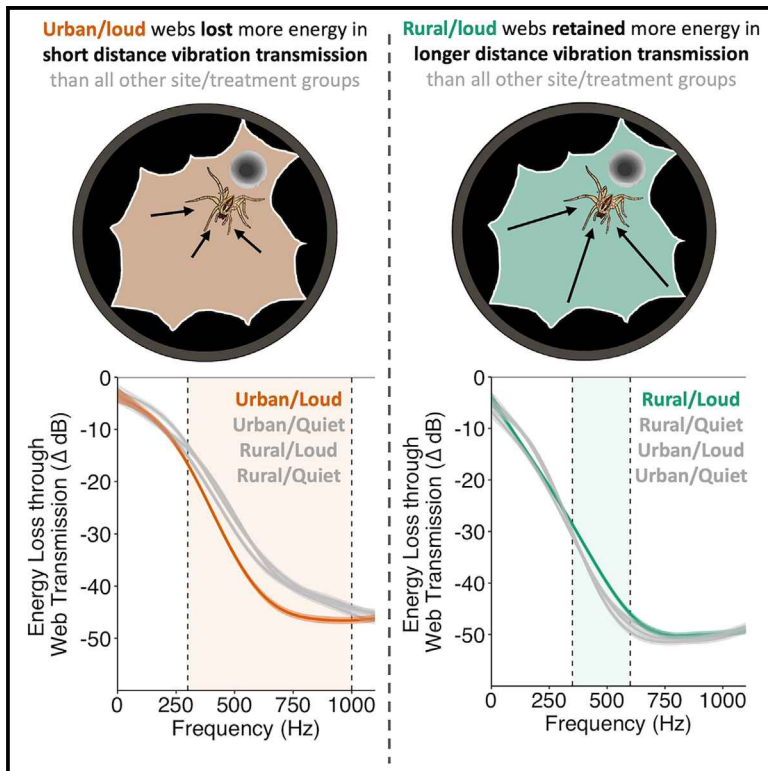


Current Biology

Web transmission properties vary with a spider's past and current noise exposure

Graphical abstract



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In brief

Pessman and Hebets show that the funnel-weaving spider's past and current exposure to environmental noise shapes web vibration transmission. Under loud noise, rural webs retained energy in longer-range vibrations, whereas urban webs attenuated short-range vibrations. This flexibility may enhance information reception in dynamic, noisy environments.

Highlights

- Rural/urban field-collected spiders built webs under quiet/loud vibratory playback
- Urban/loud webs lost energy in short-range vibrations, damping persistent noise
- Rural/loud webs retained energy in biologically relevant longer-range vibrations
- Variation in web transmission may enhance sensory reception amid varying noise

Article

Web transmission properties vary with a spider's past and current noise exposure

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SUMMARY

Animals rely on the reception of accurate information for survival and reproduction. Environmental noise, especially from human activity, challenges information acquisition by disturbing sensory channels and masking relevant cues. Investigations into how animals cope with noise have been heavily biased toward plasticity in information production, often overlooking flexibility in information reception. Studying internal sensory structures is challenging, but web-building spiders offer a unique opportunity to investigate external sensory surfaces—their webs. Here, we explored the potential of the funnel-weaving spider, *Agelenopsis pennsylvanica*, to influence information reception amid vibratory noise. During web construction, we exposed spiders to a 2 × 2 fully-crossed design: rural/urban collection sites and quiet/loud noise treatments, reflecting natural vibratory noise variation. On the resulting webs, we compared frequency-dependent energy loss between site/treatment groups as vibrations transmitted short and longer distances from an artificial stimulus to the spider's hunting position. Under loud vibratory noise, rural webs retained more energy in longer-distance vibratory stimuli across a narrow frequency range (350–600 Hz) than all other groups, potentially to improve the reception of relevant prey and mate cues. Conversely, urban/loud webs lost more energy in short-distance vibrations across a broader frequency range (300–1,000 Hz) than all other groups, likely to prevent sensory overload from constant, high-amplitude urban noise. Variable web transmission was related to spiders' prior (ancestral and/or developmental) and current noise exposure. Our study highlights the capacity of animals to influence information reception amid environmental noise and emphasizes the importance of a holistic approach to studying information flow in dynamic environments.

INTRODUCTION

The accurate reception of information—whether about the presence of predators, prey, potential mates, or the environment—is critical for animals to make informed behavioral decisions.¹ It is not surprising, then, that numerous studies across disparate taxa provide a strong foundation of understanding (both ultimate and proximate) regarding the transmission and reception of information.^{2–4} Whether in the context of communication⁵ or predator-prey interactions,^{6,7} information serves to reduce a receiver's uncertainty about the source's identity, condition, location, or intention, among others. Yet, environmental noise can interfere with effective information flow by distorting or masking signals or cues.^{8,9}

Although natural noise has shaped animal behavior throughout evolutionary history,¹⁰ surges in human activity since the Industrial Revolution have introduced novel noise. In addition to being more intense and persistent than natural sources,¹¹ anthropogenic sources (e.g., traffic, industrial equipment, etc.) overlap spectrally with biologically relevant frequencies.⁸ The emergence of these novel noise landscapes has incited a recent push to investigate the diverse strategies

animals adopt to mitigate the detrimental effects of environmental noise.

Compared with predator-prey interactions, our understanding of animal communication in noise has a stronger conceptual framework, so we draw on this literature for examples. When noise drowns out signals and/or overlaps spectrally, animals may adjust signal timing or structure to improve the signal-to-noise ratio. For instance, some birds delay their dawn chorus until there is a reduction in aircraft noise¹² or insect choruses,¹³ treehoppers pause signaling during periods of high wind noise,¹⁴ brown tree frogs increase the pitch of their songs to avoid overlapping with traffic noise frequencies,¹⁵ and Australian lizards switch from continuous to intermittent tail flicking in windy conditions to improve signal visibility against a noisy visual background.¹⁶ These examples emphasize the importance of identifying biologically relevant noise frequencies and highlight ways in which animals can preserve signal efficacy in noisy environments.¹⁷

Despite research focusing on how signalers enhance the production and transmission of information amid noise, the fundamental question of how animals detect and discriminate information remains understudied.^{3,18} This research gap means that we

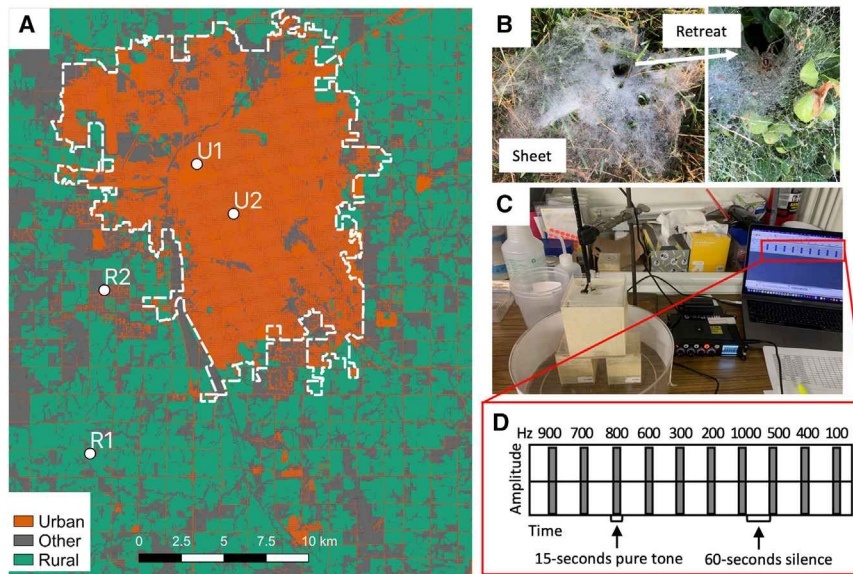


Figure 1. Collection and experimental setup of spider responses to pure tone frequencies (A and B) (A) Geographic locations where (B) *Agelenopsis pennsylvanica* spiders were collected in 2022 and 2023. Rural sites (R1 and R2) were private properties outside of Lincoln's city limits (dashed white line), and urban sites were the University of Nebraska-Lincoln's city campus (U1) and a private property (U2). Rural, urban, and other areas are based on the planted/cultivated, developed, and all other classes, respectively, from the 2019 National Land Cover Database (<https://www.mrlc.gov/data/legends/national-land-cover-data-base-class-legend-and-description>). (B) *Agelenopsis pennsylvanica* construct funnel-shaped webs that consist of a sheet where vibratory information is produced and a retreat (the narrow, tubular part of the web) where the spider sits and awaits incoming information. The left photo is adapted from Pessman et al.²⁸ (C) To test spiders' responses to pure tone frequencies, we rested a linear resonant actuator (LRA) on the surface of each web built under ambient lab conditions. The LRA was connected to a laptop through a MixPre-6 interface.

(D) We played 15-s pure tone vibrations from 100 to 1,000 Hz in 100-Hz increments, with 60 s of silence between each stimulus. We had 10 files, each with a different random order of frequencies and unique first frequency, which we randomly assigned to the spiders. We observed the spiders during each tone for attack behavior (defined as making contact with the LRA).

know little about the putative flexibility of animal sensory systems¹⁹ and likely stems from the challenges of studying sensory systems in naturally behaving animals.²⁰ Nonetheless, identifying how noise impacts the reception of information and how animals might overcome it is crucial to understanding the full impact of anthropogenic noise on animal interactions and survival.

This study explores the potential for animals to influence their reception of relevant information in the presence of noise. To do this, we focus on spiders and their webs—an external structure that functions as an extension of the spider's internal sensory processing. With over 100 million years of evolution,²¹ spider webs are highly specialized sensory devices whose vibration transmission enables these architects to detect and capture prey, identify and assess mates, and sense and evade predators.^{22–24} Despite proposed hypotheses that spiders can manipulate how vibrations propagate across their webs by adjusting silk properties, web geometry, and active tensioning,²⁵ webs have never been tested for their propensity to variably regulate vibration transmission. Here, we explore this capacity with respect to environmental vibratory noise.

The funnel-weaving spider (or grass spider), *Agelenopsis pennsylvanica*,²⁶ constructs funnel-shaped webs (Figure 1B) that lack sticky silk,²⁷ leaving spiders to rely on vibratory cues (e.g., frequency, attenuation, and direction) and their own speed to detect, locate, assess, and capture prey before escape.²⁴ Vibratory information (from prey, predators, mates, etc.) is introduced onto the web sheet and travels across its surface to the narrow, tubular part of the web funnel (hereafter, the retreat), where the spider resides and monitors the web for vibratory information (Figure 1B). These spiders are found across urban-rural gradients,^{28,29} likely across the genus' North American range. Urban areas, where these spiders are especially abundant,²⁸

exhibit daily vibratory noise levels that can reach up to 22 dB higher than rural areas.²⁹ The frequency bandwidth of this environmental noise also overlaps with biologically relevant frequency ranges (<1 kHz),²⁹ and the webs of *A. pennsylvanica* are inextricably connected with surfaces (e.g., bushes, trees, grass, rocks, and buildings) that propagate vibrations from noise-producing sources, such as traffic and harvesting equipment. Consequently, vibratory noise likely interferes with the ability of *A. pennsylvanica* to acquire critical vibratory information from their webs.²⁹

Prior research documenting biologically relevant environmental noise for *A. pennsylvanica*²⁹ led us to propose the following questions. (1) What range of frequencies within known environmental noise is relevant to *A. pennsylvanica* foraging? (2) Do vibrations travel differently across webs built by rural and urban spiders under different vibratory noise treatments? If vibratory noise disrupts the accurate reception of vibratory information, then spiders may influence how information travels across the web to mitigate the effects of noise. This investigation of a spider's web as an external sensory structure represents a gateway to assessing the internal mechanisms of information reception and its flexibility in environmental noise.

RESULTS

Spiders' responses to pure tone frequencies

To determine what range of frequencies within known environmental noise are relevant to *A. pennsylvanica* foraging, we assessed attack rates of rural and urban spiders to artificial frequency stimuli that overlap with field-recorded vibratory noise (<1 kHz). Under ambient laboratory conditions, we rested a linear resonant actuator (LRA) on webs built by spiders collected from rural ($n = 95$) and urban ($n = 94$) environments and provided pure

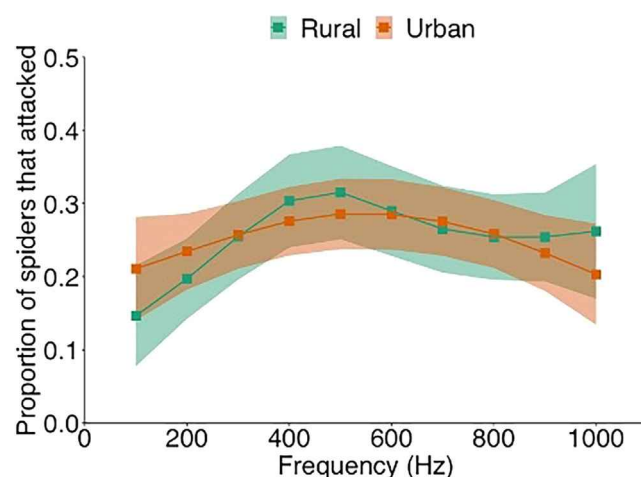


Figure 2. Results from spider responses to pure tone frequencies

We tested the proportion of spiders that attacked within the frequency range of field-recorded vibratory noise (<1 kHz). We used a binomial generalized additive model to test variation in the probability of rural and urban *A. pennsylvanica* attacking pure tone frequencies from 100 to 1,000 Hz in 100-Hz increments. The points and error ribbon represents the proportion of spiders that attacked at each frequency and the 95% confidence interval from the model. Some spiders had prior playback experience (see Table S1), but this was dropped from the model as it did not significantly affect model fit. Rural and urban spiders attacked all frequencies with approximately equal probability. When we controlled for habituation by testing only responses to the first frequency, we found similar results (see Figure S1).

tone vibrations between 100 and 1,000 Hz in 100-Hz increments and in random order, ensuring that all frequencies vibrated at the same amplitude (Figures 1C and 1D). We observed whether spiders (not fed within the 24 h before trial) attacked the LRA during each 15-s tone, separated by 60 s of silence. For the analysis, we only included spiders that attacked at least one of the ten frequencies (rural = 58 out of 95, urban = 63 out of 94). Future research exploring potential differences in sensory capabilities, motivation, or boldness (among others) is necessary to understand why 36% of tested spiders did not respond. Collection sites (R1, R2, U1, and U2, Figure 1A), years (2022 and 2023), participation in previous experiments (i.e., microhabitat use or web construction under playback; see Table S1), and age were all dropped from the binomial generalized additive model as random effects, as their inclusion did not significantly improve model fit. The final model included frequency as a smoothed term varying by rural/urban. Although this model explained little of the variance ($R^2 = 0.009$), the inclusion of the smoothed term significantly improved the model fit compared with the (null) model with rural/urban removed ($F = 2.578$, $p = 0.015$, $\Delta AIC = 6.124$). This suggests that the shape of the relationship between frequency and attack likelihood might differ between rural and urban spiders.

However, rural (Figure 2, $edf = 3.012$, $X^2 = 8.422$, $p = 0.072$) and urban (Figure 2, $edf = 2.545$, $X^2 = 3.744$, $p = 0.202$) spiders attacked all frequencies (100–1,000 Hz) with approximately equal probability, suggesting that spiders do not rely on a specific vibratory frequency range for prey detection but instead attack broadly across the range of noise. When we controlled for habituation (see Figure S1A) by testing only responses to the first frequency, we

found similar results (Figure S1B; rural: $edf = 1.236$, $X^2 = 0.127$, $p = 0.911$; urban: $edf = 1.956$, $X^2 = 3.693$, $p = 0.208$). Rural and urban spiders did not differ in average attack likelihood (Figure 2, $df = 1204$, $T\text{-ratio} = 0.505$, $p = 0.6133$).

Noise effects on web vibration transmission

To test whether vibrations travel differently across webs built by rural and urban spiders under different vibratory noise treatments, we exposed rural and urban adult female *A. pennsylvanica* to quiet or loud vibratory noise playback for 4 days, during which they built new webs. We provided white-noise (<1 kHz) vibrations that differed in amplitude (signal-to-noise ratio 0–1,000 Hz; quiet = 4.20 ± 0.23 dB, loud = 31.96 ± 0.32 dB) similar to differences recorded in the field (~22 dB daily average range).²⁹ Our artificial vibrations were coupled to the web-building substrate (Figure S2) using a custom-built arena connected to a subwoofer (Figure 3A). After 4 days of noise exposure, we removed the arena from the subwoofer and measured vibratory energy loss (or attenuation/damping) through transmission across the newly constructed web (Figures 3B–3D). We introduced vibrations to the web sheet (Figure 1B) via an artificial vibration stimulus (white noise < 2 kHz from a mini shaker) and measured resultant vibrations with a laser vibrometer at the spider's typical foraging position (the "retreat", or narrow, tubular web section, see Figure 1B). We measured transverse wave transmission because prey impact is typically perpendicular to the web plane.³⁰ Our spider groups (rural/quiet, rural/loud, urban/quiet, and urban/loud) did not differ in days since maturation ($F_{3,56} = 0.425$, $p = 0.736$) or body condition ($F_{3,56} = 0.551$, $p = 0.650$). We tested 15 webs built by separate spiders (each constructing a single web) for each unique rural/urban, quiet/loud combination (i.e., a total of 60 independent webs).

Short-distance vibration transmission

To measure how vibrations produced close to a foraging spider transmit, we applied the vibration stimulus at three different positions 3.5 cm from the opening of the web retreat, where the spider forages (Figure 1B, the position of all recordings). We ran three trials at each of the three positions and averaged across trials and positions (transmission was similar between positions; Figure S4). The generalized additive model testing the variation in energy loss across frequencies by the unique site/treatment groups (rural/quiet, rural/loud, urban/quiet, and urban/loud) explained much of the variance ($R^2 = 0.748$) and was a significantly better fit than the (null) model with the groups removed ($F = 1665$, $p < 0.001$, $\Delta AIC = 29,930.8$). These results suggest that the shape of the relationship between frequency and energy loss differs between site/treatment groups.

To test for site/treatment-specific variation in vibratory stimulus energy loss, we explored patterns of energy loss in two distinct frequency ranges: (1) below 1,000 Hz (overlapping known noise frequencies) and (2) above 1,000 Hz (outside the range of known noise). Differences among all site/treatment groups were assessed through pairwise comparisons. Significant differences were further examined for non-overlapping 95% confidence intervals, allowing us to evaluate how each group compared with others within these frequency ranges (Table 1; Figure 4A). Below 1,000 Hz, transmission of webs built by urban, but not rural, spiders differed by the treatment conditions (quiet versus loud web construction) (Table 1; Figure 4A). For short-distance vibrations, urban/loud webs lost more energy,

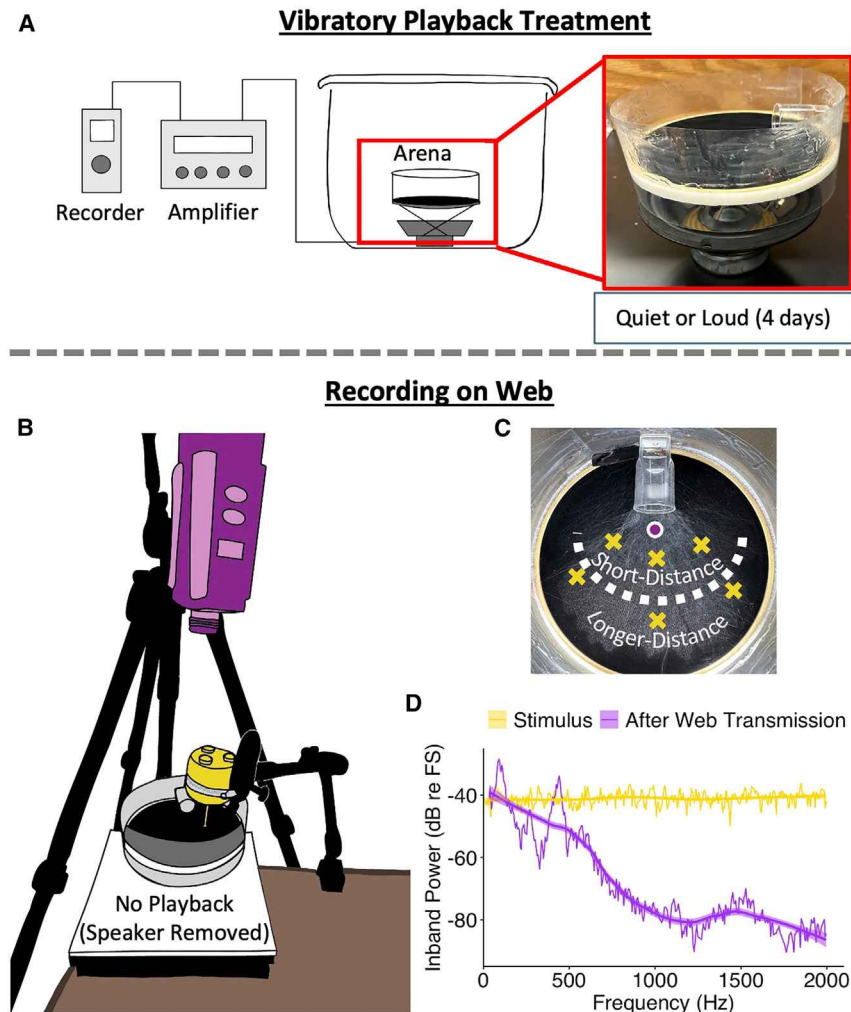


Figure 3. Experimental setup of web vibration transmission

(A and B) (A) We placed 60 adult female rural and urban *A. pennsylvanica* under quiet or loud vibratory playback treatments (see Figure S2) produced by a speaker in a custom-made arena (15 spiders per site/treatment group). During four nights of web construction, vibrations were introduced to the web directly via anchor, or attachment, points (Figure S7), and indirectly through airborne sound produced by the speakers. After four nights of web construction under playback treatments, (B) we removed the speaker and used a laser vibrometer (purple) to record resultant vibrations at the opening of the web retreat from controlled white-noise vibrations produced by a mini shaker (yellow, stimulus) elsewhere on the web.

(C) Although the laser vibrometer recorded from the same position on each web, we provided the stimulus at six positions on the web: three short distances from the stimulus to the retreat and three longer distances.

(D) The shaker produced vibrations adjusted to have equal vibration amplitudes from 0.5 to 2,000 Hz. The graph represents the amplitude (as inband power in decibels relative to the full scale, dB re FS) of a recording directly from the mini shaker (yellow, stimulus) and a trial recorded from the retreat after transmission through the web (purple) analyzed in 5.38-Hz bins. We calculated the energy lost as the vibrations traveled from the stimulus to the retreat (see Figure S3 for calculations). The raw data are shown along with the line and error ribbon representing the fit and 95% confidence interval of a loess model.

or attenuated/damped, between about 300 and 1,000 Hz compared with other webs (see urban/loud; Table 1; Figure 4A). This increased energy loss close to the foraging position may function to decrease the perception of environmental noise in this frequency range. Urban/quiet webs also damped vibrations in comparison with any rural web, particularly in the range of 300–600 Hz (Table 1). Above 1,000 Hz, short-range web vibrations only differed between urban/loud and rural/quiet—urban/loud were damped compared with rural/quiet (Table 1; Figure 4A).

Longer-distance vibration transmission

We also applied vibratory stimuli at three different positions 7 cm from the opening of the web retreat (Figure 1B). Again, the generalized additive model assessing attenuation across frequencies for the site/treatment groups explained a considerable amount of the variance ($R^2 = 0.753$) and was a better fit than the (null) model with the groups removed ($F = 1656.9$, $p < 0.001$, $\Delta AIC = 29,500.7$). Above 1,000 Hz, webs built by urban/loud spiders were damped in comparison with any rural web (Table 1; Figure 4B). At longer transmission distances, below 1,000 Hz, urban spider webs transmitted vibrations similarly between treatments (Table 1; Figure 4B), in contrast to their previously described apparent damping of 300–1,000-Hz short-range vibrations.

webs built by all other groups (see rural/loud; Table 1; Figure 4B). Within each site/treatment group, we also found that longer-distance vibrations lost more energy than short-distance vibrations across the entire measured frequency spectrum (Figure S5).

Following vibration transmission tests, for each web we recorded the wet mass of the total silk used and the dry mass following 48 h in a 50°C drying oven. Neither rural/urban, the noise treatment, nor their interaction significantly predicted the dry silk mass used per spider body mass, nor did rural/urban predict the percent silk moisture (Figure S6). However, there was a non-significant trend wherein webs built under loud conditions had higher moisture in their silk than webs built under quiet conditions, but this was driven primarily by an increase in silk moisture for rural/loud versus rural/quiet webs (Figure S6B).

DISCUSSION

Our study provides evidence of significant flexibility in information acquisition from an external sensory structure—spider webs—in response to environmental noise: flexibility that is dependent on the spider's collection location (rural/urban). We have shown previously that natural vibratory noise predominantly occurs at frequencies below 1,000 Hz for *A. pennsylvanica*,²⁹ which may

Table 1. Results from comparing average energy loss between site/treatment groups

Transmission distance	Above or below 1,000 Hz	More energy lost (damped)	More energy retained (amplified)	Non-overlapping frequency range (Hz)	Statistics
Short range	below	urban/loud	rural/quiet	100–1,000	$df = 10854$, $T\text{-ratio} = 8.835$, $p < 0.001^*$
		urban/loud	rural/loud	250–1,000	$df = 10854$, $T\text{-ratio} = 10.479$, $p < 0.001^*$
		urban/loud	urban/quiet	300–1,000	$df = 10854$, $T\text{-ratio} = 5.863$, $p < 0.001^*$
		urban/quiet	rural/quiet	100–700	$df = 10854$, $T\text{-ratio} = 2.983$, $p = 0.015^*$
		urban/quiet	rural/loud	300–600	$df = 10854$, $T\text{-ratio} = 4.624$, $p < 0.001^*$
		rural/quiet	rural/loud	N/A	$df = 10854$, $T\text{-ratio} = 1.635$, $p = 0.359$
	above	urban/loud	rural/quiet	1,000–1,100, 1,500–1,700	$df = 10809$, $T\text{-ratio} = 3.301$, $p = 0.005^*$
		urban/loud	rural/loud	N/A	$df = 10809$, $T\text{-ratio} = 1.526$, $p = 0.422$
		urban/loud	urban/quiet	N/A	$df = 10809$, $T\text{-ratio} = 1.667$, $p = 0.341$
		urban/quiet	rural/quiet	N/A	$df = 10809$, $T\text{-ratio} = 1.647$, $p = 0.352$
		urban/quiet	rural/loud	N/A	$df = 10809$, $T\text{-ratio} = 0.115$, $p = 0.999$
		rural/quiet	rural/loud	N/A	$df = 10809$, $T\text{-ratio} = 1.736$, $p = 0.305$
Longer range	below	rural/quiet	rural/loud	300–600	$df = 10488$, $T\text{-ratio} = 4.167$, $p < 0.001^*$
		urban/quiet	rural/loud	250–700	$df = 10488$, $T\text{-ratio} = 4.743$, $p < 0.001^*$
		urban/loud	rural/loud	350–900	$df = 10488$, $T\text{-ratio} = 5.901$, $p < 0.001^*$
		urban/quiet	rural/quiet	N/A	$df = 10488$, $T\text{-ratio} = 0.577$, $p = 0.939$
		urban/loud	rural/quiet	N/A	$df = 10488$, $T\text{-ratio} = 1.735$, $p = 0.306$
		urban/loud	urban/quiet	N/A	$df = 10488$, $T\text{-ratio} = 1.157$, $p = 0.654$
	above	urban/loud	rural/quiet	1,450–1,650	$df = 10546$, $T\text{-ratio} = 2.948$, $p = 0.017^*$
		urban/loud	rural/loud	1,350–1,600	$df = 10546$, $T\text{-ratio} = 3.347$, $p = 0.005^*$
		urban/loud	urban/quiet	N/A	$df = 10546$, $T\text{-ratio} = 1.261$, $p = 0.588$
		urban/quiet	rural/quiet	N/A	$df = 10546$, $T\text{-ratio} = 1.711$, $p = 0.318$
		urban/loud	rural/loud	N/A	$df = 10546$, $T\text{-ratio} = 2.103$, $p = 0.152$
		rural/quiet	rural/loud	N/A	$df = 10546$, $T\text{-ratio} = 0.374$, $p = 0.982$

We used pairwise comparisons of estimated marginal means from the generalized additive model to compare average energy loss below 1,000 Hz (overlapping noise) and above 1,000 Hz (outside of noise range) between site/treatment groups. Frequency ranges where significantly differing pairs were distinct are the approximate ranges where 95% confidence intervals did not overlap. Placement of site/treatment group into energy lost/retained designation is ambiguous for non-significant pairs.

Significant differences ($p < 0.05$) are indicated with an asterisk.

pose a significant challenge to the reception of cues or signals produced by prey and mates. In this study, we first demonstrate that *A. pennsylvanica* exhibits predatory behavior across the entire spectrum of natural vibratory noise frequencies, confirming the relevance of this frequency range for their sensory ecology. Next, we provide empirical evidence suggesting that the spider's exposure to environmental noise—both previous/ancestral exposure to noise in their natural habitat (rural versus urban) and their recent experience with noise during web construction (quiet versus loud playbacks)—influences how vibration frequencies transmit across their web's surface. When constructed under loud conditions, webs of rural and urban spiders exhibited distinct differences in web vibration transmission in three key ways: (1) the breadth of the frequency range modified (narrow in rural/broad in urban), (2) whether energy was retained (rural) or lost (urban), and (3) the transmission distance affected (short in urban/longer in rural). Rural/loud webs *retained more energy* (amplified) in a *narrow* frequency range (350–600 Hz) compared with all other groups (rural/quiet, urban/quiet, and urban/loud) during *longer-distance* transmission. On the other hand, urban/loud webs *lost more energy* (attenuated and/or damped) in a *broad* frequency range

(300–1,000 Hz) compared with all other site/treatment groups when vibration stimuli were produced *closer* to the retreat. Interestingly, the frequency ranges of modified transmission aligned with the simulated noise frequencies produced by our experimental playback (Figure S2). These contrasting patterns between rural/loud and urban/loud treatments may help spiders balance prey detection and manage environmental noise, and this balancing act is dependent on the spider's collection site (rural/urban). Notably, it is also possible that rural/urban spiders are genetically distinct, in which case different responses to noise may not reflect developmental experience per se but may be genetically linked. Regardless of the reasons for the differences (developmental experience or genetic differences), the webs built by rural versus urban spiders under loud conditions showed clear distinctions in their transmission properties.

Environmental noise can mask vital sensory information when both overlap in the same spectral frequencies. Because natural vibratory noise in the habitats of *A. pennsylvanica* occurs below 1,000 Hz,²⁹ we tested the predatory responses of rural and urban spiders within this range. Both groups broadly responded to pure tone vibrations across frequencies that align with vibrations

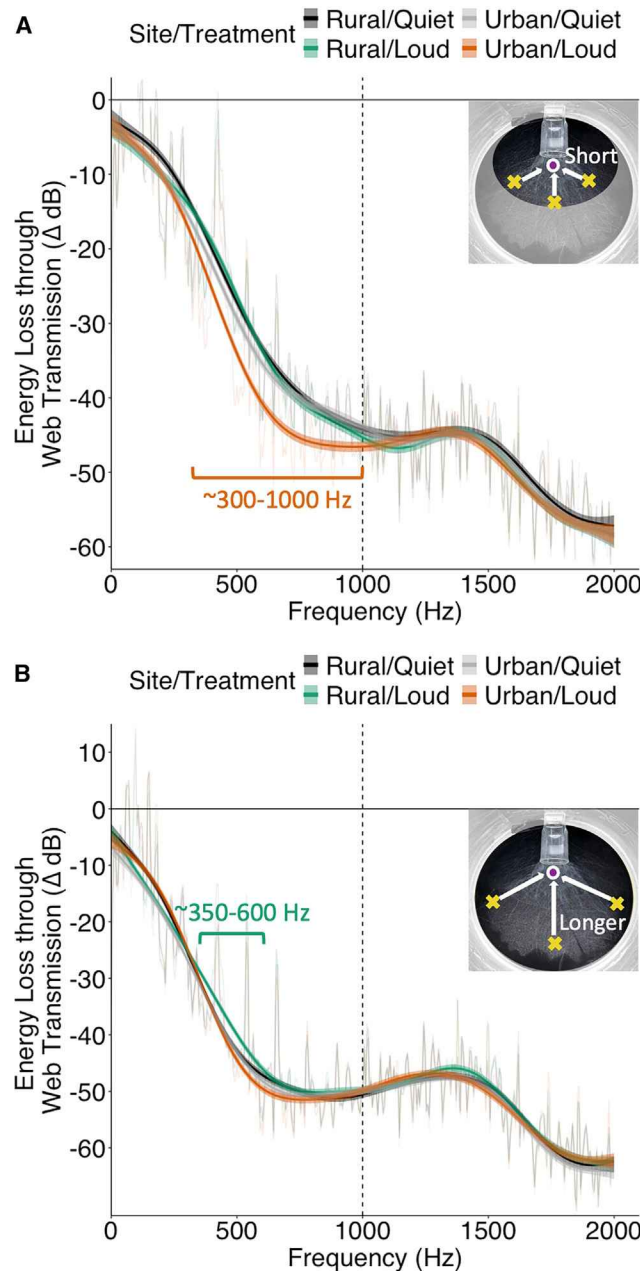


Figure 4. Results from the web vibration transmission experiment

We showed how vibrations propagated across the web's surface from the stimulus to the web retreat over (A) short distances and (B) longer distances. We measured the energy loss, or attenuation, of stimulus vibrations ($<2,000$ Hz) as they traveled across webs of rural and urban spiders constructed for four nights under quiet or loud vibratory noise treatments (15 webs each). Background lines are the calculated means across webs for each group, whereas lines and error ribbons show generalized additive model predictions with 95% confidence intervals. For each web, we averaged across trials and stimulus positions (see Figure S3 for calculations) for each transmission distance (9 trials each) because transmission was similar across positions (Figure S4). The dashed line at 1,000 Hz separates frequencies overlapping with field-recorded and playback treatment vibratory noise (<1 kHz) from those outside it (>1 kHz). We performed pairwise comparisons of the site/treatment groups using the estimated marginal means of energy loss below and above 1 kHz (Table 1) and then used non-overlapping 95% confidence

intervals to determine the specific frequency ranges where site/treatment pairs differed. Above 1,000 Hz, only urban/loud webs exhibited damping compared with rural webs (only rural/quiet at short range). (A) Short-distance vibrations on urban/loud webs lost more energy (attenuated/damped) across a broad frequency range (300–1,000 Hz) compared with all other groups. (B) Rural webs constructed under loud noise retained more energy (amplified) in longer-distance vibrations in a narrow frequency range (350–600 Hz) compared with all other groups. Longer-distance vibrations always lost more energy than short-distance vibrations (Figure S5).

produced by a struggling juvenile cricket (~ 250 –700 Hz, personal observation) and prey more generally.^{31,32} Thus, elevated noise levels within this frequency range are likely to mask important information. Given the temporal and spatial variability of rural and urban noise levels,²⁹ spiders in more variable habitats may generalize their attention to a wider frequency range to cope with challenges from information masking. Our findings of frequency-independent attacks support the idea that variable noise conditions may favor generalized responses to vibratory information, conforming to prior studies of other animals that demonstrate generalist strategies that allow foragers to be flexible in rapidly changing conditions,³³ particularly in urban areas (e.g., in moths³⁴ and in birds³⁵). Finally, the frequencies that initiated attacks in our first experiment coincided with frequency-specific modifications of rural/urban web vibration transmission under loud noise, suggesting a predatory advantage of enhancing salient cues amid environmental noise. We note that there were limited differences in energy loss outside the range of noise ($>1,000$ Hz, Figure 4; Table 1).

In general, signals and cues produced further (versus closer) from the foraging spider are more likely to be masked by noise because vibratory information loses more energy as transmission distance increases. Despite this, vibrations that traveled longer distances on rural/loud webs arrived at the spider's foraging retreat with more energy in a narrow, but extremely relevant, frequency range than other site/treatment groups at this distance, effectively amplifying and retaining high transmission efficacy of the pertinent information. This frequency-specific change to the transmission of vibratory stimuli presumably increases the spider's capacity for detecting relevant signals/cues under noisy conditions. Similar tuning has been demonstrated in the internal sensory systems of spiders, as electrophysiological recordings from an important vibration receptor on spider legs (the metatarsal lyriform organ) have exhibited heightened sensitivities to frequencies consistent with prey vibrations (increasing sensitivity up to 1,000 Hz)³⁶ and potentially to predator cues (up to 5,000 Hz).³⁷ Our results support the idea that webs act as extensions of the spider's sensory system³⁸ and can be adaptively tuned.

If the narrow range of energy retention observed in rural/loud webs is highly relevant for prey capture, one might ask why we did not see more attacks of rural spiders to this frequency range. Though there was a trend in this direction (Figure 2), there was also more than 30% of spiders that did not attack. It is likely that additional cues (e.g., visual) may be important in initiating attacks, and future work should explore attack probabilities of natural prey at higher resolution to get a finer-scale understanding of the relationship between vibratory cues and attack probabilities. Finally, we note that vibratory conspecific communication also

intervals to determine the specific frequency ranges where site/treatment pairs differed. Above 1,000 Hz, only urban/loud webs exhibited damping compared with rural webs (only rural/quiet at short range). (A) Short-distance vibrations on urban/loud webs lost more energy (attenuated/damped) across a broad frequency range (300–1,000 Hz) compared with all other groups. (B) Rural webs constructed under loud noise retained more energy (amplified) in longer-distance vibrations in a narrow frequency range (350–600 Hz) compared with all other groups. Longer-distance vibrations always lost more energy than short-distance vibrations (Figure S5).

occurs during courtship (~100–600 Hz, personal observation), raising the possibility that manipulations of web vibratory transmission may function in more than just prey detection and foraging.

Unlike rural environments that have lower and less-predictable noise levels, spiders in urban environments experience chronic exposure to heightened levels of vibratory noise.^{29,39} Such persistent, louder noise could lead to sensitivity impairments over time. Age-related hearing loss has only recently been examined for arthropods,^{40,41} and noise-related hearing loss has only been explored in the tympanal ear of the desert locust.⁴² We hypothesize that long-term exposure to noise might negatively impact arthropod hearing and that urban spiders use their webs to mitigate environmental sensory overload by reducing broad-band noise. Support for this hypothesis is evidenced by the dramatic and broad reduction in energy transmitted (and thus, signal-to-noise ratio), specifically within the documented range of urban noise across urban webs built under loud conditions. In further support, noise-dependent web damping only occurred for vibrations produced near the spider's retreat, suggesting that the urban spider produced a buffer zone immediately around its foraging position. Although a close buffer zone may reduce persistent broad-band noise, it may simultaneously reduce the signal-to-noise ratio, making it more challenging for urban spiders to react to prey at close distances. Future foraging studies can explore such potential sensory trade-offs as well as putative foraging strategies to overcome them (e.g., urban spiders may focus foraging reactions on longer-distance stimuli).

Although we did not observe the same vibratory damping (300–1,000 Hz) in longer-distance vibrations as seen in short-distance, longer-distance vibrations in urban/loud webs did show greater energy loss than short-distance vibrations. We suspect that distinct transmission properties across different regions of a single web—i.e., near the retreat versus at the edges—may account for discrepancies across distances. In addition, the observed damping of vibrations between 300 and 1,000 Hz near the retreat of urban/loud webs may serve to reduce vibrations from airborne noise introduced near the foraging spider. Although vibratory noise is likely introduced to the web via the anchor points connecting it to the substrate, airborne noise can also transfer vibrations directly to any part of the web.⁴³ Our playback treatments during web construction produced different levels of airborne noise (quiet = 56.78 ± 1.40 dB, loud = 67.80 ± 1.06 dB) that resembled natural levels in rural and urban habitats (60.7–74.3 dB).⁴⁴ Additional studies exploring spatial patterns of frequency transmission paired with behavioral studies are now needed to assess where and how transmission differences translate into foraging (or mating) efficiency, as well as how airborne and substrate-borne noise interact and propagate as vibrations on the web.

We also acknowledge that interpreting the biological significance of our artificial stimulus is challenging, as the introduced vibrations could be viewed either as noise traveling through the web or as relevant signals and cues. The difficulty arises because observed energy loss could reflect a reduction in both noise and relevant signals, whereas, ideally, webs would function to increase the signal-to-noise ratio, characterized by noise reduction and signal amplification. Future empirical playback studies and theoretical models should test how noise and

relevant signals/cues interact as they transmit simultaneously across webs with different transmission properties.

The extent to which previous experience with noise shapes real-time plastic behavioral responses is understudied, particularly in arthropods. Evidence from Lampe et al.⁴⁵ suggests a role for developmental plasticity in response to noise, as grasshoppers exhibited adjustments to adult signal frequency (Hz) based on noise exposure during development. Further, there is likely a complex interplay between previous experience with noise and plastic responses to current noise conditions⁴⁶ because variable noise environments tend to persist into adulthood. In our study, we could not distinguish between developmental plasticity, maternal effects, and/or genetic differentiation as underlying the observed differences between rural and urban spiders. Although gene flow between rural and urban populations is likely due to the ballooning dispersal mode⁴⁷ of *A. pennsylvanica* (personal observation), genetic differentiation or maternal effects may still be at play. To further elucidate these potential mechanisms, future research should rear F2 generations of rural and urban spiders in quiet or loud vibratory treatments.

We identified potential material or structural differences that may underlie the differential propagation of vibratory information, though further investigation is necessary to explore these and other mechanisms in detail. Variations in silk stiffness (modulus) and tension (pre-stress) affect the amplitude- and frequency-filtering capacities of webs.^{25,48} Factors such as the silk length,⁴⁹ connectivity of strands,³¹ mesh size,⁵⁰ and number of attachments with the substrate⁵¹ contribute to the web's structure and distinct vibratory transmission properties. For example, Gomes et al. found a correlation between *Larinioides patagiatus* web structure and environmental noise in the field, but suggest that prey abundance may mediate this effect.⁵² However, a previous laboratory study on *Araneus diadematus* found no adjustments to web geometry when anchor points were attached to moving substrates,⁵³ suggesting that this ability may be species-specific or that the silk properties, rather than web geometry, may potentially drive web transmission differences. Although we found no differences in dry silk mass (Figure S6A), webs constructed under loud conditions showed a trend toward higher silk moisture than those built under quiet conditions (Figure S6B), though this was largely driven by increased silk moisture for rural/loud versus rural/quiet webs. This may suggest a potential role of supercontraction—a unique property of spider silk where added moisture leads silk to shrink up to 50%,²⁵—though whether spiders have control over silk supercontraction is unknown. Anecdotally, we also observed that webs built under loud conditions often had larger anchor points (i.e., places where the web attached to the substrate; Figure S7), which appeared to more strongly resist detachment during silk collection. Although quantifying these anchor point characteristics was not feasible for the present study, we hypothesize that thicker, stronger anchor points may damp substrate-borne noise before it is introduced to the web's surface by influencing the web's geometry or silk properties, such as tension and stiffness. Future experiments are necessary to directly assess the functional significance of these observed differences in anchor points.

This study has unveiled the extraordinary potential of web-building spiders to create a structure, the web, which can alter the spider's perception of information when environmental noise

is present. Our findings demonstrate that the web functions as a pre-processor or filter of information before perception by the spider. Our results provide empirical support for Miller and Mortimer's hypothesis⁵⁴ that spiders exhibit morphological computation by manipulating the vibratory environment of their webs to preemptively mitigate the effects of noise before information reaches the central nervous system (CNS). If webs can pre-process information, they may alleviate the processing demands when noise masks or overwhelms the system.⁵⁵ For a complete understanding of how animals may, or may not, cope with environmental noise, we must include how information is received and processed, an angle that is too often overlooked. The accurate reception of information is necessary for survival and reproduction, facilitating precise identification, evaluation, and localization of prey, threats, and mates. To date, only a few systems have been explored with respect to how animals might manipulate their sensory environment for increased information acquisition. The ground burrows of *Eupsophus* frogs can amplify incoming (in addition to outgoing) signals and cues from other frogs and nocturnal owls; however, it is unclear whether these amplifications are intentional or a by-product of using the burrow as a refuge.⁵⁶ Similarly, cavity-nesting black-capped chickadees excavate tree-cavity nests in the direction of extra-pair partners to improve signal detection during the dawn chorus.⁵⁷

We unveil the first evidence that a spider that relies on its self-made web for vibratory information acquisition can control its vibration transmission in response to differing levels of vibratory noise. The plastic changes in this extended phenotype highlight inter-individual variation in the receiver's ability to cope with biologically relevant noise. Moreover, a history of noise exposure, either during development or across generations, appears to further influence noise-related web modifications. With the rise of intense and rapid changes to animals' sensory landscapes brought on by anthropogenic noise, we advocate for future research to adopt a more holistic approach that is inclusive of information reception, hidden sensory channels like the vibratory channel, and previous exposure. We anticipate that this research will open doors for further investigation into the flexibility of receivers' sensory systems.

RESOURCE AVAILABILITY

Lead contact

Further information requests should be directed to and will be fulfilled by the lead contact, Brandi Pessman (bjpessman@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data are accessible at https://github.com/brandipessman/vibration_transmission.
- All code used in this study are archived on Zenodo (<https://doi.org/10.5281/zenodo.14866876>).
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact, Brandi Pessman (bjpessman@gmail.com), upon request.

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AUTHOR CONTRIBUTIONS

B.J.P. and E.A.H. conceptualized and designed the study. B.J.P. performed the experiments and conducted data analysis under the supervision of E.A.H. Both authors contributed to the writing and editing of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw and analyzed data	This paper	GitHub: https://github.com/brandipessman/Vibration_Transmission ; Zenodo: https://doi.org/10.5281/zenodo.14866876
Experimental models: Organisms/strains		
<i>Agelenopsis pennsylvanica</i>	Field-caught; Lancaster County, Nebraska	Stored in collections at the University of Nebraska-Lincoln
Software and algorithms		
ImageJ	Abrámoff et al. ⁵⁸	https://imagej.net/ij/
Raven Pro	K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology ⁵⁹	https://www.ravensoundsoftware.com/
Audacity	Audacity Team ⁶⁰	https://www.audacityteam.org/
R	R Core Team ⁶¹	https://www.R-project.org/
RStudio	RStudio Team ⁶²	https://www.rstudio.com/
R package 'mgcv'	Wood ⁶³	https://cran.r-project.org/package=mgcv
R package 'car'	Fox and Weisberg ⁶⁴	https://CRAN.R-project.org/package=car
R package 'flextable'	Gohel and Skintzos ⁶⁵	https://cran.r-project.org/package=flextable
R package 'tidyverse'	Wickham et al. ⁶⁶	https://CRAN.R-project.org/package=tidyverse
R package 'emmeans'	Lenth ⁶⁷	https://CRAN.R-project.org/package=emmeans
Calibration of the Interface	Michael et al. ⁶⁸	https://doi.org/10.1007/978-1-4939-9458-8_15
Signal-to-Noise Ratio Calculations	Ringler et al. ⁶⁹	https://doi.org/10.1007/s00265-017-2340-2

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

We collected data for these experiments across two years: 2022 and 2023. In 2022, we collected 129 juvenile female *Agelenopsis pennsylvanica* in their penultimate instar from four sites – two rural (Figure 1A; 32 from R1 and 33 from R2) and two urban (Figure 1A; 39 from U1 and 25 from U2) August 4–10. In 2023, we collected 60 juvenile female *A. pennsylvanica* in their penultimate instar from one rural and one urban site (30 each, R1 and U1) August 1–3. In both years, we housed spiders individually in 8.3 x 8.3 x 8.3 cm opaque containers suspended over a tub of water with chicken wire mesh to receive ad libitum water through a cotton wick provided through a hole in the bottom of the container. We fed the spiders two 1/8-inch crickets twice a week and checked for molts every other day. The room maintained a temperature of 25°C with a 12:12 hour light:dark cycle starting at 07:00. Spiders matured between mid-August and early-September.

METHOD DETAILS

Spiders' Responses to Pure Tone Frequencies

To determine what range of frequencies within known environmental noise (< 1 kHz)²⁹ are relevant to *A. pennsylvanica* foraging, we measured spiders' responses to pure tone frequencies below 1000 Hz. We used a 10-mm Linear Resonant Actuator (LRA) to deliver pure tone vibrations onto each web through contact with the web's surface (Figure 1C). We produced pure tone frequencies in Audacity⁶⁰ (v. 3.4.0) for 100 to 1000 Hz in 100 Hz increments. When generating the tones, we set the amplitude (with options 0 for silence to 1 for maximum amplitude without clipping) for each frequency to 0.5 except for 100 Hz, which we set with an amplitude of 1. We did this because 100 Hz vibrated at quieter amplitudes than the other frequencies as measured by a Polytec Portable Digital Vibrometer (Model 100), and we wanted all frequencies to vibrate at the same amplitude. To calibrate the relative amplitudes of the input (vibrometer) and output (LRA) through our audio interface (MixPre-6), we calibrated the interface input gain (20 dB with an output volume of 90) using an analog oscilloscope (Hameg Instruments, Model: HM303-6) and determined a particle velocity of 1.5 mm/s at 500 Hz following the methods of Michael et al.⁶⁸ We did not filter the playback because the peak frequencies from these tests matched the intended frequencies.

We produced ten playback files where the 15-second pure tone frequencies were in a different random order in each file and separated by 60 seconds of silence (Figure 1D). We randomly selected from 10 uniquely ordered playback files for each spider but ensured

equal distribution of the ten files between groups. Each of the 10 playback files began with a unique frequency of the 10 possible frequencies, allowing us to perform an additional test of the responses to only the first frequency to control for habituation (see [Figure S1](#)). As spiders typically built and rested in a retreat in a corner of the square container, we lowered the LRA to just touch the web surface between the center of the web and the opposite corner of the container, about 7 cm from the spider. The same observer ran all trials to ensure equal forces were applied to each web at the point of contact with the LRA. We observed whether each spider attacked the LRA (defined as making contact with the LRA) within the time that the pure tone played on the web. For analysis, we included only the spiders that attacked at least one of the ten pure tone frequencies, which brought our sample size to 45 rural spiders in 2022 (out of 65), 41 urban spiders in 2022 (out of 64), 13 rural spiders in 2023 (out of 30), and 22 urban spiders in 2023 (out of 30). Many spiders participated in these trials after participating in an additional playback study (see [Table S1](#) about participation in previous experiments). The observer was blind to the spider's collection site and any previous participation in experiments ([Table S1](#)).

Noise Effects on Web Vibration Transmission

We wanted to test whether vibrations travel differently across webs built by rural and urban *A. pennsylvanica* under distinct vibratory noise treatments. We used the 60 female *A. pennsylvanica* spiders collected in 2023 and conducted this experiment before testing their response to different pure tone frequencies described above.

Vibratory Playback Treatments During Four Nights of Web Construction

We randomly assigned adult rural and urban spiders to construct webs under one of two vibratory playback treatments: quiet or loud. To provide a controlled vibratory environment, we crafted an arena ([Figure 3A](#)) using an 8-inch diameter subwoofer (Skar Audio, Model: FSX8-8) with the cone removed to eliminate disturbance in the near-field.⁷⁰ We connected an 8-inch diameter embroidering loop to the speaker using a wooden skewer scaffold, secured by mounting putty and hot glue ([Figure 3A](#)). To provide a substrate for the spider to construct its web and allow an observer to easily view and photograph the web, we cut black photography velvet to fit tightly in the embroidering loop. Arenas were housed in 18-gallon plastic, opaque storage bins with holes cut in the lid for light to enter and to reduce visual and acoustic disturbance. The tubs also rested on acoustic foam to reduce vibratory disturbances. We connected the speaker to a four-channel stereo microamp (Behringer, Model HA400) with a custom double alligator clip-to-3.5 mm stereo cable ([Figure 3A](#)). The microamp was connected to a digital recorder (Tascam TEAC Corporation, Model DR-05X) which played low-frequency white noise as vibrations through the speaker. We built six arenas in total to simultaneously run six trials at a time.

For the vibratory playback file, we created the white noise in Audacity⁶⁰ (v. 3.4.0) using a low pass filter with a cutoff of 1000 Hz and a 6 dB per octave roll-off to mimic ambient vibratory noise in the field, which was concentrated below 1000 Hz.²⁹ The microamp had 10 amplitude settings, which could be individually adjusted for each of the four channels. We used settings 1 (quiet treatment) and 8 (loud treatment) to produce vibrations at the center of the black velvet (signal-to-noise ratio 0–1000 Hz; quiet = 4.20 ± 0.23 dB, loud = 31.96 ± 0.32 dB) that varied similarly to field recordings of rural and urban sites by amplitude (~ 22 dB daily average range)²⁹ and shape of frequency profiles ([Figure S2](#)). We note that the lab playback was recorded using a laser vibrometer, while field recordings were collected using a contact microphone,²⁹ so comparisons of amplitudes (apart from range comparisons) between the field and lab recordings are not possible. We also measured airborne sound levels at the center of the arena using a handheld sound level meter (Cadrim; frequency range: 31.5–4000 Hz; resolution: 0.1 dB).

Mature female *A. pennsylvanica* constructed webs under either quiet or loud conditions for four consecutive nights between September 5 and October 17, 2023. We chose four days as we observed a plateau in silk addition around the fourth day, though *Agelenopsis* spiders continue adding silk beyond the fourth day. Future research should therefore examine web transmission across different days of web construction. For each unique combination of rural/urban and treatment (rural/quiet; rural/loud; urban/quiet; urban/loud), our sample size was 15 webs built by different females. We randomly assigned each spider to one of the six arenas and ensured an even distribution of site/treatment groups across the six arenas. The temperature and light cycle during playback were similar to the previously mentioned lab conditions. Spiders were not fed or provided water during these four days but were fed two 1/8-inch crickets within 24 hours of their introduction to the arena. Since age influenced how this species used a microhabitat that varied in vibratory noise levels in a previous study,²⁹ we reduced variation in spider age as much as possible. We weighed and photographed spiders with a size standard prior to their introduction to the playback. With these photographs, we measured the spider's body condition⁷¹ by calculating the residuals of the linear relationship between the log-transformed body mass and cephalothorax width measured in ImageJ.⁵⁸ We added the spider to the arena in a collection vial ([Figure 3](#), fastened in place using Velcro) to encourage retreat construction in the vial. We wrapped the embroidering loop with a six-cm-high six-mil mylar using Velcro to prevent escape and coated the mylar in Vaseline to prevent silk attachment to the mylar. We covered the top with cling wrap to further prevent escape. At the end of each trial, the velvet was replaced with new, and the collection vial was washed with dish soap.

Measuring Web Vibration Transmission

Immediately following four nights of web construction, we removed the speaker from the arena and rested the arena on a granite slab that sat on top of two squares of acoustic foam ([Figure 3B](#)). In doing so, no vibratory playback occurred during recording, and ambient vibrations were damped as much as possible. We attached a laser vibrometer (Polytec PDV-100) to a tripod, each leg of which also rested on granite and acoustic foam. We set the laser vibrometer to record from the opening of the retreat, as that is the spider's typical foraging position where it rests its legs to receive incoming vibratory information from the web sheet. We recorded from a small (2 mm x 2 mm) piece of white copier paper that we rested on the web using a low-pass of 22 kHz, no high-pass, and a

velocity of 5 mm/s/V. The laser vibrometer had a frequency range from 0.5 to 22 kHz. We recorded from the same location for all trials and for each spider (purple in [Figure 3C](#)).

To produce controlled vibrations on the web (hereafter, stimulus), we used a mini shaker (Brüel & Kjær, Model: 4810) with a #10 32-2 inch round head machine screw. We powered the shaker (without amplification) with a power amplifier (Brüel & Kjær, Model: 2718). The shaker was attached to a moveable arm (Manfrotto, Model 244, with camera bracket and clamp) using a four-inch worm gear clamp. Since *A. pennsylvanica* webs are not sticky, the shaker could be moved to different locations on the web without damaging the web with the head of the screw resting on the web surface ([Figure 3B](#)). We created the stimulus file by first producing a file of white noise between 0 and 2000 Hz. We chose this range because the vibratory playback was concentrated below 1000 Hz, and we wanted to know whether vibratory frequencies above the range of noise differed in transmission between groups. We then calibrated the surface of the shaker's tip to vibrate all frequencies 0.5–2000 Hz at approximately equal amplitude ([Figure 3D](#)) using an analog oscilloscope (Hameg Instruments, Model: HM303-6) and MixPre-6 interface, following the methodology of Michael et al.⁶⁸ The input gain of the MixPre-6 interface was calibrated to 28 dB and the output volume was set to 100. We determined that the particle velocity of the surface of the shaker was 2.2 mm/s at 300 Hz.

We produced a one-second stimulus of calibrated and filtered white noise at six different positions on each web, thus varying the distance that vibrations traveled to the retreat: three close (3.5 cm) to the retreat (hereafter short-distance transmission) and three far (7 cm) from the retreat (hereafter longer-distance transmission) ([Figure 3C](#)). We repeated the one-second vibratory stimulus three times at each position on the web, repositioning the shaker between each trial. As a result, we measured vibration transmission 18 times on each web (three trials at six positions). Simultaneously with the vibration stimulus from the shaker, we used Audacity⁶⁰ to record the resulting vibrations after transmission across the web with the laser vibrometer. Thus, any recorded deviations (purple line, [Figure 3D](#)) from the frequency profile of the shaker stimulus (yellow line, [Figure 3D](#)), would tell us the energy lost across different frequencies as they traveled across the web. We added one second of silence to the beginning of the stimulus file to record ambient vibrations.

To investigate vibration energy dynamics in a relatively fine-scaled, frequency-dependent manner, we used Raven Pro⁵⁹ (v. 1.6.5) to measure the inband power (FFT length 8192, Hann window, 50% overlap, 0.186 s time resolution, 5.38 Hz frequency grid spacing) in 5.38 Hz bins, because this was the smallest frequency bin size for this time-frequency resolution. We took these measurements from 0 to 2000 Hz (the last bin was 4.02 Hz from 1995.98 to 2000 Hz) for 0.5 seconds of ambient vibrations before the stimulus ('ambient') and during vibrations from the stimulus ('test') ([Figures S3A](#) and [S3B](#)). All recordings were processed as a waveform format with a 16-bit depth and a sampling rate of 44.1 kHz.

To remove background noise (i.e., calculate the signal-to-noise-ratio) for each recording and determine the energy loss relative to the vibrations introduced by the stimulus, we followed the calculations outlined by Ringler et al.,⁶⁹ with additional details provided in [Figure S3](#). The calculations involved converting from the logarithmic (decibel, dB) scale to linear units. To remove any equipment or room noise, we used the 'ambient' and 'test' 0.5-second segments from the same recording to calculate the signal-to-noise ratio of each trial ([Figure S3F](#)). Similarly, we recorded directly from the surface of the stimulus using the vibrometer to measure the energy being introduced to the web at the point of contact and calculated the signal-to-noise ratio from 0.5-second ambient and test segments of this recording ([Figure S3E](#)).

While it would have been ideal to record the stimulus directly at the point of contact for each recording, this was not feasible because the shaker needed to be perpendicular to the web, and the base of the shaker would block the laser. To help account for any slight variation in masses on the web, we averaged the nine trials of short-distance transmission and the nine trials of longer-distance transmission from the retreat of each web because vibration transmission was similar across positions of similar transmission distances ([Figure S4](#)). We computed these averages using the linear scale of the signal-to-noise ratio to avoid the mathematical distortion of averaging logarithmic values. After averaging the linear values, we converted all signal-to-noise values back to the more familiar logarithmic (dB) scale. Last, because the signal-to-noise ratio resulted in a stimulus that lacked a flat response across the frequency range ([Figures 3D](#) and [S3E](#), yellow line) we subtracted the signal-to-noise ratio of the stimulus from each recorded vibration trial at each frequency bin. This new metric measures the energy loss (or attenuation, in dB) of the recorded signal as the vibrations transmitted across the web from the point of production by the stimulus (now, 0 dB energy loss).

Upon removing the arena from the speaker, the spider retreated to the back of the retreat and did not move during the recordings. Preliminary trials where the spider was removed did not show a difference in the frequency profile of the web, suggesting that the spider's mass in this location had negligible effects on the overall vibration dynamics.

QUANTIFICATION AND STATISTICAL ANALYSIS

Spiders' Responses to Pure Tone Frequencies

To test whether rural or urban spiders exhibited differences in the range of frequencies they attacked (a range within known environmental noise that is relevant to *A. pennsylvanica* foraging), we used a binomial generalized additive model (attacked = 1, did not attack = 0) with frequency as a smoothed term varying by rural/urban. In the global model, we included collection site ([Figure 1A](#), R1, R2, U1, or U2), year (2022 or 2023), age, and previous lab treatment experience (none, microhabitat use, quiet, or loud, see [Table S1](#)) as random effects. Although some spiders had prior vibratory experience in previous experiments, we do not believe this influenced the results, as it was dropped from the model for lack of improving model fit (see [results: spider responses to pure tone frequencies](#)). Moreover, all webs in this experiment were constructed under the same ambient lab conditions since our web

transmission experiment shows that webs are significantly impacted by the vibratory conditions during web construction (see [Figure 4](#)). However, further research is needed to understand how the duration of noise exposure and time elapsed since such exposure affects behaviors like foraging. We used a basic dimension (k) of 10, which diagnostic tests suggested was an adequate value. We used backward selection by dropping non-significant terms one-by-one. To determine if the variables in the final model played a meaningful role in explaining spider attack behavior, we tested the final model against the null model using an ANOVA with a Wald Chi-Square statistic and compared the Akaike Information Criterion (AIC) values. We repeated this analysis on the order of frequencies presented (to test for habituation), and responses to the first frequency only (to control for habituation). To test whether overall attack probabilities differed between rural and urban spiders, we used pairwise comparisons of estimated marginal means.

Noise Effects on Web Vibration Transmission

To first test for differences in age and body condition, we performed an ANOVA with a Wald Chi-Square statistic for the interaction between rural/urban and treatment. To look for differences in energy loss of different frequencies as they travel across webs built by rural and urban spiders and under quiet or loud vibratory treatments, we used a generalized additive model (GAM) with a smoothed term across frequencies by unique rural/urban x treatment groups (rural/quiet; rural/loud; urban/quiet; urban/loud). We used a single variable for rural/urban x treatment so that we could test for differences between the four groups, and because GAMs do not handle interactions within smoothed terms. We used a basic dimension (k) of 10 for the smooth term. While increasing k improved model fit due to the noisiness of the raw data, it did not change the results. We performed separate analyses for short-distance versus longer-distance vibration transmission from the stimulus with a sample size of 15 webs per rural/urban x treatment group. To determine if the variables in the final model played a significant role in explaining energy lost during web transmission, we compared this model to the null model (the model lacking any predictor values) using an ANOVA with a Wald Chi-Square statistic and using AIC values. To compare average energy loss between site/treatment groups in relevant frequency ranges, we performed pairwise comparisons of the estimated marginal means from generalized additive models. Specifically, we performed separate analyses for frequencies below 1000 Hz (overlapping with known noise) and above 1000 Hz (outside the range of known noise). For significant pairwise differences (based on Tukey-adjusted P-values), we examined non-overlapping 95% confidence intervals to identify the specific frequency ranges where energy loss varied between pairs.

We also tested the properties of the silk (total silk mass and percent moisture) of the webs built during vibratory noise playback following recording web vibration transmission, and we provided these findings in supplemental material (see [Figure S6](#)).

All statistical analyses and visualizations were performed using R⁶¹ (v. 4.2.2) in RStudio⁶² (v. 2023.09.0+463). We used the mgcv package⁶³ to perform generalized additive models, the emmeans package⁶⁷ to perform pairwise comparisons, and the tidyverse package⁶⁶ to graph the model predictions. We used the car package⁶⁴ to perform ANOVA tests. The tables were produced using the flextable package⁶⁵ or Microsoft Word. All data and code are accessible at https://github.com/brandipessman/vibration_transmission.

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Supplemental Information

Web transmission properties vary with a spider's past and current noise exposure

Brandi J. Pessman and Eileen A. Hebets

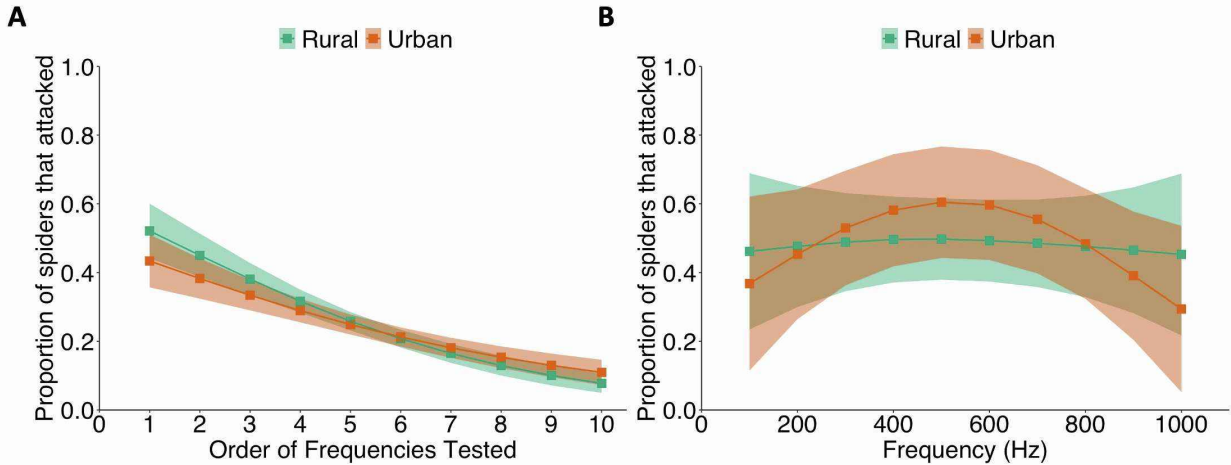


Figure S1. Results from spider responses to pure tone frequencies, Related to Figure 2. We tested the proportion of spiders that attacked within the frequency range of field-recorded vibratory noise (< 1 kHz) (A) with the order of frequencies experienced in the trial and (B) only using the first frequency presented. Each playback file contained all frequencies in random order and began with a unique frequency. The points and error ribbons represent the proportion of spiders that attacked and the 95% confidence interval from the binomial generalized additive model. (A) Both rural ($edf = 1.003$, $\chi^2 = 60.01$, $p < 0.001$) and urban ($edf = 1.099$, $\chi^2 = 34.74$, $p < 0.001$) spiders decreased in their probability of attack throughout the trial. (B) Using only the first frequency presented, rural and urban spiders attacked all frequencies at similar rates.

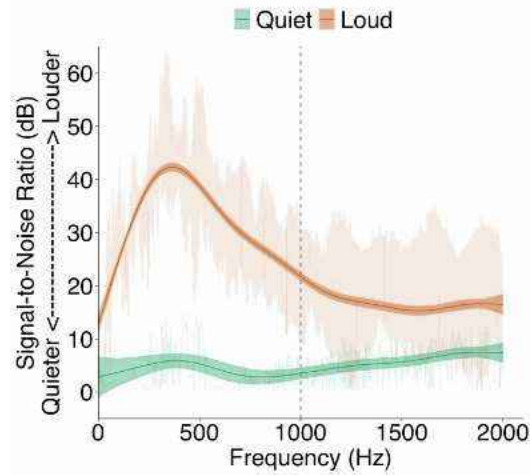


Figure S2. Recorded frequency profile of the vibratory playback treatments, Related to Figure 3. We used a laser vibrometer to record vibrations at the center of the black velvet substrate where spiders constructed webs during playback. We recorded the quiet and loud treatment settings for each of the six custom-built arenas. Background lines are the raw data for each arena. The lines and error ribbons represent the fit and 95% confidence intervals from a generalized additive model across frequency as a smooth term by treatment. The dashed line shows the frequency above which rural and urban field recordings suggest noise is negligible.^{S1}

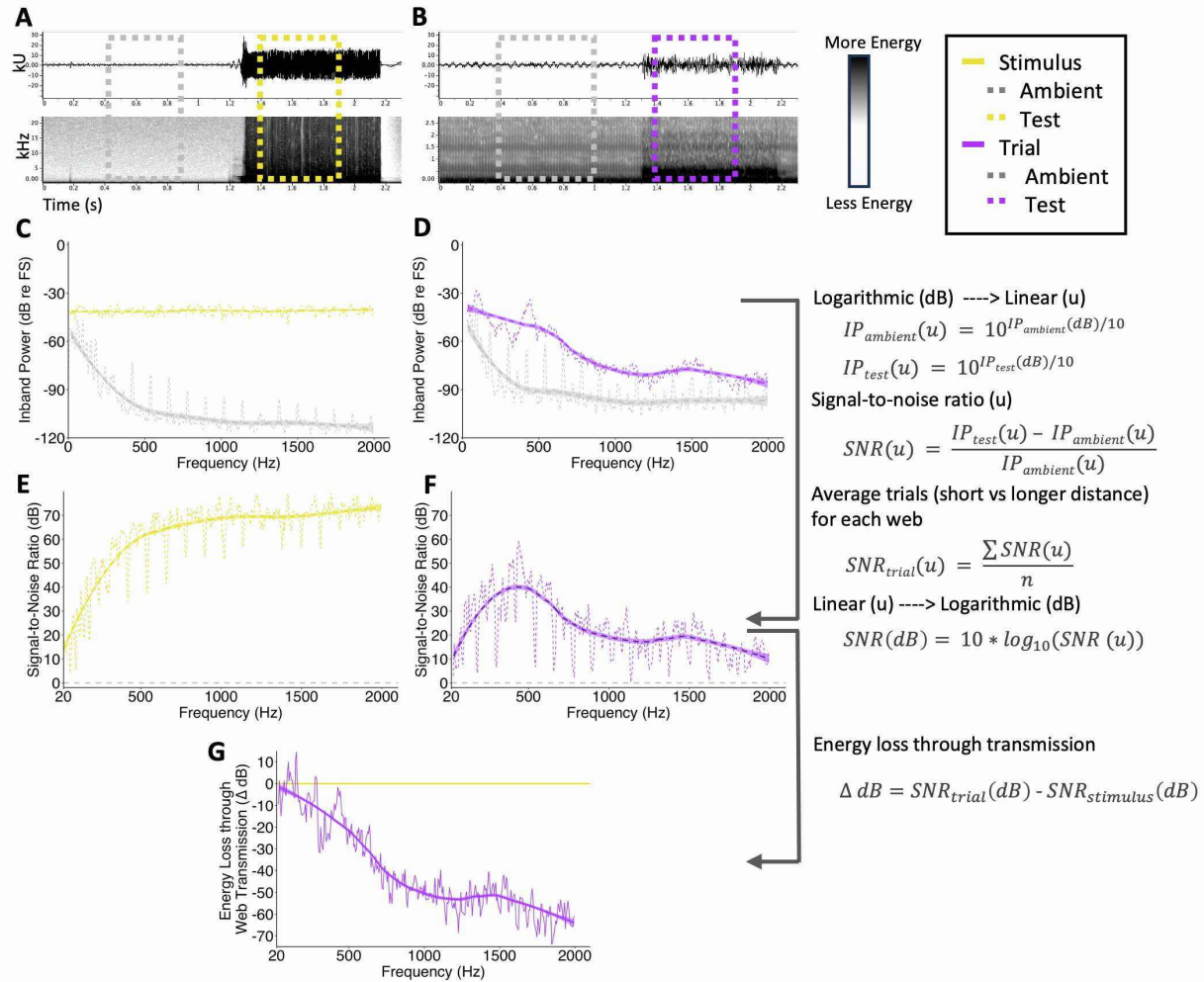


Figure S3. Breakdown of the calculations performed on the vibration transmission recordings, Related to Figure 3 and 4. We measured the inband power in 5.38 Hz bins from 0-2000 Hz using (A-B) 0.5-second portions of silence before the stimulus ('ambient', grey) and vibrations during the stimulus ('test', yellow for the stimulus recording, purple for the trial recording). (C-D) We graphed the raw inband power values (in decibels relative to the full scale, dB re FS) across the frequency range of the ambient and test portions measured. (E-F) We converted the logarithmic decibel units to linear units. Then, we calculated the signal-to-noise ratio of (E) the stimulus from a single recording and (F) the resultant recording from each trial and averaged the nine short-distance transmission trials and nine longer-distance transmission trials for each web. We converted back to the more familiar logarithmic (dB) scale and (G) calculated energy loss through web transmission. IP = inband power, SNR = signal-to-noise ratio, u = linear units, dB = logarithmic decibel units.

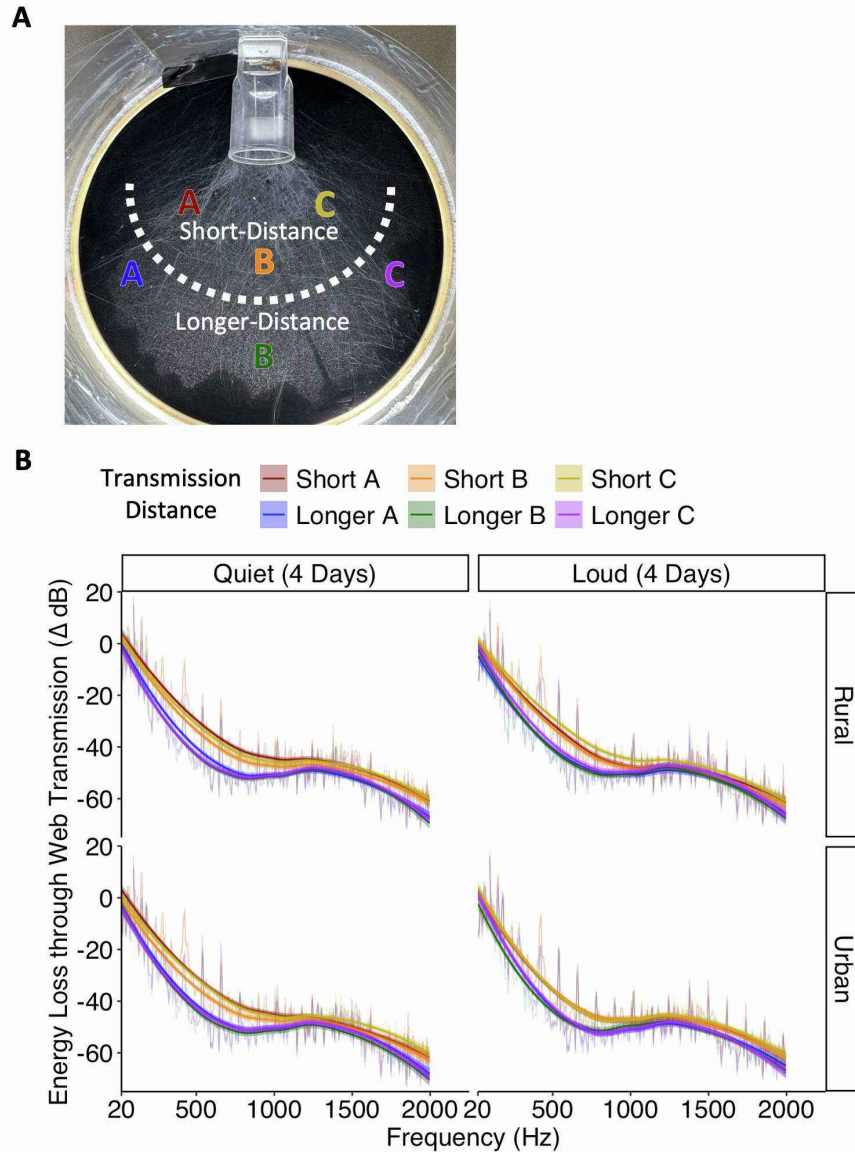


Figure S4. Short- and longer-distance vibration transmission across the web from controlled white noise provided at six different positions, Related to Figure 4. (A) We played low-frequency (0-2000 Hz) white noise vibrations at six different positions on the web. (B) We measured the loss of energy, or attenuation, of different frequencies as they arrived at the opening of the retreat for three trials at each position. Each unique color represents a different position. Background lines are the raw calculated means (across 15 webs each) for each group. Lines and error ribbons represent the mean and standard error from a smooth loess curve, respectively, after averaging across the three trials for each web. Vibrations transmitted similarly between positions A-C for short- and longer-distance vibration transmission. Yet, vibrations that transmitted longer distances showed greater energy loss (attenuation) than those that transmitted short distances.

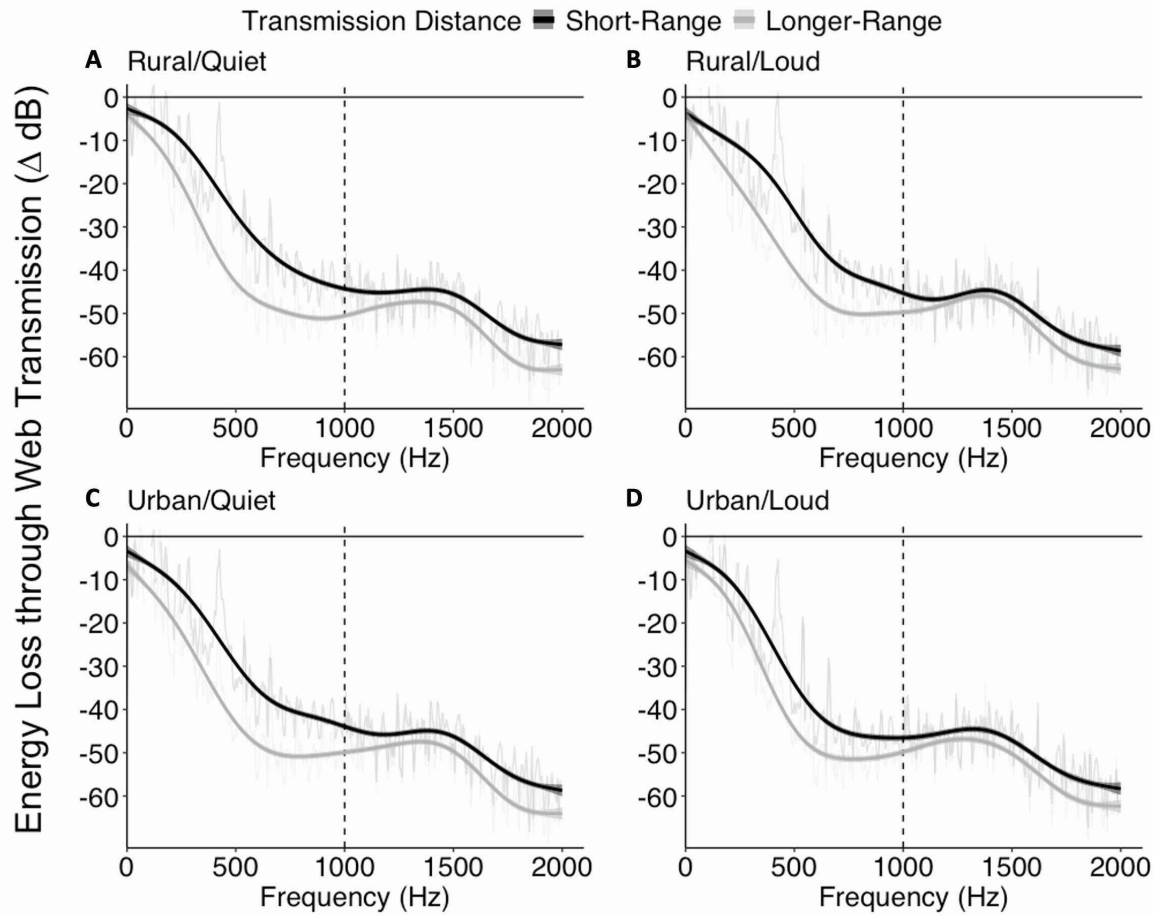


Figure S5. Results of web vibration transmission comparing short (black) and longer (grey) transmission distances within site/treatment groups, Related to Figure 4. The dashed line at 1000 Hz separates frequencies overlapping with field-recorded and playback treatment vibratory noise (< 1 kHz) from those outside it (> 1 kHz). Background lines are the calculated means across webs for each group and transmission distance, while lines and error ribbons show generalized additive model predictions with 95% confidence intervals. Short transmission distances lost significantly less energy than longer transmission distances across observed frequencies within (A) rural/quiet ($df = 10728$, $T\text{-ratio} = 13.510$, $p < 0.001$), (B) rural/loud ($df = 10706$, $T\text{-ratio} = 9.245$, $p < 0.001$), (C) urban/quiet ($df = 10646$, $T\text{-ratio} = 12.879$, $p < 0.001$), and (D) urban/loud ($df = 10688$, $T\text{-ratio} = 6.503$, $p < 0.001$) site/treatment groups from pairwise comparisons of estimated marginal means.

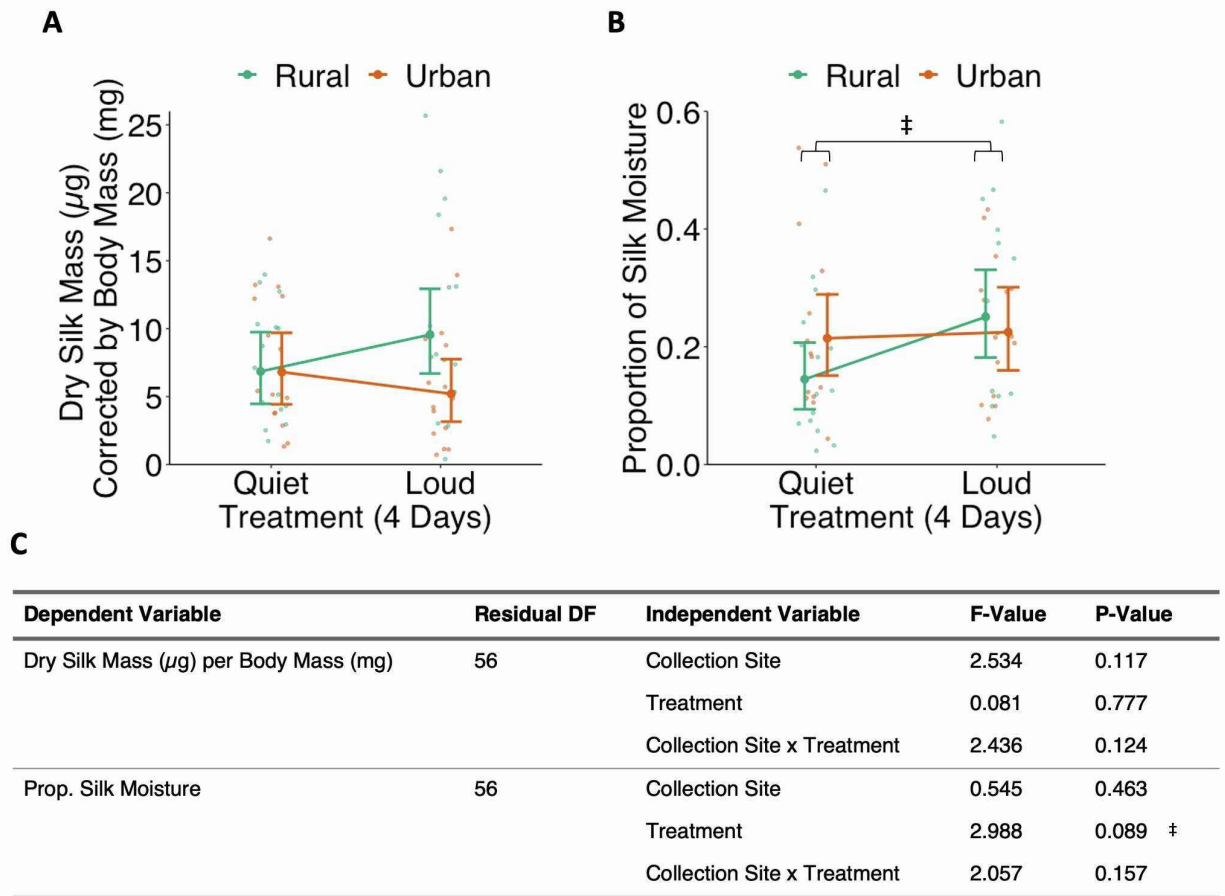


Figure S6. Properties of the silk from rural and urban webs built under quiet or loud conditions, Related to STAR Methods. After the web vibration transmission measurements, we collected all of the silk in the arena on a 4 cm pre-dried, pre-weighed fishing line and weighed the silk before (wet mass) and after (dry mass) drying in a drying oven at 50°C for 48 hours. (A) We divided the dry silk mass by the body mass of the spider that laid it. (B) We subtracted the measured dry mass from the wet mass and divided by the wet mass to get the proportion of silk moisture. For both A and B, jittered points are the raw data while the points and error bars represent the mean and 95% confidence intervals of the model predictions. (C) Results from the ANOVAs for the effects of rural/urban and treatment on dry silk mass and proportion of silk moisture. The data were square root-transformed prior to testing to fit a normal distribution and back-transformed for visualization. Despite finding no differences in dry silk mass, there was a non-significant trend that suggested that webs built under loud conditions had higher silk moisture than webs built under quiet conditions, though this appears to be largely driven by rural webs. This is intriguing because the humidity in the room was constant, and spiders received ad libitum water before testing and no water during the trial. Notably, the size of the experimental arena likely did not constrain web architecture since the arena provided for four days of web-building (324 cm^2) was comparable to measured natural web areas constructed over longer periods ($552 \text{ cm}^2 \pm 1.46 \text{ cm}^2$). Asterisks indicate significance levels ($p < 0.10$ ‡).

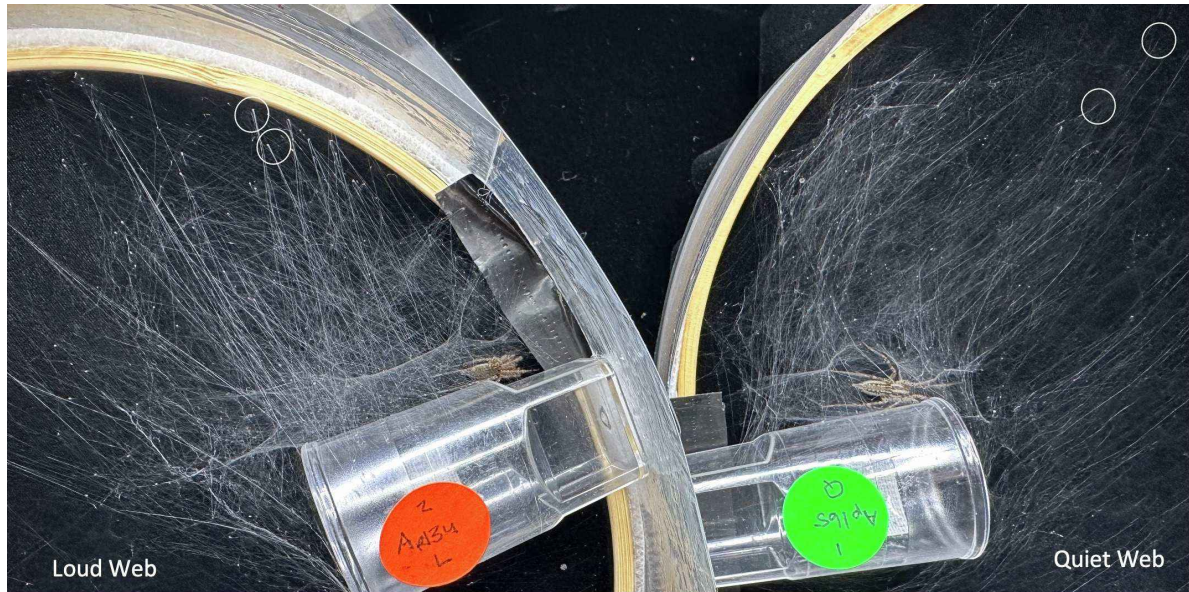


Figure S7. Observed differences in web anchor points, Related to Figure 3. Anchor points (a couple of examples circled) are where the web attaches to the substrate for webs built under loud (left) or quiet (right) conditions (see Figure 3 for details). Anchor points of webs constructed under loud conditions were often more visible and added noticeable resistance when collecting the silk from the substrate for loud webs compared to webs constructed under quiet conditions.

Experiment (Year)	Range of Time Since Exposure (days)	Mean ($\pm$ SE) Time Since Exposure (days)	Number of Rural Spiders (Quiet/Loud)	Number of Urban Spiders (Quiet/Loud)
None (2022)	NA	NA	5	0
Microhabitat Use (2022)	31 to 69	49.6 ($\pm$ 1.36)	27	30
Web Construction Quiet/Loud (2022)	6 to 47	23.8 ($\pm$ 2.06)	13 (6/7)	11 (7/4)
Web Construction Quiet/Loud (2023)	7 to 45	27.6 ($\pm$ 1.98)	13 (7/6)	22 (12/10)

Table S1. Descriptive statistics for the previous experiments prior to response to pure tone frequencies, Related to Figure 2. We included only spiders that attacked at least once during the frequency response trials. “None (2022)” spiders did not have any prior experience in lab-based manipulations of vibratory environment, apart from ambient lab conditions. “Microhabitat Use (2022)” was an experiment completed by Pessman et al.⁵¹ where spiders explored a microcosm for four nights that played both quiet and loud vibrations on opposing sides. All remaining spiders experienced only the current experiment’s four nights of quiet or loud vibrations during web construction in the described arena (Figure 3A). When included in the model, previous experiments were designated as “none”, “microhabitat use”, “loud”, or “quiet”.

Supplemental Reference

- S1. Pessman, B.J., McGinley, R.H., and Hebets, E.A. (2024). Spatial and temporal variation in ambient vibratory noise and its impact potential on a common urban arthropod. *Entomol. Exp. Appl.* 172, 1196–1216. <https://doi.org/10.1111/eea.13487>.