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Vibration-induced freezing in *Aegorhinus nodipennis* (Coleoptera: Curculionidae): implications for pest management in hazelnuts

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The weevil *Aegorhinus nodipennis* (Coleoptera: Curculionidae) (Hope, 1834) is a polyphagous woodboring beetle of economic concern in Chile and southern Argentina, mainly affecting berries and hazelnut. Although insecticides may be applied in hazelnut orchards, their effectiveness is limited and can be environmentally impactful, underscoring the need for alternative, sustainable control strategies. Attempts to exploit semiochemicals for attraction or repellence have yielded only modest results, failing to support effective trapping or deterrence. This study investigates substrate-borne vibrations as a complementary behavioral management tool by examining their potential to induce defensive responses in *A. nodipennis*. We demonstrate that walking individuals exhibit a stereotyped freezing response to vibrational stimuli, with peak sensitivity at 50 to 150 Hz (median threshold at 0.71 m/s^2) and a secondary sensitivity increase at 1–2 kHz. The duration of the immobile phase increases strongly with stimulus duration, with a median around 200 s following a 5 s stimulus, but is much less affected by amplitude once the threshold is exceeded. In addition, weevils exhibit a marked postfreeze locomotor suppression, with walking speed reduced to 25% to 30% of prestimulus levels. These findings suggest that extended low-amplitude vibrational stimuli could effectively suppress activity and feeding. This offers a novel, nonchemical, and potentially economically viable approach in managing this pest. Deterrent vibrations could be deployed directly on host plants or on structural barriers in orchards. This study provides a foundation for integrating vibrational cues into pest management frameworks for *A. nodipennis* and related weevils, though results are currently limited to females.

Keywords: substrate-borne vibration, locomotor suppression, vibrational deterrence, applied biotremology

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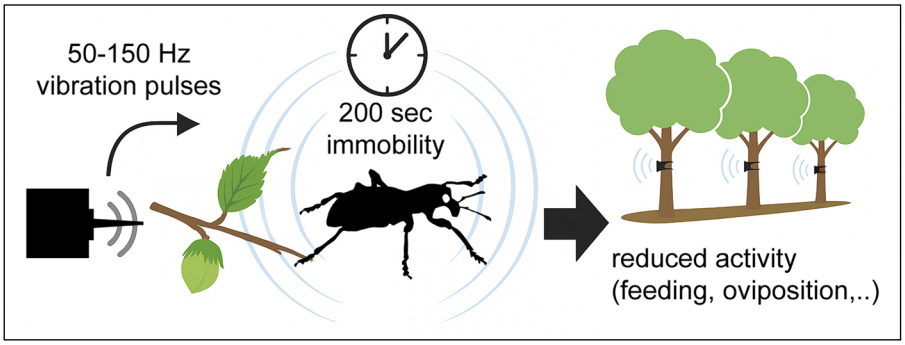
Graphical abstract



Introduction

Weevils of the genus *Aegorhinus* (Coleoptera: Curculionidae: Aterpini) are flightless beetles endemic to temperate forests of southern South America, particularly Chile and parts of southern Argentina, where *A. nodipennis* (Hope, 1834) and *A. superciliosus* (Guérin-Méneville, 1830) have become serious pests in perennial crops (Elgueta and Marvaldi 2006, Zavala et al. 2011). In Chile, *A. nodipennis* is the most widespread species, now heavily infesting berry species and European hazelnuts (*Corylus avellana* L., Betulaceae) (Lencinas et al. 2021, Navarro et al. 2022). Its larvae feed within the root crown, often killing plants, while adults damage branches and foliage, reducing yield (Ellena et al. 2014, Navarro et al. 2022). The rapid expansion of hazelnut cultivation in Chile, currently exceeding 49,000 hectares (ODEPA 2025), has amplified the economic significance of this pest that threatens one of the country's most dynamic agro-industries.

Control of *Aegorhinus* species has relied mainly on insecticides, but their efficacy is limited because larvae stay protected inside the plant (Lencinas et al. 2021). Combined with concerns over environmental safety and pollinator exposure, this underscores the urgency for alternative, more sustainable pest management strategies. Attempts to exploit semiochemicals have shown some potential for monitoring or disruption of these species. In the closely related *A. superciliosus*, males respond behaviorally to R-limonene, a compound emitted by females (Mutis et al. 2010). Some plant-based attractants and repellents have also been identified, but have shown modest and inconsistent effectiveness in the field (Tampe et al. 2020a, b). Thus, despite offering useful insights, semiochemical tools have not yet delivered robust standalone control methods, and pest management of the *Aegorhinus* genus, particularly in hazelnuts, remains largely dependent on insecticides.

As an alternative, recent research has focused on substrate-borne vibrations as an emerging tool in pest management (Mazzoni et al. 2019, Takanashi et al. 2019, Strauβ et al. 2021, Yanagisawa et al. 2024). Vibrational signals and cues play key roles in insect communication and predator avoidance (Cocroft & Rodríguez 2005, Virant-Doberlet et al. 2019, 2023), based on the widespread presence of specialized vibration-detecting organs in insect legs (Strauβ et al. 2021, 2024). Insects are particularly dependent on vibrational cues in plant habitats, where plant tissues transmit vibrations with high efficiency (Polajnar et al. 2012, Čokl et al. 2021).

In biotremology, the study of animal interactions via substrate vibrations (Hill and Wessel 2016), most applied work has focused on mating disruption, typically by interfering with vibrational courtship through the playback of rival signals or noise. This approach has been successfully used in several Hemiptera: the leafhopper *Scaphoideus titanus* Ball, 1932 (Cicadellidae), the sharpshooter *Homalodisca vitripennis* (Germar, 1821) (Mazzoni et al. 2017), and psyllids such as *Bactericera cockerelli* (Šulc, 1909) and *Diaphorina citri* Kuwayama, 1908 (Mankin 2019, Avosani et al. 2020). More recently, vibrational signals have also been adapted for active trapping of the brown marmorated stink bug *Halyomorpha halys* (Stål, 1855) (Pentatomidae) (Zapponi et al. 2023), broadening the potential of vibrational approaches in managing pests that use vibrations in the sexual context.

In addition, there is growing interest for the use of more generalized vibrational cues that trigger defensive behaviors in insects, such as immobility, startle and escape (Tsubaki et al. 2014, Takanashi et al. 2016, Takanashi and Kojima 2021, Parent et al. 2022, Macdougall et al. 2025). Unlike sexual signals, these "hardwired" responses are broadly expressed in response to stimuli mimicking predator cues and offer potential for pest management. They can cause immediate disruption of feeding, oviposition, and movement, while also inducing longer-term effects thorough increased energetic costs and predator-related stress that reduce survival and fecundity (Foster and Harris 1997, Takanashi et al. 2019, Pekas et al. 2024, Yanagisawa et al. 2024). Among Coleoptera, vibration-induced defense responses, such as freezing, startle and tonic immobility, have been documented across many families (Takanashi and Kojima 2021, Davis et al. 2023) and explored as potential crop protection strategies in some pest cerambycid and chrysomelid species (Acheampong and Mitchell 1997, Tsubaki et al. 2014, Takanashi et al. 2016, Takanashi and Nishino 2022).

For *A. nodipennis* and Curculionidae in general, defensive vibrational behaviors have not yet been studied. Here, we investigated the freezing response, that is, a transient cessation of movements, in walking individuals to pulsed vibrational stimuli. Specifically, we determined the frequency thresholds and the effects of stimulus intensity and duration on the duration of the immobile phase and postfreeze locomotor inhibition. Our findings provide the basis for developing a non-chemical

management tool for *A. nodipennis* in hazelnut orchards based on vibrational deterrence.

Materials and Methods

Animal Collection and Rearing

At the beginning of November 2024, we collected adult *A. nodipennis* from hazelnut orchard in southern Chile (Araucanía Region; Fig. 1A). The insects were kept in plastic terraria (dim. 35×20×20 cm) in groups of up to 50 individuals, at 23 to 25 °C with a natural light: dark cycle. They were provided with fresh hazelnut twigs, leaves, and water *ad libitum*. Prior to testing, individuals were isolated in 50 ml vials at least 24 h before the experiment. Each vial was supplied with a fresh twig and water-soaked cotton.

After completion of the experiments, all tested individuals were prepared and sexed, together with several additional weevils collected in the first half of November 2024. All experimental individuals were confirmed to be females, and only a single male was found in the entire sample, which could suggest that females may emerge earlier than males, but this requires further confirmation. Thus, the responses reported are based on females, and while we expect the general patterns to be similar in males, this assumption requires confirmation.

Experimental Set-up

The experimental set-up consisted of a 20 cm long wooden rod (diameter of 1.5 cm), marked at 2 cm intervals. The rod was attached with its central point perpendicularly to the direction of stimulation to a vibration exciter (type 4180, Brüel & Kjær, Denmark). The vibration exciter was fixed by a steel base at an angle of 45°, resulting in the same inclination of the test rod (Fig. 1B). The behavior of the weevils on the rod was videorecorded (HC-VXF990, Panasonic, Japan), showing lateral and top views.

Generation of Vibrational Stimuli

Vibrational stimuli were sinusoidal pulses of various durations (100 to 5,000 ms; all with 10 ms rise and fall times), carrier frequencies (30 to 2,000 Hz), and acceleration amplitudes (0.0126 to 12.6 m/s^2) applied depending on the test type. The stimuli were synthesized in Audacity (Audacity Team) at 44.000 Hz resolution and applied to the minishaker via a computer in-built sound card and a power amplifier (Rigol Pa1011, Suzhou, China). For calibration, stimuli were measured by the laser vibrometer (Polytec, PDV-100, Waldbron, Germany) at the center of the rod—the point of its attachment to the minishaker, and on the output of the vibration calibration exciter (Brüel and Kjær, 4294, Denmark) providing the reference signal (10 mm/s) for the amplitude calculation.

Experiments

We experimentally tested the characteristics of the vibrational freezing response elicited during walking in *A. nodipennis*. Each test was conducted by gently placing an individual at the lower end of the rod and letting it walk upwards along it. The test stimulus was applied once the weevil's midlegs reached the center of the rod. If walking did not start within 1 min, we replaced the individual. Subsequent tests with the same individual were conducted at a minimum interval of 1 min to avoid habituation. We investigated the frequency-threshold sensitivity of the freezing response (i.e., immobility), the effects of stimulus intensity and stimulus duration on the duration of the immobile phase, as well as the effects of stimulus intensity and duration on the change in postfreezing walking velocity relative to prestimulus velocity.

In the threshold test, we applied a 500 ms long stimulus at the carrier frequencies of 30, 50, 70, 100, 150, 200, 300, 500, 700, 1,000, and 2,000 Hz, with acceleration amplitudes varied between 0.126 and 12.6 m/s^2 in 5 dB steps. We randomized the order of test frequencies across the individuals and tested for

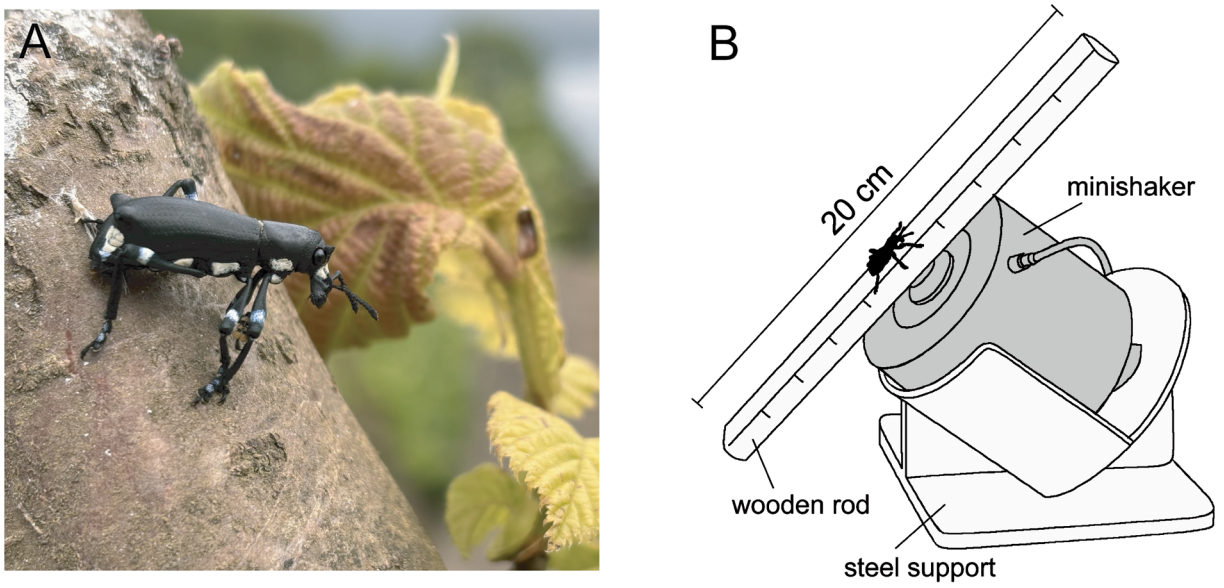


Fig. 1. *Aegorhinus nodipennis* A) on a hazelnut trunk in a commercial orchard, Araucanía Region, Chile, and B) in the experimental set-up (schematic). In the experiment, a weevil was placed at the bottom of a rod attached to a minishaker and left walking along it. The test stimulus was applied once the weevil's midlegs reached the central point of the rod.

the threshold at only one frequency at a time (with the individual returned to its vial between the tests). The starting intensity was also randomly applied and then increased (if no response was observed) or decreased (if a response occurred). We tested 10 to 12 individuals per frequency, using a total of 21 individuals in the threshold test (some were replaced due to inactivity during the 5-day testing period).

In the intensity test, we applied a 100 Hz, 500 ms long stimulus at acceleration amplitudes increasing from 0.126 to 12.6 m/s^2 in 5 dB steps. In the duration test, we applied a 100 Hz stimulus of 4 m/s^2 acceleration with durations of 100, 250, 500, 1,000, 2,000, and 5,000 ms, applied at a randomized order to each individual. In both tests, the same set of individuals (n = 10) was used across all stimulus conditions, including 3 that were not part of the threshold test. In total, 24 individuals were used in all experiments.

Behavioral Analysis

The behavior was analyzed from the video records in a frame-to-frame manner. In most cases, the weevil's movement between the subsequent video frames preceding the stimulus was continuous. We defined the threshold as the lowest stimulus intensity triggering the cessation of all movements for the duration of at least 2 video frames. In case movement was already discontinuous prior to the stimulus, the threshold was defined as the intensity that prolonged the poststimulus inactivity period for at least 2 video frames compared to the preceding one.

Following the termination of the freezing response, weevils typically exhibited a slow-down in waking speed, revealing a delayed effect of the stimulus. To analyze this change in walking velocity, we measured the time each individual required to cross a 4 cm section of the rod both before and after stimulus application. To ensure precision, equivalent walking phases based on body and leg positions were analyzed. Poststimulus walking velocity was then normalized to prestimulus velocity, producing a relative measure of change across stimulus intensities and durations.

Statistical Analysis

Diagrams were generated in Microsoft Excel, while all statistical analyses were performed in Python (3.12). Statistical methods followed established procedures: a linear model fitted by ordinary least squares regression for threshold comparisons (Kutner et al. 2005), Wilcoxon signed-rank test for paired nonparametric comparisons (Wilcoxon 1945), and false discovery rate (FDR) correction to control for multiple testing (Benjamini and Hochberg 1995).

Differences between thresholds were analyzed using a linear model, with the minimum stimulus intensity (m/s^2) at which an individual exhibited a freezing response (i.e., threshold) representing the response variable. Stimulation frequency (30 to 2,000 Hz) was included as a categorical fixed effect, with 70 Hz (with lowest median threshold) set as the reference level. This design allowed us to test for differences in sensitivity across frequencies relative to the baseline.

Changes in freezing response duration and walking speed were analyzed using the Wilcoxon signed-rank test, suitable for small samples and non-normally distributed data. A one-sided test was applied when comparing responses against a defined baseline (threshold amplitude for stimulus intensity tests, shortest stimulus for stimulus duration tests, and prestimulus walking velocity for postfreeze slow-down). When comparing responses across different stimulus amplitudes or durations, we used two-sided tests, since no directional prediction was made. To control for type I error across multiple comparisons, P-values were adjusted using the FDR correction.

Data are reported as medians with interquartile range (IQR).

Results

Vibrational stimuli induced a freezing response; an abrupt cessation of all activities of varying duration. At higher stimulus amplitudes, the inactivity period typically commenced with a startle; a transient jerk of the body with a pronounced leaning of the head and the antennae toward the substrate (Supplementary Video S1).

The freezing response expressed the main sensitivity peak between 70 and 150 Hz with the median threshold at 0.71 m/s^2, reduced sensitivity in the 500 to 700 Hz range with threshold at 4 to 7.1 m/s^2, and a secondary sensitivity peak at 1 kHz with threshold at 1.75 m/s^2 (Fig. 2). Thresholds at 500 Hz (β = +4.58, P < 0.001) and 700 Hz (β = +4.32, P < 0.001) were most significantly elevated from the reference level at 70 Hz, while the threshold at 1000 Hz was not significantly elevated from the baseline (GLMM; β = +1.54, P < 0.064; Fig. 2). Also frequencies between 30 and 200 Hz did not significantly differ from 70 Hz, suggesting a plateau of sensitivity at low frequencies. Such nonmonotonic, bimodal tuning was observed consistently across individuals.

As absolute stimulus amplitude increased, the median freezing response duration to a 100 Hz stimulus rose from 0.17 (IQR: 0 to 0.57) s at 0.71 m/s^2 (the median threshold at 100 Hz), to 2.84 (IQR: 2.09 to 3.63) s at 7.1 m/s^2, before declining again at higher amplitudes (Fig. 3A). Statistically significant increases compared to threshold level response were observed at 4 m/s^2 and higher amplitudes (Wilcoxon singed-ranks test, FDR corrected; P = 0.022 to 0.032). When stimulus amplitude was expressed in decibels (dB) relative to individual thresholds, the median response duration increased from 0.29 (IQR: 0.21 to 0.65) s at threshold to a peak of 3.42 (IQR: 1.61 to 4.34) s at 15 dB above threshold. At higher amplitudes response duration declined to values between 1.57 (IQR: 1.3 to 1.83) sec and 2.29 (IQR: 1.78 to 4.69) s (Fig. 3B). Statistically significant increases relative to

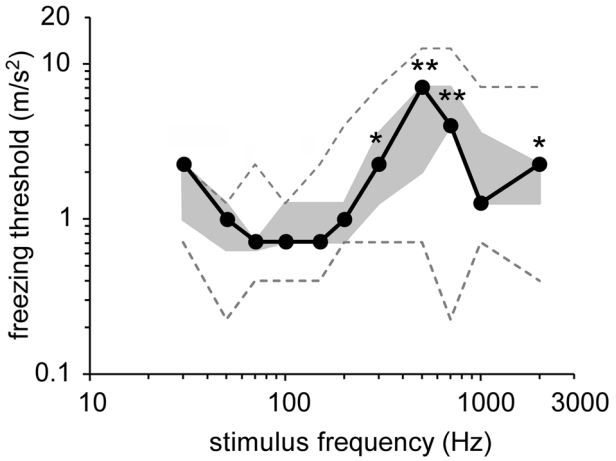


Fig. 2. Threshold tuning of the vibrational freezing response in *A. nodipennis*. Data show median threshold with interquartile ranges (grey area) and the extreme values (dashed lines). Statistical differences from the reference level (at 70 Hz) were assessed using GLMM with stimulus frequency treated as a categorical predictor. Significant differences are indicated by asterisks (*P < 0.05, **P < 0.001).

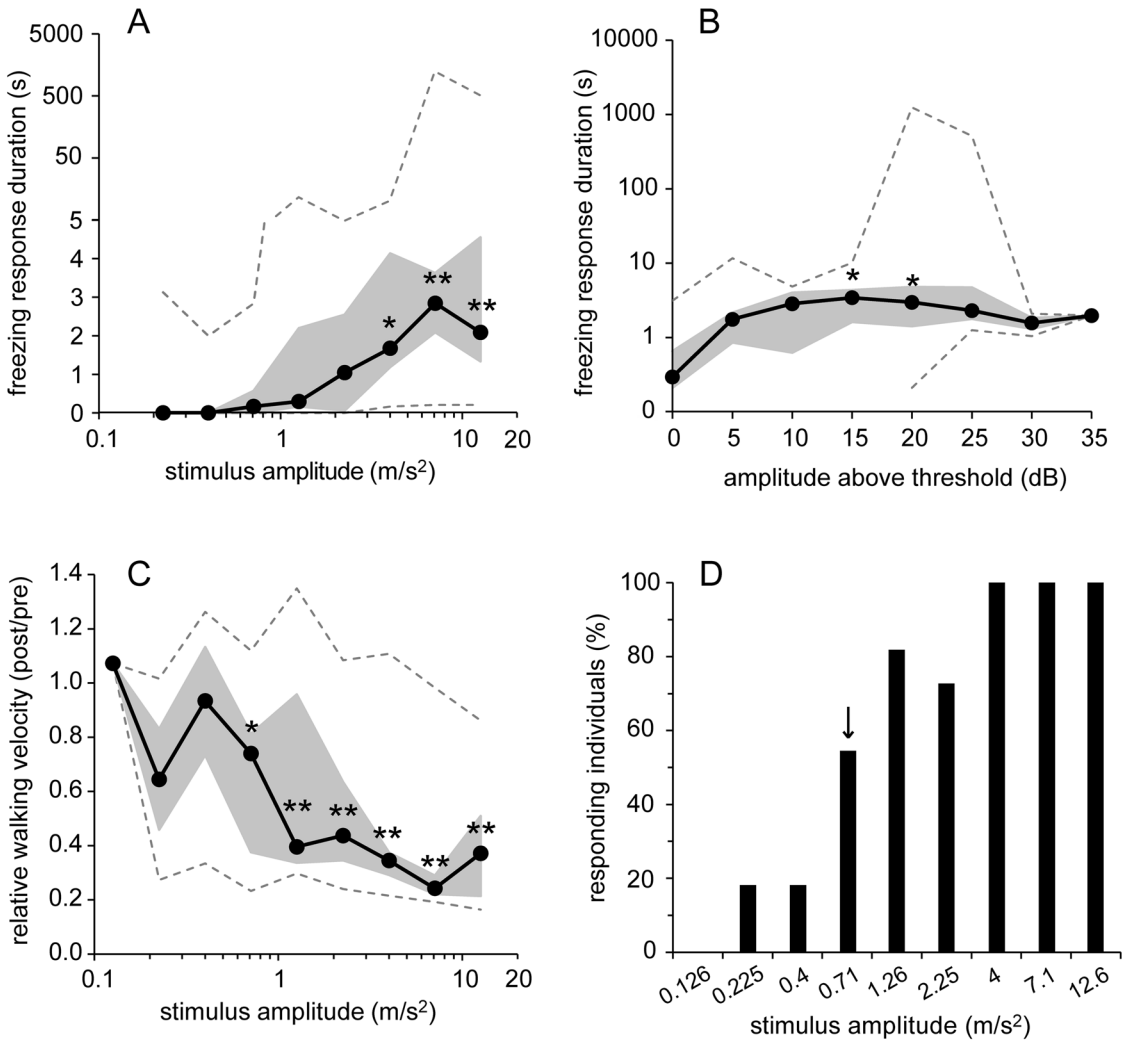


Fig. 3 Behavioral responses of *A. nodipennis* to increasing vibration amplitudes (100 Hz, 500 ms stimuli). A) Duration of freezing response as a function of absolute stimulus amplitude. B) Duration of freezing response as a function of relative stimulus amplitude (in dB) to the individual threshold level. C) Reduced velocity after freezing, as the ratio of poststimulus to prestimulus walking velocity (post/pre), show against absolute stimulus amplitude. D) Percentage of individuals expressing the freezing response, and slowdown, as a function of absolute stimulus amplitude. The arrow indicates the median threshold amplitude. Pannels A–C show medians (lines) with interquartile ranges (grey areas) and extreme values (dashed lines). Asterisks indicate significant differences from threshold (Wilcoxon signed-rank test, one-sided, FDR-corrected; * $P < 0.05$, ** $P < 0.01$). The y-axis in A is linear up to 5 s and logarithmic above.

threshold were observed only at 15 dB and 20 dB (Wilcoxon Singed-Ranks test, FDR corrected; $P = 0.042$), confirming a transient amplification of the response followed by a plateau rather than a continuous increase with stimulus intensity.

A significant slow-down in walking following the freezing response was already evident at the median threshold amplitude (0.71 m/s²) and intensified with increasing stimulus intensity, reaching a plateau between 2.25 and 12.6 m/s². Within this range, the normalized walking velocity dropped to between 0.24 and 0.44 of that prior the stimulus, and the effect was statistically significant (Wilcoxon singed-ranks test, FDR corrected; $P = 0.010$ to 0.002; Fig. 3C). Thereby, the percentage of individuals exhibiting freezing response and postfreeze slow-down increased from 18% at 0.225 m/s² to 100% at 4.0 m/s² (Fig. 3D).

The freezing response duration was also influenced by the increased stimulus duration, which appeared to have a much stronger effect than stimulus amplitude increase. The median response duration increases across the test stimulus durations from 0.17 (IQR: 0.14 to 1.11) s at 100 ms to 206.7 (74.4 to 443.9) s at 5,000 ms (Fig. 4A), without saturation. Compared to the 100 ms treatment, the effect was statistically significant at all subsequent stimulus durations (Wilcoxon singed-ranks test, FDR corrected; $P = 0.004$ to 0.005). Pairwise comparison revealed statistical response increases also between 250 and 500 ms, and 1,000 and 5,000 ms steps (both $P = 0.029$, Wilcoxon singed-ranks test, FDR corrected). Thereby, the percentage of responding individuals was 80% with the 100 ms long stimulus and 100% at all longer stimulus durations.

By contrast, the reduction of walking velocity following freezing evoked by stimuli of different durations was comparable to the effect seen with increased stimulus amplitude. This reduction was significant with all stimulus durations (Wilcoxon signed-ranks test, FDR corrected; $P = 0.002$–0.004; Fig. 4B), with the most pronounced slow-down at 500 ms (median: 0.35, IQR: 0.23 to 0.57) and 1,000 ms stimuli (median: 0.31, IQR: 0.23 to 0.48). However, pairwise comparison between stimulus

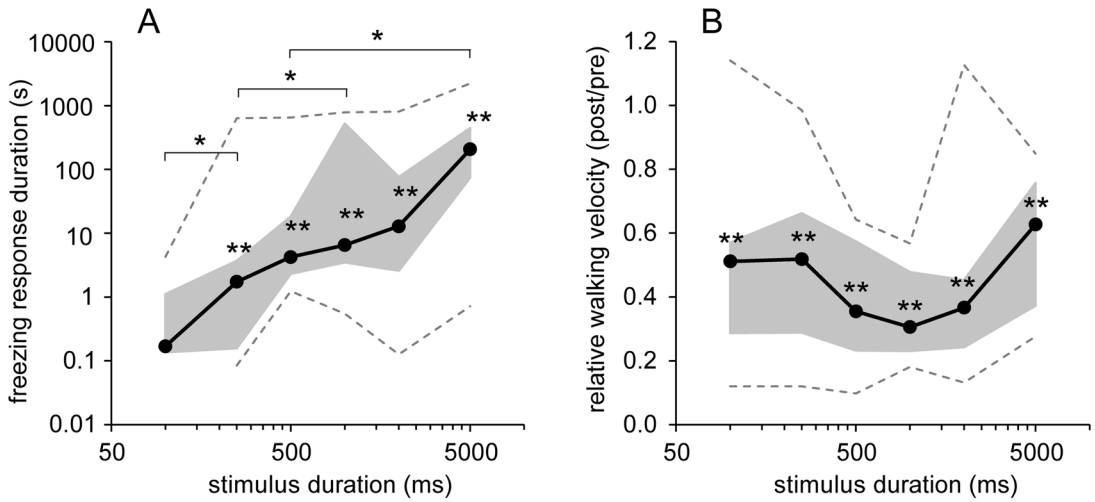


Fig. 4. Behavioral responses of *A. nodipennis* to increasing vibrational stimulus durations. A) Duration of freezing response and B) reduced velocity after freezing, as the ratio of poststimulus to prestimulus walking velocity (post/pre), evoked by a 100 Hz stimulus at 4 m/s^2 acceleration amplitude. Data show medians with interquartile ranges (grey area) and extreme values (dashed lines). Asterisks above the medians indicate significance levels in the comparisons to the shortest stimulus in A) and to prestimulus velocity in B) (Wilcoxon signed-rank test, FDR corrected; $*P<0.05$, $**P<0.01$). Asterisks between the data pairs indicate significant differences in pairwise comparisons (FDR corrected; $P>0.05$).

durations did not reveal significant differences (Wilcoxon singed-ranks test, FDR corrected; $P=0.29$ to 0.95).

Discussion

Our results show that *A. nodipennis* exhibits a characteristic freezing response to substrate vibrations, with heightened sensitivity at frequencies between 50 and 150 Hz and notably low amplitude thresholds. In addition, prolonged immobility and postfreeze reduced walking velocity were triggered even by stimuli of moderate duration and intensity. These response characteristics are promising for the development of vibrational deterrence strategies for crop protection in this species.

While the low-frequency tuning of the freezing response in *A. nodipennis* is broadly comparable to that of vibrationally elicited defensive behaviors in other Coleoptera (Tsubaki et al. 2014, Takanashi et al. 2019), the Chilean curculionid responds to substantially lower stimuli amplitudes. This enhanced sensitivity, ranging between 5 and 30 dB at peak frequencies, is advantageous for field application where signal attenuation through plant structures is unavoidable. We also observed a secondary sensitivity peak between 1 and 2 kHz in *A. nodipennis*, not seen in other beetles (Takanashi et al. 2019), expanding the range of potentially deterrent stimuli. This peak suggests ecological relevance of multiple frequency bands to this species. Notably, the frequency spectra of plant vibrations differ characteristically for biotic and abiotic sources. When generated by abiotic factors such as wind, vibrations are typically dominated by low frequencies peaking between 5 and 30 Hz (e.g., McNett et al. 2010, Guedes et al. 2012, Tsubaki et al. 2014). In contrast, biotic sources like insect walking or landing produce vibrations with significantly greater energy at higher frequencies (Castellanos and Barbosa 2006, Tsubaki et al. 2014). These differences were shown to be crucial for prey species like caterpillar larvae to discriminate predator-generated cues from those of herbivores or abiotic sources, leading to distinct behavioral responses (Castellanos and Barbosa 2006). Considering these findings, the elevated sensitivity of *A. nodipennis* in the higher frequency range may enhance its ability to discriminate and selectively respond to biologically relevant stimuli, while ignoring nonthreatening abiotic disturbances.

Importantly, our findings reveal that the freezing response duration is strongly influenced by stimulus duration but only weakly by stimulus intensity once the response threshold is exceeded. Extending the stimulus from 100 ms to 5 s (i.e., 50 times) elicited immobility periods with median duration increase from below 1 to over 200 s, without saturation. In contrast, increasing amplitude up to 30 dB (i.e., for 56-times; a comparable factor than in the amplitude treatment) above threshold did not prolong the response above the median of 3.5 s. Interestingly, this response pattern contradicts that found in Colorado potato beetle (*Leptinotarsa decemlineata* (Say, 1824), Chrysomelidae), where the freezing recovery time depended primarily on stimulus amplitude, while it was unrelated to stimulus duration (Acheampong and Mitchell 1997). From a practical perspective, the strong duration-dependence in *A. nodipennis* offers a major advantage for field application, as generating longer vibrations may be considered much less energy-demanding than producing higher-amplitude ones, which would require especially powerful actuators (namely, the mechanical power required to generate vibrations is proportional to the square of the amplitude). Moreover, when targeting woody plants such as hazelnut, the mechanical impedance of the plant tissue plays a critical role, substantially increasing the power required to induce vibrations in the structure at a desired amplitude (Olesen and Randal 1979). This makes high-amplitude excitation in woody plants not only energetically demanding but also technically challenging (see Takanashi et al. 2019). In this system, longer stimuli of moderate amplitude, found to be highly efficient for *A. nodipennis*, thus offer a more energy-efficient solution for field application. At the same time, the plateau in the freezing response in this species expressed across a wide range of stimulus amplitudes suggests that the desired behavioral inhibition could be achieved more easily throughout the plant, or other protection structures in the orchard (see below), considering signal attenuation. These characteristics make the defensive behavior of *A. nodipennis*

particularly well-suited for exploitation in pest control via vibrational deterrence.

In addition to the freezing response, *A. nodipennis* showed a postfreeze behavioral inhibition, with walking velocity significantly reduced after the immobile state ended. For both increased stimulus duration and intensity, postfreeze walking velocity was reduced to as low as 25%–30% of the prestimulus level. In both cases, the strongest slow-down occurred at intermediate stimulus values—particularly when intensity was considered relative to threshold—suggesting a generalized rather than parameter-dependent effect. This extended behavioral inhibition has not been reported in beetles previously studied for vibrational responses. This feature may be expected to prolong reductions in feeding or oviposition, thereby amplifying the protective effect of vibrational treatments.

In addition, inclination of the substrate represents another important factor, which has been shown to influence the expression of defense and escape behaviors in insects. Prior work in beetles (*Paraglenea fortunei* (Say, 1824), Cerambycidae) has shown that the freezing response sensitivity is reduced on vertical compared to horizontal substrates (Tsubaki et al. 2014). Similarly, in cave crickets (*Troglophilus cavicola* (Kollar, 1833), Rhaphidophoridae) escape behavior becomes less likely on steeper surfaces (Kastberger 1982). In our study, weevils were tested on a 45° inclined substrate, which may be considered representative of the stance of an insect on typically inclined plant twigs and branches. Nevertheless, it would be valuable to investigate response characteristics on substrates with different inclinations, representing situations from vertical stems to horizontal branches, which would further refine our understanding of how vibrational deterrence could be applied under field conditions.

Beyond application, this study also contributes new insights into the behavioral and physiological mechanisms of vibrationally induced freezing. Notably, we observed considerable individual variability in the response threshold and duration of the immobile state. This is unlikely to reflect the response sensory basis alone, but points to behavioral gating where internal states modulate responsiveness. In the Colorado potato beetle, the probability and duration of freezing immobility were shown to be modulated by hunger, decreasing both response parameters (Acheampong and Mitchell 1997). A study on the patent-leather beetle, *Odontotaenius disjunctus* (Illiger, 1800) (Passalidae), demonstrated strong and sex-specific variation of the freezing response under nematode infection, with males and females expressing opposite trends under parasitism (Davis et al. 2023). Similarly, in *A. nodipennis*, gating of the response could have been influenced by internal physiological conditions such as nutritional state and parasitic load.

Furthermore, response variation can also arise from prior exposure to stimuli, with effects generally depending on both timing and repetition. In the Colorado potato beetle, stimuli delivered during the immobile state prolonged the duration of immobility, while those applied postrecovery elicited either sensitization or habituation, depending on stimulus interval and rank (Acheampong and Mitchell 1997). Similarly, escape responses in the larvae of the sap beetle *Phenolia picta* (Macleay, 1825) (Nitidulidae) showed a nonlinear dependence on stimulus interval (Kishi and Takanashi 2019), indicating a complex interplay between sensory input and central processing. In our study, we employed a consistent 1-min stimulus interval in all experiments to avoid response decline through habituation. Future experiments in *A. nodipennis* shall explore whether variations in stimulation regimes, such as shorter intervals or stimuli delivered during the immobile phase, might enhance the freezing response through sensitization. Also, to assess the risk of long-term habituation due to repeated stimulation protocols (see Bernal-Gamboa et al. 2021), future studies should consider testing for cumulative response decline over extended periods and employ stimulus presentations at randomized intervals, reducing the likelihood of long-term habituation effects. These studies should also include testing male individuals, which were not available during our experiments. While we do not expect major qualitative differences, differences in the frequency or intensity of the response are sometimes observed between sexes even in generalized antipredator behaviors of insects (Dou et al. 2021, Matsumura and Miyatake 2023). In addition to sex difference, evaluating vibrational responsiveness at different age, times of the year and physiological conditions, such as mating and dispersal stages, would provide further insight into how internal and environmental states modulate behavioral inhibition.

In conclusion, our study carries important practical insights for the behavioral control of *A. nodipennis* using vibrational cues. We showed that the freezing response in this species is strongly dependent on stimulus duration, with prolonged immobility achieved even at moderate amplitudes, and remains stable across a wide amplitude range. The additional phase of postfreeze locomotor inhibition further enhances the suppressive effect. These features suggest that even brief, intermittent vibrational stimuli can induce sustained behavioral suppression, offering an energy-efficient and potentially field-deployable control method through deterrence, expected to suppress behaviors such as feeding, mating, oviposition and residence on host trees (Foster and Harris 1997, Takanashi et al. 2019). As such, vibrational deterrence represents a promising, sustainable tool for reducing activity of this insect pest, with potential for integration into broader management frameworks in hazelnut and other orchards. As knowledge of when and where adults are active is also crucial for field deployment, future research should clarify aspects of the seasonal activity and movement of adult *A. nodipennis*—for example, whether adults stay at orchard margins or move between fields—as such movements would directly inform the placement and timing of vibrational deterrent barriers. To achieve this, the development of a powerful, low-cost, and autonomous vibration exciter is essential for practical field application. Preliminary steps in this direction have already been taken (Takanashi et al. 2019), but further innovation is required to create an autonomous system with programmable control. Vibrational stimuli could be applied not only to the plants but also to perimeter structures, such as protective fences surrounding the orchards, to create deterrent zones. Such "behavioral barriers" would exploit the weevil's reliance on walking to enter orchards.

Future research should also aim to evaluate how vibrational deterrents perform under field conditions, particularly in terms of signal transmission through plants, as well as the behavioral effects of repeated or prolonged exposure. In addition, investigating mating behavior is essential to determine whether vibrational signals also play a role in sexual communication of *A. nodipennis* and could complement deterrents in the push–pull strategies. In the next step, this approach should be integrated with other control methods, such as semiochemical attractants or repellents, to enhance overall efficiency. Such integrated tools

may be especially valuable for crops such as hazelnuts where pesticide efficiency is constrained by the weevil's biology. Also, recent bans on highly toxic substances and the rollout of new regulatory frameworks in Chile, such as Resolución 243 Exenta and enhanced ecotoxicological requirements, indicate an accelerating need for alternative, sustainable control methods.

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Supplementary Material

Supplementary material is available at *Journal of Economic Entomology* online.

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Conflicts of Interest

None declared.

References

Acheampong S, Mitchell BK. 1997. Quiescence in the Colorado potato beetle, *Leptinotarsa decemlineata*. *Entomologia Exp. Applicata*. 82:83–89. https://doi.org/10.1046/j.1570-7458.1997.00116.x

Avosani S, Sullivan TES, Ciolli M, et al. 2020. Vibrational communication and evidence for vibrational behavioural manipulation of the tomato potato psyllid, Bactericera cockerelli. *Entomol. Gen.* 40:351–363. https://doi.org/10.1127/entomologia/2020/0984

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Statist. Soc. B*. 57:289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Bernal-Gamboa R, García-Salazar J, Gámez AM. 2021. Analysis of habituation learning in mealworm pupae (*Tenebrio molitor*). *Front. Psychol.* 12:745866. https://doi.org/10.3389/fpsyg.2021.745866

Castellanos I, Barbosa P. 2006. Evaluation of predation risk by a caterpillar using substrate-borne vibrations. *Anim. Behav.* 72: 461–469. https://doi.org/10.1016/j.anbehav.2006.02.005

Cocroft RB, Rodríguez RL. 2005. The behavioral ecology of insect vibrational communication. *Bioscience*. 55:323–334. https://doi.org/10.1641/0006-3568(2005)055[0323:TBEOIV]2.0.CO;2

Čokl A, Žunič-Kosi A, Stritih-Peljhan N, et al. 2021. Stink bug communication and signal detection in a plant environment. *Insects*. 12:1058. https://doi.org/10.3390/insects12121058

Davis AK, Ladd RRE, Smith F, et al. 2023. Sex-specific effects of a parasite on stress-induced freezing behavior in a natural beetle-nematode system. *PLoS One*. 18:e0281149. https://doi.org/10.1371/journal.pone.0281149

Dou Z, Madan A, Carlson JS, et al. 2021. Acoustotactic response of mosquitoes in untethered flight to incidental sound. *Sci. Rep.* 11:1884. https://doi.org/10.1038/s41598-021-81456-5

Elgueta M, Marvaldi A. 2006. Lista sistemática de las especies de Curculionoidea (Insecta: Coleoptera) presentes en Chile, y su sinonimia (in Spanish with English abstract). *Boletín MNHN*. 55:113–153. https://doi.org/10.54830/bmnhn.v55.2006.274

Ellena M, Sandoval P, Gonzalez A, et al. 2014. Chilean hazelnut situation and perspectives. *Acta Hortic*. 1052:329–342. https://doi.org/10.17660/ActaHortic.2014.1052.46

Foster SP, Harris MO. 1997. Behavioral manipulation methods for insect pest-management. *Ann Rev Entomol* 42:123–146. https://doi.org/10.1146/annurev.ento.42.1.123

Guedes RNC, Matheson SM, Frei B, et al. 2012. Vibration detection and discrimination in the masked birch caterpillar (*Drepana arcuata*). *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* 198:325–335. https://doi.org/10.1007/s00359-012-0711-8

Hill PS, Wessel A. 2016. Biotremology. *Curr. Biol.* 26:R187–R191. https://doi.org/10.1016/j.cub.2016.01.054

Kastberger G. 1982. Evasive behaviour in the cave-cricket, *Troglophilus cavicola*. *Physiol. Entomol* 7:175–181. https://doi.org/10.1111/j.1365-3032.1982.tb00287.x

Kishi M, Takanashi T. 2019. Escape behavior induced by substrate-borne vibrations in larvae of the sap beetle, Phenolia (Lasiodites) picta (Coleoptera: Nitidulidae) (In Japanese with English abstract). *Jpn. J. Appl. Entomol. Zool.* 63:150–154. https://doi.org/10.1303/jjaez.2019.150

Kutner MH, Nachtsheim CJ, Neter J, Li W. 2005. *Applied linear statistical models*. 5th Edition, McGraw-Hill

Lencinas MV, Martínez Pastur G, Soler R, et al. 2021. *Aegorhinus nodipennis* (Curculionidae) attack in forest plantations and orchards of Tierra del Fuego ranches: an incipient invasion? (in Spanish with English title). *An. Inst. Patagon* 49:10. https://doi.org/10.22352/AIP202149010

Macdougall MS, Nelson X, Stringer LD. 2025. Harshing the vibes: behavioural responses to predation and deterrent vibrational playback in Scolypopa Australis (Hemiptera: Ricaniidae). *J. Appl. Entomol* 149:1–11. https://doi.org/10.1111/jen.13412

Mankin RW. 2019. Vibrational trapping and interference with mating of Diaphorina citri. In: Hill PSM, Lakes-Harlan R, Mazzoni V, Narins P, Virant-Doberlet M, Wessel A, editors. *Biotremology: studying vibrational behavior. Animal signals and communication*, vol 6. Springer, Cham. p. 399–413. https://doi.org/10.1007/978-3-030-22293-2_20

Matsumura K, Miyatake T. 2023. Latitudinal cline of death-feigning behaviour in a beetle (*Tribolium castaneum*). *Biol. Lett.* 19:20230028. https://doi.org/10.1098/rsbl.2023.0028

Mazzoni V, Lucchi A, Čokl A, et al. 2009. Disruption of the reproductive behaviour of *Scaphoideus titanus* by playback of vibrational signals. *Entomologia Exp. Applicata*. 133:174–185.) https://doi.org/10.1111/j.1570-7458.2009.00911.x

Mazzoni V, Gordon SD, Nieri R, et al. 2017. Design of a candidate vibrational signal for mating disruption against the glassy-winged sharpshooter, *Homalodisca vitripennis*. *Pest Manag. Sci*. 73: 2328–2333. https://doi.org/10.1002/ps.4619

Mazzoni V, Nieri R, Eriksson A, et al. 2019. Mating disruption by vibrational signals: state of the field and perspectives. In: Hill PSM, Lakes-Harlan R,Mazzoni V, Narins P, Virant-Doberlet M,Wessel A, editors. *Biotremology: studying vibrational behavior. Animal signals and communication*, vol 6. Springer, Cham. p. 331–354. https://doi.org/10.1007/978-3-030-22293-2

McNett GD, Luan LH, Cocroft RB. 2010. Wind-induced noise alters signaler and receiver behavior in vibrational communication. *Behav. Ecol. Sociobiol*. 64:2043–2051. https://doi.org/10.1007/s00265-010-1018-9

Mutis A, Parra L, Manosalva L, et al. 2010. Electroantennographic and behavioral responses of adults of raspberry weevil *Aegorhinus superciliosus* (Coleoptera: Curculionidae) to odors released from conspecific females. *Environ. Entomol*. 39:1276–1282. https://doi.org/10.1603/EN10009

Navarro PD, Palma-Millanao R, Ceballos R, et al. 2022. *Steinernema australe* enhanced its efficacy against *A. nodipennis* larvae in berry orchards after an artificial selection process. *Agronomy*. 12:1128. https://doi.org/10.3390/agronomy12051128

ODEPA (Oficina de Estudios y Políticas Agrarias). 2025. Chile proyecta convertirse en segundo productor mundial de avellano europeo. La Tribuna. Accessed August 18, 2025. https://www.latribuna.cl/agro-forestal/2025/07/11/chile-proyecta-convertirse-en-segundo-productor-mundial-de-avellano-europeo.html

Olesen HP, Randall RB. 1979. *A guide to mechanical impedance and structural response techniques*. Brüel & Kjær Sound & Vibration Measurement A/S

Parent JP, Laidlaw R, Abram PK. 2022. Disruptive effects of non-specific airborne and substrate-borne vibrations on aphids. *J. Pest Sci*. 95:949–958. https://doi.org/10.1007/s10340-021-01425-9

Pekas A, Mazzoni V, Appel H, et al. 2024. Plant protection and biotremology: fundamental and applied aspects. *Trends Plant Sci*. 29:32–39. https://doi.org/10.1016/j.tplants.2023.06.021

Polajnar J, Svenšek D, Čokl A. 2012. Resonance in herbaceous plant stems as a factor in vibrational communication of pentatomid bugs (Heteroptera: Pentatomidae). *J. R Soc. Interface* 9:1898–1907. https://doi.org/10.1098/rsif.2011.0770

Strauß J, Stritih-Peljhan N, Nieri R, et al. 2021. Communication by substrate-borne mechanical waves in insects: from basic to applied biotremology. *Adv. Insect Physiol*. 61:189–307.https://doi.org/10.1016/bs.aiip.2021.08.002

Strauβ J, Stritih-Peljhan N, Nishino H. 2024. Vibration receptor organs in the insect leg: neuroanatomical diversity and functional principles. 61: 101153 https://doi.org/10.1016/j.cois.2023.101153

Tampe J, Pacheco B, Bardehle L, et al. 2020a. Attractant effect of *Eucalyptus globulus* (Labill) and *Foeniculum vulgare* (Mill.) essential oils on *Aegorhinus superciliosus* (Guérin) (Coleoptera: Curculionidae). *J. Soil Sci. Plant Nutr*. 20:775–783. https://doi.org/10.1007/s42729-019-00164-2

Tampe J, Espinoza J, Chacón-Fuentes M, et al. 2020b. Evaluation of *Drimys winteri* essential oil as insecticide against *Acanthoscelides obtectus* and *Aegorhinus superciliosus*. *Insects*. 11:335. https://doi.org/10.3390/insects11060335

Takanashi T, Fukaya M, Nakamuta K, et al. 2016. Substrate vibrations mediate behavioral responses via femoral chordotonal organs in a cerambycid beetle. *Zool. Lett*. 2:18. https://doi.org/10.1186/s40851-016-0053-4

Takanashi T, Uechi N, Tatsuta H. 2019. Vibrations in hemipteran and coleopteran insects: behaviors and application in pest management. *Appl. Entomol. Zool*. 54:21–29. https://doi.org/10.1007/s13355-018-00603-z

Takanashi T, Kojima W. 2021. Vibration-induced immobility in coleopteran insects. In: Sakai M, editor. *Death-feigning in insects*. Entomology monographs. Springer, Singapore. p. 73-92. https://doi.org/10.1007/978-981-33-6598-8_6

Takanashi T, Nishino H. 2022. Exploitation of vibration sensing for pest management in longicorn beetles. In: Hill PSM, Mazzoni V, Stritih-Peljhan N, Virant-Doberlet M, Wessel A, editors. *Biotremology: Physiology, ecology, and evolution. Animal signals and communication*, vol 8. Springer, Cham. p.495–510. https://doi.org/10.1007/978-3-030-97419-0_20

Tsubaki R, Hosoda N, Kitajima H, et al. 2014. Substrate-borne vibrations induce behavioral responses in the leaf-dwelling cerambycid, *Paraglenea fortunei*. *Zoolog. Sci*. 31:789–794. https://doi.org/10.2108/zs140029

Virant-Doberlet M, Kuhelj A, Polajnar J, et al. 2019. Predator-prey interactions and eavesdropping in vibrational communication networks. *Front. Ecol. Evol*. 7:203. https://doi.org/10.3389/fevo.2019.00203

Virant-Doberlet M, Stritih-Peljhan N, Žunič-Kosi A, et al. 2023. Functional diversity of vibrational signaling systems in insects. *Annu. Rev. Entomol*. 68:191–210. https://doi.org/10.1146/annurev-ento-120220-095459

Wilcoxon F. 1945. Individual comparisons by ranking methods. *Biometrics Bull* 1:80–83. https://doi.org/10.2307/3001968

Yanagisawa R, Tatsuta H, Sekine T, et al. 2024. Vibrations as a new tool for pest management—a review. *Entomologia Exp. Applicata* 172:1116–1127. https://doi.org/10.1111/eea.13458

Zapponi L, Nieri R, Zaffaroni-Caorsi V, et al. 2023. Vibrational calling signals improve the efficacy of pheromone traps to capture the brown marmorated stink bug. *J. Pest Sci*. 96:587–597. https://doi.org/10.1007/s10340-022-01533-0

Zavala A, Elgueta M, Abarzúa J, et al. 2011. Diversity and distribution of the *Aegorhinus* genus in the La Araucanía Region of Chile, with special reference to *A. superciliosus* and *A. nodipennis*. *Cienc. Inv. Agr*. 38:367–377. http://dx.doi.org/10.4067/S0718-16202011000300006

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