



Spatial and temporal variation in ambient vibratory noise and its impact potential on a common urban arthropod

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Abstract

Recent, rapid arthropod declines have been tied to human activity. Yet, the propensity for human-produced noise to disturb the substrate-borne (vibratory) channel remains virtually untested despite arthropods' ubiquitous use of vibratory information. Characterizing the vibratory landscape at biologically relevant scales is an essential initial step. We aimed to measure vibratory noise across space and time to assess its potential overlap with the urban–rural range and season of a funnel-weaving spider, *Agelenopsis pennsylvanica* (C.L. Koch) (Araneae: Agelenidae), a common urban arthropod. We assessed 24-h ambient vibrations (hereafter vibratory “noise”) at 23 sites across urban–rural Lincoln, Nebraska (NE, USA), during the adult season of *A. pennsylvanica* (August–October). Vibratory noise (amplitude, Leq) varied by ~15 dB across sites overlapping with frequencies within *A. pennsylvanica*'s sensitivity (20–1000 Hz). Urban vibratory noise was positively correlated with the principal component containing estimates of traffic-induced vibrations (e.g., traffic volume, road proximity, and impervious cover), whereas rural noise levels correlated with probable harvest times. Our findings indicate spatial variation in noise in urban areas and seasonal noise variability in rural areas. We also tested how *A. pennsylvanica*—collected from four distinct noise survey sites—use their vibratory microhabitat. We assessed daily spider position and dry silk mass within a microcosm that played loud and quiet vibrations (white noise differing by ~15 dB) in separate but connected chambers. Age affected the chamber choice (hereafter “microhabitat use”) of spiders collected from the loudest site, as younger adults associated with and used more silk in the loud chamber, but this effect decreased with age. As our data demonstrate that vibratory noise varies with *A. pennsylvanica*'s microhabitat and season with a high potential for impacting behavior, we hypothesize that this environmental noise likely impacts other arthropods as well.

KEY WORDS

Agelenidae, *Agelenopsis pennsylvanica*, agriculture, anthropogenic noise, biotremology, funnel-weaving spider, microhabitat use, silk, spider webs, substrate-borne, traffic noise, urban–rural gradient

INTRODUCTION

More than 90% of arthropods rely on substrate-borne (hereafter “vibratory”) information to assess and interact with the world around them (Cocroft & Rodríguez, 2005). This information channel, however, is not readily available to humans, which may be partially responsible for the relative

lack of vibratory communication research studies compared with auditory, visual and olfactory communication until recent years (Hill, 2009; Roberts & Wickings, 2022). The vibratory sensory channel is incredibly important, however, as many animals, especially arthropods, use vibrations for conspecific communication (Cocroft & Rodríguez, 2005), prey detection (Virant-Doberlet et al., 2019), and predator

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evasion (Oberst et al., 2017). How vibratory information is produced, received, and processed by animals, and its resulting impact on behavior, is a driving question of the recently termed and rapidly growing field of biotremology (Hill et al., 2019; Hill & Wessel, 2016).

As the largest animal phylum, arthropods rely on vibrations to perform several ecologically vital roles including (but not limited to) pest control, pollination, and decomposition (Prather et al., 2013). Unfortunately, these vital roles are at risk because arthropods are rapidly disappearing at unprecedented rates because of increased human activity—an event recently termed the insect apocalypse (Goulson, 2019). These declines can be especially prominent in urban areas (Piano et al., 2020), which represent hubs of intense human activity. Urban areas are prone to disturbances that can interrupt, mask, or degrade sensory channels (hereafter “noise”), particularly in the form of light, chemical, and sound pollution (Halfwerk & Slabbekoorn, 2015). Accumulating evidence suggests that these forms of noise can negatively impact animal communication channels (reviewed in, e.g., Barber et al., 2010; Candolin & Wong, 2019; Classen-Rodríguez et al., 2021; Jürgens & Bischoff, 2017). However, we lack an understanding of how vibratory noise, specifically, affects animals that use vibratory information. Nonetheless, vibratory noise could be a major contributing factor to the behavior, survival, and ultimately success of vibration-orienting arthropods, making this gap in knowledge of critical concern.

To investigate how urban animals cope with environmental disturbances, it is essential to first understand how the disturbance varies across biologically relevant spatial and temporal scales (Vardi & Berger-Tal, 2022). We know a fair amount about airborne sound disturbance from soundscape ecology—the study of airborne acoustic noise from biological, geophysical, and anthropogenic sources. This term was coined in 2011 with the first study to assess anthropogenic airborne noise across an urban–rural gradient (Joo et al., 2011) and the development of a conceptual framework for the subfield (Pijanowski et al., 2011). However, studying the vibratory environment to elucidate ecological processes, or ecotremology, lags with a conceptual framework published very recently (Šturm et al., 2022) and no accompanying assessment of the urban–rural vibroscape. Most of what we know of anthropogenic vibratory noise comes from seismic (ground vibration) monitoring stations for tracking changes in Earth's surface, especially earthquakes and volcanic eruptions (McNamara & Buland, 2004). These studies identify, measure, and remove anthropogenic vibrations from recordings to increase the signal-to-noise ratio of geophysically relevant signals (McNamara & Buland, 2004).

Only recently have studies recording the vibroscape emerged. Šturm et al. (2021) recorded the vibroscape of a hay meadow—focusing on vibrations produced by insect communities—and found that the community composition varied temporally by season and spatially by plant species and location. In another study monitoring

the vibroscape in a vineyard, insect vibratory signaling was found to vary temporally in relation to wind and temperature fluctuations (Akassou et al., 2022). A study by Choi et al. (2024) found variation in forest floor vibroscape that led to plastic responses of *Schizocosca* wolf spiders. Importantly, the recorded vibroscape included both substrate-borne vibrations and airborne sound from biological and anthropogenic sources (Choi et al., 2024), because airborne sound can travel through the substrate as vibrations (Caldwell, 2014). More studies measuring vibratory landscapes with an animal-centric approach are needed, and no studies to our knowledge have measured an animal's urban–rural vibroscape.

Once the variation in the vibratory landscape is quantified, it is vital to measure the degree to which the focal animal may overlap with the disturbance both spatially and temporally. It is now apparent, for example, that anthropogenic vibratory noise spectrally overlaps relevant frequencies for arthropod communication—both typically occur at frequencies below 1000 Hz (Raboin & Elias, 2019). Also, vibrations that travel along the ground surface share the same wave types that travel across spider webs (longitudinal and transverse; Mortimer, 2017), although the web wave types produced by the transition of ground waves are unclear. As low frequencies do not attenuate as rapidly as high frequencies, anthropogenic vibrations could potentially be detectable at considerable distances from the source. Measurements taken from seismic monitoring stations using geophones and seismometers suggest that anthropogenic noise can travel as far as 1 km from the source (Díaz et al., 2022; Lecocq et al., 2020; Lehujer et al., 2015), but it is unclear whether the recorded vibrations could be perceived by animals, as these equipment record low-frequency ground vibrations (<120 Hz). There is some evidence that vibrations relevant to arthropod signals (500–800 Hz) could travel several meters on the same substrate (McVean & Field, 1996), but the vibroscape is complex and unpredictable as vibrations move between different materials (Šturm et al., 2021), and the distance that noise can travel to disturb communication is unclear. In an environment where noise varies over space and time, animals may assess the vibratory environment and control where (microhabitat use) and when (activity patterns) they perform behaviors to decrease noise impacts (Lowry et al., 2013).

Animals may actively avoid areas where vibratory noise is present to reduce spatial overlap with disturbances, as is the case with earthworms near wind turbines (Velilla et al., 2021) and African elephants, *Loxodonta africana* (Blumenbach), in response to human-generated white noise (Mortimer et al., 2021). However, Bunkley et al. (2017) found mixed results for ground-dwelling arthropod families in the presence of compressor noise—the presence of some families was negatively correlated with noise levels whereas others were positively correlated or unaffected by noise. Animals may also modify the rate or timing of their calls in response to natural and anthropogenic sources of

noise. For a vertebrate example, the call rate of the toad, *Alytes obstetricans* (Laurenti), is significantly reduced during heightened wind speed (7–8 km/h, De Luca et al., 2023) and in the presence of vibratory noise from wind turbines and traffic (Caorsi et al., 2019). There is also evidence for invertebrates adjusting their calling based on gaps in wind noise. For example, male treehoppers, *Enchenopa binotata* "Ptelea" (Say), initiated signaling when the wind was absent and females reduced responses to signals during windy conditions (McNett et al., 2010). Also, male katydids, *Copiphora brevirostris* (Stål), produced fewer tremulations during bouts of increased wind velocity (Velilla et al., 2020). Detecting gaps in wind may be context-dependent as vibroscape monitoring of insect vibratory communities revealed conflicting results with signaling activity decreasing in the vineyard (Akassou et al., 2022) and increasing in the hay meadow (Šturm et al., 2021) in the presence of wind. Although we see spatial and temporal adjustments in situations where noise is concentrated in space (wind turbines, compressors) and time (wind), it is unclear whether these strategies would be successful for invertebrates in cities where noise is widespread and persistent (Barber et al., 2010). If animals cannot adjust spatially or temporally, they may exhibit other forms of behavioral plasticity (e.g., plastic spider web characteristics, as in Sandoval, 1994, or song modification, as in Orci et al., 2016) to cope with variable environments.

Spiders are abundant urban predators that likely play an essential role in pest control in cities, making them a great system for investigating the effects of urban environments on animal behavior. A few common species in urban areas have already been studied in the context of urbanization and web spatial patterns—for example, *Brigittea civica* (Lucas) (Mammola et al., 2018) and *Lactrodectus hesperus* (Chamberlin & Ivie) (Trubl et al., 2012). Of particular interest are web-building spiders that rely on web-borne vibrations to gather sensory information about their surroundings, such as the assessment of prey, mates, and threats (Mortimer, 2019). Their webs are inextricably attached to the substrate, meaning that background vibrations in the substrate could transfer to the web's surface, potentially compromising signals and cues (Wu & Elias, 2014). The funnel-weaving spider *Agelenopsis* sp. (Araneae: Agelenidae) is commonly found across North America and across an urban–rural gradient of landscapes. *Agelenopsis* spiders possess webs that lack the sticky silk that is often used to retain prey, so the genus relies entirely on their vibratory sense and rapid movement to detect and secure prey (Riechert & Tracy, 1975). It seems likely that the urban–rural habitats that *Agelenopsis* spiders inhabit have distinct vibratory profiles.

In this study, we use *Agelenopsis pennsylvanica* (C.L. Koch) to address three questions. (i) To what degree do vibratory noise levels vary across an urban–rural habitat of *A. pennsylvanica*? (ii) How do vibratory noise levels vary across the season of *A. pennsylvanica*? (iii) Does the vibratory environment of the collection site (noise level) influence

vibration-based microhabitat use by adult female *A. pennsylvanica*? We predicted that vibratory noise levels would be highly variable across the microhabitat of *A. pennsylvanica* and would depend on proximity to heavily traveled roads. We suspected that vibratory noise in urban areas would remain consistently high across the *A. pennsylvanica* season, but that rural areas would see an increase in vibratory noise during harvest. We also expected adult female *A. pennsylvanica* to avoid areas of high vibratory noise, as the close relative, *Agelenopsis aperta* (Gertsch), is known to actively select web locations based on environmental conditions (Riechert & Tracy, 1975).

MATERIALS AND METHODS

Survey sites

We recorded ambient vibrations at 21 private properties in Lancaster County, NE, USA, in 2020 and added an additional private property and the University of Nebraska-Lincoln (UNL) city campus in 2022 (Figure 1A). To acquire access to the properties, we sent an email to listservs of the School of Biological Sciences and Department of Entomology at UNL in 2020 asking for volunteers to allow us to record ambient vibrations at their properties. We received permission to access private properties for the duration of the study from participants randomly scattered across Lincoln, NE, USA, and into the surrounding rural area (Figure 1A). We added the two sites in 2022 because we collected some *A. pennsylvanica* spiders from these sites for microhabitat use experiments.

We sorted the 23 sites into two site types based on land cover class: rural and urban (Figure 1D). We determined land cover class with QGIS (v.3.16.3-Hannover, ESRI 102704), which allowed us to calculate the area of each land cover class from the 2019 National Land Cover Database (Dewitz & U.S. Geological Survey, 2021; 30-m resolution) within a 1-km radius of each site. We chose a 1-km radius because anthropogenic sources of vibratory noise are thought to travel up to 1 km from the source (Lecocq et al., 2020). As such, we defined agricultural areas as those designated "Planted/Cultivated" and urban areas as those designated "Developed" from the NLCD legend (<https://www.mrlc.gov/data/legends/national-land-cover-database-class-legend-and-description>). We defined "other" area by grouping all remaining NLCD designations. We categorized sites as rural if they had more agricultural than urban areas and sites as urban if they had more urban than agricultural areas (Figure 1D).

Recording ambient vibratory noise

To record ambient vibrations, we deployed recording units (Figure 1B) at each of the sites. We recorded ambient vibrations by attaching a contact microphone (Kmise,

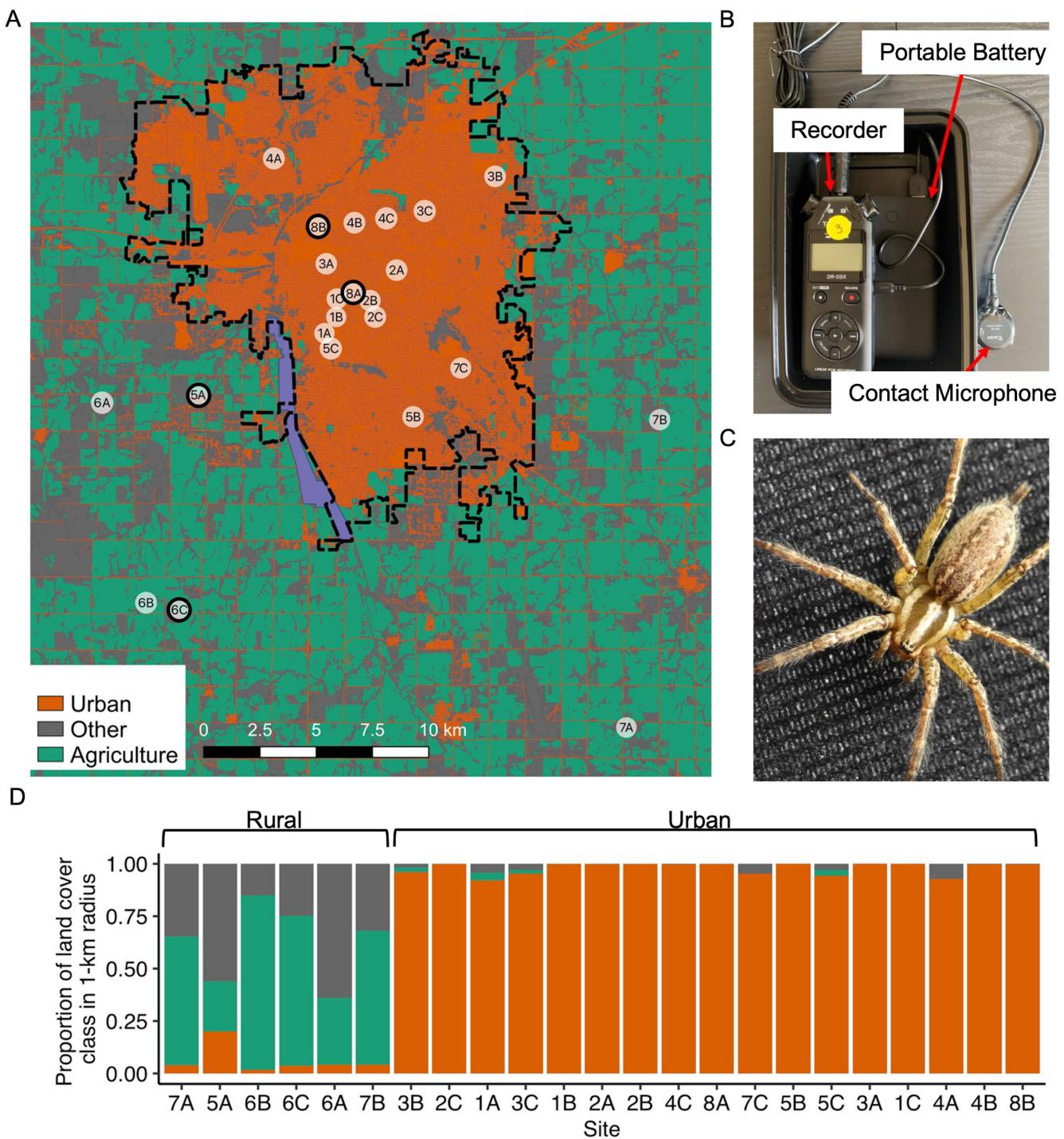


FIGURE 1 (A) Map of Lincoln, Nebraska, USA (city limits in dashed border) and the surrounding area marked with sites where substrate-borne (vibratory) noise was recorded using (B) recording units at the location of (C) female *Agelenopsis pennsylvanica* webs. Most recordings occurred in 2020, whereas recordings at sites 8A and 8B occurred in 2022. Site labels outlined in black indicate sites where *A. pennsylvanica* were collected for the microhabitat use test. The purple area shows Wilderness Park, where some *A. pennsylvanica* were collected for activity monitoring (see "Spider activity patterns across 24 h" section in Supporting Information). (D) Designation of site type (rural or urban) was based on the proportion of land cover class in a 1-km radius of each site (ordered by PC1 axis in Figure S1A). Agriculture (green) includes the 2019 National Land Cover Database (NLCD) classes Pasture/Hay and Cultivated Crop. Urban (orange) includes NLCD classes Developed Open Space, Developed Low-Intensity, Developed Medium-Intensity, and Developed High-Intensity. Other (gray) includes all other NLCD classes. Sites with more agricultural land than urban land are categorized as rural and the rest as urban.

Model KP-01, China) to substrates (Table S1) using XFasten double-sided tape. Although the frequency response of the contact microphone is unknown, similar models

exhibit a frequency range from at least 100 Hz to 4 kHz. The microphone was connected to a Tascam DR-05X digital recorder (TEAC Corporation, Tokyo, Japan) where the files

were stored on a Sandisk 32 GB microSD card. We used a waveform format with a 24-bit depth and a sampling rate of 48 kHz. The recorders have a frequency response of 20 to 22 000 Hz, a signal-to-noise ratio of 94 dB or higher, and the maximum input level is –4 dBV. The recorder was powered by a 10 000 mAh portable battery (Onn, Walmart, 3x charge, Bentonville, AR, USA), which could power the recorder for approximately 24 h. We stored the recorder and portable battery in Ethenet plastic 830-mL container (22 × 15.5 × 7 cm) covered in moisture- and UV-resistant Gorilla Tough and Wide White Duct Tape and applied caulk around the entrance of the audio cable leading to the microphone. Once a week, we coated the containers and microphones in Repels-All Animal Repellent, a mild nasal irritant, to safely deter wildlife from tampering with the equipment.

We used 12 recording units in total. At each of the sites in 2020, we deployed four recording units to record ambient vibrations for 24 h next to webs of female *A. pennsylvanica* (Figure 1C), as males typically leave their webs shortly after maturation (Singer et al., 2000). We could survey three sites in a single day. Of the four recording units, we attached two to plant substrates and two to manmade substrates (e.g., cement, paneling, wood fences/porches, and metal) to explore whether artificial versus natural substrates differ in vibratory noise levels (Table S1). We repeated recordings on the same substrates during three subsequent visits, for a total of four visits that occurred between August 3 and October 24, 2020. We chose this specific period because we tend to see *A. pennsylvanica* reach their penultimate instar in early August, mature in late August/early September, and survive until mid-late October in the field (personal observation). Thus, our survey could record how vibratory noise varies across *A. pennsylvanica*'s penultimate and adult cycles.

Visits to the same sites occurred approximately every 3 weeks (visit 1 = August 3–August 20; visit 2 = August 31–September 21; visit 3 = September 22–October 8, visit 4 = October 12–October 24). We only recorded on weekdays because vibratory noise is often reduced on weekends compared with weekdays (Lecocq et al., 2020). We also only recorded on days when the chance of rain was below 20% (both to protect the recording units and remove vibratory noise from rain) and the temperature was not forecasted to exceed 33°C (to protect the recording units). We switched out the portable battery for a fully charged battery approximately 10 h after deployment to ensure the recorders remained charged throughout data collection (see Table S2 for data on start, check, and end times). We excluded recordings where the microphone fell from the substrate at any point during recording (75 out of 370, Table S3).

In 2022, we added one private property (8A, Figure 1A) and UNL city campus (8B, Figure 1A) to determine vibratory noise levels at sites where *A. pennsylvanica* spiders were collected for microhabitat use experiments. We deployed six recording devices (three on plants and three on manmade substrates) at the private property (8A) for three

consecutive days (August 11–13, 2022). We deployed four recording devices (two on plants and two on manmade substrates) on UNL city campus (8B) for four consecutive days (August 17–20, 2022). We returned approximately every 24 h to replace the portable batteries.

To measure vibratory noise levels, we used Raven Pro (v.1.6.1) to divide each 24-h recording into 5-s time bins. We chose small bins to explore variation in noise at high time resolution, as 5 s was similar to the length of time of a car passing. We calculated the relative amplitude as the equivalent continuous sound pressure level (Leq, units = decibels relative to full scale, or dB re FS) for each bin. Where dB is often used as an absolute measure of airborne vibrations, using 20 mPa as the reference value, dB re FS uses the maximum amplitude of the system (at which clipping occurs) as a reference value, as substrate vibrations likely require a different reference value than air vibrations. As we could not calibrate the system, relative amplitudes are given as negative values. Calculated amplitude values are not absolute, meaning comparisons should only be made within the confines of this study, and we caution against making comparisons with other studies, especially if different recording equipment was used. We measured the relative amplitude for the frequency range of 20–1000 Hz as anthropogenic noise occurs predominantly below 1000 Hz (Raboin & Elias, 2019). We removed the first 5 min of each recording to ensure that disturbance from setup was not included in the analysis. For the same reason, we removed about 1 min of the recording where we replaced the battery. The only other instances of clipping occurred when the microphone was tampered with and fell, and in these cases, the trial was always removed (Table S3).

Vibratory noise across space

First, to assess the range of vibratory noise that *A. pennsylvanica* is exposed to, we computed the site average for each of the 23 sites by averaging the noise amplitude for all 5-s time bins recorded at a site. For further analysis, we calculated the daily average amplitude by averaging the noise levels of all 5-s time bins for each 24-h recording (unique by site, visit, and microphone, see Table S3).

We predicted that vibrations from nearby traffic likely contributed significantly to the recorded ambient vibrations. To test this, we first gathered four variables related to the traffic impact potential for each site. (i) Impervious cover (i.e., building and pavement) in a 1-km radius. We used the 2019 Impervious Cover Data from the National Land Cover Database (Dewitz & U.S. Geological Survey, 2021; 30-m resolution). In QGIS, we polygonized the file and used the intersection tool to calculate the percent cover for the entire 1 km buffer region for each site (as in, Pessman et al., 2023). (ii) Average daily vehicles passing on the nearest road. We used data from the Lincoln Transportation and Utilities (<https://www.lincoln.ne.gov/City/Departments/LTU/>

Transportation/Traffic-Engineering/Average-Daily-Traffic-Volume) and the NebraskaMAP Street Centerlines (<https://www.nebraskamap.gov/maps/1cfb967a70dd4b0abee9d38249c06b0a/about>) to determine the average number of vehicles per day that pass the nearest road for each site. (iii) Distance to nearest road. We calculated the shortest distance from the site to the road of its associated traffic data. (iv) Total length of roads in a 1-km radius. We used QGIS to sum the lengths of all of the roads within a 1-km radius of each site. We reduced the four traffic impact potential variables through principal component analysis (PCA; [Figure S1](#)) and used principal components 1 and 2 for statistical analyses, which we refer to as the potential traffic impact.

Statistical analysis

For all analyses of vibratory noise, we used linear mixed-effect (LME) models with site as a random factor as each site had multiple recordings. As our data frequently had outliers ([Figure S2](#)), we also tested identical robust LME models. We report the LME model results if the robust LME models produced similar results.

We wanted to see the degree of variation in vibratory noise levels across large-scale space (by site type—rural vs. urban and across 23 sites) and small-scale space (between substrates—manmade vs. plant). We first looked for differences in daily average amplitude by rural/urban to assess large-scale differences in vibratory noise levels. To determine whether vibratory noise levels are correlated with potential traffic impact and substrate type, we tested the daily average noise amplitude against the potential traffic impact (PC1), substrate type, and the interaction as predictor variables. We also repeated this analysis while subsetting the data by rural/urban to see whether rural and urban areas experienced different relationships between daily average noise amplitude and the potential traffic impact. We used separate models to investigate the potential traffic impact because the rural/urban were separated across PC1 ([Figure S1A](#)), making it difficult to interpret model predictions. We reported the results of the robust LME model for the rural subset.

We also assessed principal component 2 (PC2) of the potential traffic impact, this time including rural/urban as an interacting predictor variable because the rural/urban were integrated across the PC2 axis ([Figure S1A](#)). Because the global model included a three-way interaction (PC2 × Substrate × Rural/Urban) we used the drop1 function to perform backward selection. We performed a Type II Wald χ^2 test on the final LME model as the model included two multilevel variables (substrate and rural/urban).

Lastly, we visualized the frequency profiles across the substrates of the three loudest (8B, 5C, and 4A) and three quietest (5A, 6C, and 6B) sites during the hour of highest activity of *A. pennsylvanica* (21:00–22:00; see “Spider activity patterns across 24 h” section in [Supporting Information](#)). Using Raven Pro, we assessed the inband power (Fast

Fourier Transform length 8192, Hann window, 50% overlap, 0.171 s time resolution, 5.86 Hz frequency grid spacing) of ambient vibrations in 5.86 Hz frequency bins from 20 to 1000 Hz.

Vibratory noise across time

To determine whether vibratory noise exhibits a pattern by rural/urban across a 24-h period, we averaged the noise amplitude from the 5-s time bins by each hour (i.e., daily average amplitude broken down by the hour) to get the hourly average noise amplitude. We then calculated and graphed the mean and standard error across 24 h for rural/urban. To see whether 24-h patterns change over time, we also graphed this information by visit (1–4).

Further, we investigated whether vibratory noise varies temporally across the season throughout the penultimate instar and adulthood of *A. pennsylvanica* (August–October). For this analysis, we restricted our data to those collected in 2020, as 2022 data were collected across three or four consecutive days in August 2022, which makes it not possible to assess vibrations across the season in 2022. We looked for relationships in the daily average noise amplitude between each visit (1–4) and rural/urban and the interaction between visit and rural/urban. We performed a Type II Wald χ^2 test on the LME model as visit has more than two levels. As a post hoc test, we performed a Tukey’s pairwise comparison. We refrained from using date as a continuous variable as the data suggested a non-linear pattern across time.

We predicted that vibratory noise from harvesting equipment was a significant source of vibratory noise in rural areas. To test this, we used the United States Department of Agriculture’s (USDA) National Agriculture Statistics Service data (<https://quickstats.nass.usda.gov/>) about the end-of-the-week percent harvested values for Nebraska in August–October 2020, specifically using crops that are most common in Lancaster County, NE: corn and soybeans. We graphed these values across the season (August 3–October 24, 2020), including the calculated mean of the percent harvested for corn and soybeans, to compare to the vibratory noise levels by visit. To directly assess if harvesting is related to rural vibratory noise levels, we tested the daily average noise amplitude of rural sites against the percent harvested by matching the week from the harvest data to the week of the recording. We reported the results of the robust LME model.

Spider microhabitat use in response to vibratory environment

To assess how spiders with experience in specific vibratory environments respond to variation in vibratory environments, we collected 69 female *A. pennsylvanica* in their penultimate instar across four sites (Sites 5A, 6C, 8A, and 8B; [Figure 1A](#)). We chose to use females because

females continue to construct webs in adulthood whereas adult males leave their webs in search of females. These sites varied in the recorded vibratory noise levels (5A and 6C [rural] = -69 dB re FS, 8A [urban] = -64 dB re FS, 8B [urban] = -55 dB re FS) where decibel values closer to 0 dB are louder. We collected spiders within 1 week's time (August 4–10, 2022) and housed them in the lab under ambient vibratory conditions in $8.3 \times 8.3 \times 8.3$ cm plastic containers until the vibration microhabitat use test. The spiders received ad libitum water from a cotton wick inserted in the bottom of each container. We suspended the containers over a tub of water with metal chicken wire. We fed the spiders two crickets twice a week and each cricket was approximately half of their abdomen length. The spiders were maintained at 25°C and a L13:D11 photocycle that began at 07:30 h. We checked for molts every other day to determine the day of maturation.

Our experimental design allowed spiders to construct a web in a microcosm that varied in vibratory noise levels. The microcosm was custom-made from two $8.3 \times 8.3 \times 8.3$ cm acrylic containers connected by a smaller ($5.8 \times 2.6 \times 2.6$ cm) acrylic container using acrylic plastic cement (Weld-On 16) to keep the material as consistent as possible for vibration transmission (Figure 2). Hereafter, we refer to each container as a chamber. The microcosm was suspended in acoustic foam (Figure 2B) to reduce vibrations from traveling between chambers. We attached Hylaea clear anti-slip tape (5 cm wide) to the sides of the larger chambers to produce rough surfaces for silk attachment. We applied Vaseline above the anti-slip tape to discourage silk attachment to the lid of the larger chambers. On the bottom inside of each large chamber, we placed black masking tape to better observe the silk. Centered on the bottom of each larger chamber, we attached a piezoelectric disk (Pagow 3-in-1 transducers) that played continuous vibrations from the same audio recorders used to collect ambient vibrations in the field (Figure 1B). This allowed us to present a different vibratory environment on each chamber of the microcosm: one loud and one quiet. These treatments were produced from white noise, filtered to be concentrated in low frequencies (<1000 Hz) with a 6 dB decrease per octave. We used white noise to control the amplitude and frequencies that the spiders experienced (see Figure S3 for frequency profiles from the field and chambers). The treatments differed only in amplitude, similar to the variation in ambient vibrations from the noise survey (~15 dB, Figure 2). The treatments played continuously across the experiment, powered by the same power banks from field recordings (exchanged every 24 h).

We had 18 microcosms in total and ran four iterations of trials for a total of 69 spiders. At the time of the trial, we weighed each spider and photographed it with a size standard to calculate body size from the cephalothorax width using ImageJ (v.1.8.0_172). To avoid any chamber bias based on the chamber that we initially placed the spider in, we added the spider to a random chamber (loud or quiet)

and encouraged it to the other chamber with a paintbrush before trapping it in the smaller chamber (hereafter tunnel) connecting the two larger for the start of the trial. After a 10-min acclimation period in the tunnel, we removed the barriers and the spider was allowed to explore the microcosm and build its web for four nights. In between each trial, we thoroughly cleaned the microcosm with soap and water and randomly rotated each microcosm before a new spider was introduced. We fed spiders on the third day of their trial with two crickets, one thrown in each larger chamber of the microcosm. We conducted this experiment from September 13 through October 7, 2022—within the natural adult season of this species.

On each of the 4 days of the microhabitat use experiment for each spider, we recorded their position once between 10:00 and 15:00, which is the time of day when they show the least activity (see "Spider activity patterns across 24 h" section in [Supporting Information](#)) and are often observed in the field either at the entrance of the retreat or deep into the retreat (personal observation; Riechert & Tracy, 1975). Thus, this was meant to be a measure of their resting microhabitat preference. At the end of the 4 days, we used pre-dried, pre-weighed fishing lines (4 cm long) to collect the silk from each chamber separately. We dried the silk at 50°C for 48 h in a drying oven and recorded the dry mass to the nearest 1 mg. Silk mass was meant to quantify where the spiders were laying their silk.

Statistical analysis

We used spider age (no. days since maturation) and body condition at the time of trial as predictors in all our models. We considered a spider to be 1 day old on the day when the final molt was found. We calculated body condition by obtaining the residuals of the linear model between body mass and cephalothorax width (both log-transformed, following Jakob et al., 1996) at the beginning of the microhabitat use trial. We first used linear models to explore whether age and body condition of spiders differed by the site where the spider was collected (rural vs. urban). We also tested whether age and body condition were correlated and found that they were (see "Spider microhabitat use in response to vibratory environment" section). Thus, we refrained from including their interaction in any model, but we retained both in the global model due to the low R^2 value (0.165). For each final model where two or more continuous predictors remained in the model, we scaled and centered all continuous variables in the global model and ensured the variance inflation factor remained below two for each of the variables in the final model. We used backward selection to select the best fit model.

Given the variation in noise levels between loud and quiet vibratory environments, we wanted to test whether spiders collected from sites with different vibratory profiles would vary in their use of a variable vibratory microhabitat. To determine whether the vibratory environment

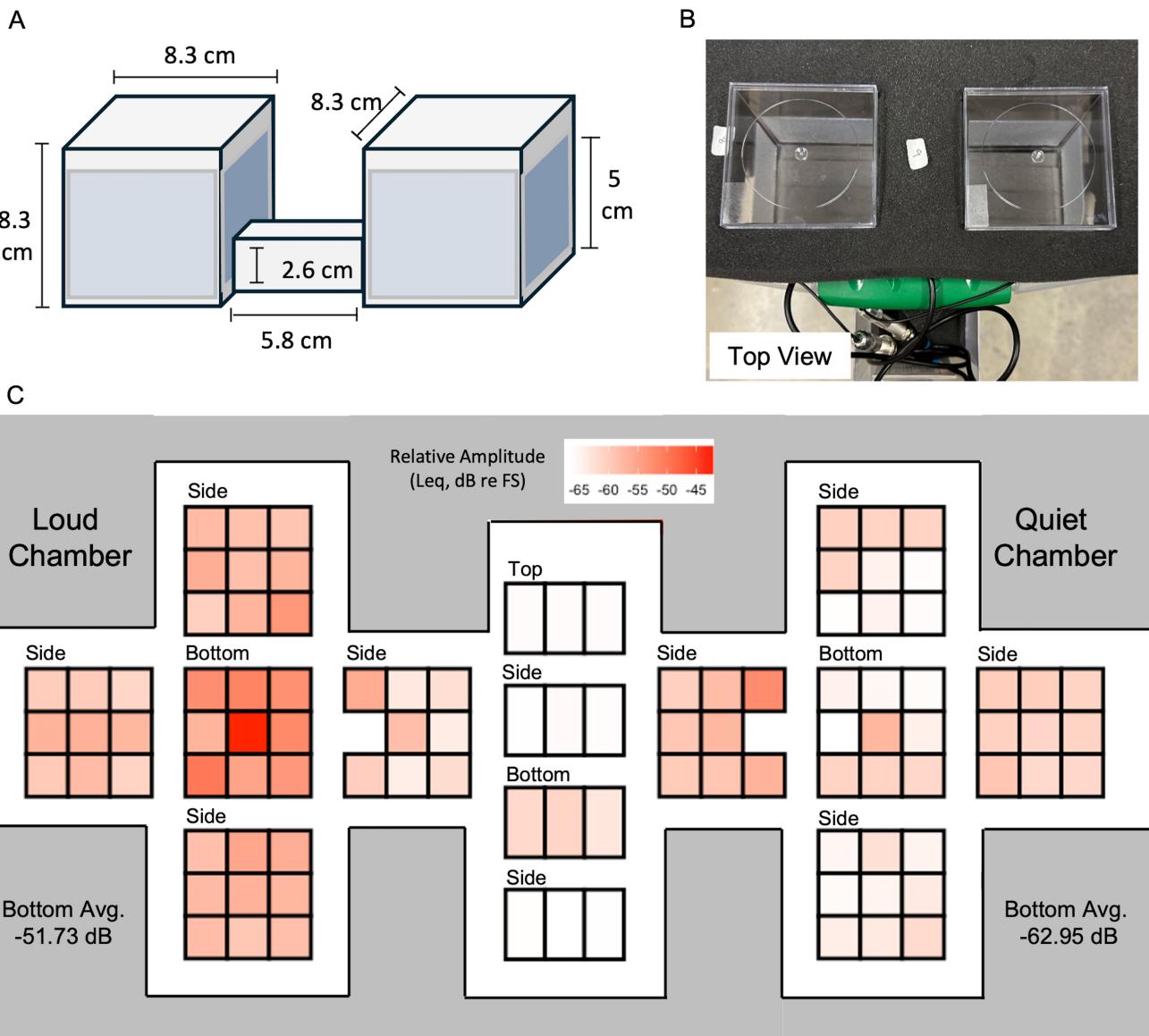


FIGURE 2 Experimental setup of the microhabitat use trials. (A) The microcosm was constructed from two large clear acrylic chambers and one smaller tunnel (B) suspended in acoustic foam, with a piezo electric contact microphone attached to the bottom of each chamber. In the large chambers we played low-frequency (<1000 Hz) white noise vibrations that varied in noise amplitude similar to field recorded variation (~15 dB), with one chamber playing loud vibrations and the other quiet. (C) The results from testing the resultant vibrations, recorded for 30 s during playback at points all across a microcosm using the same recording system as was used in the field recordings. The colors and numbers represent the relative amplitude (measured as Leq, in units dB re FS).

influenced microhabitat use, we quantified the degree to which spiders were found in the loud versus quiet chamber. We used (i) observations of spiders in the loud versus quiet chamber as well as (ii) the chamber (loud vs. quiet) where the spiders placed more silk as proxies of microhabitat use. Next, to determine whether spiders use silk differently across the microcosm, (iii) we measured the proportion of silk spiders placed in each chamber. Thus, (ii) assessed whether there was a bias toward the loud or quiet chambers whereas (iii) measured the strength of that bias and included silk use in the tunnel. Last, (iv) we assessed chamber fidelity by measuring the probability of staying in the same chamber for each of the 4 days of observation.

(i) To investigate predictors of a spider being found in the loud (1) or quiet (0) chamber, we used a binomial generalized linear model using site noise amplitude, age, and day of observation as interacting variables. We took a mixed model approach by adding spider ID as a random effect. (ii) In addition to spider position, we assessed microhabitat use using dry silk mass. We built a model similar to (i) where spiders with higher silk mass in the loud chamber were coded (1) and more silk mass in the quiet chamber (0). We removed day of observation because silk mass was collected once at the end of the trial. (iii) We first assessed total dry silk mass by each spider using a negative binomial generalized linear model with

site amplitude \times age and site amplitude \times condition. As total silk mass varied by age (see “[Spider microhabitat use in response to vibratory environment](#)” section), we tested variation in the proportion of silk mass by chamber \times amplitude \times age and chamber \times amplitude \times condition using a beta regression generalized additive model. (iv) We used a binomial generalized linear model to determine whether site amplitude \times age and amplitude \times body condition predicted the probability of a spider being observed in the same chamber each day (1) or moving between chambers (0). We also performed similar tests for each response variable to assess variation by age and condition within each of the four sites.

We also investigated *A. pennsylvanica* activity patterns across 24 h. See [Supporting Information](#) (section “[Spider activity patterns across 24 h](#)”) for detailed methods and results.

All analyses were completed in RStudio (v.2023.03.0+386). We performed a PCA using the FactoMineR (Lê et al., [2008](#)), factoextra (Kassambara & Mundt, [2020](#)), and corrrplot (Wei & Simko, [2021](#)) packages. We calculated LME model predictions from 1000 simulations of bootstrapping using the bootMer function in lme4 (Bates et al., [2014](#)). As a default, we obtained *p*-values with the base summary function. However, we loaded the lmerTest package (Kuznetsova et al., [2017](#)) for the LME models, and we used the anova function in the car package (Fox & Weisberg, [2019](#)) for models with a categorical variable with more than two levels. Tukey post hoc analyses were completed using the emmeans package (Lenth et al., [2023](#)). To run robust LME models and get model predictions for the robust LME models, we used the robustlmm package (Koller, [2016](#)) and the allEffects function in the effects package (Fox, [2003](#)), respectively. We used the insight package (Lüdecke et al., [2019](#)) to calculate the R^2 values for each LME model. For backward selection, we used the buildmer package (Voeten, [2023](#)) for LME models or the base function step for other models. We also used the mgcv package (Wood, [2011](#)) to build the generalized additive model. We used the tidyverse (Wickham et al., [2019](#)), ggrepel (Slowikowski et al., [2023](#)), ggpubr (Kassambara, [2023](#)), viridis (Garnier et al., [2021](#)), and ggExtra (Attali & Baker, [2023](#)) packages to build the graphs. For the maps, we used ggmap (Kahle & Wickham, [2013](#)) and ggsn (Baquero, [2019](#)) packages. Tables were made using the flextable package (Gohel & Skintzos, [2022](#)) or the Word document table function. All data and code are available at https://github.com/brandipessman/Vibratory_Noise.

RESULTS

Vibratory noise across space

Site average noise amplitude varied by about 15 dB across the 23 sites—the loudest vibrations came from site 8B at -55 dB re FS and the quietest vibrations from site 6B at -70 dB re FS ([Figure 3A](#)). Urban sites varied from -66 to -55 dB re FS and rural sites varied from -70 to -66 dB re FS ([Figure 3A](#)). In

the recordings, insects, such as crickets and cicadas, can be frequently heard at rural and urban sites, but the observed calls occur at frequencies above 1000 Hz and would thus not likely impact our noise analysis ([Video S1](#)). Cars passing by produce vibrations below 1000 Hz and are the major vibration source heard in the recordings ([Video S1](#)).

When reducing our four traffic impact potential variables through PCA, the first principal component (PC1) explained 70.9% of the variation, whereas PC2 explained 18.3% ([Figure S1A](#)). All variables contributed to PC1, but only traffic (average daily vehicles) had a substantial contribution to PC2 ([Figure S1B](#)). Daily average noise amplitude significantly varied by site type (rural vs. urban), with urban sites exhibiting higher noise amplitude than rural sites ([Table 1](#)). Overall, daily average amplitude showed a significant positive relationship with potential traffic impact (PC1), and manmade substrates carried significantly louder vibrations than plant substrates ([Figure 3B; Table 1](#)). There was not a significant interaction between potential traffic impact (PC1) and substrate, overall ([Table 1](#)). When we subset the data by rural/urban, daily average noise amplitude for rural sites did not significantly correlate with potential traffic impact (PC1) or substrate, and there was not a significant interaction between potential traffic impact (PC1) and substrate ([Figure 3C; Table 1](#)). For the urban subset, we found similar results to that found overall ([Figure 3D; Table 1](#)). We also found similar results for PC2 ([Figure S4](#)).

Furthermore, the three loudest urban sites showed heightened noise levels below about 500 Hz compared to the three quietest rural sites ([Figure S3](#)). Of the six sites for which we assessed frequency profiles, four sites had recordings from the same manmade material and two sites had recordings from different manmade materials ([Figure S5](#)). Frequency profiles at sites with recordings on the same material overlapped ([Figure S5](#)). At the quietest site, recordings on different materials showed similar frequency profiles ([Figure S5](#)). However, when noise is heightened at an urban site, we anecdotally noticed a potential divergence in the frequency profiles of concrete and paneling: concrete vibrations were louder at low frequencies (<500 Hz) and quieter at higher frequencies than paneling. As our sample size was small in this case, tests directly addressing the role of substrate material in anthropogenic noise propagation are needed.

Vibratory noise across time

By graphing the trends in the hourly average noise amplitude across 24 h, we observed that vibratory noise in rural and urban areas goes through similar daily patterns ([Figure 4A](#)). Noise levels are highest in the morning, with an additional peak in the afternoon before decreasing and maintaining low levels during the night ([Figure 4A](#)). Rural noise levels stay consistently lower than urban noise levels throughout the 24-h span ([Figure 4A](#)). Peaks appeared to have occurred around rush hours (08:00 in urban, 09:00 in rural, 15:00 both).

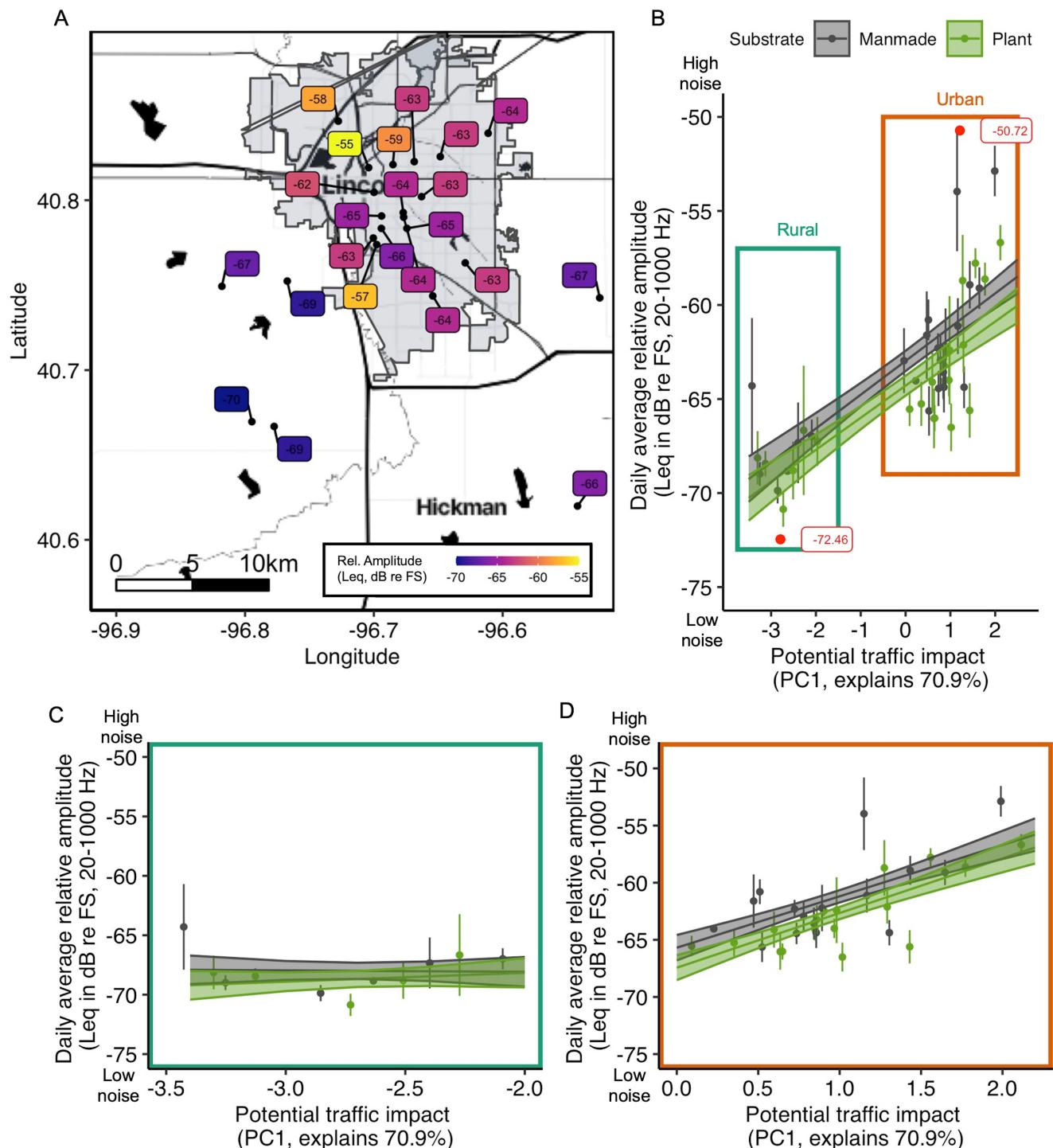


FIGURE 3 Results of spatial analysis of vibratory noise. (A) Site mean of the daily average noise amplitude (measured as L_{eq} in units dB re FS) across all 23 sites is given in the text label and represented by color (quieter in blue, louder in yellow). Site mean noise amplitude ranged from -55 dB to -70 dB re FS. Major highways and interstates are represented by thick, dark lines. (B–D) Raw data (mean \pm SD) and model predictions (line \pm ribbon = mean \pm SE) from linear mixed effect (LME) model of daily average noise amplitude by the potential traffic impact (PC1, see principal component analysis in Figure S1) and substrate (gray = manmade, green = plant) with site as a random effect. Results are shown for (B) data overall, [(C) robust LME] rural sites, and (D) urban sites. Green boxes represent rural sites and orange boxes represent urban. (B) The red dots and text show the lowest and highest daily average noise amplitude readings. Overall, (B) noise levels were positively related to the potential traffic impact, and manmade substrates carried significantly louder vibrations. However, no relationships between noise and potential traffic impact or substrate were found in the rural subset, suggesting (D) that these patterns are driven by variation in urban areas.

TABLE 1 Results of linear mixed effect (LME) models (site as a random factor) assessing spatial and temporal variation in vibratory noise amplitude (measured as Leq in units dB re FS).

Noise variation	Data (subset by)	Variable	Test statistic	N	p	Cond. R ²	Marg. R ²
Spatial	Daily average	Rural/urban	-4.269	295	<0.001	0.79	0.36
	Daily average	Potential traffic impact (PC1)	5.856	295	<0.001	0.81	0.51
		Substrate	-5.904	295	<0.001		
		Potential traffic impact (PC1) × substrate	-0.691	295	0.49		
	Daily average (rural)	Potential traffic impact (PC1)	-0.081 ^a	78	0.94	0.64	0.05
		Substrate	1.006 ^a	78	0.32		
		Potential traffic impact (PC1) × substrate	1.468 ^a	78	0.15		
	Daily average (urban)	Potential traffic impact (PC1)	4.152	217	<0.001	0.76	0.44
		Substrate	-3.212	217	0.002		
		Potential traffic impact (PC1) × substrate	0.573	217	0.57		
Temporal	Daily average (2020)	Visit	7.360 ^b	268	0.061	0.75	0.39
		Rural/urban	20.490 ^b	268	<0.001		
		Visit × rural/urban	3.490 ^b	268	0.32		
	Daily average (2020, rural)	Percent weekly harvest	1.874 ^a	78	0.065	0.57	0.02

Note: Test statistic is *t* unless otherwise noted.

^aResults from a robust linear mixed effects model.

^bResults from a Type II Wald χ^2 test of a linear mixed effect model (test statistic: χ^2).

When looking across the season as *A. pennsylvanica* mature and proceed through adulthood, we found significant variation in vibratory noise levels. There was a trend that daily average noise amplitude varied by visit (Figure 4B; Table 1). A Tukey's post hoc test revealed a significant increase in noise from visit 2 to visit 3 ($t=-3.00$, $df=241$, $p=0.016$). We still saw a significant effect of rural/urban where rural sites are quieter than urban sites, and there is no interaction between visit and rural/urban overall (Table 1). Because we were interested in the potential role of harvesting, we ran a Tukey post hoc analysis to compare visits 2 and 3 and rural/urban, and we found a near-significant increase in noise amplitude from visit 2 to 3 from rural sites ($t=2.52$, $df=241$, $p=0.059$), but no difference between visits to urban sites ($t=1.63$, $df=241$, $p=0.36$). Across visits, rural sites showed variability in noise levels across 24 h, whereas urban sites seemed to maintain relatively consistent patterns (Figure S6). During the third visit, we saw high noise levels at night in rural areas that nearly match nightly recordings in urban areas (Figure S6). During the fourth visit, rural areas showed heightened daily noise levels (Figure S6).

Using the USDA data on harvest rates for corn and soybeans in Nebraska, we found that most of the corn harvest (51%) occurred during the fourth visit whereas most of the soybean harvest (70%) occurred during the third visit (Figure 4C). As a result, the mean harvest of corn and soybeans was at its peak during the third visit (Figure 4C), coinciding with the increase in daily average amplitude at

the third visit (Figure 4B). When we tested to see whether the mean percent harvest was correlated with the daily average amplitude of rural sites, we found a positive trend from the robust LME (Table 1) that was significant in the LME ($t=2.12$, $df=71$, $p=0.037$).

Spider microhabitat use in response to vibratory environment

We collected spiders from four different sites that varied in average noise amplitude (5A: -69 dB re FS, 6C: -69 dB re FS, 8A: -64 dB re FS, 8B: -55 dB re FS). We first tested whether spiders differed in age or body condition by site. Spiders from different sites did not vary by age at the time of the trial ($F_{3,65}=1.40$, $p=0.25$). Body condition showed marginally no difference between sites ($F_{3,65}=2.62$, $p=0.058$). A Tukey's post hoc test showed a trend that site 8A spiders were in better condition than spiders from sites 8B ($t=-2.57$, $df=65$, $p=0.059$) and 6C ($t=0.247$, $df=65$, $p=0.075$) but not 5A ($t=2.18$, $df=65$, $p=0.14$). We also found that age and condition have a significant positive correlation ($t=3.80$, $df=67$, $p<0.001$, adj. $R^2=0.165$).

Direct observations of microhabitat use

- (i) Site noise amplitude and age had no effect on a spider's probability of being found in the loud or quiet chamber

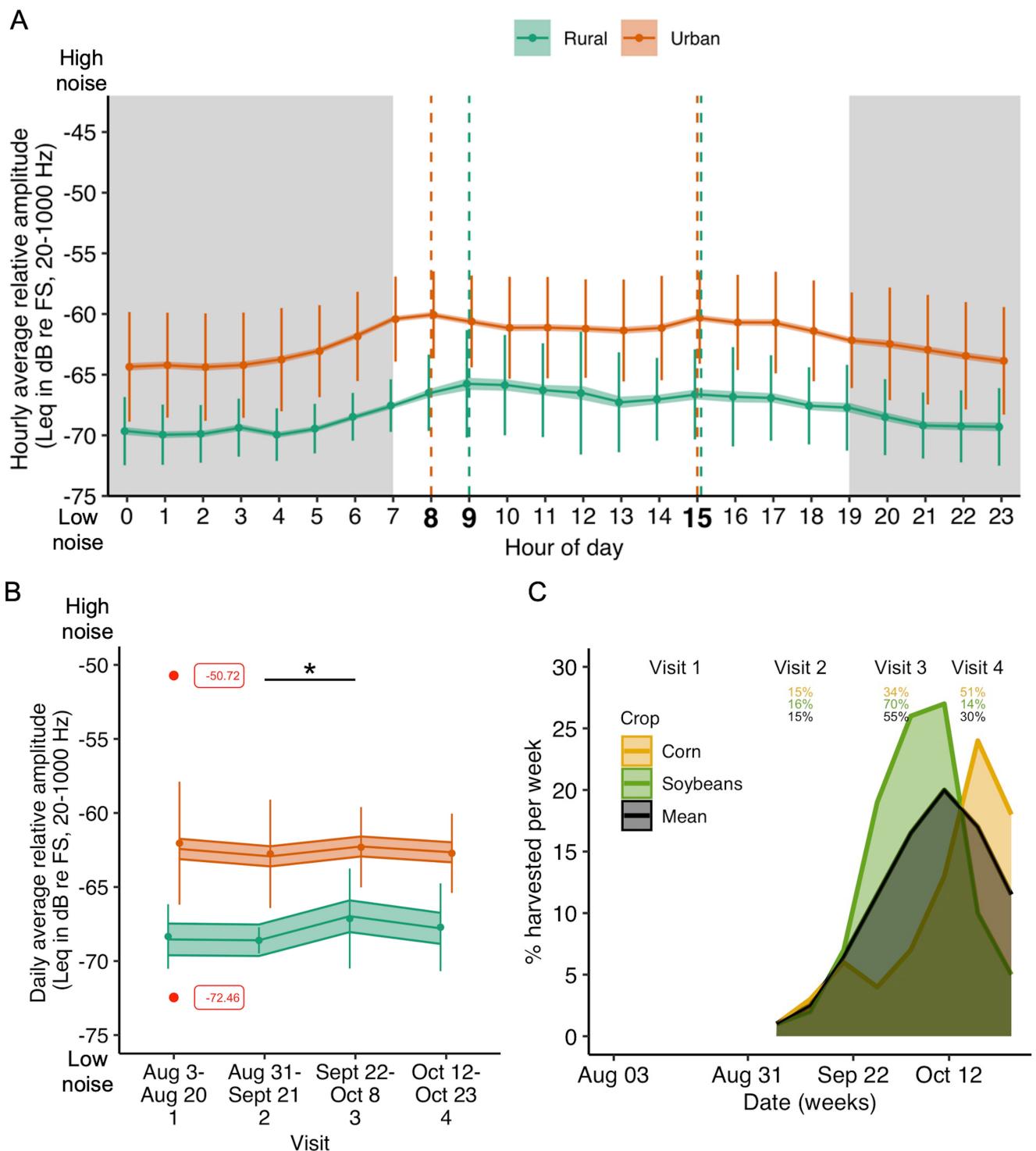


FIGURE 4 Results of temporal analysis of vibratory noise in 2020. (A) The calculated mean (\pm SD error bars, \pm SE ribbon) hourly average noise amplitude (measured as Leq in units of dB) across 24 h by rural/urban. Vertical dashed lines and bolded hour represent peaks of the associated site type. Darkened areas represent nighttime. Vibratory amplitude was highest around 08:00/09:00 and 15:00 h and lowest throughout the night, but urban sites remained consistently louder than rural sites across 24 h. (B) Raw data (mean \pm SD) and model predictions (line \pm ribbon = mean \pm SE) from linear mixed effect model of daily average noise amplitude by visit (1–4 throughout *Agelenopsis pennsylvanica* penultimate juvenile/adult season) and rural/urban (green = rural, orange = urban) with site as a random factor. The red dots and text show the lowest and highest daily average noise amplitude reading. Line and asterisk indicate the results of a Tukey pairwise comparison post hoc test (* $p < 0.05$). Noise levels were higher at urban than rural sites, and there was a trend that noise amplitude varied by visit. The post hoc test showed that there was an increase in noise amplitude from visit 2 to visit 3. (C) USDA data on percent of annual crops harvested at the end of each week in 2020 across Nebraska for two major crops in Lancaster County: corn and soybeans. Vertical lines show the boundaries of each visit for vibratory noise recording. Percentages represent the percent of the harvest of the associated crop that occurred during the visit. Corn and soybean harvest increased around the third visit when we saw a subsequent increase in noise levels.

TABLE 2 Final model results of the statistical analyses investigating predictors of spiders' microhabitat use under a variable vibratory environment.

Measurement	Distribution	Response	Predictor	Test statistic ^a	Residual df	p	R ²
Spider position	Binomial	(i) Loud (1) or quiet (0)	Amplitude	0.30	244	0.76	0.655 ^b
			Age	-0.36			
			Amplitude×age	-1.75			
Silk mass	Binomial	(ii) Loud (1) or quiet (0)	Amplitude	1.11	65	0.27	0.072
			Age	-0.72			
			Amplitude×age	-1.94			
	Beta	(iii) Proportion of silk mass	Chamber	168.44	195	<0.001	0.469
			Amplitude	1.05			
			Age	0.04			
Spider position	Binomial	(iv) Stay (1) or move (0)	Chamber×amp.	6.23	65	0.044	0.038
			Chamber×age	0.40			
			Chamber×amp.×age	11.63			
Spider position	Binomial	(iv) Stay (1) or move (0)	Body condition	0.11	65	0.91	0.12
			Amplitude×condition	-1.57			

Note: The amplitude (amp.) is measured as Leq and has units dB re FS.

^aThe test statistic was z for all tests except for beta regression where it was χ^2 .

^bThis test was a mixed model with spider ID as a random effect. As such, the R² value is the conditional R². The marginal R² value was 0.055.

(Table 2). Yet, there was a non-significant trend exhibited in the interaction between noise amplitude and age (Table 2)—that is, spiders from louder sites decreased in the probability of being found in the loud chamber as age increased whereas age effects diminished for spiders from quieter sites (Figure 5A). We found further support for this finding when we looked for age effects within sites and found a trend for site 8B spiders (the loudest site, $z_{2,84} = -1.71, p = 0.088$) but no effect of age for spiders from other sites ($p > 0.36$). We observed the spiders' positions daily, but there were no trends associated with the day of observation and it was dropped from the model.

(ii) The results for the chamber with more dry silk mass (regardless of the extent of the difference) were similar to the findings from spiders' positions (Table 2; Figure 5B). We also found a trend that spiders from the loudest site decreased in likelihood of putting more silk in the loud chamber (a proxy of microhabitat choice) with age ($z_{2,22} = -1.74, p = 0.083$) but there were no age effects for the rest of the sites ($p > 0.14$).

(iii) As total silk mass increased with age ($z_{1,66} = 3.94, p < 0.001$), we used the proportion of silk mass between chambers to test the extent to which spiders differentially apportioned silk between chambers. Site noise amplitude, age, and the interaction between chamber and age did not significantly predict the proportion of silk (Table 2). There was a significant effect of the chamber on the proportion of silk (Table 2), where spiders invested more silk in the larger chambers than in the tunnel (following a Tukey's post hoc test). We also found a significant interaction between chamber and noise amplitude (Table 2). Exploring this interaction post hoc revealed significant interactions

between the loud versus quiet chambers ($t = 3.973, df = 195, p < 0.001$) and quiet versus tunnel ($t = -3.011, df = 195, p = 0.008$) but not loud versus tunnel ($t = 0.636, df = 195, p = 0.80$) chambers at the 25th percentile age. In other words, spiders from increasingly louder sites used proportionally more silk in the tunnel and loud chambers and less in the quiet (Figure 5C). At the median age, there was only a trend for the interaction between quiet and tunnel silk proportions with site noise amplitude ($t = -2.184, df = 195, p = 0.076$). At the 75th percentile age, there were no significant interactions between chambers and site noise amplitude. There was also a significant three-way interaction between chamber, amplitude, and age (Table 2; Figure 5C). When we compared chambers pairwise for interacting age trends for each site noise amplitude, the only significant finding was that spiders from the loudest site decreased silk in the loud chamber and increased in the quiet chamber as age increased ($t = -3.109, df = 195, p = 0.006$). We tested for chamber×age within sites, and spiders from each site had a significantly higher proportion of silk in the loud and quiet chambers compared to the tunnel (8B: $\chi^2 = 28.58, p < 0.001$; 8A: $\chi^2 = 8.58, p = 0.014$; 6C: $\chi^2 = 5.93, p = 0.052$; 5A: $\chi^2 = 6.42, p = 0.040$, all df=2). The loudest site also had a higher proportion of silk in the loud than quiet chamber ($t = 3.29, df = 66, p = 0.004$).

Fidelity of vibratory microhabitat

(iv) Site noise amplitude, body condition, and their interaction did not significantly predict whether a spider was

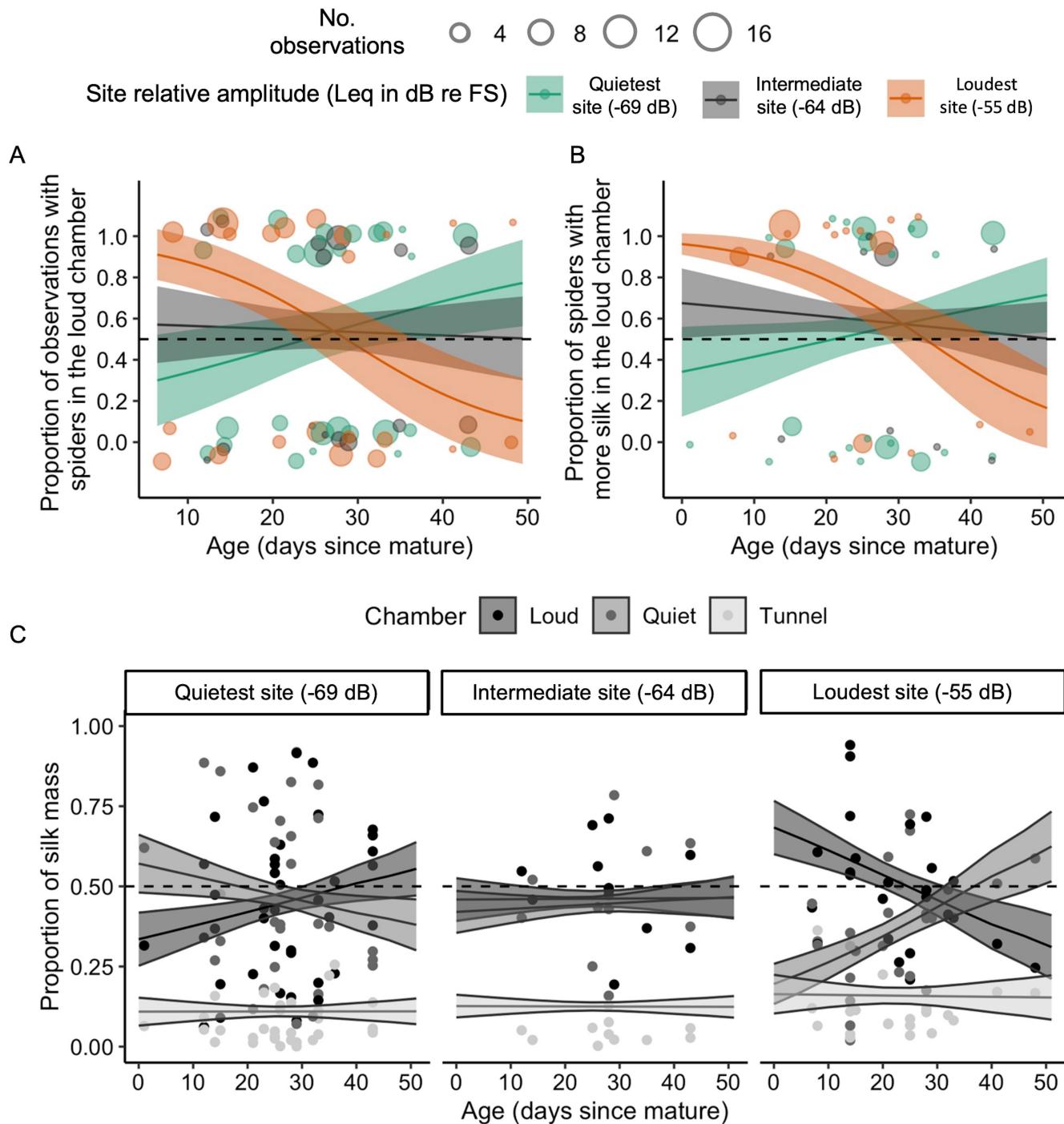


FIGURE 5 Results of microhabitat use experiment. (A) The proportion of observations of spiders' positions and (B) the proportion of spiders with more dry silk mass in the loud chamber (vs. the quiet chamber) of the microcosm for spiders of different ages and from sites with different vibratory noise amplitudes (measured as Leq in dB re FS). From quietest to loudest, the site amplitudes are -69 dB re FS to -55 dB re FS, respectively. For both (A) the spider's position and (B) the silk mass, we found a trend in the interaction between site noise amplitude and age. Spiders from the loudest site were more often observed in the loud chamber as recently matured individuals but the effect decreased with age. (C) The proportion of total dry silk mass found in the chambers (loud, quiet, or tunnel) for spiders of different ages and from sites with differing noise amplitude. Spiders put the lowest proportion of silk in the tunnel. At the 25th percentile age, spiders used more silk in the tunnel and loud chambers and less in the quiet as their site noise levels increased. However, these relationships weakened and became non-significant as age increased. For all graphs, the lines (\pm SE) represent the mean (\pm SE) from the model predictions, respectively. Points represent the raw data. Because (A, B) represents binomial data (i.e., crowding of points at 0 and 1), point size represents the number of observations at that age. Lack of association with a particular chamber is represented by the dashed line at 50%.

found in the same chamber (loud, quiet, or tunnel) all 4 days of observation (Table 2), and age was dropped from the model entirely. When we looked for variation within sites, only spiders from site 8B (the loudest site) were less likely to stay in the same chamber as age increased ($z_{2,22} = -2.02, p = 0.043, R^2 = 0.174$).

In summary, we found that vibratory noise levels vary spatially and temporally across urban–rural Lincoln, NE, with respect to *A. pennsylvanica*'s habitat and season. Noise levels differed by up to 15 dB, on average, across the sites tested. The majority of spatial variability occurred in urban areas, where noise amplitude was correlated with potential traffic impact. On the other hand, rural areas exhibited more seasonal variation in noise levels, with the harvest season suspected to increase noise levels. Vibratory noise levels vary significantly between urban and rural environments throughout the night when *A. pennsylvanica* are most active (see "Spider activity patterns across 24 h" section in Supporting Information). We tested how *A. pennsylvanica* used a variable vibratory microhabitat and found that only young spiders from the loudest site associated more with a particular chamber—surprisingly, the loud chamber.

DISCUSSION

We took an animal-centric approach to measure the spatiotemporal variation in vibratory noise levels across an urban–rural landscape and season of a common urban arthropod, *A. pennsylvanica*. We recorded ambient vibrations next to *A. pennsylvanica* webs. Vibratory noise amplitude (Leq) varied significantly across space in urban areas, showing a positive correlation with proximity to high-traffic areas, as predicted. Vibratory noise also varied seasonally in rural areas, and this was coincident with the timing of harvest. We also assessed the microhabitat use of *A. pennsylvanica* by allowing spiders to construct webs in a microcosm with a loud (high Leq) vibratory environment on one end (chamber) and quiet on the other. In contrast to our prediction, *A. pennsylvanica* did not avoid high-noise areas. On the contrary, a trend showed young spiders collected from the loudest site spent more time and used more silk in loud conditions. Our findings indicated that *A. pennsylvanica* experiences high variation in vibratory noise across the urban–rural gradient they inhabit and across the season, and in laboratory conditions, they do not actively avoid using loud microhabitats.

We found that vibratory noise has more spatial variation in urban as compared to rural areas. Across all measured sites, vibratory noise levels varied by about 15 dB (−55 to −70 dB re FS), on average. Recent airborne acoustic noise surveys have observed a similar degree of variation in ambient noise (Fiedler & Zannin, 2015), including an animal-centric survey that found a correlation between airborne

acoustic noise and great tit behavior (Akçay et al., 2020). Within the measured range, we found that urban sites were responsible for a broader part of the range (−55 to −66 dB re FS) than rural sites (−66 to −70 dB re FS).

Vibratory noise across our urban sites was highly correlated with estimated traffic impacts. This finding adds to prior research demonstrating that human activity can have substantial impacts on the vibratory landscape. For example, seismic measurements taken before and during COVID-19 lockdowns showed a 50% reduction in seismic noise across the globe (Lecocq et al., 2020). Proximity to roads was previously found to predict ambient airborne noise (Turner et al., 2018) and is thought to be a key source of terrestrial vibratory noise (Roberts & Howard, 2022). Because airborne and substrate-borne vibrations can transition between media (Šturm et al., 2022), it is difficult, if not impossible, to untangle the two sources in substrate-borne recordings. Traffic, for example, likely adds substrate-borne noise indirectly via transfer of airborne noise to the substrate and directly through wheels contacting the ground. We also mention anecdotally that sites with the highest noise levels were frequently found near high-traffic routes, such as highways and interstates (see Figure 3A). Recent studies have shown that vibroscapes within habitats can exhibit vast spatiotemporal variation, especially with respect to biological noise produced by vibration-producing arthropods (Akassou et al., 2022; Šturm et al., 2021). Biological noise likely contributed to the ambient vibrations recorded in the field in this study. As arthropod vibratory communication (Šturm et al., 2021) and anthropogenic sources of noise likely overlap spectrally (<1000 Hz), we were unable to untangle these noise sources. A lack of distinguishable arthropod-related vibratory signals may be the result of signal timing (we reviewed *A. pennsylvanica*'s most active hour: 21:00–22:00), avoidance of areas near spider webs where we recorded, or traffic being a louder source of noise in that range (Video S1).

On a smaller scale, our data showed that manmade substrates carried louder vibrations than plants in urban, but not rural areas. This contrasts with the findings of Wu and Elias (2014) who found higher noise levels on natural substrates compared to artificial substrates. There are a couple of possible explanations for this difference. First, Wu and Elias (2014) used a laser vibrometer to record ambient vibrations whereas we used contact microphones which added weight to the plant. This additional weight may have reduced wind-induced noise—a major source of plant noise. Although wind may have partially contributed to the measured noise levels, we do not believe it played a big role, as we found noise to be louder in urban areas which often exhibit lower surface wind speeds than the surrounding area due to drag produced by buildings (Collier, 2006). Second, we recorded vibrations at private properties, and the microphone attachments on manmade substrates were often hotspots of daily activity, including garages with cars entering and exiting and porches of dog owners with dogs coming and going from the house. Still, these sources of

noise are likely reflective of what the animals living near these structures experience on a daily basis.

In addition to variation in noise levels between rural/urban habitats and substrates, we also found differences in the frequency profiles (Figures S3 and S5). Differences in vibratory noise between rural and urban areas was especially prevalent below 500 Hz, and urban sites exhibited more variation in noise levels in this range than rural sites. The shape of the power spectrum is similar to another study measuring anthropogenic vibratory noise (Wu & Elias, 2014), with lower frequencies containing more energy. There was far more variation between rural/urban sites than between substrates within sites, suggesting that the noise level is a better predictor of the vibroscope amplitude than the material of the substrate, but this remains to be tested directly. Still, within a site with high noise levels, concrete and paneling exhibited different frequency profiles, with concrete carrying louder low-frequency vibrations (<500 Hz) and quieter high-frequency vibrations than paneling. It remains unclear, however, if spiders could sense this variation and choose web site locations accordingly.

The shape of the noise level curves across 24 h varied with each visit for rural and urban areas (Figure S6). Consistency in traffic patterns varies depending on land use across urban areas, and workplace and school commute routes are strong contributors to predictable traffic schedules (Zahnow & Abewickrema, 2023). Perhaps a lack of a school commute during the first visit explains, in part, the flatter urban vibratory noise curve (Figure S6). In our study, the traffic estimates were based on annual averages, and thus do not capture seasonal or daily variations in traffic patterns.

In rural areas, an increase in vibratory noise levels during the third visit (September 22–October 8) coincided with the peak of Nebraska field corn and soybean harvest. We point out, however, that these were broad estimates of crop harvest across the entire state and as such are a potential underestimate of this relationship. Had we noted crop harvesting events for each site and surrounding fields, we believe we would have seen a stronger effect of harvest on the vibratory noise levels. This assertion is further supported by our observation of an increase in rural vibratory noise levels during the middle of the night on the third visit (Figure S6), as farmers frequently harvest during the night when temperatures are cooler (personal observation and communications). Furthermore, we note that agricultural equipment can produce high-amplitude airborne and substrate-borne noise in a frequency range relevant to the current study (<1000 Hz; Koppel et al., 2012; Sümer et al., 2006), and vegetation can serve as noise attenuators, with seasonal changes in vegetation density (e.g., crop harvest) potentially impacting vibratory noise levels (Gaudon et al., 2022). Unfortunately, the noise-absorbing properties of crop fields have only been tested in regard to airborne sound, and crops are most effective at absorbing airborne sound at frequencies above 4 kHz (Bashir et al., 2015). It is unknown whether crops can attenuate substrate-borne noise.

When assessing vibratory-based microhabitat use, we found that all spiders utilized the entire space provided by the artificial microcosm. For a subset of spiders observed throughout the 1st night of web-building, no spiders were exclusively seen in a single chamber suggesting that they were fully exploring the microcosm (Figure S9). We also frequently observed spiders in different chambers from day-to-day. Contrary to our predictions, *A. pennsylvanica* did not avoid high-noise conditions. Rather, most spiders spent relatively equal time in either chamber and laid relatively equal silk mass in each large chamber. One possible explanation for this is that the use of white noise to produce an artificial vibroscape may not be an accurate representation of the natural vibroscape (Figure S3). Vertebrate studies, for example, have shown that synthetic vibratory noise is less effective than recorded vibratory noise to elicit animal responses (Caorsi et al., 2019; De Luca et al., 2023). Future research should include recorded playback and field studies. Also, the quiet chamber remained louder than the daily average of any rural site, so instances of equivalent silk use in each chamber may be a result of both chambers being considered ‘loud’. We also caution that the loud chamber had higher noise levels than the quiet chamber for frequencies above 500 Hz where noise does not appear to be present in the field (Figure S3).

Still, the microhabitat use experiment revealed that spiders from sites with distinct vibratory profiles respond to vibratory microhabitat variation in different and complex ways, especially with respect to age. Young spiders collected from the loudest site were more frequently observed in the loud chamber of the microcosm, seemingly choosing a familiar vibratory environment. We similarly observed the greatest proportion of silk in the loud chamber for this subset of spiders. These aging effects call into question whether spiders experience age-related declines in sensory sensitivity and/or age-related decrease in choosiness. In the past couple of years, evidence of age-related auditory hearing loss in arthropods has emerged (Austin et al., 2023; Keder et al., 2020). Whether age-related declines occur in other modalities is unknown for arthropods. There is also evidence that adult female wolf spiders exhibited age-related declines in choosiness for male traits beyond about 3 weeks of post-maturation (*Schizocosa ocreata* [Hentz], Uetz & Norton, 2007; *Rabidosa rabida* [Walckenaer], Wilgers & Heberts, 2012).

For spiders collected from the loudest site, increased time spent and use of silk in the loud chamber was most evident in the first 2 weeks following maturation. Shortly after female spiders mature in the field, males begin courting on female webs using vibratory courtship signals, which play a key role in mating success for *Agelenopsis* spiders (Singer et al., 2000). Thus, the vibratory environment where the spider builds its web could impact mating success if vibratory noise disrupts or masks the reception of vibratory signals. Yet, young spiders from loud sites use the loud microcosm chamber for web construction whereas other spiders exhibit approximately equivalent microhabitat use across the

microcosm. We suggest two potential explanations for our observed patterns of spider sightings and silk mass that are not mutually exclusive. In both cases, we suspect that juvenile experience influenced adult behavior.

First, *A. pennsylvanica* may be actively choosing or selecting a particular vibratory environment to construct their web. They may prefer a vibratory environment and due to their preference for the location, they may accumulate more silk there. As support for this hypothesis, young, loud-reared spiders invested more silk and spent more time in the loud microcosm chamber. Yet, we note that spiders were not often observed in the same microcosm chamber on all 4 days, suggesting an incomplete potential preference. Also, the spider's position did not always match the chamber that the spider spent the most time in during the first night or the chamber with the highest proportion of silk mass (Figure S9). Still, *A. aperta* (a close relative) actively selects sites for web construction, and the thermal environment (Riechert & Tracy, 1975) and vegetation (Riechert, 1976) have been shown to be important during selection. Artificial light at night, another form of human-induced sensory pollution, has been shown to guide microhabitat use by an orb-weaving spider, *Eriophora biapicata* (Koch) (Willmott et al., 2019). Even airborne noise (in the form of river noise) appears to influence web site selection for web-building spiders (Araneidae and Tetragnathidae; Gomes et al., 2021). Animals may select adult habitats that match natal habitat conditions—a phenomenon called habitat imprinting (Davis & Stamps, 2004). For example, the crab spider, *Misumena vatia* (Clerck), was found to preferentially hunt on flower species that match the flower of their final instar (Morse, 1999). Thus, *A. pennsylvanica* collected from loud sites may be actively selecting web construction sites based on the natal vibratory environment but experiments directly aimed at assessing the habitat imprinting hypothesis are necessary to support this hypothesis.

Second, experience-dependent microhabitat-based silk use may help explain why young spiders from loud sites exhibited increased use of the loud chamber with more silk laid. If using more silk when in a loud vibratory environment improves vibratory information transfer across the web, spiders may increase silk investment when in a noisy environment and increased silk investment likely requires more time. In relation to our data, juveniles that experienced loud environments during development may have spent more time in the loud chamber, laying more silk to mitigate the effects of noise. Other spiders have shown similar plasticity in web structure in response to external cues including prey type and size (Blamires, 2010; Dahirel et al., 2019). Existing evidence for plasticity in web construction is currently biased toward orb-weaving spiders, and the degree to which environmental conditions can affect web construction in most spiders is unclear. Still, web-building spiders can control how vibrations travel across their web by manipulating different properties of the web, including supercontraction of silk or active tensioning of the web (Mortimer et al., 2016). Research directly

addressing how increased silk use changes the transfer of vibratory information is needed to further explore microhabitat choice and microhabitat-dependent silk use, especially in *A. pennsylvanica*.

There are several notable aspects or concerns related to our study. First, there are outliers in the vibratory measurements of sites due to unexpected weather (pop-up storm cell at visit 1 of sites 2A–C) and some high-amplitude human activity—mowing (7A visit 1 and 6A visit 2), a tree being cut down (3A visit 1), and yard work (1B visit 3)—as we told property owners to carry out their normal activities. The positive of this is that it gave us the opportunity to see the breadth of vibratory disturbances across sites. Second, as we measured relative amplitudes of noise, it is challenging to know whether the observed noise levels are relevant for *A. pennsylvanica*. Yet, we know that the lyriform organ—a vibration sense organ found at the distal end of a spider's metatarsus—is highly sensitive to vibrations (Barth & Geethabali, 1982) and that anthropogenic vibratory noise is capable of influencing prey cues for another web-building spider (Wu & Elias, 2014). Third, although the acoustic foam in the microhabitat-use trials reduced vibration transmission between microcosms, the playback also produced airborne noise. Zhou et al. (2022) found that airborne acoustic waves can transfer and carry as web-borne vibrations through the webs of the orb-weaving spider, *Larinoides sclopetarius* (Clerck). However, both the vibratory amplitude (Figure 2C) and sound amplitude (varying by 14.3 ± 0.5 dB) were distinct between our loud and quiet chambers. Thus, we believe that the added airborne noise did not weaken the differences in vibratory environment between chambers. Fourth, the microcosms were small (1183 cm^3) compared to the field-measured web area of *A. pennsylvanica* that participated in the microhabitat use trials ($1963 \pm 130 \text{ cm}^2$). This means that spiders may have simply filled all the available space with web. We accounted for this possibility by limiting the time that the spiders had to build (four nights) as preliminary trials suggested that this was adequate time to see differences before space filling occurred. Finally, the direct role that a site's noise amplitude had on the observed differences in microhabitat use is unclear. The collection sites for the microhabitat use trials likely differed by a number of different conditions, including (but not limited to) artificial light at night, temperature, and food availability. To control for these confounds, an experiment using spiders reared in the laboratory under different vibratory conditions would need to be conducted.

Conclusions

Vibratory noise is an understudied human disturbance. Like airborne acoustic noise, it has the potential to overlap spectrally, spatially, and temporally with animal communication and foraging signals/cues. This gap in research is concerning because the use of vibratory information is ubiquitous across ecologically critical arthropods. We

stress the importance of understanding how vibratory noise (and any environmental disturbance) varies across the microhabitat and season of the study organism to identify potential overlaps. In the present study, we have shown that vibratory noise varies across space and time relevant to *A. pennsylvanica* habitat (across urban–rural space) and adult season (August–October). Vibratory noise had stronger spatial variation in urban areas related to estimated traffic disturbance and strong seasonal variation in rural areas related to timing of harvest. Vibratory noise was quieter during the night, when *A. pennsylvanica* are most active, compared to the day. Still, *A. pennsylvanica* may be impacted by the louder nighttime vibroscape in urban compared to rural habitats. Young *A. pennsylvanica* collected from vibrationally loud sites exhibited increased microhabitat use of loud vibratory environments. These findings raise several new questions. How does experience with vibratory noise impact behavioral plasticity? Can plastic silk use or web design allow spiders to adjust to variable vibratory environments? Does age-related sensory sensitivity decline affect a spider's ability to assess and react to its environment? Vibratory noise is as widespread and persistent as airborne acoustic noise and we urge the study of its impact across vibrationally-orienting animals, particularly arthropods. Further research is vital to determine the role vibratory noise may play in the disappearance of arthropods and their essential ecosystem services from urban spaces.

AUTHOR CONTRIBUTIONS

Brandi J. Pessman: Conceptualization (equal); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (equal); validation (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Rowan McGinley:** Conceptualization (supporting); formal analysis (supporting); investigation (supporting); methodology (supporting); validation (equal); visualization (supporting); writing – review and editing (equal). **Eileen A. Hebets:** Conceptualization (equal); formal analysis (supporting); funding acquisition (supporting); investigation (supporting); methodology (equal); project administration (lead); resources (lead); supervision (lead); validation (equal); visualization (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest to declare and no disputes over ownership of the data.

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DATA AVAILABILITY STATEMENT

All data and code that support the findings of this study are available at https://github.com/brandipessman/Vibratory_Noise.

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REFERENCES

- Akassou, I., Zapponi, L., Verrastro, V., Ciolfi, M. & Mazzoni, V. (2022) Extending the vibroscape to agroecosystems: investigating the influence of abiotic factors and monitoring insect vibrational signaling. *PeerJ*, 10, e14143. Available from: <https://doi.org/10.7717/peerj.14143>
- Akçay, Ç., Porsuk, Y.K., Avşar, A., Çabuk, D. & Bilgin, C.C. (2020) Song overlapping, noise, and territorial aggression in great tits. *Behavioral Ecology*, 31, 807–814. Available from: <https://doi.org/10.1093/beheco/araa030>
- Attali, D. & Baker, C. (2023) *ggExtra: add marginal histograms to "ggplot2", and more "ggplot2" enhancements*.
- Austin, T.T., Thomas, C.L., Lewis, C., Blockley, A. & Warren, B. (2023) Metabolic decline in an insect ear: correlative or causative for age-related auditory decline? *Frontiers in Cell and Developmental Biology*, 11, 392.
- Baquero, O.S. (2019) *ggsn: north symbols and scale bars for maps created with "ggplot2" or "ggmap"*.
- Barber, J.R., Crooks, K.R. & Fristrup, K.M. (2010) The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution*, 25, 180–189. Available from: <https://doi.org/10.1016/j.tree.2009.08.002>
- Barth, F.G. & Geethabali. (1982) Spider vibration receptors: threshold curves of individual slits in the metatarsal lyriform organ. *Journal of Comparative Physiology A*, 148, 175–185. Available from: <https://doi.org/10.1007/BF00619124>
- Bashir, I., Taherzadeh, S., Shin, H.-C. & Attenborough, K. (2015) Sound propagation over soft ground without and with crops and potential for surface transport noise attenuation. *The Journal of the Acoustical Society of America*, 138, 101–108. Available from: <https://doi.org/10.1121/1.4913000>

- Society of America, 137, 154–164. Available from: <https://doi.org/10.1121/1.4904502>
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014) Fitting linear mixed-effects models using lme4. *arXiv*. Available from: <https://doi.org/10.48550/arXiv.1406.5823>
- Blamires, S.J. (2010) Plasticity in extended phenotypes: orb web architectural responses to variations in prey parameters. *Journal of Experimental Biology*, 213, 3207–3212. Available from: <https://doi.org/10.1242/jeb.045583>
- Bunkley, J.P., McClure, C.J.W., Kawahara, A.Y., Francis, C.D. & Barber, J.R. (2017) Anthropogenic noise changes arthropod abundances. *Ecology and Evolution*, 7, 2977–2985. Available from: <https://doi.org/10.1002/ece3.2698>
- Caldwell, M.S. (2014) Interactions between airborne sound and substrate vibration in animal communication. Studying vibrational communication. In: Crocroft, R.B., Gogala, M., Hill, P.S.M. & Wessel, A. (Eds.) *Animal signals and communication*. Berlin, Heidelberg: Springer, pp. 65–92.
- Candolin, U. & Wong, B.B.M. (2019) Mate choice in a polluted world: consequences for individuals, populations and communities. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 374, 20180055. Available from: <https://doi.org/10.1098/rstb.2018.0055>
- Caorsi, V., Guerra, V., Furtado, R., Llusia, D., Roese Miron, L., Borges-Martins, M. et al. (2019) Anthropogenic substrate-borne vibrations impact anuran calling. *Scientific Reports*, 9, 19456.
- Choi, N., Miller, P. & Hebets, E.A. (2024) Vibroscape analysis reveals acoustic niche overlap and plastic alteration of vibratory courtship signals in ground-dwelling wolf spiders. *Communications Biology*, 7, 1–13. Available from: <https://doi.org/10.1038/s42003-023-05700-6>
- Classen-Rodríguez, L., Tinghitella, R. & Fowler-Finn, K. (2021) Anthropogenic noise affects insect and arachnid behavior, thus changing interactions within and between species. *Current Opinion in Insect Science*, 47, 142–153. Available from: <https://doi.org/10.1016/j.cois.2021.06.005>
- Croxford, R.B. & Rodríguez, R.L. (2005) The behavioral ecology of insect vibrational communication. *BioScience*, 55, 323–334. Available from: [https://doi.org/10.1641/0006-3568\(2005\)055\[0323:TBEOV\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0323:TBEOV]2.0.CO;2)
- Collier, C.G. (2006) The impact of urban areas on weather. *Quarterly Journal of the Royal Meteorological Society*, 132, 1–25. Available from: <https://doi.org/10.1256/qj.05.199>
- Dahirel, M., De Cock, M., Vantieghem, P. & Bonte, D. (2019) Urbanization-driven changes in web building and body size in an orb web spider. *Journal of Animal Ecology*, 88, 79–91. Available from: <https://doi.org/10.1111/1365-2656.12909>
- Davis, J.M. & Stamps, J.A. (2004) The effect of natal experience on habitat preferences. *Trends in Ecology & Evolution*, 19, 411–416. Available from: <https://doi.org/10.1016/j.tree.2004.04.006>
- De Luca, J., Zaffaroni-Caorsi, V., Bosch, J., Llusia, D., Beltrán, J.F. & Márquez, R. (2023) Effect of natural abiotic soil vibrations, rainfall and wind on anuran calling behavior: a test with captive-bred midwife toads (*Alytes obstetricans*). *Journal of Comparative Physiology A*, 209, 105–113. Available from: <https://doi.org/10.1007/s00359-022-01596-5>
- Dewitz, J. & U.S. Geological Survey. (2021) *National Land Cover Database (NLCD) 2019 products* (ver. 2.0, June 2021). U.S. Geological Survey Data Release. Available from: <https://doi.org/10.5066/P9KZCM54>
- Díaz, J., DeFelipe, I., Ruiz, M., Andrés, J., Ayarza, P. & Carbonell, R. (2022) Identification of natural and anthropogenic signals in controlled source seismic experiments. *Scientific Reports*, 12, 3171. Available from: <https://doi.org/10.1038/s41598-022-07028-3>
- Fiedler, P.E.K. & Zannin, P.H.T. (2015) Evaluation of noise pollution in urban traffic hubs—noise maps and measurements. *Environmental Impact Assessment Review*, 51, 1–9. Available from: <https://doi.org/10.1016/j.eiar.2014.09.014>
- Fox, J. (2003) Effect displays in R for generalised linear models. *Journal of Statistical Software*, 8, 1–27. Available from: <https://doi.org/10.18637/jss.v008.i15>
- Fox, J. & Weisberg, S. (2019) *An R companion to applied regression*. Thousand Oaks, CA: Sage.
- Garnier, S., Ross, N., Camargo, A.P., Sciaiani, M., Rudis, R. & Scherer, C. (2021) *Revision – colorblind-friendly color maps for R*.
- Gaudon, J.M., McTavish, M.J., Hamberg, J., Cray, H.A. & Murphy, S.D. (2022) Noise attenuation varies by interactions of land cover and season in an urban/peri-urban landscape. *Urban Ecosystems*, 25, 811–818. Available from: <https://doi.org/10.1007/s11252-021-01194-4>
- Gohel, D. & Skintzos, P. (2022) *Using the flextable R package*.
- Gomes, D.G.E., Hesselberg, T. & Barber, J.R. (2021) Phantom river noise alters orb-weaving spider abundance, web size and prey capture. *Functional Ecology*, 35, 717–726. Available from: <https://doi.org/10.1111/1365-2435.13739>
- Goulson, D. (2019) The insect apocalypse, and why it matters. *Current Biology*, 29, R967–R971. Available from: <https://doi.org/10.1016/j.cub.2019.06.069>
- Halfwerk, W. & Slabbekoorn, H. (2015) Pollution going multimodal: the complex impact of the human-altered sensory environment on animal perception and performance. *Biology Letters*, 11, 20141051. Available from: <https://doi.org/10.1098/rsbl.2014.1051>
- Hill, P.S.M. (2009) How do animals use substrate-borne vibrations as an information source? *Naturwissenschaften*, 96, 1355–1371. Available from: <https://doi.org/10.1007/s00114-009-0588-8>
- Hill, P.S.M., Lakes-Harlan, R., Mazzoni, V., Narins, P.M., Virant-Doberlet, M. & Wessel, A. (2019) *Biotremology: studying vibrational behavior*. Cham, Switzerland: Springer International Publishing.
- Hill, P.S.M. & Wessel, A. (2016) Biotremology. *Current Biology*, 26, R187–R191. Available from: <https://doi.org/10.1016/j.cub.2016.01.054>
- Jakob, E.M., Marshall, S.D. & Uetz, G.W. (1996) Estimating fitness: a comparison of body condition indices. *Oikos*, 77, 61–67. Available from: <https://doi.org/10.2307/3545585>
- Joo, W., Gage, S.H. & Kasten, E.P. (2011) Analysis and interpretation of variability in soundscapes along an urban–rural gradient. *Landscape and Urban Planning*, 103, 259–276. Available from: <https://doi.org/10.1016/j.landurbplan.2011.08.001>
- Jürgens, A. & Bischoff, M. (2017) Changing odour landscapes: the effect of anthropogenic volatile pollutants on plant–pollinator olfactory communication. *Functional Ecology*, 31, 56–64. Available from: <https://doi.org/10.1111/1365-2435.12774>
- Kahle, D. & Wickham, H. (2013) ggmap: spatial visualization with ggplot2. *The R Journal*, 5, 144. Available from: <https://doi.org/10.32614/RJ-2013-014>
- Kassambara, A. (2023) Ggpubr: "ggplot2" based publication ready plots.
- Kassambara, A. & Mundt, F. (2020) factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0.7.
- Keder, A., Tardieu, C., Malong, L., Filia, A., Kashkenbayeva, A., Newton, F. et al. (2020) Homeostatic maintenance and age-related functional decline in the *Drosophila* ear. *Scientific Reports*, 10, 7431. Available from: <https://doi.org/10.1038/s41598-020-64498-z>
- Koller, M. (2016) robustlmm: an R package for robust estimation of linear mixed-effects models. *Journal of Statistical Software*, 75, 1–24. Available from: <https://doi.org/10.18637/jss.v075.i06>
- Koppel, T., Tint, P., Karajeva, G., Reinhold, K. & Kalle, S. (2012) Vibration and noise caused by lawn maintenance machines in association with risk to health. *Agronomy Research*, 10, 251–260.
- Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2017) lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software*, 82, 1–26. Available from: <https://doi.org/10.18637/jss.v082.i13>
- Lé, S., Josse, J. & Husson, F. (2008) FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software*, 25, 1–18. Available from: <https://doi.org/10.18637/jss.v025.i01>
- Lecocq, T., Hicks, S.P., Van Noten, K., van Wijk, K., Koelemeijer, P., De Plaen, R.S.M. et al. (2020) Global quieting of high-frequency seismic noise due to COVID-19 pandemic lockdown measures. *Science*, 369, 1338–1343. Available from: <https://doi.org/10.1126/science.abd2438>

- Lehujeur, M., Vergne, J., Schmittbuhl, J. & Maggi, A. (2015) Characterization of ambient seismic noise near a deep geothermal reservoir and implications for interferometric methods: a case study in northern Alsace, France. *Geothermal Energy*, 3, 3. Available from: <https://doi.org/10.1186/s40517-014-0020-2>
- Lenth, R.V., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M. et al. (2023) *emmeans: estimated marginal means, aka least-squares means*.
- Lowry, H., Lill, A. & Wong, B.B.M. (2013) Behavioural responses of wildlife to urban environments. *Biological Reviews*, 88, 537–549. Available from: <https://doi.org/10.1111/brv.12012>
- Lüdecke, D., Waggoner, P.D. & Makowski, D. (2019) Insight: a unified interface to access information from model objects in R. *Journal of Open Source Software*, 4, 1412. Available from: <https://doi.org/10.21105/joss.01412>
- Mammola, S., Isaia, M., Demonte, D., Triolo, P. & Nervo, M. (2018) Artificial lighting triggers the presence of urban spiders and their webs on historical buildings. *Landscape and Urban Planning*, 180, 187–194. Available from: <https://doi.org/10.1016/j.landurbplan.2018.09.003>
- McNamara, D.E. & Buland, R.P. (2004) Ambient noise levels in the continental United States. *Bulletin of the Seismological Society of America*, 94, 1517–1527. Available from: <https://doi.org/10.1785/012003001>
- McNett, G.D., Luan, L.H. & Crocetti, R.B. (2010) Wind-induced noise alters signaler and receiver behavior in vibrational communication. *Behavioral Ecology and Sociobiology*, 64, 2043–2051. Available from: <https://doi.org/10.1007/s00265-010-1018-9>
- McVean, A. & Field, L.H. (1996) Communication by substratum vibration in the New Zealand tree weta, *Hemideina femorata* (Stenopelmatidae: Orthoptera). *Journal of Zoology*, 239, 101–122. Available from: <https://doi.org/10.1111/j.1469-7998.1996.tb05440.x>
- Morse, D.H. (1999) Choice of hunting site as a consequence of experience in late-instar crab spiders. *Oecologia*, 120, 252–257. Available from: <https://doi.org/10.1007/s004420050855>
- Mortimer, B. (2017) Biotremology: do physical constraints limit the propagation of vibrational information? *Animal Behaviour*, 130, 165–174. Available from: <https://doi.org/10.1016/j.anbehav.2017.06.015>
- Mortimer, B. (2019) A spider's vibration landscape: adaptations to promote vibrational information transfer in orb webs. *Integrative and Comparative Biology*, 59, 1636–1645. Available from: <https://doi.org/10.1093/icb/icz043>
- Mortimer, B., Soler, A., Sivior, C.R., Zaera, R. & Vollrath, F. (2016) Tuning the instrument: sonic properties in the spider's web. *Journal of the Royal Society Interface*, 13, 20160341. Available from: <https://doi.org/10.1098/rsif.2016.0341>
- Mortimer, B., Walker, J.A., Lolchuragi, D.S., Reinwald, M. & Daballen, D. (2021) Noise matters: elephants show risk-avoidance behaviour in response to human-generated seismic cues. *Proceedings of the Royal Society B: Biological Sciences*, 288, 20210774. Available from: <https://doi.org/10.1098/rspb.2021.0774>
- Oberst, S., Bann, G., Lai, J.C.S. & Evans, T.A. (2017) Cryptic termites avoid predatory ants by eavesdropping on vibrational cues from their footsteps. *Ecology Letters*, 20, 212–221. Available from: <https://doi.org/10.1111/ele.12727>
- Orci, K.M., Petróczki, K. & Barta, Z. (2016) Instantaneous song modification in response to fluctuating traffic noise in the tree cricket *Oecanthus pellucens*. *Animal Behaviour*, 112, 187–194. Available from: <https://doi.org/10.1016/j.anbehav.2015.12.008>
- Pessman, B.J., Hays, M., Agpawa, E. & Hebert, E.A. (2023) Urbanization affects web abundance and aggregation of a funnel-weaving spider, *Agelenopsis pennsylvanica* (Agelenidae). *Urban Ecosystems*, 26, 1275–1292. Available from: <https://doi.org/10.1007/s11252-023-01379-z>
- Piano, E., Souffreau, C., Merckx, T., Baardsen, L.F., Backeljau, T., Bonte, D. et al. (2020) Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology*, 26, 1196–1211. Available from: <https://doi.org/10.1111/gcb.14934>
- Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M. et al. (2011) Soundscape ecology: the science of sound in the landscape. *BioScience*, 61, 203–216. Available from: <https://doi.org/10.1525/bio.2011.61.3.6>
- Prather, C.M., Pelini, S.L., Laws, A., Rivest, E., Woltz, M., Bloch, C.P. et al. (2013) Invertebrates, ecosystem services and climate change. *Biological Reviews*, 88, 327–348. Available from: <https://doi.org/10.1111/brv.12002>
- Raboin, M. & Elias, D.O. (2019) Anthropogenic noise and the bioacoustics of terrestrial invertebrates. *Journal of Experimental Biology*, 222, jeb178749. Available from: <https://doi.org/10.1242/jeb.178749>
- Riechert, S.E. (1976) Web-site selection in the desert spider *Agelenopsis aperta*. *Oikos*, 27, 311–315. Available from: <https://doi.org/10.2307/3543911>
- Riechert, S.E. & Tracy, C.R. (1975) Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. *Ecology*, 56, 265–284. Available from: <https://doi.org/10.2307/1934960>
- Roberts, L. & Howard, D.R. (2022) Substrate-borne vibrational noise in the Anthropocene: from land to sea. *Biotremology: physiology, ecology, and evolution*. In: Hill, P.S.M., Mazzoni, V., Stritih-Peljhan, N., Virant-Doberlet, M. & Wessel, A. (Eds.) *Animal signals and communication*. Cham: Springer International Publishing, pp. 123–155.
- Roberts, L. & Wickings, K. (2022) Biotremology: tapping into the world of substrate-borne waves. *Acoustics Today*, 18, 49–57. Available from: <https://doi.org/10.1121/AT.2022.18.3.49>
- Sandoval, C.P. (1994) Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. *Functional Ecology*, 8, 701–707. Available from: <https://doi.org/10.2307/2390229>
- Singer, F., Riechert, S., Xu, H., Morris, A.W., Becker, E., Hale, J.A. et al. (2000) Analysis of courtship success in the funnel-web spider *Agelenopsis aperta*. *Behaviour*, 137, 93–117. Available from: <https://doi.org/10.1163/156853900501890>
- Slowikowski, K., Schep, A., Hughes, S., Dang, T.K., Lukauskas, S., Irisson, J.-O. et al. (2023) *ggrepel: automatically position non-overlapping text labels with ggplot2*.
- Šturm, R., López Díez, J.J., Polajnar, J., Sueur, J. & Virant-Doberlet, M. (2022) Is it time for ecotremology? *Frontiers in Ecology and Evolution*, 10, 503.
- Šturm, R., Rexhepi, B., López Díez, J.J., Blejec, A., Polajnar, J., Sueur, J. et al. (2021) Hay meadow vibroscape and interactions within insect vibrational community. *iScience*, 24, 103070. Available from: <https://doi.org/10.1016/j.isci>
- Sümer, S.K., Say, S.M., Ege, F. & Sabancı, A. (2006) Noise exposed of the operators of combine harvesters with and without a cab. *Applied Ergonomics*, 37, 749–756. Available from: <https://doi.org/10.1016/j.apergo.2005.11.006>
- Trubl, P., Gburek, T., Miles, L. & Johnson, J.C. (2012) Black widow spiders in an urban desert: population variation in an arthropod pest across metropolitan Phoenix, AZ. *Urban Ecosystems*, 15, 599–609. Available from: <https://doi.org/10.1007/s11252-011-0223-2>
- Turner, A., Fischer, M. & Tzanopoulos, J. (2018) Sound-mapping a coniferous forest—perspectives for biodiversity monitoring and noise mitigation. *PLoS One*, 13, e0189843. Available from: <https://doi.org/10.1371/journal.pone.0189843>
- Uetz, G.W. & Norton, S. (2007) Preference for male traits in female wolf spiders varies with the choice of available males, female age and reproductive state. *Behavioral Ecology and Sociobiology*, 61, 631–641. Available from: <https://doi.org/10.1007/s00265-006-0293-y>
- Vardi, R. & Berger-Tal, O. (2022) Environmental variability as a predictor of behavioral flexibility in urban environments. *Behavioral Ecology*, 33, 573–581. Available from: <https://doi.org/10.1093/beheco/arac002>
- Velilla, E., Collinson, E., Bellato, L., Berg, M.P. & Halfwerk, W. (2021) Vibrational noise from wind energy-turbines negatively impacts earthworm abundance. *Oikos*, 130, 844–849. Available from: <https://doi.org/10.1111/oik.08166>
- Velilla, E., Muñoz, M., Quiroga, N., Symes, L., ter Hofstede, H.M., Page, R.A. et al. (2020) Gone with the wind: is signal timing in a neotropical katydid an adaptive response to variation in wind-induced vibratory

- noise? *Behavioral Ecology and Sociobiology*, 74, 59. Available from: <https://doi.org/10.1007/s00265-020-02842-z>
- Virant-Doberlet, M., Kuhelj, A., Polajnar, J. & Šturm, R. (2019) Predator-prey interactions and eavesdropping in vibrational communication networks. *Frontiers in Ecology and Evolution*, 7, 203.
- Voeten, C.C. (2023) *buildmer: stepwise elimination and term reordering for mixed-effects regression*.
- Wei, T. & Simko, V. (2021) *R package "corrplot": visualization of a correlation matrix*.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R. et al. (2019) Welcome to the tidyverse. *Journal of Open Source Software*, 4, 1686. Available from: <https://doi.org/10.21105/joss.01686>
- Wilgers, D.J. & Hebets, E.A. (2012) Age-related female mating decisions are condition dependent in wolf spiders. *Behavioral Ecology and Sociobiology*, 66, 29–38. Available from: <https://doi.org/10.1007/s00265-011-1248-5>
- Willmott, N.J., Henneken, J., Elgar, M.A. & Jones, T.M. (2019) Guiding lights: foraging responses of juvenile nocturnal orb-web spiders to the presence of artificial light at night. *Ethology*, 125, 289–297. Available from: <https://doi.org/10.1111/eth.12852>
- Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, 73, 3–36. Available from: <https://doi.org/10.1111/j.1467-9868.2010.00749.x>
- Wu, C.-H. & Elias, D.O. (2014) Vibratory noise in anthropogenic habitats and its effect on prey detection in a web-building spider. *Animal Behaviour*, 90, 47–56. Available from: <https://doi.org/10.1016/j.anbehav.2014.01.006>
- Zahnow, R. & Abewickrema, W. (2023) Examining regularity in vehicular traffic through Bluetooth scanner data: is the daily commuter the regular road user? *Journal of Transport Geography*, 109, 103578. Available from: <https://doi.org/10.1016/j.jtrangeo.2023.103578>
- Zhou, J., Lai, J., Menda, G., Stafstrom, J.A., Miles, C.I., Hoy, R.R. et al. (2022) Outsourced hearing in an orb-weaving spider that uses its web as an auditory sensor. *Proceedings of the National Academy of Sciences of the United States of America*, 119, e2122789119. Available from: <https://doi.org/10.1073/pnas.2122789119>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Principal component analysis of sites using variables related to potential impacts from traffic, including percent impervious cover, distance from the recording site to the nearest road, annual daily average vehicles on the nearest road, and total length of roads in a 1-km radius of the site.

Figure S2. Heat map depicting the hourly average relative noise amplitude (as Leq measured in dB re FS, 20–1000 Hz) for all recordings.

Figure S3. Frequency profiles of field recordings and microhabitat use chambers.

Figure S4. Raw data (mean \pm SD) and model predictions (line \pm ribbon=mean \pm SE) from linear mixed effect (LME) models of daily average noise amplitude (measured as Leq in units dB) with the potential traffic impact (PC2, see PCA Figure S1), substrate (grey=manmade, green=plant), and rural/urban with site as a random factor after backward selection.

Figure S5. Frequency profiles of substrates at the three loudest (top) and three quietest sites (bottom).

Figure S6. The calculated mean (\pm SD error bars, \pm SE ribbon) hourly average noise amplitude (measured as Leq in units of dB) across 24 h by rural/urban for each separate visit.

Figure S7. Raw spider activity from (A) the activity monitor experiment and (B) the microhabitat use experiment.

Figure S8. Total and peak activity for (A, B) the activity monitor experiment and (C, D) the microhabitat use experiment.

Figure S9. Visualizations from the raspberry pi images from the microhabitat use experiment taken every 2 min during the first night of web-building for a subset of tested spiders.

Table S1. Substrates used to measure vibratory noise at each site. The super script shows the recording unit number used on that substrate.

Table S2. Date and time of the start and end of each recording for each site with times that we switched the batteries in the recording units (check).

Table S3. The total number of recordings per substrate per visit at each site.

Video S1. Sample video.

Data S1. Supplementary materials and methods.

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