Characterizing the vibratory and acoustic signals of the “purring” wolf spider, *Gladicosa gulosa* (Araneae: Lycosidae)

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**ABSTRACT**

Both airborne acoustic signals and substrate-borne vibrations are prevalent modes of animal communication, particularly in arthropods. While a wide variety of animals utilize one or both of these modalities, the connection between them is still ambiguous in many species. Spiders as a group are not known for using, or even perceiving, acoustic signals, despite being well-adapted for vibratory communication. Males of the “purring” wolf spider *Gladicosa gulosa* are reported to produce audible signals during courtship, although the literature on this species is largely anecdotal. Using a laser Doppler vibrometer and an omnidirectional microphone in controlled conditions, we recorded and characterized the visual and mechanical (both substrate-borne and airborne) signals of this species in an attempt to provide a qualitative and quantitative overview of its signal properties. We found that the vibratory signal is composed of two primary repeating and alternating elements, consisting of pulses of stridulation and percussive strikes, as well as a less common, but repeatable, third element. We also characterized a measurable airborne component to the signal that is significantly correlated with the amplitude of the vibratory signal, which we suggest is a by-product of the strong vibration. Neither modality correlated significantly with male body size or condition. Although the exact role of the acoustic component is unclear, we speculate that the unique properties of signalling in this species may have value in answering new questions about animal communication.

**KEYWORDS**

Vibration; spider; acoustic; communication

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**Introduction**

While acoustic communication is widely recognized as a standard mode of communication for a variety of animal species (Bradbury and Vehrencamp 2011), it is also intrinsically connected with vibration as a means of communication (Hill 2008; Cocroft et al. 2014). “Sound” (airborne) and “vibration” (substrate-borne) constitute different facets of a coupled mechanical signal and are differentiated primarily by the medium through which they flow. Increasingly, vibration is gaining recognition as a prominent modality, with hundreds of thousands of species potentially utilizing substrate-borne vibratory signals for conspecific
communication (Cocroft and Rodríguez 2005; Hill 2008; Cocroft et al. 2014). Studies on animal vibration elucidate a previously understudied but highly prevalent mode of communication, and are beginning to shed light on the evolutionary origins of airborne acoustic communication (Cocroft and Rodríguez 2005; Hill 2008; Cocroft et al. 2014). While there are numerous examples of animals that utilize both sound and vibration, particularly in arthropods (Cocroft and Rodríguez 2005), the degree of connection between these two modalities is still largely unknown for many species, as true “bimodal” acoustic signalling can be difficult to demonstrate (Caldwell 2014), and is largely dependent on the physiological independence of the receptor organs in the target receiver. Thus, the connection may be even more ambiguous for species that do not possess structures adapted to sense both airborne sound and substrate-borne vibration.

Wolf spiders (Araneae: Lycosidae) are known to communicate using multiple modalities, including chemical (Searcy et al. 1999; Persons and Rypstra 2000; Persons et al. 2001; Barnes et al. 2002; Roberts and Uetz 2005; Gasket 2007; Sweger et al. 2010), visual (McClintock and Uetz 1996; Clark et al. 2011, 2012; Uetz et al. 2011), and vibratory (Rovner 1967, 1975; Elias et al. 2006; Gibson and Uetz 2008; Gordon and Uetz 2012; Hebets et al. 2013) signals, and in some cases, species will use multimodal communication (Hebets and Uetz 1999; Uetz and Roberts 2002; Hebets 2005; Rypstra et al. 2009; Uetz et al. 2009, 2013; Gordon and Uetz 2011; Stafstrom and Hebets 2013). However, male courtship in many species involves complex vibrations with structural components of the courtship often serving as one of the defining behavioural differences between closely related species (Uetz and Denterlein 1979; Stratton and Uetz 1981).

With several thousand species worldwide, the prevalence of substrate-borne vibratory signalling across lycosid spiders is not fully understood, and is further complicated by the convolution of terminology related to airborne and substrate-borne signals. However, several key genera have been studied extensively in relation to mechanical signalling during courtship. Rovner’s work in the genus Rabidosa documented the production of and response to male signals (1967), and while his initial work identified them as “acoustic” in nature, his follow-up work identified a substrate-coupled mechanism not only in Rabidosa but in several North American genera (1975), suggesting that the primary mechanical signalling modality was substrate-borne. Since that time, the genus Schizocosa has been perhaps the most well-studied in relation to substrate-borne vibration. Several members of this genus utilize multi-component signals, consisting of stridulation, body tremulation and active percussion with the whole or part of the body (Stratton and Uetz 1981; Elias et al. 2006; Gibson and Uetz 2008), and substrate-borne vibration is believed to be ancestral to the more derived visual and multimodal signals that are present in several species (Hebets et al. 2013). Despite a mixture of terminology for the mechanical signals, and a few references to “audible” signals (Rundus et al. 2010), the literature largely suggests that mechanical communication in wolf spiders is substrate bound. While research increasingly suggests that spiders are capable of responding to airborne acoustic stimuli (Gordon and Uetz 2012, Lohrey et al. 2009; Caldwell 2014), there is no evidence of tympanal organs capable of direct pressure reception, there is little to no concrete evidence that they utilize airborne acoustic signals in intraspecific communication, and there are few species that seem capable of producing a sufficient airborne signal to effectively communicate.

To our knowledge, only two species have been described as “audible” at a substantial distance from the focal spider. The European drumming spider Hygrolycosa rubrofasciata
has been documented as having a substantial airborne sound associated with the drumming
behaviour inherent to its substrate-borne communication (Kronestedt 1996). Females of this
species appear to respond to both forms of the signal (Parri et al. 2002) and the percussive
signal has been extensively studied in connection with female preference (Parri et al. 1997,
2002), male quality and viability (Kotiaho et al. 1996, 1998, 1999; Mappes et al. 1996; Rivero
et al. 2000) and the evolution of chorusing behaviour (Kotiaho et al. 2004). However, this
European species bears a more distant lineage to North American lycosid species, and does
not appear to utilize multi-component mechanical signals.

The “purring” wolf spider, *Gladicosa gulosa*, a ground-dwelling wolf spider that occupies
deciduous forest habitats throughout the mid-western and eastern United States (Brady
1986; Dondale and Redner 1990), has also been described as “audible” to observers at
c onsiderable distances. However, unlike *Hygrolycosa*, this species is not well-studied, and
what little literature exists is largely anecdotal. The focal point of nearly every published
anecdote is the audible nature of male courtship in this species (Davis 1904; Lahee 1904;
Allard 1936; Kaston 1936; Harrison 1969), with some authors suggesting that males can be
heard anywhere from 10 feet (Allard 1936) to upwards of 6-m away (Harrison 1969). While
the majority of the claims are nearly a century old and empirically unfounded, Harrison
(1969) does provide the only published recordings of the species, noting its volume in the
study. It remains unclear if the initial suggestion about airborne acoustic communication
in this species is an artefact, given that we lack updated and properly controlled recordings
of male courtship. However, if this species does have the potential to produce a sufficient
airborne component, it could serve as useful system to evaluate the evolution of new signal
modalities.

Our objective was to record and characterize the courtship signals of this species, and
provide an assessment of any visual or mechanical (both substrate-borne and airborne)
signals that males may produce when courting. Here, we characterize the presence of various
signals and their constituent components, provide qualitative and quantitative descriptions
of spectral and temporal aspects of the male courtship signal, and realistically evaluate
historic claims regarding this species. We also discuss its potential as a model for the future
study of acoustic and vibratory communication in animals.

**Methods**

**Spider collection and maintenance**

All male and female spiders used in this study were collected post-maturity in leaf litter
from a deciduous forest location in New Richmond, OH in August and September of 2013.
Spiders were brought into the laboratory at the University of Cincinnati and maintained on
a Spring photoperiod (13:11 h light:dark) in stable environmental conditions (23–25 °C,
65–75% humidity). Each individual was housed in a small deli dish (approx. 9.5-cm dia. at
base) and were fed 2–3 house crickets (*Acheta domesticus*) twice per week and given water
*ad libitum*. Prior to trials, each individual was photographed using a stereo dissecting scope
(OMAX CS-W43C2-D3-L144L-C90) using ScopeImage 9.0 imaging software, and weighed
using a microbalance (RadWag AS220/C/2) to determine size, mass and body condition.
Condition indices were determined from residuals of the regression of mass × cephalotho-
rax width using the method described in Jakob et al. (1996). Post-trial, male spiders were
euthanized with CO₂ and stored in 75% ethanol for cataloguing purposes.
**Recording and assessing male behaviours**

We recorded 14 individual male *G. gulosa* in this study. To stimulate courtship, a female conspecific spider was placed on a clean Fisherbrand P8 filter paper substrate (09-795F) for approximately 2 h prior to recording. In many wolf spider species, males will respond to chemotactile cues from females in isolation. Prior to recording, we removed the female, and placed a male on the filter paper substrate inside a hollow rectangular arena (13 cm × 7 cm). We then simultaneously recorded any vibratory, acoustic or visual signal produced by males during courtship. All signals were recorded inside an anechoic and vibration-isolated booth. Video was recorded using a Sony Handycam (HDR-XR260), and male visual behaviours (if present) were evaluated from video recordings. Substrate-borne vibrations were recorded using a PDV-100 laser Doppler vibrometer (125 mm/s/V sensitivity, 500 mm/s max, 96-mm standoff distance), and airborne acoustic signals were recorded using an iSEMcon omni-directional microphone (1/4″ front end, 125 dB max, 20-cm standoff distance) (see Supplementary Figure S1). Both instruments were connected to an external sound card (Roland QuadCapture) and calibrated with a 1-kHz tone (LDV at 50% FS, Microphone at 94 dB). Digital signal processing of male acoustic and vibratory signals was conducted in SpectraPLUS-SC (24 kHz sampling rate, 2048 FFT, Hanning window), with independent scaling and calibration for each signal. After initial qualitative evaluation of the airborne acoustic signal, a 100-Hz high-pass filter was applied in order to facilitate cleaner quantification of signal levels, as most of the acoustic signal was completely masked below this frequency.

**Results**

**Elements of the substrate-borne signal**

The substrate-borne vibratory signal in this species is composed of three discrete and simple elements (Figure 1), two of which were prominent in every recording. The first is a stridulatory element generated through a pulse of the pedipalps, striking the *plectrum* across the *pars stridens* in a stridulatory organ first described by Rovner (1975). Each stridulatory pulse is short (370.3 ± 24.0 ms) and contains anywhere from 6 to 25 separate rapid (31.95 ± 0.90/s) impulses (with each impulse containing a series of strikes across the teeth

![Figure 1. A waveform of an example of the substrate-borne vibratory courtship signal in male *G. gulosa*, with the three characterized elements of the signal – (1) stridulation; (2) percussion; (3) third “tick” element. The hatched line indicates a large temporal gap between segments, though both segments are scaled to the same relative amplitude.](image-url)
of each *pars stridens*), that are generally connected in a train of 2–6 pulses. Pulse amplitude can vary (6.58 ± 0.56 mm/s RMS), and each pulse occupies a fairly broad frequency range, with most of the signal ranging from 100 to 4500 Hz. Males generally do not move around while producing this stridulatory element, as the pedipalps need to be in contact with the substrate in order to properly conduct the vibration (Rovner 1975).

The second element consists of a sharp percussive strike using the abdomen. These strikes are short (6.67 ± 0.56 ms) and high amplitude (68.47 ± 6.08 mm/s RMS). Males frequently move around the arena while generating percussive strikes in a series of about 5–10 over the course of several seconds. Like most percussive signals, each strike occupies a broad range of frequencies, with signal energy extending from low frequencies up through 12,000 Hz (the upper limit of instrument recording capacity).

In four of the total recordings, a third discrete element was present. While the element was not present in every male recorded, it was repeatable and distinct in the four males that produced it. It consists of a low amplitude (0.578 ± 0.02 mm/s RMS) signal resembling 3–4 “ticks” that are produced with considerable regularity once every 1–2 s over the course of several minutes. The ticks occupy relatively low frequencies compared with the other elements (100–2000 Hz) and they do not occur alongside the other two elements. During production of this third element, the spider remains completely still with only subtle movement from the pedipalps, not beginning movement again until returning to full courtship with the first two elements, at which point the third element is no longer present.

Temporal structure of the signal, while varied, has a qualitative pattern, as shown in Figure 1. Elements 1 and 2 are almost always produced repeatedly in a series, with each series consisting of only one of the elements and alternating the elements between separate series. The visual behaviour of males follows a similar pattern, with each male pausing to generate a series of stridulatory pulses, followed by movement around the arena while creating a series of percussive strikes. This courtship occurs in discrete bouts of 1–2 min, followed by a pause of several minutes before the next bout. It is during this intermediate time interval that the third element, if present, is produced.

**Presence of the airborne signal**

We found that an acoustic component to this signal is qualitatively present, as each male spider was audible at up to 1-m away (Sweger and Uetz, personal observation). The acoustic component is also quantifiable, though at low levels (37.3 ± 1.0 dB SPL) above background noise (32.5 ± 1.0 dB SPL). The quiet acoustic “purring” that occurs is temporally associated with the stridulatory component of the vibratory signal and is largely masked on a waveform by low-frequency background noise. However, when looking at the spectrogram of both signals (Figure 2), the airborne signal is visible for both elements, and at higher frequencies than most of its vibratory component. The third element, when present, is sufficiently masked by background noise such that it is not quantitatively or qualitatively identifiable in the acoustic recording.

**Gross morphology and signal production**

We sampled multiple segments of courtship containing both primary elements of the signal and compared them to natural variations in size and body condition among males. We
found no significant association between size and amplitude of either signal (Vibratory: \( N = 14, R^2 = 0.0010, p = 0.9123 \); Acoustic: \( N = 14, R^2 = 0.0017, p = 0.8868 \)), nor did we find an association between body condition and either signal (Vibratory: \( N = 14, R^2 = 0.0503, p = 0.4406 \); Acoustic: \( N = 14, R^2 = 0.08846, p = 0.3017 \)). However, we found a significant positive correlation between the relative amplitude of the vibratory and acoustic signals (\( N = 14, R^2 = 0.3120, p = 0.0379 \)) (Figure 3).

Figure 2. Two spectrograms showing the relative amplitude for both primary elements of the substrate-borne and airborne signal. Both spectrograms represent separate modality recordings of the same 1.5-s interval.
Discussion

This species utilizes two different mechanisms in producing vibration – stridulation and percussion – both of which are prominent mechanisms in both substrate-borne and airborne mechanical communication. Each element is produced with an independent mechanism, and these elements are discrete and repeated, influencing both the temporal structure of the vibratory signal and the visual behaviour of the male during courtship. Given the previous evidence for both visual and vibratory signals influencing female mate choice in wolf spiders (McClintock and Uetz 1996; Hebets and Uetz 1999, 2000; Hebets 2005; Gibson and Uetz 2008) with particular emphasis on the substrate-borne vibratory signal (Kotiaho et al. 1996; Hebets et al. 2013), the discrete and repeatable structure of this courtship signal may make this species useful dissecting signal complexity within a specific modality. Future studies can easily manipulate signal elements in relation to varying courtship rate, element ratios and overall pattern. While our current data do not suggest a direct connection between signal amplitude and body size, additional studies could explore connections between individual signal parameters and aspects of male quality or female preference, and given the role of these signal facets in female preference in *Hygrolycosa* (Parri et al. 1997, 2002), we hypothesize that *G. gulosa* may follow similar trends.

The third element of the vibratory signal raises additional questions about signals, their production and their function, both within this species and in arthropod communication networks as a whole. Its mechanism for production is unknown, though visually there appears to be subtle movement of the male pedipalps during its production, suggesting a similar mechanism to the stridulatory element. Its role within the broader courtship signal is also unknown, and could possibly be an artefact of the spider “warming up” for the substantially stronger elements of the substrate-borne signal, similar to a behaviour described in *Hygrolycosa* (Kohler and Tembrock 1987). However, given its dramatically lower amplitude relative to other elements, its distinct regularity and its presence exclusively

![Figure 3. Regressions of the vibratory signal against a scaling metric (left), and the substrate-borne signal against the airborne signal (right). While gross morphology did not appear to correlate with signal strength, amplitudes of the separate modalities were tightly correlated.](image)
between bouts of more pronounced courtship, we speculate that it could also have a role as some sort of timing mechanism, though the theoretical intended receiver for this timing is not immediately clear. Regardless, its production and function may raise questions about conspecific communication that translate to other species utilizing similar mechanisms.

In characterizing the various components and possible modalities inherent to this signal, we might speculate about its value in the context of a variety of unanswered questions in arthropod communication. Based exclusively on our recordings, it remains difficult to determine the relevance of any airborne acoustic signal. Its temporal and spectral correlation with the substrate-borne signal suggests that it is a physical by-product of the strong vibratory signal. However, in flat frequency weighting, the airborne signal is masked almost entirely at lower frequencies, and is difficult (if possible) to visualize on a waveform. The signal is clearly visible above the background much more readily at mid-to-high frequencies, though still quantitatively low amplitude, especially in comparison to species that traditionally utilize airborne sound. Despite this, the qualitative presence of the airborne signal is clear. In both lab and field settings, a quiet environment allows males of this species to be heard easily at upwards of 1 m (Sweger and Uetz, personal observation). While not traditionally “loud”, it does represent a considerable signal for a species that is not known to use acoustic communication, and given that this species seems to breed in very early spring (Brady 1986; Dondale and Redner 1990), the acoustic environment may be more accommodating to low-amplitude acoustic signals. At the very least, anecdotal reports of airborne acoustic signals in this species are not far off, although controlled measures of the signal create a much more realistic portrait of the acoustic component.

Though studies are needed to confirm the function (if any) of the airborne signal, the lack of tympanal organs in lycosids suggests that bimodal acoustic signalling is unlikely in this species. We hypothesize that a more likely function for this signal is in the extension of the active space of the signal. Substrate-borne signals are highly attenuated by breaks in the solid communication medium, and an airborne signal capable of inducing vibration in nearby substrates could potentially extend the active range of a signalling male (Mazzoni et al. 2014). It is also unclear to what degree individual male behaviour influences the production of the airborne component. Previous studies in Schizocosa suggest a flexibility in microhabitat choice and relative production of different signal components based on available habitat (Hebets et al. 2008; Gordon and Uetz 2011), and varying shapes, sizes and species of deciduous litter are likely to have equally varying acoustic properties. Additional recordings and behavioural studies in this species could determine which substrates contribute most to the production of the airborne signal, and if they are utilized as such.

This species and its courtship signals may present opportunities to investigate the unique conditions under which new modes of communication might have evolved. Independent reception and usage of substrate-borne and airborne signals is rare, but not unprecedented, even in arthropods (Latimer and Schatral 1986, Hill and Shadley 2001; Caldwell 2014). Certain environmental conditions, combined with current variations in behaviour, signal production and mate choice pressures may create opportunity for the adaptation of a signal that would otherwise be a simple redundancy or biophysical artefact. Combined with the complex patterning and discrete signal elements of courtship in this species, communication in this wolf spider could serve as an atypical, but elegant, model for the evolution of signals and their functions.
Supplementary material

Supplementary material for this article is available via the supplementary tab on the article’s online page at http://dx.doi.org/10.1080/09524622.2016.1160328.

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