

The buzzOmeter system: In situ audio recordings of pollinators in flight

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Abstract

1. The role of sounds produced by free-flying insects is challenging to research due to technical difficulties in obtaining audio recordings suitable for playback experiments. Experimental studies using flight sounds are needed to understand if buzzes carry information and by whom it is perceived.
2. We developed the 'buzzOmeter system' for recording untethered, flying insects in their habitat, followed by file processing that allows precise measurements of acoustic parameters, including those dependent on the distance of the sound source from the microphone, that is signal magnitude measurements. The system consists of commercially available elements and open source software.
3. We provide a practical guide for the assembly and use of two alternative setups of the buzzOmeter system, followed by a video tutorial on file processing and an R script for the assignment of audio recordings to the corresponding species based on mixture discriminant analysis. Recordings of nine insect species (bees, wasps and lepidopterans) obtained with the use of our system in various habitats demonstrate its feasibility for field studies.
4. Diverse species interactions are based on sound, and our new tool can aid researchers studying acoustical signalling in predator–prey, pollinator–plant and mimic–model complexes, among others.

KEYWORDS

audio, buzz, flight, insect bioacoustics, pollinators, predator–prey interactions, sound, wingbeat frequency

1 | INTRODUCTION

Hisses, clicks, chirps, trills, rattles and buzzes—insects produce diverse sounds to convey information to their receivers. Their aim varies: some seek mates through audible sexual displays (Hou et al., 2022), others scare away intruders via acoustical warning signals (Dowdy & Conner, 2016). Predators and ectoparasites can detect insect prey following the sounds they produce (Tomás & Soler, 2016)

and even plants react to noisy pollinators (Veits et al., 2019). The production of buzzing sounds is primarily associated with hymenopterans whose bright colouration is a display of their ability to defend themselves, a phenomenon known as aposematism. Predators could potentially associate not only colouration, but also sound with the risk of being painfully stung or bitten (Quicke, 2017). However, experimental evidence for an aposematic role of buzzing sounds, as pointed out by Chatelain et al. (2023), is scarce. King

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et al. (2007) played the sounds of disturbed honey bees to African elephants and found that elephants responded aversively by moving away from artificial buzzing hives (although the sounds were played at a volume impossible to achieve by live bees—twice the recorded value). Jablonski et al. (2013) performed playback experiments with Oriental tits (*Parus minor*) by placing miniature speakers playing buzzing sounds of bumblebees in nest boxes. The birds showed signs of distress in response to the buzzes. Wood demonstrated as early as 1976 (Wood, 1976) that audible buzzes of treehoppers deter predatory coccinellid beetles (ladybugs) from attacking them. These experiments indicate the acoustical aposematic function of certain insect buzzing sounds.

Demonstrating the effect of insect sounds on other organisms requires playback experiments, in which an animal is exposed to an audio cue and its reaction is analysed. Obtaining suitable audio files for such experiments is technically challenging, especially when the sound studied is produced by a small animal in motion, such as a buzzing insect. Many studies of flight have been restricted to tethered insects (Barber & Kawahara, 2013; Cator et al., 2010) and although that approach allows for the analysis of defence or alarm signals, it fails to consider implications of sound production by nondistressed animals and risks causing biases due to human manipulations (e.g. de Silva et al., 2015 demonstrated differences in wingbeat frequencies between tethered and free-flying midges). There have been many advances in recording free-flying insects in recent years, including optical and ultrasonic approaches that produce signals that are uncontaminated by background noise. Optical methods of recording insect flight allow species identification based primarily on wingbeat frequency (Batista et al., 2011; Rydhmer et al., 2022). However, the insect is recorded only when it crosses the laser beam for a fraction of a second, resulting in very small flight samples. Moreover, signals generated by optical sensors are filtered and amplified before being recorded as audio data, and precise signal magnitude values cannot be extracted from the resulting files. Thus, optical sensors are a promising solution for the purpose of insect classification based on brief wingbeat recordings, but they are not suitable for playback experiments. An interesting new solution is the ultrasonic recording methodology, which produces significantly longer signals (Staunton et al., 2020). This approach was designed to obtain mosquito wingbeat frequencies for classification purposes. It has not been developed to produce audio files suitable for use in animal response studies. In this method subjects are placed in a flight chamber (vial) and can be recorded as long as they continue flying. Yet many insects will either crash against a flight chamber wall or simply not fly within a small enclosure. Moreover, any sort of manipulation of insects may cause distress and behaviour alteration, which in turn can result in the production of alarm signals instead of plain free-flight sounds.

We present the “buzzOmeter system”, a tool for simultaneous video and sound pressure recording of free-flying insects in their habitat, which produces files suitable for playback experiments and for the extraction of both frequency and sound pressure derived parameters.

The sound pressure level and derived metrics, which depend on the distance of the insect from the microphone/sensor, are biologically significant parameters that must be determined before studying animal response to sound. In a number of published acoustic studies, the distance between the sound source and the recording device had not been precisely determined (Gradišek et al., 2017; Kawakita & Ichikawa, 2019), yet signal magnitude parameters were still considered and compared between species. It is crucial to consider sound pressure in playback experiments, which otherwise lead to misinterpretations, for example observed aversive behaviours of receivers might simply be a result of sounds being played at a higher volume than those produced by the insect in nature. Moreover, different animal taxa detect different components of an acoustic signal and experiments must take into consideration how sound is perceived by the receiver. Most terrestrial vertebrates respond to sound pressure (Beason, 2004; Warren & Nowotny, 2021), including snakes that were long thought to be deaf (Zdenek et al., 2023). Hearing in invertebrates is highly variable: some cannot detect airborne sound at all, whereas others have multiple auditory organs finely tuned to specific frequencies. Insects that can hear have either antennal or tympanal ears, or both. Tympanal insect ears respond to sound pressure via a sound-receiving eardrum; antennal ears detect the particle velocity component of sound (Göpfert & Hennig, 2016). The buzzOmeter system is designed to produce and analyse recordings based on their frequency and sound pressure components. The recordings can be used to expand our understanding of the aposematic and antipredator role of sound, to determine whether the production of buzzing in bees and wasps is part of their displayed Müllerian mimicry and whether this acoustic aspect of antipredator defence is exploited by Batesian mimics. Additionally, audio recordings of flying insects can serve to study the evolution of pollinator-plant interactions in the expanding field of studies on plants' reactions to sound.

Our low-cost system is easy to assemble from commercially available elements, can be adapted to different cameras and microphones and further data processing can be performed in free software. We provide instructions for tool assembly and field recordings, an R script to verify the assignment of audio recordings to the corresponding species based on mixture discriminant analysis, and a video tutorial showing the process of file synchronization and audio selection in open access software.

2 | buzzOmeter SYSTEM—DESIGN, ASSEMBLY AND FILE PROCESSING

2.1 | Hardware

The brand (and thus cost) of the buzzOmeter system components can be selected by the user (Table 1). The buzzOmeter system consists of a directional (cardioid) lavalier microphone with good bass reproduction (we used a Sennheiser MKE 40-EW with frequency response 40–20,000 Hz) attached with a wire and sponge pad for shock

absorption to a selfie stick, mounted with a clamp to either a photography light stand (Setup 1, Figure 1, see Supplementary Practical guide) or the centre column of a tripod/monopod with head (Setup 2, Figures S4 and S5), a camera with manual focus lens, a PCM recorder (we used a TASCAM DR-60D MKII linear PCM recorder,

Figure S1) with headphones and a wireless microphone system (we used a Sennheiser Evolution G2 wireless system). The selfie stick allows for easy adjustment of the distance between the microphone and the camera. To reduce wind noise, we recommend using a foam cover for the microphone in slightly windy conditions. An additional

TABLE 1 Components of the buzzOmeter system.

buzzOmeter system components		
Component	Properties	Exemplary model
Audio recorder	Quality of recordings at least 24-bit wav; XLR mic input; frequency response starting from at least 60Hz; possibility to precisely define gain value; possibility to charge with powerbank	TASCAM DR-60D MKII
Microphone	Directional (cardioid), type lavalier; frequency response starting from at least 60Hz	Sennheiser MKE 40-EW
Wireless audio system	Frequency response starting from at least 60Hz; possibility to precisely define gain value	Sennheiser Evolution ew100 G2
Photography clamp 2x	Robust enough to support a digital camera with lens	Manfrotto super clamp
Light stand	Adjustable height (depending on registered insect but preferably 60–250 cm), lightweight	Light stand Amazon Basics
Tripod column	Lightweight, preferably aluminium (used for handheld setup)	Manfrotto 122B (Backlite)
Selfie stick	Adjustable length	Handlife selfie stick
Digital camera	Interchangeable lens; possibility to set focus manually	Sony α6500
Lens	Minimum focusing distance around 30 cm from camera sensor	7artisans 25 mm f/1.8
Mini ball tripod head	Robust enough to support a digital camera with lens	Mini ball tripod head Manfrotto

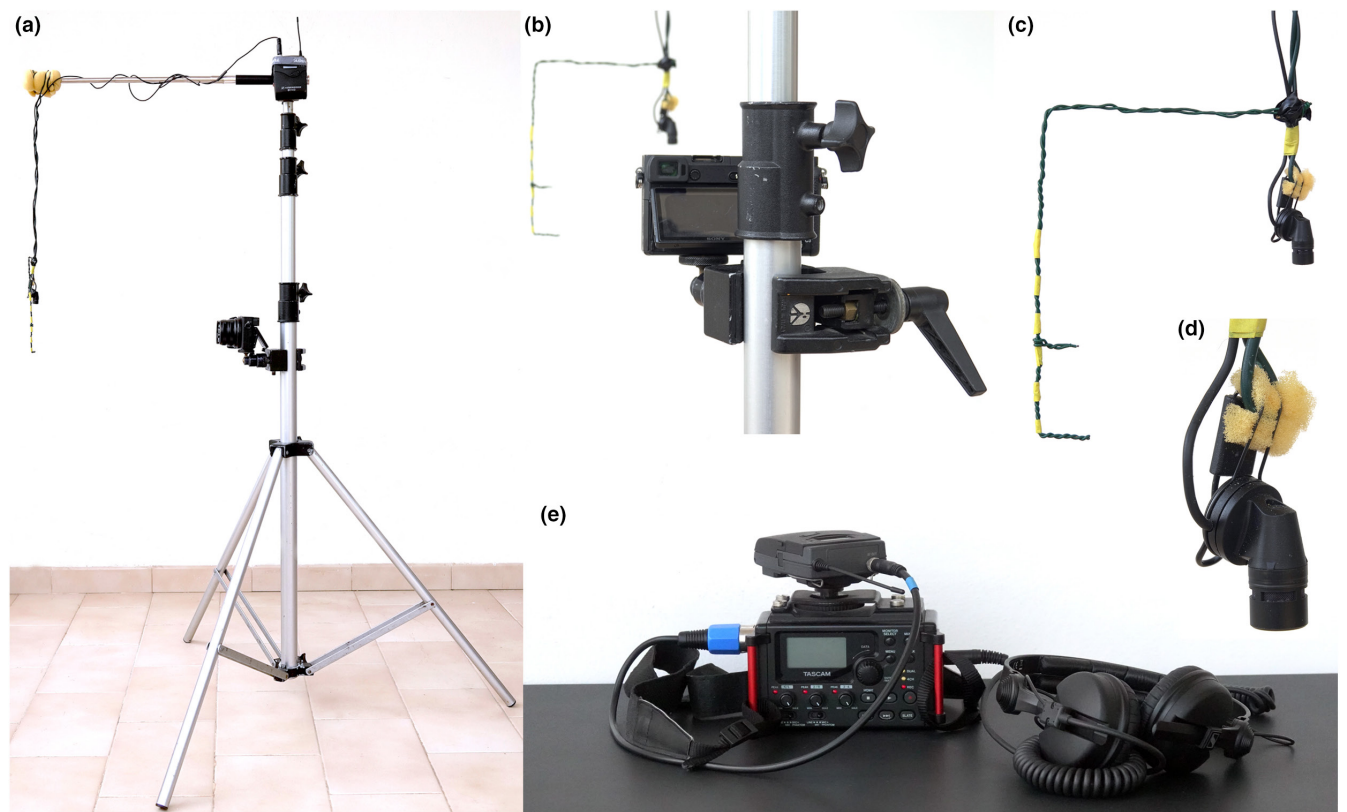


FIGURE 1 The buzzOmeter system. (a) Setup 1 (stationary) consisting of a light stand, selfie stick attached with a clamp, microphone, transmitter of wireless mic system and camera attached to stand with a clamp and mini ball tripod head; (b) close-up of camera attachment; (c) microphone and wire indicating distance from sound source; (d) close-up of microphone attachment; (e) PCM recorder with receiver and headphones.

clamp with a mini ball tripod head is needed for setup 1 to mount the camera. Audio files are registered in uncompressed wav format at a 48 kHz sample rate and 24-bit audio depth because compressed audio formats (e.g. MP3) introduce artefacts that may interfere with later analyses. It is important to note the level of microphone gain settings in both the PCM recorder and the wireless microphone system for later acoustic analyses (see the Supplementary [Practical guide](#)).

Different models of microphones, wireless mic systems and PCM recorders can be used to build the buzzOmeter system, however, it is important to make sure that they all have a frequency response starting at low frequencies.

2.2 | File synchronization and sound selection in open access software

As a result of field recordings, two files are obtained: an uncompressed audio file generated by the PCM recorder and a video file with compressed audio. The next step is to synchronize these two files by aligning the two audio waveforms (to aid this operation, a distinct signal is added at the end of each field recording, see Supplementary [Practical guide](#)). After synchronization, the compressed audio file (i.e. the one recorded by the video camera) is deleted and only the uncompressed one is used for acoustical analyses. The audio and video files generated by the buzzOmeter system are first visualized and synchronized in DaVinci Resolve, an open source software for filmmakers. The synchronized files are exported through DaVinci Resolve and audio fragments for further analyses are selected in the free software Praat (Boersma & Weenink, 2020; see Supplementary Video [SV1](#) for a detailed tutorial). The described approach might not be suitable for playback experiments with insects responding to particle velocity rather than sound pressure. For playback experiments with sound pressure detecting animals, it is important to carefully consider the speakers to be used: many models do not reproduce frequencies as low as the buzzes of insects, and even high-quality speakers may distort the original sound. To overcome this obstacle, sounds emitted by a speaker are re-recorded using the same equipment, parameters and distance from the sound source as were applied for a given insect species during field recordings. The sounds are then compared in Praat and adjusted with an equalizer (we used the Poweramp equalizer for Android) to properly recreate insect buzzes.

3 | PROOF-OF-CONCEPT

3.1 | Field recordings

We recorded nine species of flying insects with the buzzOmeter system from May 2020 to July 2021 in variable types of habitat (forests and forest edges, meadows, lowland heaths, raspberry shrubs, gardens, artificial insect nests, [Figure S2](#)) in several locations in eastern

Poland: Biebrza and Wigierski National Parks, Ostoja Knyszyńska. Our focus was on hymenopterans (*Vespa crabro*, *Dolichovespula media*, *Bombus terrestris*, *Bombus pascuorum*, *Polistes dominula*, *Sphex funerarius*) and lepidopterans (*Hemaris fuciformis*, *Hemaris tityus*, *Macroglossum stellatarum*) that produce buzzing sounds in flight. The park authorities gave permission to record insects within the Biebrza and Wigierski national parks.

3.2 | Setup

The most suitable setup for each species was selected based on previous observations of insect behaviour in situ. In general, those insects that return to a fixed spot, for example nest or burrow entrance, source of pheromone, limited food source, for example sap from tree wound, can easily be recorded by one person using the stationary Setup 1. It is more feasible to record insects foraging on flowers, as well as those entering multiple nesting sites, using Setup 2, which requires two operators. We were able to record species which varied in size, habitat (meadows, forests, mountain scrublands, artificial nests) and foraging habits (hornets drinking sap on tall trees vs. bumblebees, sphecids foraging on low vegetation). It is important to understand the biology of the studied species nesting/feeding/mating behaviour before attempting to record them and we recommend that at least a day is spent at each new location to observe the insects to be recorded. Synthetic pheromones have been developed for a number of taxa, including lepidopterans, dipterans and coleopterans and the use of such attractants in the buzzOmeter system is very efficient. The pheromone lure is placed in a plastic delta trap (without sticky liner) with the microphone suspended above the entrance to the trap ([Figure S3](#)). Using a delta trap is helpful because the attracted insect hovers slightly before entering the trap, resulting in longer audio recordings. We recorded insects at 10 cm from the microphone (for details, see Supplementary [Practical guide](#) and video tutorial).

3.3 | Analysis of acoustical data and results

To validate the reliability of the new method described here, we analysed the buzzing sounds obtained for the nine species of insects (see above). After video and audio synchronization, we selected signal fragments of flying insects from videos in DaVinci Resolve. This process is possible due to the distance-indicating wire, which is filmed along with the flying insect (see Supplementary [Practical guide](#)). Care was taken to select fragments when the middle of the insect body (in the horizontal plane) was aligned with the tip of the wire. However, because the system is designed to record free-flying insects in their habitat, it is not always feasible to select exactly the same aspect of the insect, hence we decided to select insects flying within a range of 2 cm (distance of $10\text{ cm} \pm 1\text{ cm}$ from the microphone). Spectrograms showing the sound produced by each species are shown in [Figure 2](#). The duration of the audio unit for analysis can

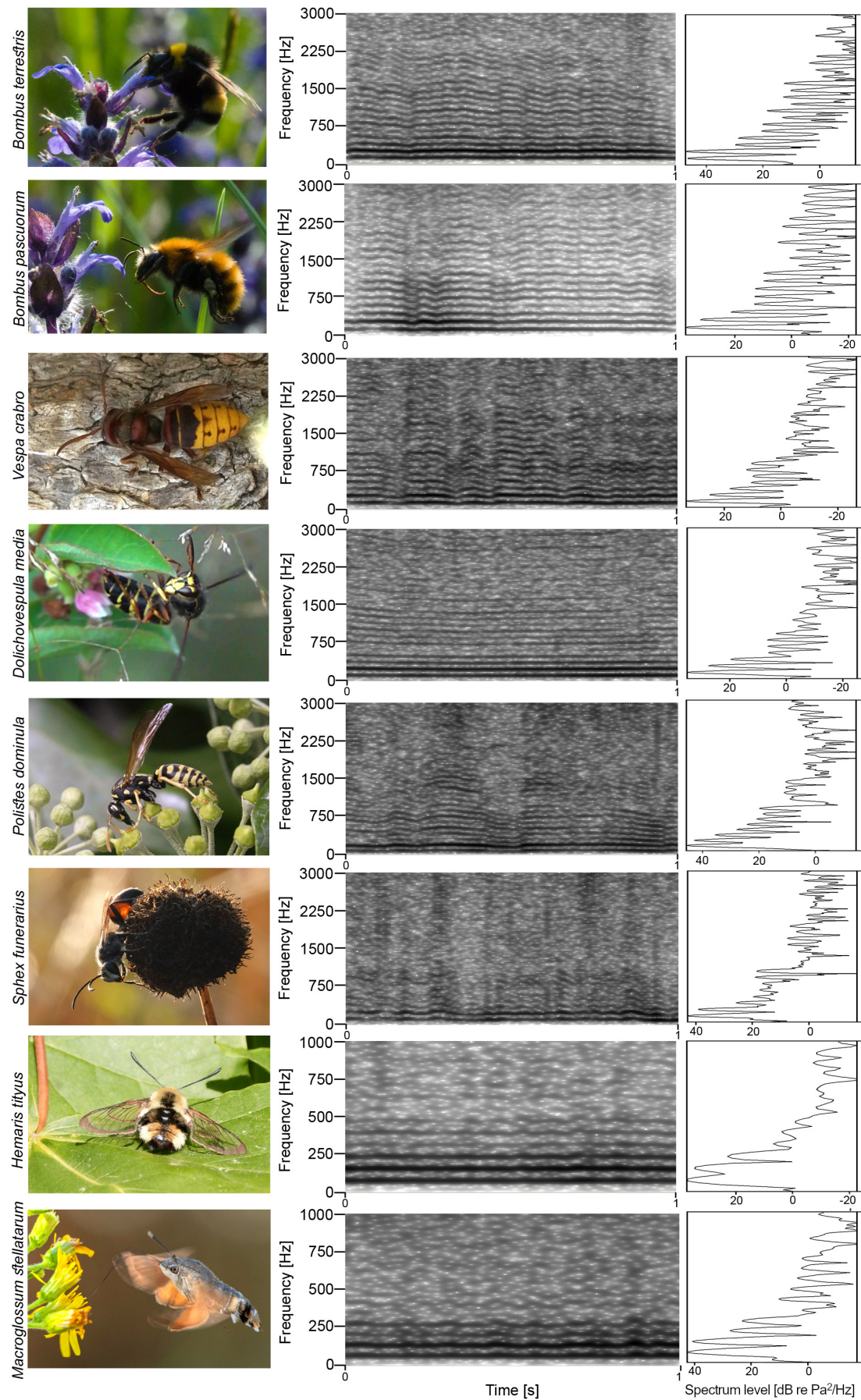


FIGURE 2 Spectrograms and spectra slices of buzzing sounds produced by the pollinator species analysed. Spectrograms generated by Fourier transform, using Gaussian window shape, 1000 time steps, 250 frequency steps.

be defined by the user because the buzzing sound of an insect in flight is a continuous, harmonic signal not divided into specific elements. In our example, acoustic variables were calculated in Praat (see Table S1 for definitions) based on at least two 0.3-s audio fragments (units) per individual. Seven of them were frequency measurements: fundamental frequency F0 (the “pitch” or lowest harmonic, Hz), frequencies of the first F1 and second F2 harmonics (first and second frequency components above the fundamental frequency, Hz), dominant frequency (Hz), first, second (centroid frequency) and

third frequency quartiles (Hz) and standard deviation of the centroid frequency (Hz). The remaining variables obtainable through the buzzOmeter system measured the magnitude of the signal: sound pressure level (dB), sound pressure (Pa), power (Pa^2), energy ($\text{Pa}^2 \times \text{s}$), root mean square of sound pressure (Pa), sound levels of each of the first three frequency components (dB) and the proportions between each of the first three frequency components. The dominant frequency was excluded from the analysis since it varied even between sounds produced by the same individual. After eliminating highly correlated

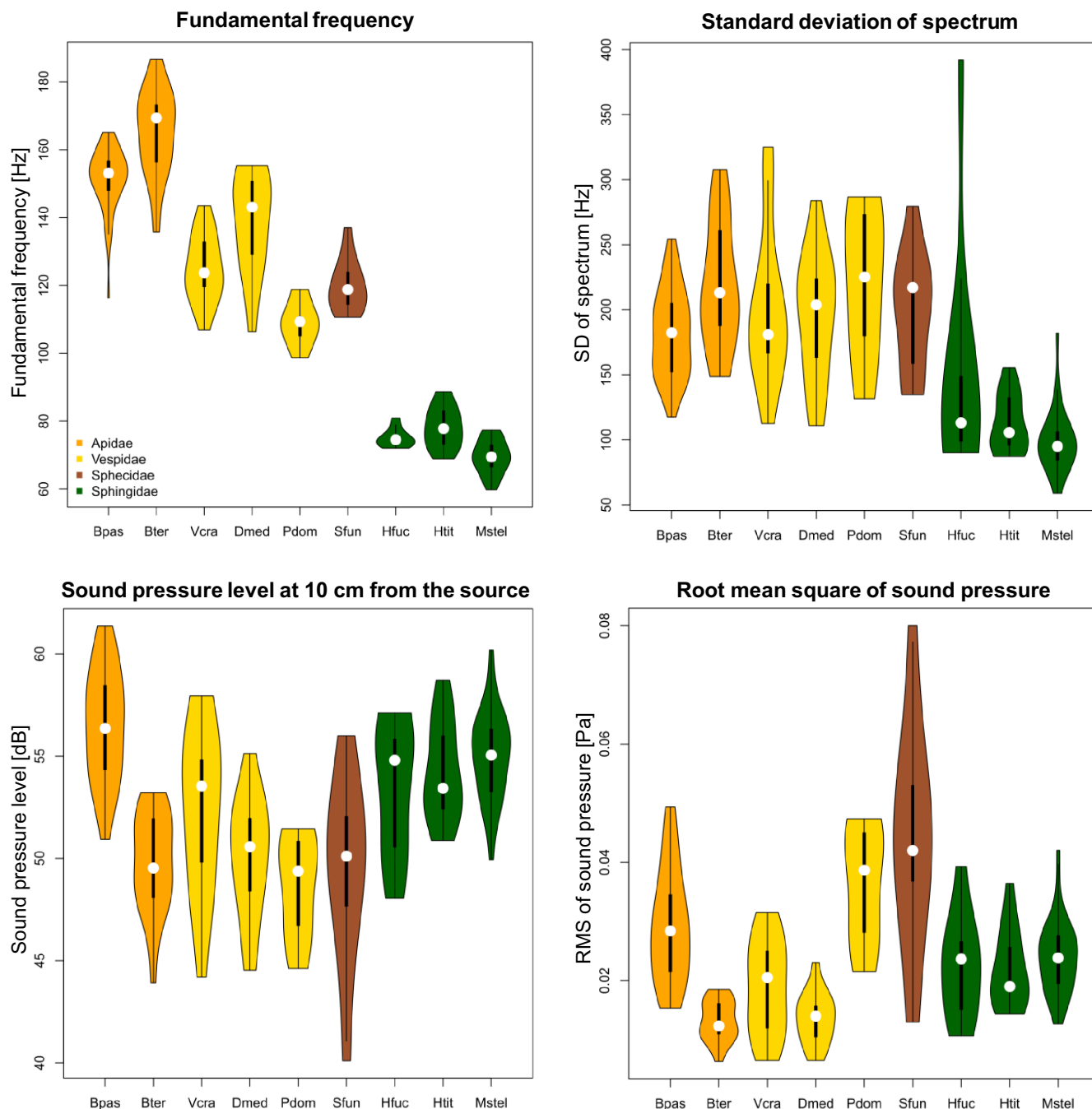


FIGURE 3 Median values of four selected acoustical parameters of the buzzing sounds produced in flight by insects recorded at 10 cm from the microphone using the buzzOmeter system. Abbreviations: Bpas—*Bombus pascuorum*, Bter—*Bombus terrestris*, Vcra—*Vespa crabro*, Dmed—*Dolichovespula media*, Pdom—*Polistes dominula*, Sfun—*Spheg funerarius*, Hfuc—*Hemaris fuciformis*, Htit—*Hemaris tityus*, Mstel—*Macroglossum stellatarum*.

variables based on a Pearson correlation matrix (Pearson $R > 0.80$), the following parameters were considered for further analysis: sound pressure level (dB), sound pressure (Pa), RMS of sound pressure (Pa), first frequency quartile (Hz), SD of centroid frequency (Hz), F0 (Hz), sound pressure levels of F0, F1 and F2 (dB), proportions between F1&F0 and F2&F0 (Figure 3). Praat may generate unreliable values if there is too much background noise (in our case this was either wind or rustling leaves), mostly altering the low-frequency values. These biased recordings typically resemble each other in their fundamental frequency. For this reason, a pass Hann band with a smoothing level of 10 Hz was used to select frequency ranges within which the studied sounds are audible (80–4000 Hz for *P. dominula* which was recorded in slightly windy conditions and 50–4000 Hz for all other species) and hierarchical clustering was applied to identify groups of diverging units. Data were scaled and centred, a Bray–Curtis dissimilarity among recordings was calculated and the data clustered through the unweighted pair group method with arithmetic mean (R packages and script are included in Supplementary Material). The dendrograms were examined and cut to eliminate highly divergent units. The cut heights and number of individuals remaining for analysis per species were as follows: *B. pascuorum* 0.15, $n = 49$; *B. terrestris* 0.2, $n = 24$; *D. media* 0.2, $n = 17$; *P. dominula* 0.2, $n = 10$; *V. crabro* 0.16, $n = 17$; *H. tityus* 0.15, $n = 13$; *H. fuciformis* 0.4, $n = 10$; *M. stellatarum* 0.15, $n = 30$; *S. funerarius* 0.2, $n = 11$ (hierarchical cluster plots can be inspected running the Supplementary script).

Only individuals for which at least two units remained after selection by hierarchical clustering were used: ultimately 567 units corresponding to 182 individuals (details on location and dates of recordings are given in dataset S1; recordings are available here: <https://doi.org/10.5061/dryad.mw6m90627>). The different units

for each individual were aggregated by computing the average for each variable.

Mixture discriminant analyses (mda R package) were performed on the square-root transformed, scaled and centred data (to improve normality and homoscedasticity) to verify the possibility to assign the averaged recordings to their species based on the acoustical parameters (Figure 4). Compared to other algorithms, mda allows the user to specify the number of subclasses for each group (here: species). This can be useful to account for intraspecific differences in sound production corresponding to sex, size, caste, type of activity, etc. We used from 1 to 4 subclasses and compared the classification success. Individuals were blindly attributed to species using a jackknife (leave-one-out) procedure (see R script for details). In the first series of analyses, we considered variables obtainable through other insect flight recording methods (F0, SD of centre of gravity, first frequency quartile). The results were then compared to the identification success of mdas based on uncorrelated variables obtainable with the buzzOmeter (i.e. including those dependent on the distance of the source from the microphone). When using only frequency-related variables, we obtained a species recognition rate of 61.9%, 57.4%, 54.7% and 60.2% for 1 to 4 subclasses, respectively. When both frequency and sound pressure parameters were added, the identification success increased considerably to 80.7%, 79.0%, 80.1%, 79.0% for 1 to 4 subclasses. The highest attribution success for a single subclass indicates that intraspecific variation in produced sound was low. Among the 35 misidentifications obtained using one subclass, 17 were among the three very closely related lepidopterans, eight were misclassifications between the two Vespinae wasps, *V. crabro* and *D. media* (so these two species were misidentified in about 30% of cases). Notably, we only scored two

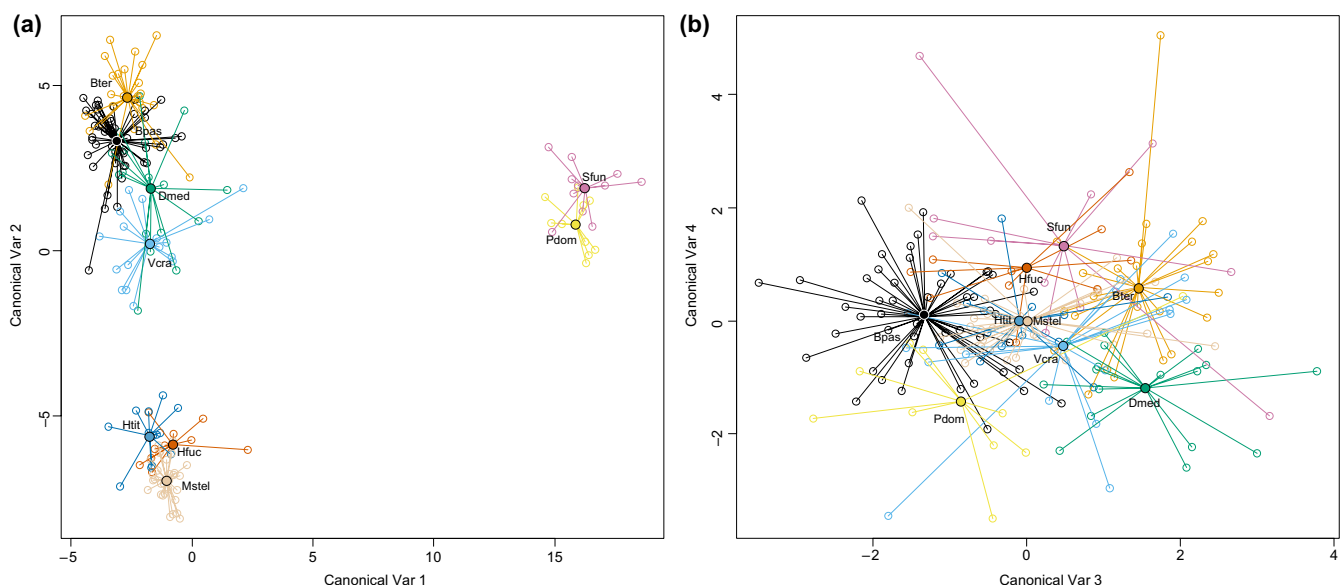


FIGURE 4 Mixture discriminant analysis showing species differentiation based on eleven acoustical parameters of the buzzing sounds of insects in flight. (A) canonical variates 1 and 2, (B) canonical variates 3 and 4. Abbreviations: Bpas—*Bombus pascuorum*, Bter—*Bombus terrestris*, Vcra—*Vespa crabro*, Dmed—*Dolichovespula media*, Pdom—*Polistes dominula*, Sfun—*Spheg funerarius*, Hfuc—*Hemaris fuciformis*, Htit—*Hemaris tityus*, Mstel—*Macroglossum stellatarum*.

misidentifications between congeneric *B. terrestris* and *B. pascuorum* (see Supplementary Confusion Table S2).

4 | DISCUSSION

The buzzOmeter system was designed primarily to obtain recordings of sounds produced by insects in flight, which would be suitable for playback experiments. Although we focused on large insects, the high sensitivity levels of modern microphones allow recording much smaller organisms, such as midges and fruit flies. The system could also be used to record insects that produce sounds in different contexts, for example buzz pollinators releasing pollen, chirping crickets or cicadas calling for a mate. The audio recordings obtained allow for precise calculations of acoustical parameters, including sound pressure and sound level. In our proof of concept we obtained a high (80.7%) recognition rate when we included all non-correlated variables obtainable through the buzzOmeter system. This level dropped to 61.9% when we excluded those variables that depend on the distance from the microphone, indicating the importance of the sound pressure level and derived metrics in differentiating species. These recognition rates could possibly be increased if the sounds were recorded in a noise-free environment (e.g. under laboratory conditions). However, our system is meant to be used in ecological field studies, and we argue that the presence of low levels of background noise obtained in natural surroundings affects the reliability of sound to a much lesser extent than the stressful conditions to which insects are subjected in the lab. Moreover, in nature, animals will never hear an isolated sound like those registered in acoustical chambers, but instead they must be able to discriminate and identify cues on a rich acoustical background. Although alternative methods (e.g. ultrasonic) of insect flight recordings might be more efficient in animal classification based on frequency, they produce a proxy of the real sound, whereas we provide a means of obtaining audio files that can serve both for identification and for studying species interactions in a biologically meaningful context.

Can predators remember past unpleasant encounters based on sound? Which parasitoids locate their hosts by eavesdropping? Does the buzzing of blood-sucking or stinging insects cause aversive behaviours across different taxa? Do mimics imitate model species' buzzes, calls or hisses to avoid attack? Obtaining decent recordings of insect auditory signals is the starting point for addressing the role of sound in the complex network of animal and plant-animal interactions.

AUTHOR CONTRIBUTIONS

Paolo Volponi conceived the idea of, designed and assembled the recording system, and helped in video processing. Marta Skowron Volponi designed the pilot study, processed audio and video recordings and wrote the manuscript. Marta Skowron Volponi and Paolo Volponi carried out field recordings and took photos, Marta Skowron Volponi and Leonardo Dapporto analysed data. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14224>.

DATA AVAILABILITY STATEMENT

Data, recordings and script available via the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mw6m90627> (Volponi et al., 2023).

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SUPPORTING INFORMATION

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

Supplementary file. Practical guide: How to build and use the buzzOmeter system.

Figure S1. TASCAM PCM recorder with receiver plugged in.

Figure S2. Paolo Volponi placing the buzzOmeter system in front of a hornet nest entrance.

Figure S3. Setup 1 placed in front of a custom-made delta trap with a pheromone lure.

Figure S4. Hand-held setup 2 consisting of the centre column of a tripod with camera attached to tripod head, selfie stick, microphone and transmitter of wireless mic system.

Figure S5. The authors using setup 2 of the buzzOmeter system to record *Macroglossum stellatarum* foraging on *Solidago virgaurea*. *S. virgaurea* flowers were attached to the microphone for camouflage.

Table S1. Definitions of calculated acoustic parameters with abbreviations used in analysed dataset (dataset S1) and explanation of the applied bandpass filter. Equations and figure are from Praat v. 6.1.09.

Table S2. Confusion table showing species assignment based on 11 acoustical parameters of buzzing sounds of insects in flight.

Video SV1. Video tutorial showing the process of file synchronization and audio selection in open access DaVinci Resolve and Praat software.

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