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SOUNDS OF THE SUNSET COAST

Effectiveness of nonlinear time series analysis for the analysis and classification of bee wingbeat-generated sounds

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ABSTRACT

Bees are among the most important pollinators for crops and wild plants. Surveys show global food production is affected due to the decline in the bee population and activity. Most of these studies concerned with the honeybees and their monitoring have been developed for commercial purposes, however, recent research highlights the vital role solitary bee species play in native ecosystems, serving as highly effective pollinators for specific plants. In contrast, honeybees may pose an ecological threat by competing for food resources, potentially disrupting local pollinator dynamics. Hence, there have been efforts to understand the ecology of pollination using acoustic signal detection through passive monitoring with classification to analyse ecosystem dynamics. In general, these studies are based on the identification of the frequency-related features in the signal using machine learning and artificial neural networks, e.g., harmonics, spectral power, and distribution of spectrum. As the flying sound generated by the bees is due to the aeroacoustics of flapping wings, it is difficult to identify species with similar size and wing beat frequencies. However, there has been little understanding of using time series analysis for feature extraction and identification in their acoustic signals. In this study, we show that time series analysis, which is also able to discover nonlinear features, can overcome the above issue. Using the European honeybee (*Apis mellifera*) as a readily available model species, prior to aiming at analysing solitary bees, we analyse the acoustic signals of the species recorded in the wild with nonlinear time series analysis, especially recurrence quantification analysis (RQA) to show the difference between flying behaviour for the species. RQA shows that recurrence time and recurrence time entropy for *hovering* are higher than leaving a flower signal at a statistically significant level. Furthermore, using the dynamic feature preserving geometric filter-*GHKSS*-we could resolve the phase-space trajectory from noisy information, which shows time varying phase-space trajectory for the signal.

1 INTRODUCTION

Insects, especially bees, are an integral part of ecology and food production (Sluijs and Vaage, 2016). Most of the human crop pollination is due to the honeybees (Rother et al., 2022), while, in general, flies and other pollinators such as solitary bees are responsible for plant-specific pollination (Schenk et al., 2018). On the other hand, invasive bee species compete directly and indirectly in the local ecosystem, causing decline in the native bee population (Geslin et al., 2017; Da Silva et al., 2021). Therefore, there is a growing interest in ecosystem monitoring of different bee species through their acoustic signals (Alberti et al., 2023; Truong et al., 2023; Kohlberg et al., 2024).

Bees produce sound because of their flapping wing during flight. Traditionally, the wingbeat-generated sound of insects has been studied using frequency domain-based approaches, based on the fast Fourier transformation, like spectrograms, mel-spectrogram, and mel-frequency cepstral coefficients (Truong et al., 2023). These methods have been successful in identifying insects with distinct acoustics (Kohlberg et al., 2024). With the help of Machine Learning and Neural Network-based algorithms these methods have been further developed to identify individual bee species with good accuracy (Ferreira et al., 2023; Truong et al., 2023). However, the challenge remains in recording good-quality audio in their natural habitat for training of the algorithms (Ferreira et al., 2023). Nonetheless, the effect of nonlinearity in signals is little understood, and with it, the distinct features of wingbeat-generated sounds. Hence, there are very few applications of nonlinear time series analysis (NTSA) applied to pollinator sounds. To monitor the pollination and the effects on ecosystems, it would be of interest to understand the flying behaviour of bees and the associated airborne sound generation. Further, using ethograms (Kazlauskas et al., 2016), we can estimate the pollination efficiency through acoustic monitoring of bee visits to and departures from the flower. Recently, NTSA was used in the form of recurrence plot spectrograms and convolutional neural networks (Hertramph and Oberst, 2024) to classify the flying behaviours of bees (Mohapatra et al., 2024).

Recurrence plot (RP) has been extensively used for time series analysis and nonlinear dynamics (Marwan et al., 2007). RP is a visual representation of the recurrence of states and dynamics. Recurrence quantification analysis (RQA) is used to find the patterns and structures within RP. Both RP and RQA are powerful tools to check the periodicity, determinism, or chaos among many other properties in a time series (Webber and Marwan, 2015). RP has been applied as a popular tool to analyse biomedical signals, e.g., EEG and ECG, to predict irregularity in physiology (Ouyang et al., 2008; Mathunjwa et al., 2021). Aboofazeli et al. (2008) have shown the difference in swallowing and breathing sounds with the help of RP and RQA. Oberst et al. investigated the chaos and nonlinearity in friction-induced vibrations, space applications, dynamics in geological systems, and biomechanics using NTSA and RP (Oberst and Lai 2011; Oberst and Tuttle, 2018; Oberst et al. 2018a, b). However, there is no study on nonlinearity and the use of RP and RQA for the analysis of wingbeat-generated sounds, as nonlinearity is undoubtedly important when it comes to the aerodynamics of flexible flapping wings, which involves solving Navier-Stokes equations and fluid-structure-acoustic interactions (Wang et al., 2020). Also, species-specific sounds and cues are likely to be distinguished using more complex measures than those developed for the frequency domain.

Furthermore, acoustic signals are an essential medium of communication for animals (Alexander, 1967; Ladich and Winkler, 2017). Both vertebrates and arthropods use acoustics to signal information regarding health, sex, social behaviour, or to avoid predators in inter- and intraspecific communication (Kirchner, 1997; Ladich and Winkler, 2017; Schönrogge et al., 2017; Wu et al., 2021; Muir et al., 2025). Acoustic communication in social insects, including honeybees, has been researched for over a century (Kirchner, 1997; Nerse and Oberst, 2022). These insects use acoustic communication for recruitment, health of the colony, and alarm signals, and also, warning signals in intra- and interspecific communication, respectively (Kirchner, 1997). Most of the studies on insect acoustic communication focus on the signal's frequency content (Kirchner, 1997; Pollack et al., 2016). Nonetheless, the importance of nonlinear acoustic signals in animal vocalisation and communication has been studied across different animal species (Benko and Perc, 2007; Hughes et al., 2009; Muir et al., 2025). Frogs use nonlinear ultrasonic communication to exhibit sexual traits (Suthers et al., 2006; Wu et al., 2021). As shown in Hughes et al. (2009), nonlinearity in cicada mating calls helps in sound propagation. Although there is evidence of wingbeat-generated sound for communication in flying insects (Kirchner, 1997; Pinto et al., 2022), the nonlinearity in the signal has not been investigated. Hence, we use the honeybee (*Apis mellifera)* as a model species in this study to compare the acoustic signals of two flying behaviours: *hovering* and *leaving* a flower. We use a traditional analysis usually applied in a linear system response framework and compare that to the results of NTSA.

2 METHODS

The framework for this study was divided into three steps: (1) data recording, (2) data cleaning and labelling, and (3) nonlinear time series analysis, Figure 1. Ideally, one would proceed directly from step (2) to step (3); however, in practice, data cleaning and labelling may sometimes require basic signal processing, such as generating a spectrogram, to enhance the quality of time series analysis subsequently.

2.1 Data recording

The data were recorded in the summer of 2023, Valencia, Spain, Figure 2(a). This time of year was the peak of pollination activity for many local ecosystems (Rodrigo et al. 2021). Fieldwork was done between 11 AM and 4 PM of the day, where the temperature and humidity were recorded to be 28-35 °C and 33-54 % relative humidity, respectively. The setup included a cardioid microphone (Sennheiser MKE40-EW; sensitivity: 42 mV/Pa, ± 2.5 dB at 1 kHz; frequency range: 40 Hz to 20 kHz) connected to a Tascam DR-60DMkII audio recorder, Figure 2(b). The microphone was mounted on a pole for easy manoeuvrability. The pole was handheld or fixed on the ground, depending on the bee activity around the flowering plants. A fixed microphone was not suitable for recording the acoustic signal when the pollinators moved from plant to plant. Therefore, handheld recording had the flexibility to follow the pollinator and record with a high signal-to-noise (SNR) ratio without much compromise on quality, even in the noisy outdoor conditions. The audio was recorded at 48 kHz sampling frequency and in .WAV file

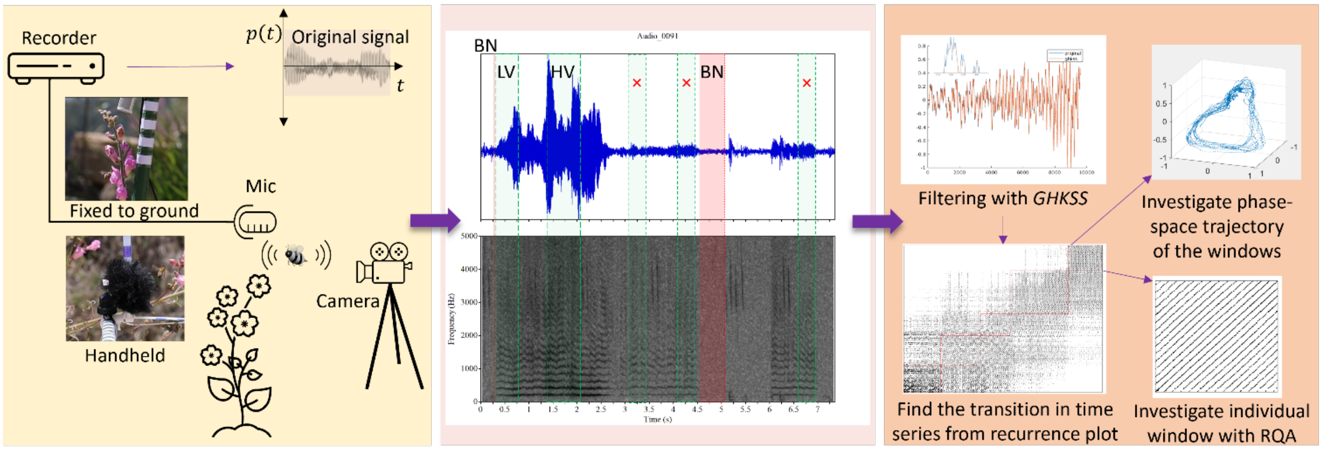


Figure 1: Three-step framework for this study. (1) Data recording: schematic of the setup for audio-visual recording. (2) Data cleaning and labelling: data preprocessing and labelling using Praat audio software. LV: leaving. HV: hovering. BN: background noise. (3) Nonlinear time series analysis. RQA: recurrence quantification

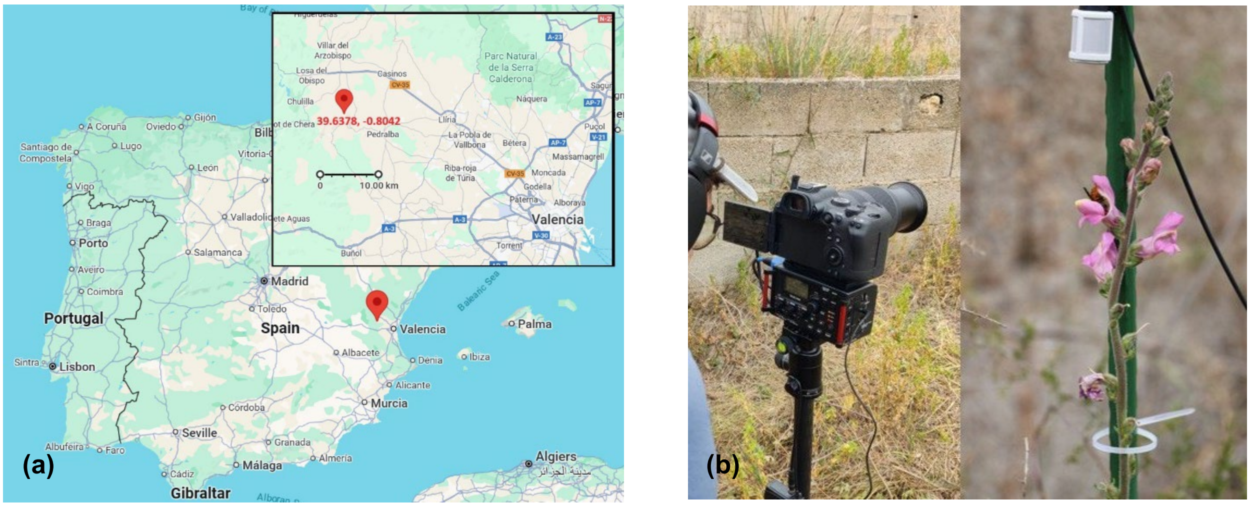


Figure 2: (a) Google Maps image of the location near Valencia, Spain used for field study. (b) Audio-visual recording setup in the field.

format with a gain of 11 dB on the microphone input signal. Simultaneously, video was recorded with a DSLR camera (Canon EOS R6 MKII) with autofocus mode to capture the flying behaviour.

2.2 Data cleaning and labelling

Praat (Boersma, 2001), an open-source audio software, was applied to the recorded audio files to check for any unwanted acoustic events like environmental noise, anthropogenic noise, birds calling, and other insect sound. The section of audio with only the pollinator sound was kept for analysis, highlighted as green windows in (2), Figure 1. This may also occasionally include audible background noise (like wind noise). To further clean the signal, the audio sections were selected when the pollinator signal was 5 dB or more above the background noise and remaining were rejected (marked as red X). The background noise in an audio file was selected, where there were no acoustic events and it was close to the pollinator sound event, shown as red windows in (2). As the background noise in the outdoors was dynamic too, we selected two windows (one before and after the pollinator window) and took the average power of the two windows. However, there were two out of nine signals (~ 22 %) with only one background noise window to quantify the SNR. Assuming additive background noise, we calculated SNR as

$$SNR = \frac{P_s}{P_b} = \frac{P_t}{P_b} - 1 \tag{1}$$

where P_s, P_b and P_t are the signal power, background noise power, and total power ($P_t = P_s + P_b$), respectively. We define a *hovering* signal when the insect is interested in the flowers (and/or the microphone) and it does not fly in a straight line, but it hovers around the flowers or microphone. This type of flight should last at least 0.2 seconds to be labelled as *hovering*. The flight that happens from the moment in which the insect leaves a flower to 0.5 seconds after is labelled as the *leaving* signal. There were a total of nine signals: four for *hovering* and five for *leaving*. However, NTSA of only one signal for each behaviour has been presented in the results because of similar observations in the remaining signals. Before NTSA, the signal was analysed for the power spectral density (PSD) and autocorrelation function (ACF) using *periodogram* (with a Hamming window) and *autocorr* function in MATLAB, respectively. Each time series was divided into signals of 0.2 s duration by shifting the window linearly. The number of windows is given by

$$N_w = \left\lfloor \frac{L-N}{N_s} \right\rfloor, \quad (2)$$

where L is the length of the time series, $N = 9{,}600$ is the length of the 0.2 s signal, and $N_s = 1{,}200$ is the window shift length.

2.3 Nonlinear time series analysis

First, we used *GHKSS* algorithm, a locally projective geometric filter, available through the *TISEAN* package (Hegger et al., 1999), which iteratively reduces the noise by projecting the time series to a low-dimensional space and removing the coordinates that do not match the neighbourhood criteria. Hence, the *GHKSS* filter aims to preserve the dynamics of the signal by not simply removing frequency content but only works if low and high-dimensional content is uncoupled and can be separated. Next, the filtered signal was subjected to delay embedding to find the time delay at the optimised embedding dimension, where the auto mutual information was minimum and the % of false nearest neighbours was zero (Wallot and Mønster, 2018). With the calculated time delay and embedding dimension, the time series vector was embedded to an m-dimensional phase-space. The delay embedded signal was used to calculate the recurrence matrix at a 10% *fixed amount of neighbours* and subsequently, to plot the RP (Marwan and Krämer, 2022). The transitions within the timeseries were qualitatively and manually determined by checking the transition of the recurrence plot along the diagonal, line of identity (LOI), as shown in Figure 1. The small windows within the RP refer to quasi-steady state as the corresponding phase-space trajectories are different from each other. Furthermore, the signal was subjected to RQA (Marwan and Krämer, 2022) on random windows of 0.2 s duration to investigate the significance of the recurrence plot for differentiating the *hovering* and *leaving* flying behaviours from their acoustic signals. The density of the random windowing while performing RQA was 20 per one second duration of the time series. In total, there are 54 and 40 samples for *hovering* and *leaving*, respectively.

3 RESULTS

3.1 *Hovering*

From PSD, the signal appears to be highly tonal, up to 8 visible peaks for the average plot in black, Figure 3(b). The average ACF of the individual time series is plotted in the darker shade compared to 0.2 s window signals, Figure 3(c). ACF has visible peaks and decays at a slow rate, which indicates that the signal is periodic. There are smaller peaks in between large peaks, also indicating the presence of higher harmonics, which is also evident from the PSD. However, the ACF is asymmetric about zero. Also, the broader peaks indicate that the periodicity varies in time. Figure 4(a) presents the recurrence plot for the *hovering* time series 1. Each red block represents the quasi-steady state within the time series. To understand the dynamics further, the phase-space trajectory of each window has been plotted in Figure 4(b), with the window number labelled on the top. The transition between the states is clear from these trajectories, and the manifolds evolve with time. It is also clear that the signal time series has high nonlinearity (w2 and w4), and the trajectory has multiple orbits, as clearly seen from w7 in Figure 4(b).

3.2 Leaving

Contrary to *hovering*, PSD of *leaving* is less tonal as the higher harmonics (4th onwards) are not as prominent as the former, Figure 5(b). Also, the average PSD peaks are less sharp compared to *hovering*. However, the ACF is more symmetric about zero and has fewer smaller peaks, Figure 5(c). Figure 6 presents the RP with quasi-steady states (marked by red blocks) and the corresponding phase-space trajectories. The time series evolves to become periodic, as can be seen from the phase-space trajectory in Figure 6(b). Moreover, the manifolds in the trajectory converge in *leaving,* in contrast to *hovering*, where it changes more in transitions. Nonetheless, by finding transitions in the recurrence plot and estimating the correct delay embedding, the phase-space trajectory of the univariate time series can be resolved, which shows complex features.

3.3 Comparison between *hovering* and *leaving* using recurrence quantification analysis

Figure 7(a)-(c) show the notched box plots of RQA variables with statistically significant differences between the *hovering* and *leaving* signal. Comparison was done with the Wilcoxon rank sum nonparametric test using MATLAB at a significance level of 0.05, Figure 7(d). Out of 13 RQA variables, we found three: recurrence time of the second type (T_2), recurrence time entropy (RTE), and maximal white vertical line length (RT_{max}), that show statistical

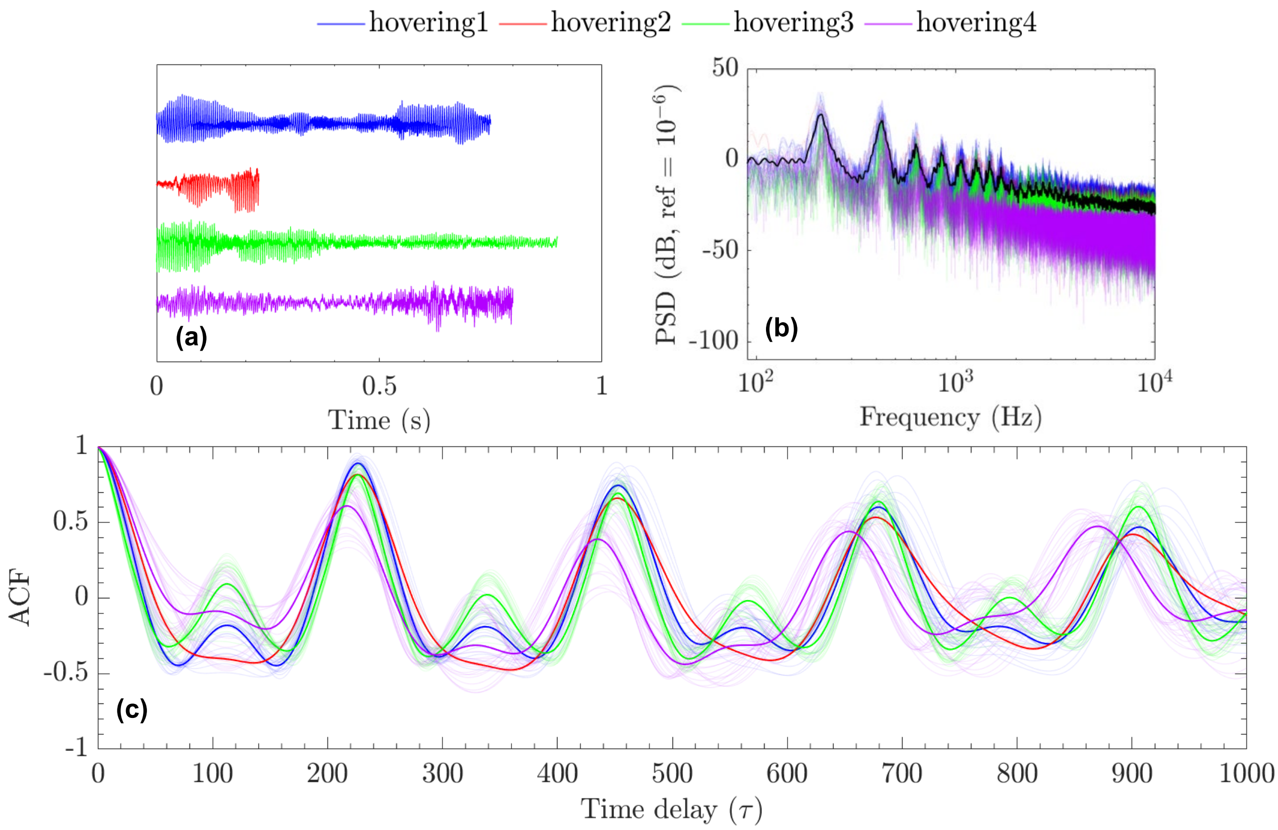


Figure 3: *Hovering* signals in (a) with corresponding power spectral density (PSD) in (b) and autocorrelation function (ACF) in (c). (b) Average PSD (in black) shows the tonality the signal with clear peaks up to 2 kHz. (c) The light shade represents the signal of 0.2 s selected by shifting the window at 0.025s of the time series and the darker shade is the average for the above. The tonal nature of the signal is also evident from the slow decaying periodic nature of ACF.

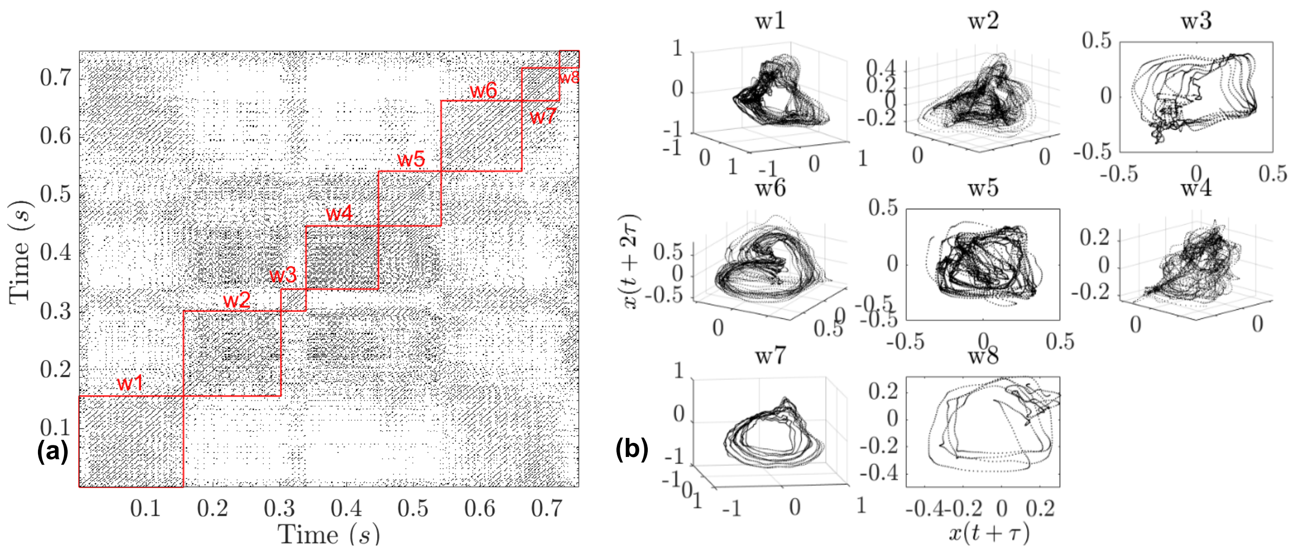


Figure 4: (a) Recurrence plot (RP) of the *hovering* time series 1. The red blocks represent the quasi-steady states within the time series. (b) The phase-space trajectory of each quasi-steady state shows a complex and evolving manifold within the time series, even though the average PSD and ACF in Figure 3 present a tonal nature of the signal.

significance. T_2 and RTE are related, as both measure the recurrence of states. As *hovering* has complex phase-space manifolds, the recurrence of states takes a longer time, as shown in Figure 7(a). Hence, T_2 and RTE for *hovering* is greater than *leaving*. However, maximal white vertical line length (RT_{max}), corresponds to the

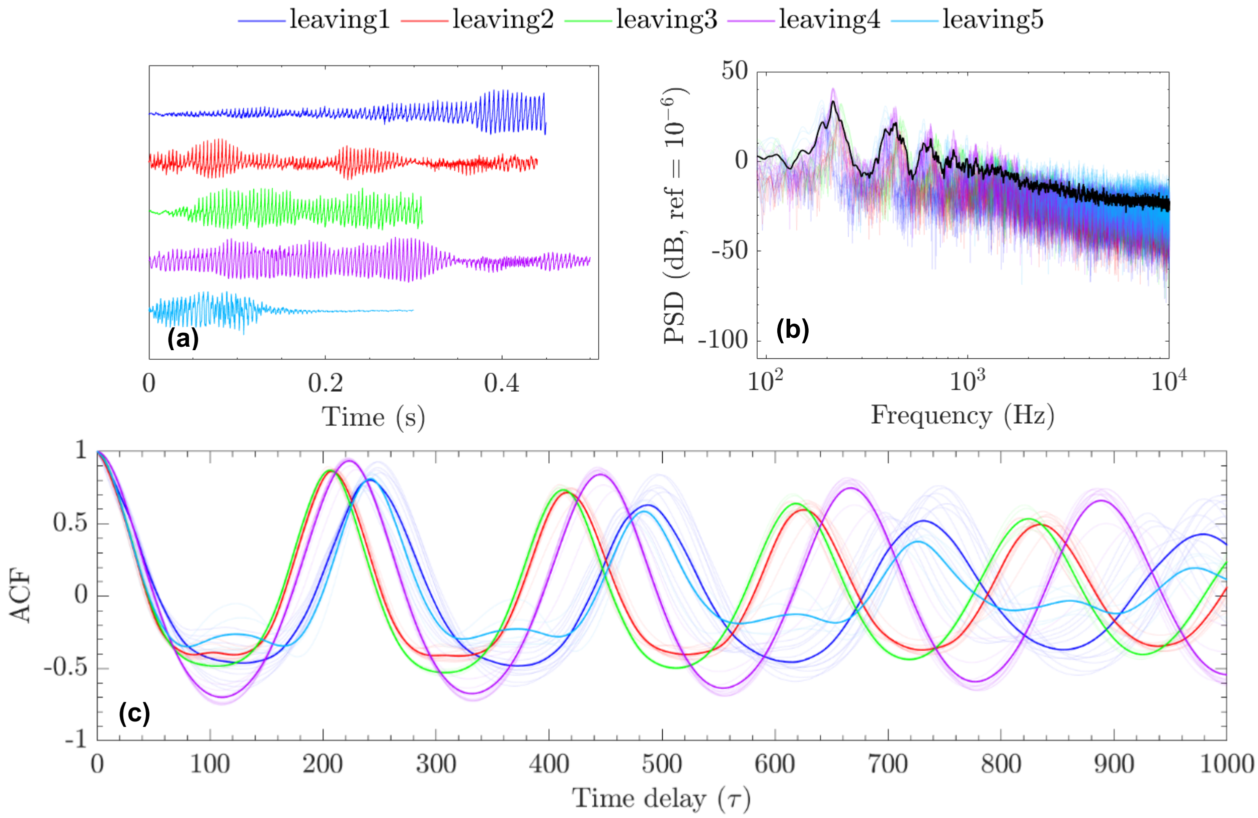


Figure 5: *Leaving* signals in (a) with corresponding power spectral density (PSD) in (b) and autocorrelation function (ACF) in (c). (b) Average PSD (in black) for all *leaving* signals is less tonal, compared to *hovering*, with clear peaks up to 4th harmonics. (c) ACF is more symmetric about zero and has fewer smaller peaks.

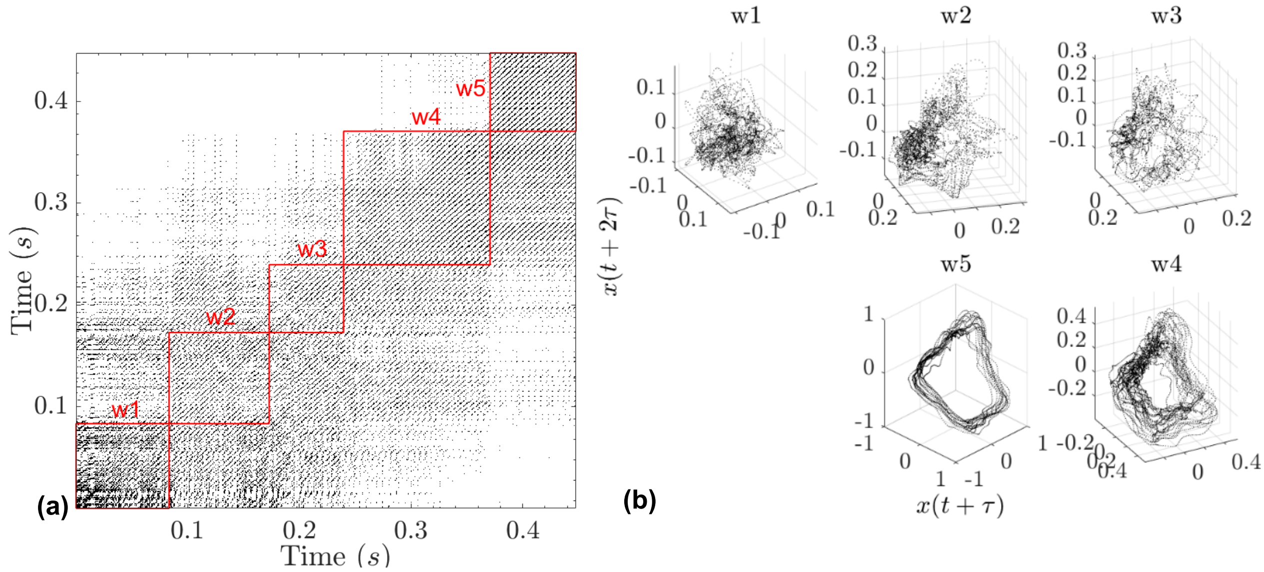
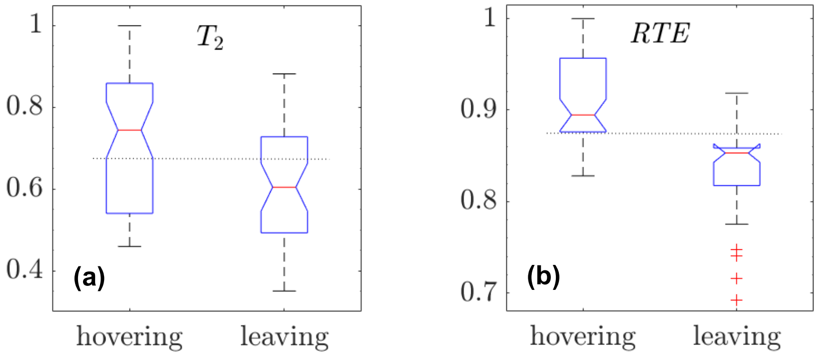
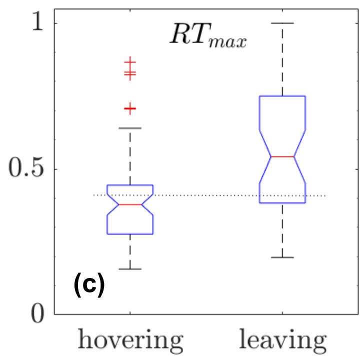


Figure 6: (a) Recurrence plot (RP) of the *leaving* time series 1 with the quasi-steady states, which are marked by red blocks. (b) The phase-space trajectories of the quasi-steady states exhibit a converging manifold.

maximum recurrence time in a recurrence plot, which is high in the case of *leaving*. The above results show that RQA of the acoustic signals can be used to distinguish different flying behaviours of bees.





(d)

Wilcoxon rank sum test	
RQA variable	probability
T_2	$\sim 10^{-3}$
RTE	$\sim 10^{-11}$
RT_{max}	$\sim 10^{-4}$

Figure 7: Notched box plots of normalised recurrence quantification analysis (RQA) variables: (a) recurrence time of the second type (T_2), (b) recurrence time entropy (RTE), and (c) maximal white vertical line length (RT_{max}). The black dotted line shows the non-overlapping notches, which indicates the significant difference between medians of the groups at 95% confidence interval. (d) Wilcoxon rank sum test to show the significant difference between *hovering* and *leaving* signal at significance level of 0.05.

4 DISCUSSION

Wingbeat-generated sound of insects has been widely studied in ecology (Clark, 2021) and for flapping wing mechanisms (Ji et al., 2022; 2024). However, the acoustic features associated with different flying behaviours have been largely ignored due to the complexity of the theoretical model and the lack of detailed experimental observations. In this study, we have presented the wingbeat-generated sound for two flying behaviours: hovering and leaving a flower. The PSD and ACF of these sounds show that the signals are mainly tonal or harmonic with prominent peaks, which has been confirmed both experimentally and numerically by Seuer et al. (2005) and Bae and Moon (2008), respectively, for flying insects. Our result confirms the nonlinearity of the time series through the RPs, which shows the complex dynamics of the signal with transitions between quasi-steady states. Moreover, we have shown that RQA can distinguish between hovering and leaving flying behaviours. The phase-space trajectories of these signals also show different and complex manifolds with multiple orbits, which is a sign of periodic and chaotic signals (Gao and Cai, 2000; Marwan et al., 2007; Webber and Marwan, 2015). This is not possible with frequency domain and linear time series analysis methods. The above analysis needs to be verified with more datasets and different species of pollinators. Also, the behaviours considered in this study are limited to only two types. The overall process of an insect approaching a flower (with the intention of landing) and leaving a flower is much more complex, and different behaviours like *landing* or *passing by* can be added as per the ethogram and the nature of the study. This may change the RQA variables further.

Although we have presented only one time series for each flying behaviour, the observation for the other remaining time series is similar to the ones presented, i.e., the *hovering* behaviour has complex phase-space manifolds and *leaving* has a more ordered trajectory. The *hovering* time series have been noted to be longer in general (> 0.5 s in three out of four cases) compared to the *leaving* time series (~0.3-0.4 s in duration). A longer signal means more variations during flying and thus, more quasi-steady states in the same time series. But the lack of order in the phase-space manifold could be the behaviour-specific feature. Nonetheless, the above analysis is sensitive to the quality of delay embedding. While using the *GHKSS* filter to reduce the noise, we selected the embedding dimension up to four and in a three-dimensional projection space because most of the nonlinear dynamic models and attractors are three-dimensional. Selecting an embedding dimension that is much less than the actual could lead to irrelevancy in a phase-space, like a noisy signal, and may not be sufficient to resolve the phase-space trajectory (Casdagli et al. 1991). Hence, the future analysis will include the sensitivity of the *GHKSS* projection dimension to the analysis.

The aeroacoustics of insect wingbeat-generated sound is dominated by the vortex shedding because of the flapping wing (Ji et al., 2024). The numerical model to understand the above phenomena involves first solving the Navier-Stokes equation for the aerodynamics, followed by solving the acoustic pressure using Ffowcs Williams-

Hawkings (FW-H) model. Studies using the FW-H model suggest that the acoustic field is highly complex and directional (Ji et al. 2022; Ji et al., 2024) even after many simplifications to the model, for example, ignoring the thickness term and Lighthill tensor term, which is related to the turbulence. During experimental and field measurements, it is impossible to control the above effects. Hence, there is a gap between the model and the experimental observations. With our analysis, we have shown that the nonlinearity in the signal is an important attribute to distinguish different flying behaviours from the acoustic signal. Moreover, it is also difficult to judge the near field or far field concerning the source, which poses further challenges in the analysis, if the near field effects due to complex fluid dynamics are not registered in the recording. Therefore, we believe this study will lead to improvements in the aeroacoustics model. Furthermore, studies show that the hovering flight of insects is unstable, as easily disturbed by external factors like wind (Liang and Sun, 2013). Hence, the continuous adjustment to balance the aerodynamic forces could be the reason for transitioning between states and such complex phase-space manifolds. *Leaving* is a relatively simpler flying behaviour, as it requires forward flight away from the flower (Wang, 2005). Another reason could be the sudden changes in directions during flight. This requires further analysis of the footage along with the transitioning states.

As shown, hovering signal has highly complex phase-space trajectory, which indicates possible chaotic regime (Gao and Cai, 2000; Webber and Marwan, 2015). A chaotic signal is broadband with subharmonics (Massenet et al., 2025), which can be argued as information-rich compared to only a harmonic or periodic signal. However, the challenge always remains in understanding the importance of these features for the intended receiver in inter- and intraspecific communication, as hearing is understood to be a nonlinear process too (Nadrowski et al., 2011). From an evolutionary point of view, it is not surprising that flying insects use the wingbeat-generated sound for acoustic communication. However, the importance of the nonlinearity for different species still needs to be investigated. Further evidence suggests that social bees have evolved to be better in chemical communication compared to the solitary bees due to the evolutionary requirement to exist in a colony (Wittwer et al., 2017). Does it mean the wingbeat-generated sound of these bees has also evolved? This requires an in-depth analysis of behaviour and species-specific nonlinearity in the signal through nonlinear time series analysis.

5 CONCLUSION

In this paper, nonlinearity in wingbeat-generated sound for different flying behaviours of honeybees (*Apis mellifera*) was analysed using RP and RQA. We demonstrated the transitions of quasi-steady states in the acoustic signals using RP. The phase-space trajectory of these quasi-steady states shows complex manifolds that evolve with time. Therefore, analysis of the signal as a stationary time series or with linear methods may lead to oversimplification and wrong interpretation. Furthermore, we can distinguish between different flying behaviours with the help of RP and RQA. Both the phase-space trajectory and RQA suggest that the *hovering* time series has complex dynamics out of the two. However, further analysis is required to fully understand the nonlinearity and the hidden dynamics. Moreover, the above analysis is possible due to the nonlinear time series analysis and cannot be done with frequency-based analysis, which is generally practiced in the bioacoustics field.

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AUTHOR CONTRIBUTION

ARM: Conceptualisation, Methodologies, Analysis, and Manuscript preparation. LB, MRT: Fieldwork, Data collection, and Methodologies. SA: Methodologies, and Technical discussion. CN: Conceptualisation, and Editing. IS, DNP, JE, GP: Editing. JTM, LPC, FB: Project administering, Funding acquisition, and Editing. SO: Conceptualisation, Methodologies, Manuscript preparation, Supervision, Resources, Project administering, and Funding acquisition.

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