habitat selection in the wolf spider *Pardosa Chelata* (OF Müller). *Oikos*, 18(1), 145–150. <https://doi.org/10.2307/3564644>
- Hauser, M. D. (1993). The evolution of nonhuman primate vocalizations: Effects of phylogeny, body weight, and social context. *American Naturalist*, 142, 528–542. <https://doi.org/10.1086/285553>
- Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: Developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, 57, 197–214. <https://doi.org/10.1007/s00265-004-0865-7>
- Hebets, E. A., Vink, C. J., Sullivan-Beckers, L., & Rosenthal, M. F. (2013). The dominance of seismic signaling and selection for signal complexity in *Schizocosa* multimodal courtship displays. *Behavioral Ecology and Sociobiology*, 67, 1483–1498. <https://doi.org/10.1007/s00265-013-1519-4>
- Hill, P. S. M. (2008). *Vibrational communication in animals*. Harvard University Press.
- Jocqué, R. (2005). Six stridulating organs on one spider (Araneae, Zodariidae): Is this the limit? *The Journal of Arachnology*, 33, 597–603. <https://doi.org/10.1636/04-107.1>
- Kaston, B. J. (1936). The senses involved in the courtship of some vagabond spiders. *Brooklyn Entomological Society*, 16, 97–167.
- Kingsley, E. P., Eliason, C. M., Riede, T., Li, Z., Hiscock, T. W., Farnsworth, M., Thomson, S. L., Goller, F., Tain, C. J., & Clarke, J. A. (2018). Identity and novelty in the avian syrinx. *Proceedings of the National Academy of Sciences*, 115, 10209–10217. <https://doi.org/10.1073/pnas.1804586115>
- Maddison, W. P., & Stratton, G. E. (1988). Sound production and associated morphology in male jumping spiders of the *Habronattus agilis* species group (Araneae, Salticidae). *The Journal of Arachnology*, 16, 199–211.
- McNett, G. D., & Cocroft, R. B. (2008). Host shifts favor vibrational signal divergence in *Enchenopa binotata* treehoppers. *Behavioral Ecology*, 19, 650–656. <https://doi.org/10.1093/beheco/arn017>
- Montealegre-Z, F. (2009). Scale effects and constraints for sound production in katydids (Orthoptera: Tettigoniidae): Correlated evolution between morphology and signal parameters. *Journal of Evolutionary Biology*, 22, 355–366. <https://doi.org/10.1111/j.1420-9101.2008.01652.x>
- Nowicki, S., & Marler, P. (1988). How do birds sing? *Music Perception*, 5, 391–426. <https://doi.org/10.2307/40285408>
- Patek, S. N. (2001). Spiny lobsters stick and slip to make sound. *Nature*, 411, 153. <https://doi.org/10.1038/35075656>
- Pfennig, D. W., & Pfennig, K. S. (2012). *Evolution's wedge: Competition and the origins of diversity* (Vol. 12). University of California press. <https://doi.org/10.1525/california/9780520274181.001.0001>
- Podos, J. (2001). Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature*, 409, 185–188. <https://doi.org/10.1038/35051570>
- Podos, J., Huber, S. K., & Taft, B. (2004). Bird song: The interface of evolution and mechanism. *Annual Review of Ecology, Evolution, and Systematics*, 35, 55–87. <https://doi.org/10.1146/annurev.ecolsys.35.021103.105719>
- Raboin, M., & Elias, D. O. (2019). Anthropogenic noise and the bioacoustics of terrestrial invertebrates. *Journal of Experimental Biology*, 222, 12. <https://doi.org/10.1242/jeb.178749>
- Read, A. F., & Weary, D. M. (1992). The evolution of bird song - Comparative analyses. *Philosophical Transactions of the Royal Society B*, 338, 165–187. <https://doi.org/10.1098/rstb.1992.0137>
- Reichert, M. S. (2013). Patterns of variability are consistent across signal types in the treefrog *Dendropsophus ebraccatus*. *Biological Journal of the Linnean Society*, 109, 131–145. <https://doi.org/10.1111/bij.12028>
- Roberts, J. A., & Uetz, G. W. (2005). Information content of female chemical signals in the wolf spider, *Schizocosa ocreata*: Male discrimination of reproductive state and receptivity. *Animal Behaviour*, 70, 217–223. <https://doi.org/10.1016/j.anbehav.2004.09.026>
- Rosenthal, M. F., & Elias, D. O. (2019). Nonlinear changes in selection on a mating display across a continuous thermal gradient. *Proceedings of the Royal Society B*, 286, 20191450. <https://doi.org/10.1098/rspb.2019.1450>
- Rosenthal, M. F., & Hebets, E. A. (2012). Resource heterogeneity interacts with courtship rate to influence mating success in the wolf spider *Schizocosa floridana*. *Animal Behaviour*, 84, 1341–1346. <https://doi.org/10.1016/j.anbehav.2012.08.028>
- Rosenthal, M. F., Wilkins, M. R., Shizuka, D., & Hebets, E. A. (2018). Dynamic changes in display architecture and function across environments revealed by a systems approach to animal communication. *Evolution*, 72, 1134–1145. <https://doi.org/10.1111/evo.13448>
- Rovner, J. S. (1967). Acoustic communication in a Lycosid spider (*Lycosa rabida* Walckenaer). *Animal Behaviour*, 15, 273–281. [https://doi.org/10.1016/0003-3472\(67\)90012-7](https://doi.org/10.1016/0003-3472(67)90012-7)
- Rovner, J. S. (1968). An analysis of display in the Lycosid spider *Lycosa rabida* Walckenaer. *Animal Behaviour*, 16, 358–369. [https://doi.org/10.1016/0003-3472\(68\)90021-3](https://doi.org/10.1016/0003-3472(68)90021-3)
- Rovner, J. S. (1975). Sound production by Nearctic wolf spiders: A substratum-coupled stridulatory mechanism. *Science*, 190, 1309–1310. <https://doi.org/10.1126/science.190.4221.1309>
- Rundus, A. S., Sullivan-Beckers, L., Wilgers, D. J., & Hebets, E. A. (2011). Females are choosier in the dark: Environment-dependent reliance on courtship components and its impact on fitness. *Evolution*, 65, 268–282. <https://doi.org/10.1111/j.1558-5646.2010.01125.x>
- Ryan, M. J., & Brenowitz, E. A. (1985). The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist*, 126, 87–100. <https://doi.org/10.1086/284398>
- Searcy, W. A., & Andersson, M. (1986). Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics*, 17, 507–533. <https://doi.org/10.1146/annurev.es.17.110186.002451>
- Stratton, G. E. (2005). Evolution of ornamentation and courtship behavior in *Schizocosa*: Insights from a phylogeny based on morphology (Araneae, Lycosidae). *The Journal of Arachnology*, 33, 347–376. <https://doi.org/10.1636/04-80.1>
- Sueur, J., Pavoine, S., Hamerlynck, O., & Duval, S. (2008). Rapid acoustic survey for biodiversity appraisal. *PLoS One*, 3, e4065. <https://doi.org/10.1371/journal.pone.0004065>
- Suzuki, R., Buck, J. R., & Tyack, P. L. (2006). Information entropy of humpback whale songs. *Journal of the Acoustical Society of America*, 119, 1849–1866. <https://doi.org/10.1121/1.2161827>
- Uhl, G., & Elias, D. O. (2011). Communication. In M. E. Herberstein (Ed.), *Spider behavior: Flexibility and versatility*. Cambridge University Press (pp. 127–190). <https://doi.org/10.1017/cbo9780511974496.006>
- Virant-Doberlet, M., & Čokl, A. (2004). Vibrational communication in insects. *Neotropical Entomology*, 33, 121–134. <https://doi.org/10.1016/b978-0-12-374144-8.00271-x>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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