



Vibratory noise in anthropogenic habitats and its effect on prey detection in a web-building spider



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ARTICLE INFO

Article history:

Received 11 September 2013
 Initial acceptance 8 October 2013
 Final acceptance 17 December 2013
 Published online
 MS. number: 13-00749R

Keywords:

anthropogenic substrate
 garden spider
 habitat change
 prey detection
 seismic noise
 substrate-borne
 vibration

In nature, animals must contend with the presence of noise, which may limit their ability to detect prey, attract mates and escape predators. Sources of noise vary and may originate from natural (e.g. animal sounds, water) or anthropogenic (e.g. traffic, construction) sources. The vibratory sensory modality has long been overlooked in the study of anthropogenic effects on wildlife. Human-induced environmental changes may introduce noise sources as well as artificial substrates that alter vibratory noise profiles, leading to maladaptive behavioural responses. We conducted field measurements of vibratory noise on various substrate types (natural and artificial) used by animals in human-developed habitats. Next, we conducted laboratory experiments on how vibratory noise affects the prey detection ability of the European garden spider, *Araneus diadematus*. We tested whether changes in vibratory noise profiles consistent with anthropogenic alterations of vibratory habitats are sufficient to alter the spider's sensitivity to prey cues. We found that overall noise amplitude on artificial substrates was lower and less variable across contexts compared with natural substrates. In experiments with different noise levels, we observed that garden spiders showed noise-dependent changes in sensitivity to prey-mimicking cues, with response thresholds lowest at intermediate noise levels. Experimental levels of intermediate noise consistent with field measurements on natural substrates suggest that spiders' predatory performance is higher when webs are constructed on natural substrates. This suggests that human-introduced substrates may interfere with spiders' predatory performance. As human activities and habitat alteration are widespread, our findings highlight the need to consider the vibratory sensory channel in assessing anthropogenic impacts on wildlife.

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Environmental noise is widespread in both natural and urban landscapes. Previous studies have revealed many negative impacts of noise on organisms, particularly from anthropogenic sources, with a focus on the airborne and waterborne sound sensory channels (Barber, Crooks, & Frstrup, 2010; Blickley & Patricelli, 2010; Celi et al., 2013; Kight & Swaddle, 2011; Nowacek, Thorne, Johnston, & Tyack, 2007; Slabbekoorn et al., 2010; Weiglart, 2007). Noise effects on animals include signal masking and physiological stress (Brumm & Slabbekoorn, 2005; Slabbekoorn & Ripmeester, 2008; Wright et al., 2007), which may have a variety of negative consequences (Barber et al., 2010; Francis, Ortega, & Cruz, 2009; Kight & Swaddle, 2011). In addition, noise interference in one sensory modality may influence performance in other sensory modalities; for example, auditory noises impair animals' performance of visual tasks through distraction (Chan, Giraldo-

Perez, Smith, & Blumstein, 2010; Maes & de Groot, 2003). As anthropogenic change becomes increasingly widespread, it is crucial to understand whether and how animals cope with noise in human-altered habitats.

In the study of the effects of anthropogenic noise on wildlife, one common sensory modality has been overlooked: the vibratory sense. Animals across a wide range of taxa utilize substrate-borne vibrations as an information source and the vibratory sense may be one of the most ubiquitous senses guiding behaviour in arthropods as well as in some vertebrate taxa (Hill, 2008; Narins, 1990, 2001; Randall, 2001; Uhl & Elias, 2011; Virant-Doberlet & Cokl, 2004). Substrate-borne vibrations are commonly used in a variety of behaviours including intraspecific communication (e.g. courtship, competition, social interactions) and interspecific interactions such as predator avoidance and prey detection (Cocroft & Rodriguez, 2005; Hill, 2009). It is known that natural sources of vibratory noise, such as those caused by rain, wind and animal songs, play important roles in modulating the aforementioned behaviours. Some organisms can discriminate between noise and 'biological' cues even when both contain overlapping spectra (Caldwell, McDaniel, & Warkentin, 2009, 2010; Guedes, Matheson,

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Frei, Smith, & Yack, 2012). However, many other organisms are subject to vibratory noise interference. For example, *Enchenopa binotata* treehoppers, communicate less efficiently during windy periods (McNett, Luan, & Coccoft, 2010). Male southern green stink bugs, *Nezara viridula*, are less responsive to female songs if there is interference from heterospecific signals (de Groot, Čokl, & Virant-Doberlet, 2010), and their mating success is reduced when wind vibratory noise is present (Polajnar & Cokl, 2008). Vibratory noise can also influence predator–prey interactions; for example, araneophagic assassin bugs, *Stenolemus bituberus*, utilize wind-induced vibration as a ‘smokescreen’ to approach their spider prey (Wignall, Jackson, Wilcox, & Taylor, 2011). These findings give rise to an interesting question: do human-induced habitat changes affect the vibratory noise profile in the field? And if so, would such changes be strong enough to elicit behavioural responses?

Human activities may alter vibratory noise in two ways: (1) providing new noise sources and (2) introducing novel, artificial substrates. Anthropogenic noise sources such as automobile traffic and construction create low-frequency substrate-borne vibrations that may overlap with frequencies commonly used by arthropods, and may propagate with only moderate attenuation (for example, the 16–250 Hz vibrations from underground rail systems; Kurzweil, 1979). Impacts of such noises may parallel those of acoustic noises such as traffic, wind turbines, shipping and seismic exploration (Hildebrand, 2009), which influence vocalization (Di Iorio & Clark, 2010; Lampe, Reinhold, & Schmoll, 2013; Lampe, Schmoll, Franzke, & Reinhold, 2012; Slabbekoorn & Peet, 2003), antipredator (Rabin, Coss, & Owings, 2006), foraging (Croll, Clark, Calambokidis, Ellison, & Tershy, 2001; Leonard & Horn, 2012; Schaub, Ostwald, & Siemers, 2008) and reproductive behaviours (Bee & Swanson, 2007; Halfwerk, Holleman, Lessells, & Slabbekoorn, 2011).

An even more prevailing yet understudied agent of vibratory noise alteration is the introduction of artificial substrates. Substrate properties affect the ability of animals to detect, attend to and respond to substrate-borne vibrations produced by prey, predators and/or conspecifics. Previous studies have demonstrated the effects of the vibratory environment on mating (Elias, Mason, & Hebets, 2010; Elias, Mason, & Hoy, 2004; Hebets, Elias, Mason, Miller, & Stratton, 2008; McNett & Coccoft, 2008), antipredator (Warkentin, 2005) and foraging behaviour (Young & Morain, 2002). In modern habitats, human-made objects such as pipelines, fences, road signs and wire rods are widespread, and in urban/suburban landscapes, many buildings are made out of concrete and glass materials. A variety of wildlife, particularly arthropods, are widespread in these areas and many make use of these artificial substrates. The transmission properties of artificial substrates may differ substantially from those of natural ones; for example, objects with homogeneous composition such as metal rods and glass are vibration resistant and have frequency-filtering properties very different from those of natural substrates such as twigs and leaves. Such transmission differences could be important since they may affect behaviours crucial to survival and reproduction. In this sense, artificial substrates could provide both opportunities and challenges for organisms that rely heavily on the vibratory sense.

Currently, we know little about vibratory noise across natural and artificial substrates in human-altered habitats. Additionally, studies on how anthropogenic vibratory noise influences behaviours are lacking. One property of environmental noise that is likely to have large effects on behaviour is overall vibratory noise amplitude. The overall noise amplitude in a substrate will depend on (1) amplitude and type of background acoustic noise (both air- and substrate-borne) and (2) how well a substrate picks up and transmits sympathetic vibrations. The degree to which a substrate vibrates in response to sympathetic vibrations is determined by its

material composition and geometry (Bishop & Johnson, 2011) which are very likely to differ between natural and artificial substrates. The overall noise amplitude for substrates that are sensitive to sympathetic vibrations is likely to change widely with any given background noise type (e.g. wind) whereas substrates that do not vibrate to sympathetic vibrations are likely to be dampened (‘noise free’) regardless of background noise.

Web-building spiders are well suited for studying vibratory noise effects for several reasons. They are highly dependent on vibratory cues generated on the web for guiding their behavioural responses (Klarner & Barth, 1982; Landolfa & Barth, 1996), and the underlying sensory biology, together with vibration characteristics of spider webs, have been the focus of decades of research (Barth, Bleckmann, Bohnenberger, & Seyfarth, 1988; Frohlich & Buskirk, 1982; Landolfa & Barth, 1996; Masters & Markl, 1981; Masters, Markl, & Moffat, 1986; Speck & Barth, 1982; Walcott, 1969). Web spiders are among the most abundant general predators in human-developed habitats, and their utilization of man-made objects has long been recognized. Spider orb webs consist of frame threads attached to surrounding materials, supporting radial threads which transmit vibrations to a central hub, and sticky spiral threads to capture prey. Webs function as an extension of the spider’s vibratory sensory space and vibrations on the web could arise from sources on the web itself (e.g. prey, potential mates), substrate-borne vibrations from the surrounding environment (e.g. vibrations transmitted from the environment into the web via the frame threads) or air-borne vibrations from the surrounding environment (wind, auditory sounds). Strong vibratory noise originating from the surrounding environment may interfere with the abilities of spiders to sense and respond to biologically relevant stimuli on the web, and may force a trade-off between missed detection and false alarms. Spiders are expected to adjust their responses according to noise level, similar to that previously shown in nestling birds (Leonard & Horn, 2012).

In this study, we investigated how overall vibratory noise amplitude may affect the prey detection ability of a common orb-weaving spider, the European garden spider, *Araneus diadematus*. We first measured vibratory noise on various natural and artificial substrates that were commonly used by *A. diadematus* as web attachment sites in urban/suburban habitats. Next, we conducted laboratory experiments on how vibratory noise alone influences prey detection sensitivity of *A. diadematus*. Behavioural thresholds to prey-mimicking strikes were tested under three levels of noise with amplitudes ranging from ‘quiet’, ambient background to extremely strong noise levels. Specifically, we tested the following hypotheses. (1) Anthropogenic sources are significant sources of substrate-borne vibratory noise. (2) Vibratory noise amplitude to a given noise source differs between artificial and natural substrates. (3) Predatory responses of *A. diadematus* depend on the vibratory noise amplitude. (4) *Araneus diadematus* perform better under noise conditions mimicking noise levels on natural substrates.

METHODS

Field Census of Spider’s Substrate Usage

We conducted field surveys on substrate usage by *A. diadematus* in four urban/suburban areas (0.06–0.34 km² in size) around the UC Berkeley campus (37°52′16.06″ N, 122°15′20.17″ W). Substrates were grouped into two categories, natural and artificial, and were further classified into morphological and compositional groups. A list of the ‘substrate types’ and ‘substrate structures’ defined in the study is provided in Appendix Table A1. We searched the areas thoroughly for webs and recorded the substrate types and structures on which individual webs were attached. The measurement

unit we used for quantifying substrate usage was individual web attachment points to a substrate, as each attachment point serves as a transducer that transfers vibrations from the substrate to the web. The number of attachment points for each substrate type was recorded, and the percentage of artificial substrate usage (i.e. percentage of attachment points on artificial substrates) was calculated for each web and across all webs.

Measuring Field Vibratory Noise

Three urban (<5 m from traffic or buildings) and three suburban habitats (>500 m from traffic or buildings) in the four study areas were chosen for measuring vibratory noise patterns, resulting in a total of six measurement sites. The measurement sites were selected to maximize the number of substrate types present given logistical constraints. We used a portable laser vibrometer (PDV; PDV-100, Polytec GmbH, Waldbronn, Germany) to measure vibratory noise. Data were recorded on Sound Devices 722HT (Sound Devices, LLC, Reedsburg, WI, U.S.A.) with a 48 kHz sampling rate. For each substrate type, at each habitat we haphazardly selected one measurement point that was accessible and used by *A. diadematus* as a web attachment point, and recorded for 3–5 min at each point. Within each measurement site, all the measurement points were within 3 m of each other and were a similar distance from the nearest street, to control for spatial heterogeneity in noise level. Measurements at each of the six sites were conducted at four time intervals (0600–0800, 0900–1100, 1200–1400, 1500–1700 hours), and were replicated three times on different dates. Evening time slots were excluded from the study because *A. diadematus* are typically not active at night.

For individual recordings, we first used Adobe Audition 2.0 (Adobe Systems Inc., San Jose, CA, U.S.A.) to examine the spectrum and removed segments of poor quality (e.g. clipped segments). Next we identified and extracted representative noise segments of three categories: (1) anthropogenic noise (e.g. traffic); (2) wind-induced noise; and (3) background noise. Background noise is defined as the baseline noise level of our recording equipment, that is, recordings in periods without detectable vibratory events. All noise categories can be easily distinguished by ear. For each segment, the noise amplitude was defined as the root-mean-square (RMS) velocity, calculated using Matlab 2009a (Mathworks, Inc., Natick, MA, U.S.A.).

Spider Maintenance

Adult and subadult female *A. diadematus* (2.8–5.7 mm in carapace length) were collected by hand from within 1 km of the UC Berkeley campus. Spiders were housed individually inside Perspex frames (TAP plastics, CA, U.S.A.; 30 cm × 30 cm × 5 cm, with duct tape linings inside), separated by PVC sheets (TAP plastics, CA, U.S.A.). Spiders were kept under a 16:8 h light:dark cycle at 25 °C. Every 3 days, they were fed one similar-sized house cricket, *Acheta domestica*, and the webs misted with water. After each feeding, old webs were destroyed using a hot soldering iron to promote building of new webs. Spiders were in captivity for 6 weeks on average, and were returned to the sites of collection at the end of the study.

Response Threshold

Instrumental set-up

We tested responses of female *A. diadematus* to prey-mimicking stimuli under three levels of vibratory noise. We manipulated vibratory noise by mounting each spider frame onto surface transducers (COM-10975, Sparkfun Electronics, Boulder, CO, U.S.A.), and playing band-limited white noise (0–2 kHz) within the spiders'

detection range (Barth, 1982) using Audacity software v2.03 (audacity.sourceforge.net). These noise stimuli transmit into the web via anchor threads. To produce prey-mimicking cues, we used a home-made vibrator with a plastic tube (5 mm in diameter) glued onto the centre of a modified woofer (SDS-160F25PRO1-08, Peerless, Tymphony HK Limited, Wanchai, Hong Kong). The vibrator was connected to a receiver (RX-4105, RadioShack Corporation, Fort Worth, TX, U.S.A.) and a signal generator (PSV 8.7 software; Fig. 1).

We chose white noise, which is widely used for studying effects of noise on behaviour, rather than field-recorded noise for noise treatments, because the latter could not be reproduced consistently (see Discussion). Two sets of experiments were conducted using different prey-mimicking stimuli: a 30 Hz sine wave stimulus, which represents a major component of prey signals on spider webs, and a 100 Hz sine wave stimulus, which represents a minor component in prey signals (Landolfa & Barth, 1996; Masters, 1984b). These were based on spectrum analysis of vibratory signals induced by Diptera and Hymenoptera species, since these two taxa constitute a large portion of the prey species of *A. diadematus* (Nentwig, 1985). Three levels of vibratory noise treatment were used: (1) low noise: 0.05 cm/s (0 dB); (2) medium noise: 0.6 cm/s (21.6 dB); (3) high noise: 3 cm/s (35.5 dB). The low and medium noise treatments approximate background (ambient) and average wind-induced noise amplitude levels on natural substrates, respectively (see Results). The high noise treatment corresponded to an unnaturally strong noise environment, for example, directly adjacent to construction sites (our unpublished data). We used the PDV to calibrate the white noise stimulus, and adjusted the input stimulus for each spider frame to ensure a flat output spectrum.

Experiment protocol

We used 27 and 22 spiders for the 30 Hz and 100 Hz experiments, respectively. Each spider was tested under the three noise treatments with the order of the three tests randomized. Trials were carried out on newly built webs only and each web was used for a single trial only. Therefore, there were at least 2 days between consecutive trials on the same individual. Each spider was also tested under similar levels of satiety (ca. 24 h after the last meal). All experiments were conducted on a vibration-isolated table (Newport Corporation, Irvine, CA, U.S.A.), and were videotaped using a CCD camera (CV-S3200, JAI, Copenhagen, Denmark). Noise and prey-mimicking stimuli were calibrated using the PDV before and after each trial to ensure consistency.

In individual trials, we gently attached the tip of the vibrator to a single radius on the web, 7–9 cm away from the spider, which was located at the centre of the web (hub). The tip was positioned within 15–30° relative to the web plane, to elicit mainly longitudinal vibrations which transmit with the least attenuation (Masters, 1984a). The test stimuli were applied in two phases.

(1) Increasing-amplitude phase. After an initial 10 min acclimation period, we introduced a series of prey-mimicking stimuli each lasting 5 s, with a 30 s pause after each stimulus. Test amplitudes started from 0 dB (corresponding to 1 μm displacement) and increased in 5 dB increments. Spiders would first start showing body movements and eventually rush out of the hub towards the vibrator; we recorded this as the 'peak' amplitude response.

(2) Decreasing-amplitude phase. A 5 min pause was given after the first rush-out event. Afterwards a second series of 5 s stimuli was introduced, starting from the 'peak' amplitude and decreased in 3 dB decrements, until the spider stopped responding to the test amplitude (showed no body movements). There was a pause of at least 5 min between any rush-out event and the subsequent stimulus to ensure the spider had stopped responding to the previous stimulus.

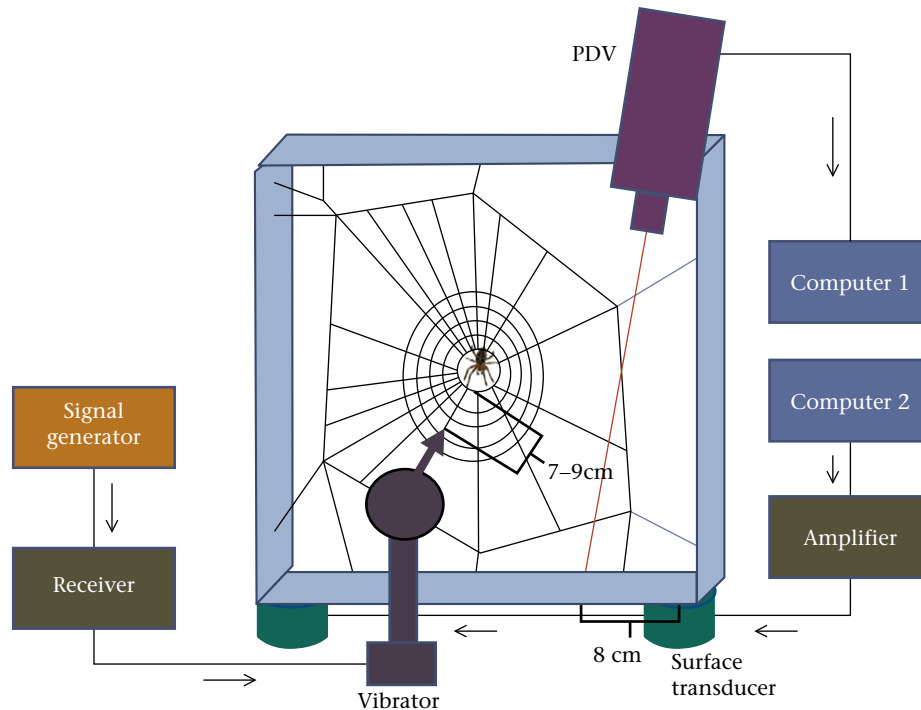


Figure 1. Experimental set-up. Noise was monitored using a laser vibrometer (PDV) 8 cm away from the centre of either one of the surface transducers. Two different computers were used to monitor and adjust noise output. A high-resolution camera was placed perpendicular to the web plane (70 cm away) and focused on the spider for video recording (not shown).

We defined the amplitude at which the spider stopped responding to the stimulus as the 'detection threshold'. This protocol follows Masters (1984b) and is designed to account for the excitation state of individual spiders and ensure an accurate measurement of true sensitivity thresholds. The maximal amplitude tested was 70 and 60 dB for the 30 Hz and 100 Hz stimuli, respectively. The lower maximal amplitude under the 100 Hz stimulus is due to instrumental constraints. If a spider did not respond to the maximal amplitude stimulus, we considered its threshold to be 3 dB higher than the maximal amplitude, after Masters (1984b). Spiders in seven of 77 and six of 59 trials for the 30 Hz and 100 Hz stimuli, respectively, did not respond at the maximal amplitude stimulus. A number of missing values ($N = 4$ and 7 for the 30 Hz and 100 Hz experiments, respectively) were present since some spiders failed to build new webs or died before completion of all three trials.

Data Analysis

We used a nonparametric Kruskal–Wallis test followed by a Dwass–Steel–Chritchlow–Fligner test for post hoc comparisons to compare average noise amplitude of the three noise source categories. Next, we used linear mixed models (LMM) to analyse the effect of substrate, habitat and time slot on field vibratory noise amplitude levels. To meet model assumptions, RMS amplitude data of background and wind noise segments were square root-transformed, and those for anthropogenic noise segments log-transformed. Transformed data were fitted to LMM (lmer function in lme4 package, R v.2.15.1, The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>) with a Gaussian error distribution. Fixed effects included substrate category (natural/artificial), habitat type (urban/suburban) and time slot (0600–0800/0900–1100/1200–1400/1500–1700 hours). Date, site, substrate type and substrate structure were included as

random effects. For each noise category, we used an AICc model selection approach first to optimize the random effect terms with all the fixed effects present (full model, including interaction terms), and then to compare models of all possible fixed effect combinations to select the model with the lowest AICc value. If the selected models failed to meet model assumptions (normality, homoscedasticity and independence of data), models with the second-lowest AICc value would be chosen. Previously excluded fixed factors were added back to models that violated the assumption of independence of data between levels of these factors, following model selection criteria suggested by Zuur, Ieno, Walker, Saveliev, and Smith (2009).

For the 30 Hz and 100 Hz response threshold experiment, the detection threshold data were square root-transformed and then fitted to LMMs using the method described above. Noise level was included as the fixed effect. Spider ID, treatment order and date (controlling for any ageing effect) were included as random effects.

The Kruskal–Wallis test was conducted using SYSTAT 13 (Systat Software Inc., Chicago, IL, U.S.A.). All other analyses were performed using R v.2.15.1.

RESULTS

Substrate Usage

A total of 50 spider webs were examined, resulting in 283 attachment points recorded. The spiders used 19 of the 25 substrate structures (10 of the 13 substrate types) for web construction. The number of attachment points per web varied from three to nine, with a median of five points per web. While 27 webs had zero artificial substrate usage, all the other 23 webs showed artificial substrate usage greater than 40% (median = 66.7% for these 23 webs), including five webs with 100% artificial substrate usage. The results suggest that artificial substrates are important web

attachment sites for *A. diadematus*. A summary of individual substrate type usage, pooled across all webs, is provided in Appendix Table A2.

Field Overall Vibratory Noise Amplitude

We performed noise measurements on 10 of the 13 substrate types used by *A. diadematus*, encompassing 89.4% of observed substrate usage (see Appendix). For the substrate types ‘Tree’, ‘Wood-like’ and ‘Other’, noise measurements are lacking because no suitable sample was present in our measurement sites. Representative power spectra of noises recorded on natural and artificial substrates are provided in Appendix Fig. A1.

Averaged across all recordings, average noise amplitude differed between anthropogenic, background and wind-induced noises (Kruskal–Wallis test: $H_2 = 277.8$, $P < 0.0001$). Anthropogenic noises were predominantly produced by nearby traffic, with amplitudes significantly higher than background noise (median + interquartile range (IQR) = $0.065 + 0.041$ versus $0.036 + 0.028$ cm/s; post hoc comparison: $P < 0.0001$). Wind-induced noises (median + IQR = $0.506 + 0.680$ cm/s) were significantly stronger than both anthropogenic (post hoc comparison: $P < 0.0001$) and background noise (post hoc comparison: $P = 0.006$), and represented the strongest noise source recorded in the study. When we pooled all noise categories, artificial substrates were lower in median amplitude (median = 0.0393 versus 0.0676 cm/s) and variation (IQR = 0.0487 versus 0.3865 cm/s) relative to natural substrates (Fig. 2). These results indicate that artificial substrates are more ‘silent’ across contexts.

Linear mixed modelling results for the effects of substrate, habitat type and time slot on individual noise categories are summarized in Table 1. Overall noise amplitude was significantly lower on artificial substrates for anthropogenic and wind noise, whereas background noise amplitude was similar across substrates (Fig. 3a, b, c). Habitat type (urban versus suburban) had no effect on noise amplitudes and was excluded from the final models. Background

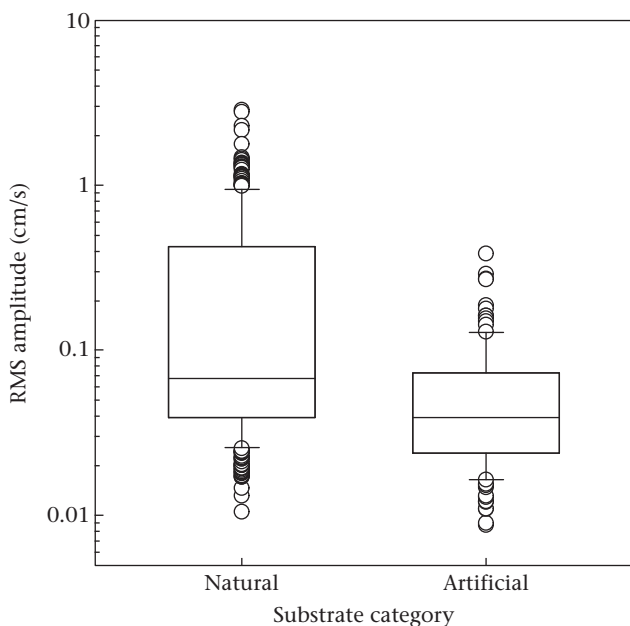


Figure 2. Field vibratory noise amplitude on artificial and natural substrates. Data were pooled across the three noise categories. $N = 339$ and 122 for natural and artificial category, respectively. Boxes show median and interquartile range. The whiskers indicate distance from the box that equals to $1.5 \times$ IQR, and open circles indicate data points that are more than $2 \times$ IQR away from the median.

and anthropogenic noise amplitudes were significantly lower during 0600–0800 hours compared to other times of day (Fig. 3d).

Response Thresholds

Overall noise amplitudes used in the medium and high noise treatments were comparable to noise amplitudes recorded on natural substrates, and were always above the amplitude range for artificial substrates (see the previous section). Linear mixed modelling results are summarized in Table 2. In the 30 Hz experiment, spiders showed significantly lower detection thresholds in medium noise treatments than low noise treatments, but not between medium and high noise treatments (Fig. 4a). In the 100 Hz stimuli experiment, noise treatments had no effect on detection threshold (Fig. 4b).

In two of the high-noise treatment trials the spiders left the web and searched for and reached the surface transducer. Such behaviour resembled the debris-removing behaviour commonly observed in the field (our personal observations), indicating that the spiders might have perceived the strong noise sources as disturbances to be removed.

DISCUSSION

Our results demonstrate anthropogenic impacts on overall vibratory noise level, predominantly via the presence of ‘silent’ artificial substrates, and showed that the resulting shifts in overall noise amplitude are sufficient to influence prey detection abilities in orb web spiders.

The effect of substrate on overall noise amplitude was prominent for not only ambient background levels but also anthropogenic and wind-induced noise sources. Human-introduced artificial substrates were lower in vibratory noise amplitude, independent of the noise source compared to natural substrates. The largest difference was observed when wind was the noise source. It is possible that artificial substrates are relatively more rigid and thus more resistant to vibratory disturbances. As a result, the average, range and variation of overall noise level experienced by animals is reduced on artificial substrates.

For orb-web spiders, web noise levels will ultimately be affected by the relative number of attachment points on artificial versus natural substrates. This will vary and span a continuum from all natural to all artificial substrate usage. In highly developed urban habitats, where the artificial-to-natural-substrate ratio is high, we predict large effects of artificial substrates with relatively lesser effects in less developed habitats. We should not, however, exclude the possibility that the presence of a few ‘noisy’ attachment points may be enough to elevate considerably the total web noise level.

Although we predicted that anthropogenic noise sources would alter vibratory noise profiles in highly developed regions (e.g. cities, industrial sites), it seemed not to be the case in our study. Amplitude differences between anthropogenic and natural background noise were significant yet not prominent, suggesting that anthropogenic noise sources are a minor contributor to the vibratory environment. Temporal patterns of anthropogenic and background noise level showed weak fluctuations, and habitat type (distance to human activity) had no effect on overall noise amplitude. These results indicate that typical human activity does not influence vibratory noise level to a large degree. We suggest that the addition of substrates is the most significant factor influencing vibratory environments in human-altered landscapes.

We found that changes in prey detection sensitivity of *A. diadematus* are dependent on the overall vibratory noise amplitude, and that the presence of intermediate-level vibratory noise increased sensitivity compared to other noise levels. Animals have

Table 1
Results of LMMs testing the effects of substrate category, habitat type and time slot on field vibratory noises

Dependent variable	Model structure*	N	Fixed effects	Estimate	SE	t	P
RMS velocity of background noise, square root-transformed	~Substrate category+Time slot+(1+Habitat Type Date)+(1+Substrate category Site)+(1+Substrate category Substrate type)	224	(Intercept)	0.145	0.022	6.535	<0.001
			Substrate category: natural	0.036	0.021	1.688	0.091
			Time slot: 0900–1100	0.034	0.010	3.320	<0.001
			Time slot: 1200–1400	0.035	0.008	4.361	<0.001
			Time slot: 1500–1700	0.025	0.008	3.050	0.002
RMS velocity of anthropogenic noise, log ₁₀ -transformed	~Substrate category+Time slot+(1+Substrate category Site)	81	(Intercept)	-1.439	0.100	-14.466	<0.001
			Substrate category: natural	0.203	0.084	2.403	0.016
			Time slot: 0900–1100	0.146	0.063	2.317	0.021
			Time slot: 1200–1400	0.104	0.057	1.821	0.068
			Time slot: 1500–1700	0.002	0.060	0.398	0.691
RMS velocity of wind noise, square root-transformed	~Substrate category+Time slot+(1+Substrate category Substrate type)	156	(Intercept)	0.240	0.069	3.474	<0.001
			Substrate category: natural	0.484	0.062	7.780	<0.001
			Time slot: 0900–1100	0.110	0.089	1.235	0.217
			Time slot: 1200–1400	0.101	0.064	1.568	0.117
			Time slot: 1500–1700	0.069	0.067	1.033	0.302

N is the number of valid noise segments used for fitting the model. P values <0.1 are in bold.

* (1 + factor|random factor) indicates a random effect with both random slope and intercept; (1|random factor) indicates a random effect with only random intercept.

been shown to alter their behaviours in response to shifts in airborne acoustic noise level (e.g. Leonard & Horn, 2012; Quinn, Whittingham, Butler, & Cresswell, 2006; Rabin et al., 2006; Slabbekoorn & Peet, 2003), and here we show that similar mechanisms could be operating on the vibratory modality as well. We hypothesize that vibratory noise (medium and high noise levels) may exert two opposing effects on web spiders' prey detection sensitivity: (1) a sensitivity-increasing effect and (2) a masking

effect. The sensitivity-increasing effect of noise could be at the periphery, as shown in a physiological study on vibration receptors of wandering spiders (Barth & Geethabali, 1982), or more centrally, similar to the vigilance response in birds (Quinn et al., 2006). In this scenario, web vibrations stronger than the background may indicate the presence of active objects on the web and thus focus a spider's attention on identifying upcoming, 'anticipated' vibratory signals. On the other hand, the presence of high levels of noise may

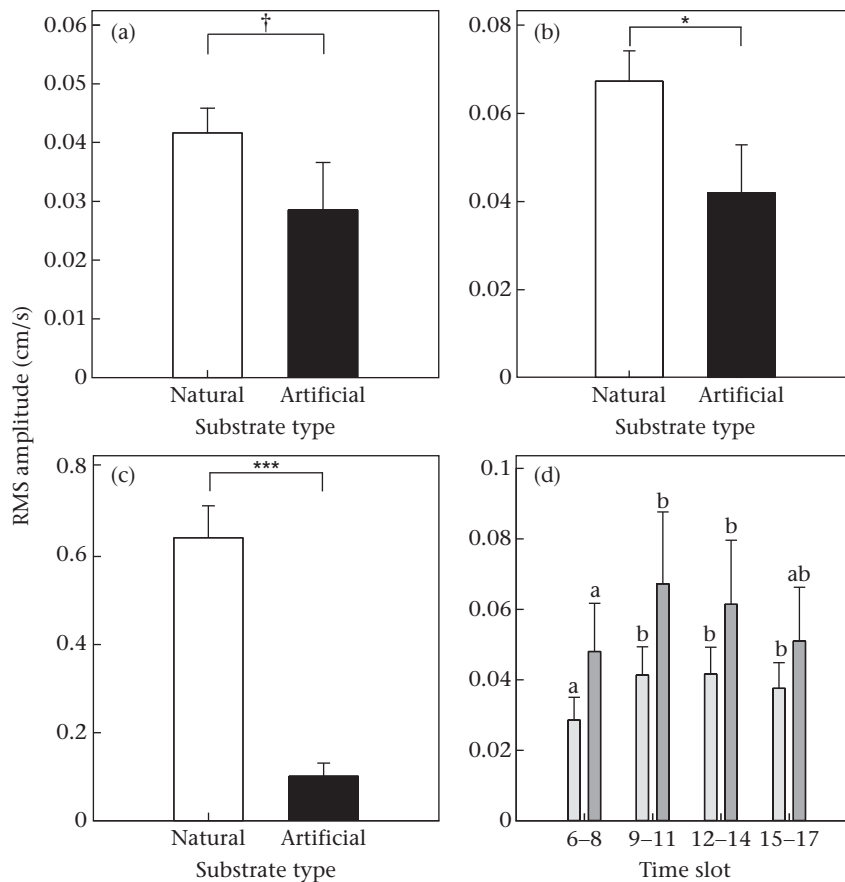


Figure 3. Field vibratory noise amplitude (mean ± SE). Differences between natural and artificial substrates for (a) background noise, (b) anthropogenic noise and (c) wind noise. (d) Temporal patterns of background (dark grey) and anthropogenic (light grey) noise amplitudes across time slots. Results of within-noise-type multiple comparisons are shown by lowercase letters. † $P < 0.1$; * $P < 0.05$; *** $P < 0.001$.

Table 2
Results of LMMs testing the effects of noise level on response thresholds of *A. diadematus*

Dependent variable	Model structure*	N	Fixed effects	Estimate	SE	t	P
Detection threshold (vibrator displacement in dB, square root-transformed (30Hz))	~ Noise level+(1+Noise level Spider ID)	76	(Intercept)	7.099	0.100	71.04	<0.001
			Noise level: low	0.246	0.134	2.111	0.035
			Noise level: loud	0.226	0.116	1.681	0.093
Detection threshold (vibrator displacement in dB, square root-transformed (100Hz))	~ 1+(1+Noise level Spider ID)	58	(Intercept)	7.028	0.096	73.12	<0.001

N is the number of trials used for fitting the model. P values <0.1 are in bold.

* (1 + factor|random factor) indicates a random effect with both random slope and intercept; models that have no fixed effects included are shown with only intercept estimates.

cause signal masking as previously shown in substrate-, air- and waterborne acoustic sensory channels (Bee & Swanson, 2007; Foote, Osborne, & Hoelzel, 2004; McNett et al., 2010; Narins, 1982). We suggest that any increase in sensitivity at high noise treatments would be counteracted by signal masking. Future work is necessary to test this hypothesis.

Combining the field and laboratory studies, we suggest that the magnitude of overall noise level difference between natural and artificial substrates is sufficient to induce changes in spiders' sensitivity to prey cues under some conditions. On artificial substrates, spiders may be less sensitive to prey cues, since overall noise amplitudes are lower and do not change appreciably under different noise conditions (Fig. 2). In this scenario, no shifts in prey sensitivity would occur in artificial substrates whereas they would occur on natural substrates. Specifically, the large differences in overall noise levels consistent with measured wind noise levels between the two substrate categories suggest that spiders on artificial substrates remain less sensitive to prey cues under natural noisy events. If sensitivity to prey cues is shaped by adaptation to natural noise levels as in other behaviours such as vocal signalling (Ficken, Ficken, & Hailman, 1974; Grafe, 1996; Lang, 1996), we may expect a mismatch between noise conditions and spiders' responses to them on artificial substrates. For example, in the presence of wind, insects are able to escape more readily from webs and if spiders do not elevate their response, they would be less likely to catch prey under these conditions. As artificial substrates are widely utilized by spiders and insects as web attachment, nesting and foraging sites, these impacts should be considered when assessing anthropogenic influences on behaviour.

Although this study suggests strong effects of anthropogenic environments on vibratory behaviour, some limitations to this study are evident. First, vibratory noise on spider webs can be

induced not only by substrate vibrations but also by airborne sounds. Vibratory noise, however, will have more energy at lower frequencies relative to airborne noise (Cremer, Heckl, & Ungar, 1973). Because webs are more likely to vibrate at lower frequencies, it is likely that vibratory noise will be a more significant contributor to the overall noise level than airborne noise. Further work is needed to disentangle these two sources of noise. Second, we did not test the frequency dependency of noise on spiders. Spiders are likely to respond differently to noise with different frequency spectra; for example, noise with power centred on lower frequencies (around 30 Hz) could impose stronger masking effects on prey cues. Experiments using various noise spectra are required to test this hypothesis. Third, we used broadband white noise instead of field noise playbacks. White noise signals are commonly used in the study of noise effects on animal behaviour (Caldwell et al., 2009; Chan, Stahlman, et al., 2010; Dooling, Lohr, & Dent, 2000; Mazzoni, Lucchi, Čokl, Prešern, & Virant-Doberlet, 2009; Schilcher, 1976; Warkentin, 2005), and can be reproduced consistently under our experimental settings. Since this study focused on overall noise amplitude rather than frequency-specific effects, the usage of white noise is valid in testing our hypotheses. Lastly, we were unable to conduct in-field behavioural experiments owing to instrumental constraints. In the field, web spiders are capable of adjusting their web location, orientation and composition in response to disturbances such as wind (Hieber, 1984; Liao, Chi, & Tso, 2009), and these adjustments could also affect web vibratory properties and predatory performance of the spiders. Further field study is also necessary to determine whether prey capture success is indeed influenced by environmental noise level.

Our study illustrates potential anthropogenic impacts on the vibratory environment via substrate effects, which have rarely been discussed or investigated. Numerous studies in the field of urban

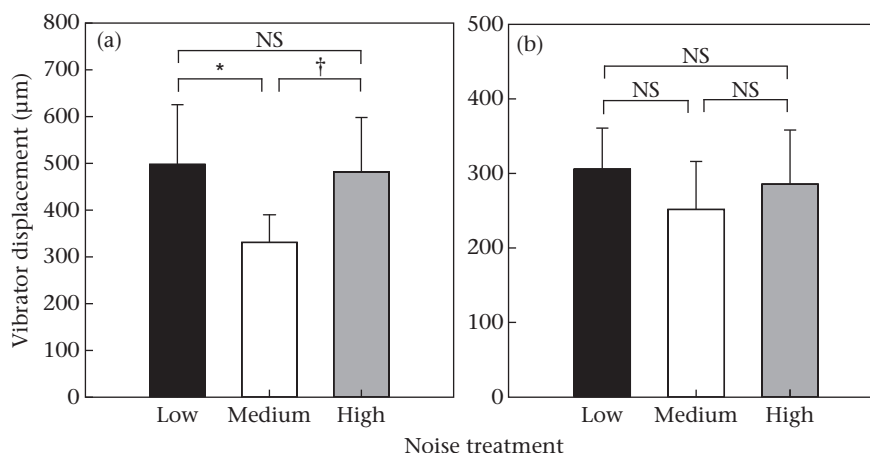


Figure 4. Detection thresholds (mean ± SE) of *A. diadematus* to (a) 30 Hz and (b) 100 Hz prey-mimicking stimuli. NS, $P > 0.1$; † $P < 0.1$; * $P < 0.05$.

noise and structural engineering have provided information on vibration properties of man-made objects (Ngai & Ng, 2002), transmission of vibrations from anthropogenic sources (Coward, Blair, Burman, & Zhao, 2003; Fiala, Degrande, & Augusztinovicz, 2007; Kurzwil, 1979) and dominating frequency characteristics of anthropogenic seismic noises (Groos & Ritter, 2009). Previous ecological studies focusing on acoustic noises have incorporated urban noise research and architectural science into producing testable hypotheses, for example that on animal signal propagation (Warren, Katti, Ermann, & Brazel, 2006). We suggest that similar, interdisciplinary works would benefit the study of vibrations, providing insight into how human activities may interfere with the ubiquitous vibratory sensory channel of animals in human-developed habitats.

To conclude, we provide evidence that human-developed habitats change the overall vibratory environment primarily through the introduction of novel artificial substrates. Artificial substrates tend to be much more stiff and resistant to vibrations. We propose that for the many animals using the vibration sensory modality, the addition of damped artificial structures provides a homogeneous vibratory environment that may not match their prevailing environmental conditions, such as wind. We suggest that this mismatch could significantly affect performance if animals are unable to respond adaptively to the appropriate environmental conditions. Appropriately responding to local conditions is key for survival and increasing lifetime fitness (Benard, 2004; Elias, Andrade, & Kasumovic, 2011; Ghalambor, McKay, Carroll, & Reznick, 2007; Kasumovic & Brooks, 2011; West-Eberhard, 2003) and as man-made substrates become increasingly widespread, the cues that animals use to assess local 'noise' conditions may be eliminated. We suggest that such substrate-mediated effects may play a nontrivial role in the fitness of animals that live in human-developed habitats.

Acknowledgments

We thank Andrew C. Mason for assistance in experimental design, Thomas Hesselberg for comments on spider maintenance, J. Patrick Kelly for assistance in statistical analysis, Madeline B. Girard, Christine Rivera for general support and assistance in the field census, and Mimi Dietrich for support in spider maintenance. We also thank the Behaviour Group at UC Berkeley, particularly Eileen Lacey and Tali Hammond for helpful comments. We thank National Taiwan University, Ministry of Education of Taiwan and University of California Education Abroad Program (UCEAP) for supporting Chung-Huey Wu's visit to UC Berkeley. Additionally, we are grateful to three anonymous referees and the Editor for insightful comments on the manuscript. This work was supported by the National Science Foundation [IOS-1021385 to D.O.E.]. We declare that we have no conflicts of interest.

References

- Barber, J. R., Crooks, K. R., & Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution*, 25(3), 180–189. <http://dx.doi.org/10.1016/j.tree.2009.08.002>.
- Barth, F. G. (1982). Spiders and vibratory signals: sensory reception and behavioral significance. In P. N. Witt, & J. S. Rovner (Eds.), *Spider communication: mechanisms and ecological significance* (pp. 67–120). Princeton, NJ: Princeton University Press.
- Barth, F. G., Bleckmann, H., Bohnenberger, J., & Seyfarth, E. A. (1988). Spiders of the Genus *Cupiennius* Simon 1891 (Araneae, Ctenidae). 2. On the vibratory environment of a wandering spider. *Oecologia*, 77(2), 194–201. <http://dx.doi.org/10.1007/Bf00379186>.
- Barth, F. G., & Geethabali. (1982). Spider vibration receptors: threshold curves of individual slits in the metatarsal lyriform organ. *Journal of Comparative Physiology*, 148(2), 175–185.
- Bee, M. A., & Swanson, E. M. (2007). Auditory masking of anuran advertisement calls by road traffic noise. *Animal Behaviour*, 74, 1765–1776. <http://dx.doi.org/10.1016/j.anbehav.2007.03.019>.
- Benard, M. F. (2004). Predator-induced phenotypic plasticity in organisms with complex life histories. *Annual Review of Ecology, Evolution, and Systematics*, 35(1), 651–673. <http://dx.doi.org/10.1146/annurev.ecolsys.35.021004.112426>.
- Bishop, R., & Johnson, D. (2011). *The mechanics of vibration*. Cambridge, UK: Cambridge University Press.
- Blickley, J. L., & Patricelli, G. L. (2010). Impacts of anthropogenic noise on wildlife: research priorities for the development of standards and mitigation. *Journal of International Wildlife Law & Policy*, 13(4), 274–292. <http://dx.doi.org/10.1080/13880292.2010.524564>.
- Brumm, H., & Slabbekoorn, H. (2005). Acoustic communication in noise. *Advances in the Study of Behavior*, 35, 151–209.
- Caldwell, M. S., McDaniel, J. G., & Warkentin, K. M. (2009). Frequency information in the vibration-cued escape hatching of red-eyed treefrogs. *Journal of Experimental Biology*, 212(4), 566–575. <http://dx.doi.org/10.1242/jeb.026518>.
- Caldwell, M. S., McDaniel, J. G., & Warkentin, K. M. (2010). Is it safe? Red-eyed treefrog embryos assessing predation risk use two features of rain vibrations to avoid false alarms. *Animal Behaviour*, 79(2), 255–260. <http://dx.doi.org/10.1016/j.anbehav.2009.11.005>.
- Celi, M., Filicetto, F., Parrinello, D., Buscaino, G., Damiano, M. A., Cuttitta, A., et al. (2013). Physiological and agonistic behavioural response of *Procambarus clarkii* to an acoustic stimulus. *The Journal of Experimental Biology*, 216(4), 709–718. <http://dx.doi.org/10.1242/jeb.078865>.
- Chan, A. A. Y.-H., Giraldo-Perez, P., Smith, S., & Blumstein, D. T. (2010). Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biology Letters*, 6(4), 458–461. <http://dx.doi.org/10.1098/rsbl.2009.1081>.
- Chan, A. A. Y.-H., Stahlman, W. D., Garlick, D., Fast, C. D., Blumstein, D. T., & Blaisdell, A. P. (2010). Increased amplitude and duration of acoustic stimuli enhance distraction. *Animal Behaviour*, 80(6), 1075–1079. <http://dx.doi.org/10.1016/j.anbehav.2010.09.025>.
- Cocroft, R. B., & Rodriguez, R. L. (2005). The behavioral ecology of insect vibrational communication. *Bioscience*, 55(4), 323–334. [http://dx.doi.org/10.1641/0006-3568\(2005\)055\[0323:Tbeoiv\]2.0.Co;2](http://dx.doi.org/10.1641/0006-3568(2005)055[0323:Tbeoiv]2.0.Co;2).
- Coward, D., Blair, D., Burman, R., & Zhao, C. (2003). Vehicle-induced seismic effects at a gravitational wave observatory. *Review of Scientific Instruments*, 74(11), 4846–4854. <http://dx.doi.org/10.1063/1.1614411>.
- Cremer, L., Heckl, M., & Ungar, E. E. (1973). *Structure-borne sound*. Berlin, Germany: Springer-Verlag.
- Croll, D. A., Clark, C. W., Calambokidis, J., Ellison, W. T., & Tershy, B. R. (2001). Effect of anthropogenic low-frequency noise on the foraging ecology of Balaenoptera whales. *Animal Conservation*, 4(01), 13–27. <http://dx.doi.org/10.1017/S1367943001001020>.
- Di Iorio, L., & Clark, C. W. (2010). Exposure to seismic survey alters blue whale acoustic communication. *Biology Letters*, 6(1), 51–54. <http://dx.doi.org/10.1098/rsbl.2009.0651>.
- Dooling, R. J., Lohr, B., & Dent, M. L. (2000). *Hearing in birds and reptiles*. In R. Dooling, R. Fay, & A. Popper (Eds.), *Comparative hearing: Birds and reptiles* (Vol. 13); (pp. 308–359). New York: Springer.
- Elias, D. O., Andrade, M. C., & Kasumovic, M. M. (2011). Dynamic population structure and the evolution of spider mating systems. *Advances in Insect Physiology*, 41, 65.
- Elias, D. O., Mason, A. C., & Hebets, E. A. (2010). A signal-substrate match in the substrate-borne component of a multimodal courtship display. *Current Zoology*, 56(3), 370–378.
- Elias, D. O., Mason, A. C., & Hoy, R. R. (2004). The effect of substrate on the efficacy of seismic courtship signal transmission in the jumping spider *Habronattus dosseus* (Araneae: Salticidae). *Journal of Experimental Biology*, 207(23), 4105–4110. <http://dx.doi.org/10.1242/jeb.01261>.
- Fiala, P., Degrande, G., & Augusztinovicz, F. (2007). Numerical modelling of ground-borne noise and vibration in buildings due to surface rail traffic. *Journal of Sound and Vibration*, 301(3–5), 718–738. <http://dx.doi.org/10.1016/j.jsv.2006.10.019>.
- Ficken, R. W., Ficken, M. S., & Hailman, J. P. (1974). Temporal pattern shifts to avoid acoustic interference in singing birds. *Science*, 183(4126), 762–763. <http://dx.doi.org/10.1126/science.183.4126.762>.
- Footo, A. D., Osborne, R. W., & Hoelzel, A. R. (2004). Environment: whale-call response to masking boat noise. *Nature*, 428(6986), 910.
- Francis, C. D., Ortega, C. P., & Cruz, A. (2009). Noise pollution changes avian communities and species interactions. *Current Biology*, 19(16), 1415–1419. <http://dx.doi.org/10.1016/j.cub.2009.06.052>.
- Frohlich, C., & Buskirk, R. E. (1982). Transmission and attenuation of vibration in orb spider webs. *Journal of Theoretical Biology*, 95(1), 13–36. [http://dx.doi.org/10.1016/0022-5193\(82\)90284-3](http://dx.doi.org/10.1016/0022-5193(82)90284-3).
- Ghalambor, C. K., McKay, J. K., Carroll, S. P., & Reznick, D. N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*, 21(3), 394–407. <http://dx.doi.org/10.1111/j.1365-2435.2007.01283.x>.
- Grafe, T. U. (1996). The function of call alternation in the African reed frog (*Hyperolius marmoratus*): precise call timing prevents auditory masking. *Behavioral Ecology and Sociobiology*, 38(3), 149–158. <http://dx.doi.org/10.2307/4601185>.
- Groos, J. C., & Ritter, J. R. R. (2009). Time domain classification and quantification of seismic noise in an urban environment. *Geophysical Journal International*, 179(2), 1213–1231. <http://dx.doi.org/10.1111/j.1365-246X.2009.04343.x>.
- de Groot, M., Cökl, A., & Virant-Doberlet, M. (2010). Effects of heterospecific and conspecific vibrational signal overlap and signal-to-noise ratio on male

- responsiveness in *Nezara viridula* (L.). *The Journal of Experimental Biology*, 213(18), 3213–3222. <http://dx.doi.org/10.1242/jeb.044024>.
- Guedes, R. N. C., Matheson, S. M., Frei, B., Smith, M. L., & Yack, J. E. (2012). Vibration detection and discrimination in the masked birch caterpillar (*Drepana arcuata*). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 198(5), 325–335. <http://dx.doi.org/10.1007/s00359-012-0711-8>.
- Halfwerk, W., Holleman, L. J. M., Lessells, C. M., & Slabbekoorn, H. (2011). Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology*, 48(1), 210–219. <http://dx.doi.org/10.1111/j.1365-2664.2010.01914.x>.
- Hebets, E. A., Elias, D. O., Mason, A. C., Miller, G. L., & Stratton, G. E. (2008). Substrate-dependent signalling success in the wolf spider, *Schizocosa retrorsa*. *Animal Behaviour*, 75(2), 605–615. <http://dx.doi.org/10.1016/j.anbehav.2007.06.021>.
- Hieber, C. S. (1984). Orb-web orientation and modification by the spiders *Araneus diadematus* and *Araneus gemmoides* (Araneae: Araneidae) in response to wind and light. *Zeitschrift für Tierpsychologie*, 65(3), 250–260. <http://dx.doi.org/10.1111/j.1439-0310.1984.tb00103.x>.
- Hildebrand, J. A. (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*, 395, 5–20. <http://dx.doi.org/10.3354/meps08353>.
- Hill, P. S. M. (2008). *Vibrational communication in animals*. Cambridge, MA: Harvard University Press.
- Hill, P. S. M. (2009). How do animals use substrate-borne vibrations as an information source? *Naturwissenschaften*, 96(12), 1355–1371. <http://dx.doi.org/10.1007/s00114-009-0588-8>.
- Kasumovic, M. M., & Brooks, R. C. (2011). It's all who you know: the evolution of socially cued anticipatory plasticity as a mating strategy. *The Quarterly Review of Biology*, 86(3), 181–197. <http://dx.doi.org/10.1086/661119>.
- Kight, C. R., & Swaddle, J. P. (2011). How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecology Letters*, 14(10), 1052–1061. <http://dx.doi.org/10.1111/j.1461-0248.2011.01664.x>.
- Klarner, D., & Barth, F. G. (1982). Vibratory Signals and prey capture in orb-weaving spiders (*Zygiella x-notata*, *Nephila clavipes*, Araneidae). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 148(4), 445–455.
- Kurzweil, L. G. (1979). Ground-borne noise and vibration from underground rail systems. *Journal of Sound and Vibration*, 66(3), 363–370. [http://dx.doi.org/10.1016/0022-460x\(79\)90853-8](http://dx.doi.org/10.1016/0022-460x(79)90853-8).
- Lampe, U., Reinhold, K., & Schmoll, T. (2013). How grasshoppers respond to road noise: developmental plasticity and population differentiation in acoustic signalling. *Functional Ecology*. <http://dx.doi.org/10.1111/1365-2435.12215>.
- Lampe, U., Schmoll, T., Franzke, A., & Reinhold, K. (2012). Staying tuned: grasshoppers from noisy roadside habitats produce courtship signals with elevated frequency components. *Functional Ecology*, 26(6), 1348–1354. <http://dx.doi.org/10.1111/1365-2435.12000>.
- Landolf, M. A., & Barth, F. G. (1996). Vibrations in the orb web of the spider *Nephila clavipes*: cues for discriminating and orientation. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 179(4), 493–508.
- Lang, F. (1996). Noise filtering in the auditory system of *Locusta migratoria* L. *Journal of Comparative Physiology A*, 179(4), 575–585. <http://dx.doi.org/10.1007/BF00192323>.
- Leonard, M. L., & Horn, A. G. (2012). Ambient noise increases missed detections in nestling birds. *Biology Letters*, 8(4), 530–532. <http://dx.doi.org/10.1098/rsbl.2012.0032>.
- Liao, C. P., Chi, K. J., & Tso, I. M. (2009). The effects of wind on trap structural and material properties of a sit-and-wait predator. *Behavioral Ecology*, 20(6), 1194–1203. <http://dx.doi.org/10.1093/beheco/arp119>.
- Maes, J. H. R., & de Groot, G. (2003). Effects of noise on the performance of rats in an operant discrimination task. *Behavioral Processes*, 61(1–2), 57–68. [http://dx.doi.org/10.1016/S0376-6357\(02\)00163-8](http://dx.doi.org/10.1016/S0376-6357(02)00163-8).
- Masters, W. M. (1984a). Vibrations in the orbwebs of *Nuctenea sclopetaria* (Araneidae). 1. Transmission through the web. *Behavioral Ecology and Sociobiology*, 15(3), 207–215. <http://dx.doi.org/10.1007/Bf00292977>.
- Masters, W. M. (1984b). Vibrations in the orbwebs of *Nuctenea sclopetaria* (Araneidae). 2. Prey and wind signals and the spiders' response threshold. *Behavioral Ecology and Sociobiology*, 15(3), 217–223. <http://dx.doi.org/10.1007/Bf00292978>.
- Masters, W. M., & Markl, H. (1981). Vibration signal transmission in spider orb webs. *Science*, 213(4505), 363–365. <http://dx.doi.org/10.1126/science.213.4505.363>.
- Masters, W. M., Markl, H. S., & Moffat, A. J. M. (1986). Transmission of vibration in a spider's web. In W. A. Shear (Ed.), *Spiders: Webs, behavior, and evolution* (pp. 49–69). Stanford, CA: Stanford University Press.
- Mazzoni, V., Lucchi, A., Cokl, A., Prešern, J., & Virant-Doberlet, M. (2009). Disruption of the reproductive behaviour of *Scaphoideus titanus* by playback of vibrational signals. *Entomologia Experimentalis et Applicata*, 133(2), 174–185. <http://dx.doi.org/10.1111/j.1570-7458.2009.00911.x>.
- McNett, G. D., & Cocroft, R. B. (2008). Host shifts favor vibrational signal divergence in *Enchenopa binotata* treehoppers. *Behavioral Ecology*, 19(3), 650–656. <http://dx.doi.org/10.1093/beheco/arn017>.
- McNett, G. D., Luan, L. H., & Cocroft, R. B. (2010). Wind-induced noise alters signaler and receiver behavior in vibrational communication. *Behavioral Ecology and Sociobiology*, 64(12), 2043–2051. <http://dx.doi.org/10.1007/s00265-010-1018-9>.
- Narins, P. M. (1982). Effects of masking noise on evoked calling in the Puerto Rican coqui (Anura: Leptodactylidae). *Journal of Comparative Physiology*, 147(4), 439–446. <http://dx.doi.org/10.1007/BF00612008>.
- Narins, P. M. (1990). Seismic communication in anuran amphibians. *Bioscience*, 40(4), 268–274. <http://dx.doi.org/10.2307/1311263>.
- Narins, P. M. (2001). *Vibration communication in vertebrates*. Springer-Verlag.
- Nentwig, W. (1985). Prey analysis of four species of tropical orb-weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. *Oecologia*, 66(4), 580–594. <http://dx.doi.org/10.1007/BF00379353>.
- Ngai, K. W., & Ng, C. F. (2002). Structure-borne noise and vibration of concrete box structure and rail viaduct. *Journal of Sound and Vibration*, 255(2), 281–297. <http://dx.doi.org/10.1006/jsvi.2001.4155>.
- Nowacek, D. P., Thorne, L. H., Johnston, D. W., & Tyack, P. L. (2007). Responses of cetaceans to anthropogenic noise. *Mammal Review*, 37(2), 81–115. <http://dx.doi.org/10.1111/j.1365-2907.2007.00104.x>.
- Polajnar, J., & Cokl, A. (2008). The effect of vibratory disturbance on sexual behaviour of the southern green stink bug *Nezara viridula* (Heteroptera, Pentatomidae). *Central European Journal of Biology*, 3(2), 189–197. <http://dx.doi.org/10.2478/s11535-008-0008-7>.
- Quinn, J., Whittingham, M., Butler, S., & Cresswell, W. (2006). Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. *Journal of Avian Biology*, 37(6), 601–608. <http://dx.doi.org/10.1111/j.2006.0908-8857.03781.x>.
- Rabin, L. A., Coss, R. G., & Owings, D. H. (2006). The effects of wind turbines on antipredator behavior in California ground squirrels (*Spermophilus beecheyi*). *Biological Conservation*, 131(3), 410–420. <http://dx.doi.org/10.1016/j.bioco.2006.02.016>.
- Randall, J. A. (2001). Evolution and function of drumming as communication in mammals. *American Zoologist*, 41(5), 1143–1156. <http://dx.doi.org/10.1093/icb/41.5.1143>.
- Schaub, A., Ostwald, J., & Siemers, B. M. (2008). Foraging bats avoid noise. *Journal of Experimental Biology*, 211(19), 3174–3180. <http://dx.doi.org/10.1242/jeb.022863>.
- Schilcher, F. (1976). The function of pulse song and sine song in the courtship of *Drosophila melanogaster*. *Animal Behaviour*, 24(3), 622–625. [http://dx.doi.org/10.1016/S0003-3472\(76\)80076-0](http://dx.doi.org/10.1016/S0003-3472(76)80076-0).
- Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C., & Popper, A. N. (2010). A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution*, 25(7), 419–427. <http://dx.doi.org/10.1016/j.tree.2010.04.005>.
- Slabbekoorn, H., & Peet, M. (2003). Ecology: birds sing at a higher pitch in urban noise. *Nature*, 424(6946), 267.
- Slabbekoorn, H., & Ripmeester, E. A. P. (2008). Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology*, 17(1), 72–83. <http://dx.doi.org/10.1111/j.1365-294X.2007.03487.x>.
- Speck, J., & Barth, F. G. (1982). Vibration sensitivity of pretarsal slit sensilla in the spider leg. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 148(2), 187–194.
- Uhl, G., & Elias, D. O. (2011). Communication. In M. E. Herberstein (Ed.), *Spider behaviour: Flexibility and versatility* (pp. 127–190). Cambridge, UK: Cambridge University Press.
- Virant-Doberlet, M., & Cokl, A. (2004). Vibrational communication in insects. *Neotropical Entomology*, 33, 121–134.
- Walcott, C. (1969). A spider's vibration receptor: its anatomy and physiology. *American Zoologist*, 9(1), 133–144.
- Warkentin, K. M. (2005). How do embryos assess risk? Vibrational cues in predator-induced hatching of red-eyed treefrogs. *Animal Behaviour*, 70, 59–71. <http://dx.doi.org/10.1016/j.anbehav.2004.09.019>.
- Warren, P. S., Katti, M., Ermann, M., & Brazel, A. (2006). Urban bioacoustics: it's not just noise. *Animal Behaviour*, 71, 491–502. <http://dx.doi.org/10.1016/j.anbehav.2005.07.014>.
- Weilgart, L. S. (2007). The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Canadian Journal of Zoology*, 85(11), 1091–1116. <http://dx.doi.org/10.1139/Z07-101>.
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. New York: Oxford University Press.
- Wignall, A. E., Jackson, R. R., Wilcox, R. S., & Taylor, P. W. (2011). Exploitation of environmental noise by an araneophagous assassin bug. *Animal Behaviour*, 82(5), 1037–1042. <http://dx.doi.org/10.1016/j.anbehav.2011.07.038>.
- Wright, A. J., Soto, N. A., Baldwin, A. L., Bateson, M., Beale, C. M., Clark, C., et al. (2007). Anthropogenic noise as a stressor in animals: a multidisciplinary perspective. *International Journal of Comparative Psychology*, 20(2), 250–273.
- Young, B. A., & Morain, M. (2002). The use of ground-borne vibrations for prey localization in the Saharan sand vipers (*Cerastes*). *Journal of Experimental Biology*, 205(5), 661–665.
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.

Appendix

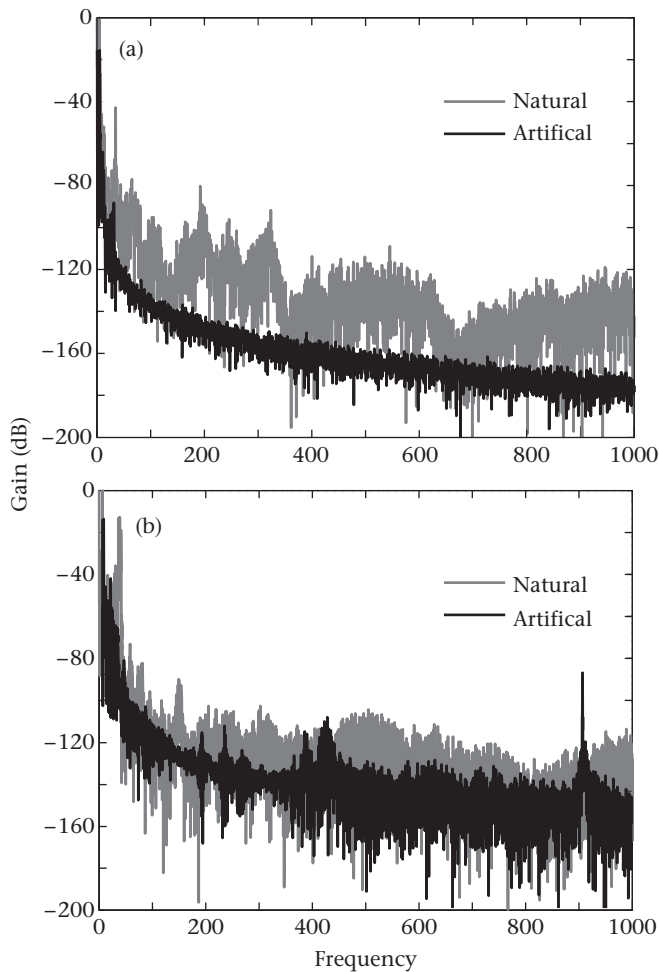


Figure A1. Representative power spectra of (a) wind-induced and (b) anthropogenic vibratory noises on natural and artificial substrates.

Table A2
Web attachment substrates for *A. diadematus*

Substrate type	Number of attachment points	Percentage usage	Geometric structure utilized
Oval leaf	25	8.8	(1)
Vine leaf	5	1.8	(1)
Long flat leaf	86	30.4	(1)
Needle leaf	15	5.3	(1)
Hard twig	30	10.6	(1),(2)
Soft twig	13	4.6	(1),(2)
Tree	23	8.1	(1)
Others	2	0.7	(1)
Sum: natural	199	70.3	
Concrete	26	9.2	(1),(2)
Glass	10	3.5	(1)
Metal	40	14.1	(1),(2),(3)
Plastic	3	1.1	(4)
Wood-like	5	1.8	(1)
Sum: artificial	84	29.7	
Sum: total	283	100.0	

Numbers of attachment points were pooled across all 50 webs observed. Numbers in parentheses correspond to the geometrical structure indices of each substrate type in Table A1.

Table A1
Classification of natural and artificial substrate types and their geometrical structures presented in the field

Substrate type	Descriptions	Geometrical structures
Substrate category: natural		
Oval leaf	Small (<15cm in length), oval or circular leaves on bush plants	(1) As description
Vine leaf	Oval or circular leaves on vines	(1) As description
Long flat leaf	Long (>15cm in length), flat leaves on ground plants	(1) As description
Needle leaf	Needle-like leaves on bush or ground plants	(1) As description
Hard twig	Small (<2cm in diameter) twigs with lignified, nonbendable linings	(1) <1cm in diameter; (2) >1cm and <2cm in diameter
Soft twig	Small (<2cm in diameter) twigs with soft, bendable linings	(1) <1cm in diameter; (2) >1cm and <2cm in diameter
Tree	Tree trunk or twig >2cm in diameter	(1) As description
Others	Nonplant, natural substrates on the ground	(1) As description
Substrate category: artificial		
Concrete	Concrete objects or walls	(1) Wall; (2) isolated object, maximum thickness >5cm; (3) isolated object, maximum thickness <5cm
Glass	Windows	(1) Thickness <1cm; (2) Thickness >1cm
Metal	Metal rods, road signs or street lights	(1) Cross-sectional length or diameter (<i>l</i> or <i>d</i>) >5cm, $R > 0.2$; (2) <i>l</i> or <i>d</i> <5cm, $R > 0.2$; (3) <i>l</i> or <i>d</i> >5cm, $R < 0.2$; (4) <i>l</i> or <i>d</i> <5cm, $R < 0.2$
Plastic	Plastic tube or rod	(1) <i>l</i> or <i>d</i> >5cm, $R > 0.2$; (2) <i>l</i> or <i>d</i> <5cm, $R > 0.2$; (3) <i>l</i> or <i>d</i> >5cm, $R < 0.2$; (4) <i>l</i> or <i>d</i> <5cm, $R < 0.2$
Wood-like	Artificial wooden objects	(1) Maximum thickness >5cm; (2) maximum thickness <5cm

For natural substrate types other than 'Hard twig', 'Soft twig', their geometrical structures were not further classified due to similarity. *l*: cross-sectional length; *d*: diameter; *R*: maximum *l* divided by minimum *l*.