PLOS Complex Systems

RESEARCH ARTICLE

Group size and environmental obstacles drive acoustic call properties for gray bats in flight: A data-driven analysis

Megan Grey[1,2], **Eighdi Aung**[3], **Nicole Abaid**[1,2]*

1 Department of Mathematics, Virginia Tech, Blacksburg, Virginia, United States of America, **2** Center for the Mathematics of Biosystems, Virginia Tech, Blacksburg, Virginia, United States of America, **3** Engineering Mechanics Program, Virginia Tech, Blacksburg, Virginia, United States of America

* nabaid@vt.edu

Citation: Grey M, Aung E, Abaid N (2026) Group size and environmental obstacles drive acoustic call properties for gray bats in flight: A data-driven analysis. PLOS Complex Syst 3(4): e0000100. https://doi.org/10.1371/journal.pcsy.0000100

Editor: Gil Ariel, Bar-Ilan University Faculty of Exact Sciences, ISRAEL

Received: July 31, 2025

Accepted: March 13, 2026

Published: April 22, 2026

Data availability statement: The data sets and Matlab codes supporting this article are available on GitHub https://github.com/nabaid/Group-size-and-environmental-obstacles-drive-acoustic-call-properties-for-wild-gray-bats.

Funding: This work was supported by the National Science Foundation (1751498 to NA).

Abstract

Unlike schools of fish or flocks of birds, social bats who use echolocation for navigation are faced with the complex challenge of signal processing while living and flying in groups. Interference between an individual's calls and those of its conspecifics can be confused, making these signals difficult to study and interpret for both animals and researchers. Moreover, it is not necessarily clear from the literature what form models that seek to predict bat echolocation behaviour should take. For example, we know that bats change their calls when flying in groups, but the literature is not consistent on what specific changes are implemented. Here, we collect and analyse data from a colony of wild gray bats, *Myotis grisescens*, to explore whether the number of bats emerging from the roost at a given time and the physical geometry of their environment influences their echolocation calls. Specifically, we explore whether the number of calls and their acoustic power are influenced by the group size and presence of obstacles using a time-series analysis tool called transfer entropy (TE). We further apply a data-driven algorithm called sparse identification of non-linear dynamics (SINDy) to describe a model for this phenomenon. Our findings reveal significant TE values, indicating that call properties are influenced by both social and environmental factors, without assuming a form for this influence. Additionally, SINDy-based models suggest how bats adjust their echolocation behaviour in response to the presence of conspecifics and environmental obstacles. These results provide new insights into the role of sociality and physical surroundings in shaping echolocation dynamics in gray bats.

Author summary

Gray bats are a social species that use echolocation during flight to navigate their environment and forage. When flying in groups, bats are faced with the task

The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

of processing sounds from their own calls and from neighboring bats. Current literature shows that many species of echolocating bats change their calls in the presence of their peers, but modelling these changes has not yet been rigorously done for animals in natural conditions. In this research, we analyze wild gray bats' calling behaviour using data-driven methods. We first explore whether the number of bats and the presence of physical obstacles influences the number and acoustic power of gray bats' calls using an information theoretic measure. We then develop a model to describe this influence using sparse identification of nonlinear dynamics (SINDy), an algorithm that fits data to a nonlinear model using a sparse number of terms. By uncovering which variables appear in the data-driven models, these tools allow us to discover underlying dynamics in systems that are otherwise unknown.

Introduction

Gray bats, *Myotis grisescens*, are a social species of microbats native to the eastern United States [1]. During flight, these bats use echolocation to visualize their surroundings [2] by emitting directional high frequency calls between 40 kHz to 80 kHz [3] which reflect off objects in the calls' paths and return to the bat via an echo. The bat is then able to determine the object's location and size based on changes in frequency and timing of the echo. However, gray bats often fly in groups, which causes an additional complexity to how well they are able to accurately interpret the echoes in their environment.

When echolocating bats fly together, the calls emitted by conspecifics may overlap with one another and cause what is known as "call jamming" [4]. If a bat's call is jammed by another bat, they may lose the ability to correctly interpret or hear the echo of their original call. This effect is often seen when bats fly with conspecifics behind them, as the calls from rear bats interfere more than the calls from bats flying in front of or towards the jammed bat [5]. Corcoran and Conner suggest that some bats, such as the Mexican free-tailed bats, *Tadarida brasiliensis*, will jam a conspecific's call intentionally in order to reduce the jammed bat's ability to locate its prey [6]. Since echolocating bats rely on being able to interpret calls for both navigation and hunting, we can expect gray bats to change their call properties in the presence of conspecifics in order to avoid potential jamming, which is known as a jamming avoidance response [4].

Researchers of bat behaviour discuss two prominent ways in which bats use a jamming avoidance response - one being changing the number of calls and the other being changing the usage of certain frequencies or power. Chiu, Xian, and Moss document that bats may suppress echolocation to avoid jamming. It was noted that, when big brown bats, *Eptesicus fuscus*, fly in pairs, the individual bat is more likely to not make calls as compared to when flying alone [7]. Similarly, Jarvis, Jackson, and Smotherman found a decrease in call emissions in groups of Mexican free-tailed bats versus single bats when bats are confined in a cage and do not fly [8]. Another study by Ulanovsky et al. discusses the jamming avoidance response associated with changes in the dominant frequencies of calls made by pairs of foraging bats of two different species. The European free-tailed bat, *Tadarida teniotis*, demonstrated a wider range of frequencies when flying in pairs versus alone, while the Egyptian tomb bat, *Taphozous perforatus*, did not display any significant changes [4]. Hence, whether or not bats experience jamming in a given condition, and how they may compensate for it if they do, is not fully understood across bats in general and specifically for gray bats.

In addition to accounting for nearby conspecifics and their calls, bats may be faced with complex environments in which they have to navigate. Bats have been known to vary the number and frequency of calls they make when approaching physical objects such as obstacles. Specifically, Jones and Moss found a decrease in number of calls and decreases in peak frequency and bandwidth when big brown bats, *Eptesicus fuscus*, were faced with obstacles [9]. Physical barriers have also been known to decrease foraging in some *Myotis* species as noted in work from Brigham et al. [10]. Physical clutter causes the calls made by bats to reflect off multiple surfaces which may additionally cause unintentional jamming interrupting the bats ability to interpret their echoes. With both group size and physical obstacles, we expect bats to change their calls in order to reduce call jamming and better navigate their environment. However, research from Orbach and Fenton suggest that there is no significant change in call duration in the presence of obstacles for little brown bats, *Myotis lucifugus* [11]. Therefore, how gray bats may change their call properties when flying with obstacles remains an open question.

While jamming avoidance responses have been researched for a subset of species, the underlying rules that bats use are not consistent between documented studies; therefore, we do not know a ground truth for how gray bats change their calls when flying with conspecifics and obstacles, or even whether changes are being made. This challenge offers an opportunity to use data-driven methods to find relationships in behavioural data that would evidence such changes. In order to identify and quantify causal relationships between data, researchers have used mathematical tools such as mutual information or transfer entropy (TE) [12,13]. TE quantitatively measures information flow from one time series to another and is sensitive to non-linear effects which may dominate in complex natural systems [14]. Current literature that uses transfer entropy to study animal social behaviour typically only includes pairs of individuals and measures the information flow between them. For example, Shaffer and Abaid use TE to measure the amount of information flow from one bat's flight patterns to another bat's change in direction and speed [15]. Additionally, a study on the collective behaviour of zebrafish focuses on finding the transfer entropy between a focal fish's position in response to a robotic conspecific [13]. Our research differs from the literature by exploring information flow between group-level properties rather than characteristic of individuals. Namely, we measure the flow of information from the time-varying local density of a group of bats to properties of the group's calls.

Although the presence of a causal relationship can be identified with a technique like TE, finding the specific nature of such a relationship may be challenging without further analysis. Recent developments in model identification tools allow for inferring and modelling the relationships between causally associated variables from data alone with some ansatz. Such techniques include linear mixed models [16], and more recently, sparse identification of non-linear dynamics (SINDy) [17] for non-linear modelling. Although the application of SINDy to animal systems is very limited currently, this technique has been used previously to model collective behaviour of engineered systems, such as Khaldi *et al.*'s work on flocking dynamics of robot teams, which uses variations of SINDy to look at heading alignment and proximity to another agent over time to model how the drones flock [18]. By taking into consideration the state of a neighbouring agents, flocking robots can navigate similar to biological systems like fish, bats, and birds. Rather than using properties of individual bat flights, our study uses the basic SINDy algorithm to build a model that captures the relationship between the number of bats and properties of their calls at the group level.

In this paper, we seek to demonstrate relationships between gray bats' use of sound (i.e., their number of calls and their acoustic power) and the presence of conspecifics, and to quantify the nature of these relationships–if they exist–when obstacles are both present and absent in their environment. We detail the collection of a novel dataset from a wild bat colony. We use transfer entropy as a tool to detect and quantify the flow of information between time series for group density and acoustic characteristics, in order to show the existence of dependencies between them. We then apply SINDy to construct a data-driven model that captures the underlying dynamics governing these relationships and relate the results in the literature. Through this approach, we aim to gain deeper insights into the behaviours of echolocating bats and how they use sound to better navigate complex environments.

Methods

Data collection

Data was collected over a span of two days in Bristol, Virginia, USA, in September 2022, at a gray bat maternity colony of approximately 10,000 members which roost in a culvert of Beaver Creek. When leaving the roost around sunset, the bats exit the culvert and typically fly upstream towards a bridge. Before sunset on both days of experimental testing, four infrared sensitive cameras (GoPro, Hero 3+, Black Edition, modified with infrared (IR) sensitive lenses, IR-Pro IRP202 Hybrid lenses) were set up on this bridge facing the culvert to collect video data. We sought to image a volume of approximately 14 m cross stream, by 7 m upstream, by 3 m deep, spanning the creek's channel with a view from the bridge deck to the water surface. These cameras were set with a frame rate of 60 frames per second and saved files approximately every seventeen minutes. In addition, four IR lights (Tendelux, CCTV Lighting, Mid-Long Range IR Illuminator) were set up to illuminate the imaged volume. As most species of bats, including *Myotis* bats, are not known to be sensitive to IR light [19], we assume that the presence of these lights do not directly affect the bats' behaviour [20]. Two ultrasonic three-microphone arrays (USG Omidirectional Electret Ultrasound Microphones, Knowles FG-O, Avisoft Bioacoustics, Nordbahn, Germany) were positioned facing outward from the bridge, such that the bats were flying towards the arrays. Audio files were saved every five minutes with a data acquisition board (UltraSoundGate 816H, Avisoft Bioacoustics, Nordban, Germany) using a sampling rate of 150 kHz. For this work, we focus on data from a single camera and microphone to demonstrate group-level calling behaviour of the bats in flight. We select the camera with the most direct line of sight of the bat flight path and minimal interference of the IR lights. The microphone located closest to this camera was used to collect the audio data.

The two data acquisition systems were synchronized by tapping two PVC pipes together approximately every five minutes within the camera's range of view, so that each audio file had a synchronization point. After data collection, the files were manually synchronized by finding the video frame and audio sample where the taps were recorded, making the greatest possible temporal accuracy of synchronization the camera frame rate, 1/60 s.

On the first day of testing, the bats were recorded with the camera and microphone arrays without intervention on their environment. On the second day, two sets of hanging obstacles, made from foam pool noodles and nylon cord, were strung across the stream perpendicular to the bats' flight paths. The obstacles extended from approximately the top of the concrete channel wall to 0.2 m above the water surface. Each line of obstacles comprised nine foam noodles, each measuring 1.4 m in length and spaced approximately 1.3 m apart (a gray bats wingspan is 0.27-0.30 m on average [1]). The experimental setup is shown in the schematic and photograph in Fig 1.

Approximately ten minutes before sunset, scouting bats began exiting the culvert, which we used as a signal to begin data collection. Data was collected for approximately 90 minutes. We selected four minutes of data from each night for analysis, two minutes when many bats were present and two minutes when few bats were present.This provided us with four two-minute blocks for our data.

Ethical note

This study followed ethical standards set by the Institutional Animal Care and Use Committee (IACUC 21–087) and was approved by the Virginia Department of Game and Inland Fisheries.

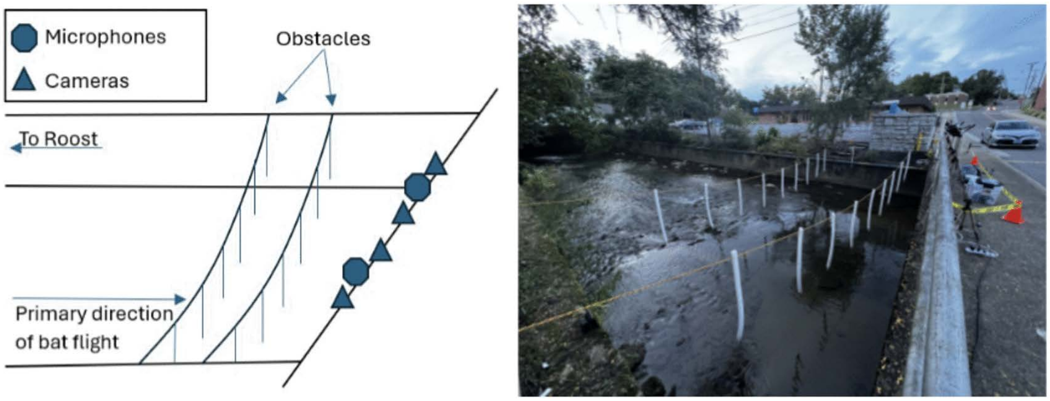

Fig 1. Experimental setup. Schematic (left) showing general setup and photograph (right) of field site with experimental setup.

https://doi.org/10.1371/journal.pcsy.0000100.g001

Data processing

From the video and audio data, we sought to extract time series for the number of bats in the imaged volume and properties of the calls they made at the same time. We define a time step of 1/60 seconds corresponding to the time of a single video frame. We note that a gray bat can fly through the imaged volume in approximately one second, and from the literature, bats make on the order of ten to twenty calls per second [1].

We measure the social interactions by counting the number of bats in each video frame manually. In the raw video files, many of the bats blended into the surrounding background, making counting individuals difficult. To combat this, each video clip was processed using a Matlab script to subtract the background and highlight any moving objects, allowing us to define the number of bats at a given time and store these values in a vector. We measure the bat calling behaviour as the total acoustic power per bat and the number of calls per bat, with the normalization of these values selected to allow us to appropriately compare instances with different numbers of bats. If the number of bats at a given time step is zero, then the auditory properties are set to zero.

We created a spectrogram to identify the bats' calls in the audio data, see Fig 2. We used a window size of 200 samples and an overlap of 160 samples, and computed spectrograms for 9/60 second intervals. To find the acoustic power per bat, the sum of sound intensity at all frequencies from 35 to 75 kHz per 1/60 second time step was taken, which was then normalized by the number of bats in the contemporaneous frame to give the acoustic power per bat.

To find the number of calls, we notice that the call of a gray bat has a general shape that starts at a high frequency of around 75 kHz and has a slight bend at a knee of around 55 kHz [3] as seen in Fig 2. In order to count the number of calls, we developed a Matlab code that first detects potential calls by finding the times when the power was above 0.02 decibels at the 70 kHz frequency. We consider the power to be zero when the power was less than 0.02 decibels to eliminate noise. With this filtered signal, we took the numerical derivative to find when the start and end of the call would be made; a positive derivative indicated the start of a call as the power increased, while a negative derivative indicated the end of a call as the power decreased. We eliminated any times where the spectrogram started or ended in a call. We considered a call to occur when the length between the start and end as defined above was over a threshold of 1.3 ms. The total number of calls was summed over the 1/60 second time step, which was then normalized by the number of bats in the contemporaneous frame to give the number of calls per bat. An example of how many calls were detected and the total power over time with respect to the given spectrogram can be seen in Fig 2.

As a comment, the cameras only captured a limited space that may not take into consideration nearby bats that could be recorded in the audio data. That is, our microphones potentially picked up calls from bats outside the given frame or

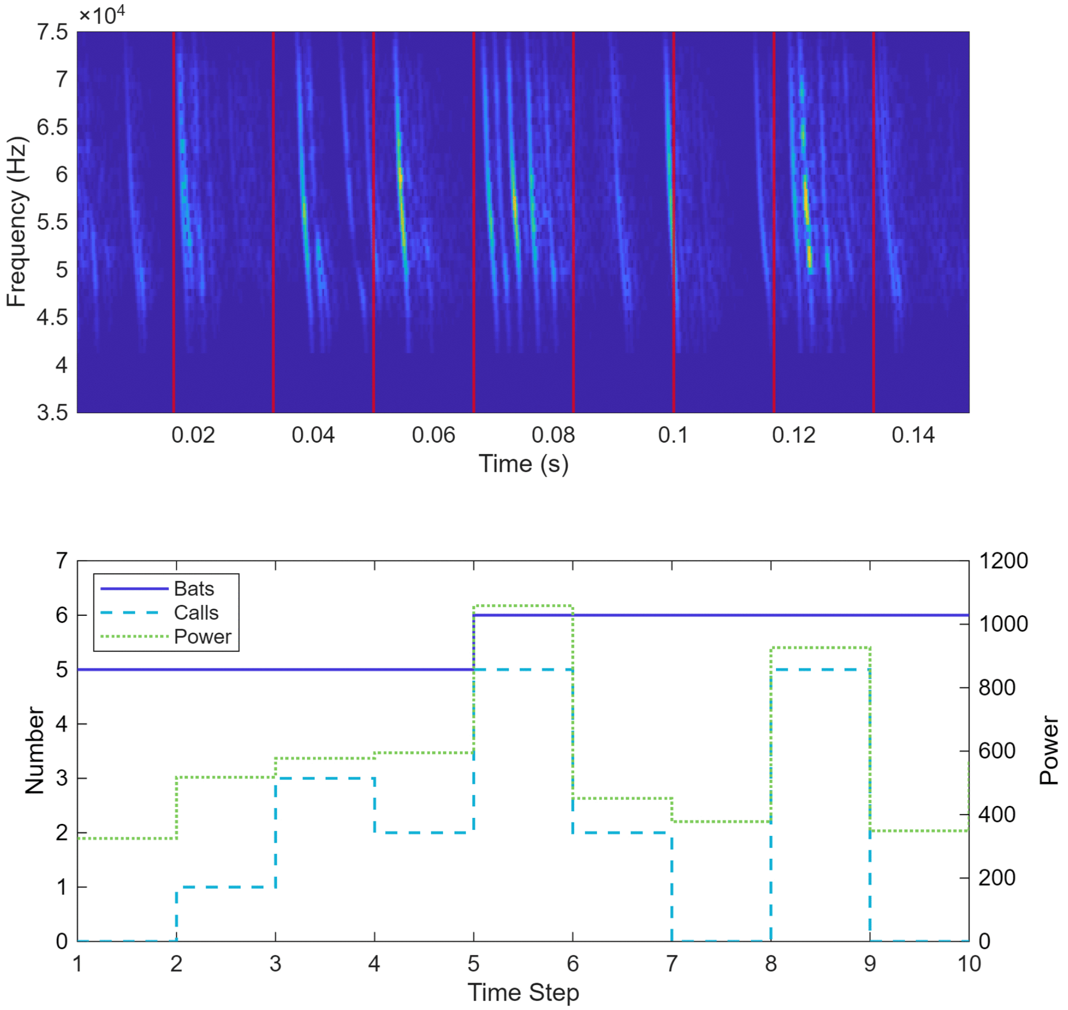

Fig 2. Extracting bat call properties from acoustic time series. Example spectrogram (top) showing a set of calls made by a group of "many" gray bats with obstacles. Red vertical lines show the bounds of each 1/60 s time step. The corresponding number of bats, detected number of calls, and total acoustic power in decibels per time step are shown in the corresponding plot (bottom).

https://doi.org/10.1371/journal.pcsy.0000100.g002

may have picked up "noisy" calls that would not be cut out by the code that counted the number of calls. As a result, the number of calls may not accurately capture only the vocalizations of the bats we see, but it is the best proxy for this quantity with the data available. Since bat calls and echoes attenuate after a few meters [21], we believe that the calls detected should at least include all calls being made by the visible bats in a given frame. Additionally, we do expect there to be some overlap between calls which would affect our time series. For this reason, we consider both properties of number of calls and acoustic power for analysis.

Numerical methods

Transfer entropy

Information theory considers information to be quantified by the amount of surprise or the amount of reduction in uncertainty one variable gives about another variable or itself. Transfer entropy (TE), denoted $T_{X\to Y}$, is the quantitative representation for the measure of information being transferred from a source time series, X, to a destination time series, Y, given what we know about the past of Y [14]. Both X and Y are one-step Markov processes. Since we seek to understand the relationship between the sociality of bats and their use of sound for sensing, the source time series X represents the number of bats at time t, while the destination time series Y represents the two call properties (i.e., number of calls and total acoustic power) at time t. The transfer entropy from X to Y then represents how much information $x(t)$ provides $y(t+1)$ conditioned on $y(t)$, where x and y are realizations of the Markov processes X and Y, respectively, and t is time. Transfer entropy from X to Y is thus defined as

$$T_{X\rightarrow Y} = \sum_{\substack{y(t)\in Y \\ x(t)\in X}} p[y(t+1), y(t), x(t)] \ln \frac{p[y(t+1)|y(t), x(t)]}{p[y(t+1)|y(t)]} \tag{1}$$

with p being a probability measure. A measured transfer entropy of zero would mean there is no information passing from time series X to Y. In general transfer entropy is asymmetric, meaning $T_{X\rightarrow Y} \neq T_{Y\rightarrow X}$.

To calculate transfer entropy, we used the Java Information Dynamics Toolkit (JIDT) [22]. In order to build a probability distribution function (PDF) that can be used in Eq 1, we use the common technique called the Kraskov, Stögbauer, and Grassberger method (KSG) in JIDT. The KSG method is an estimator for finding mutual information of continuous distributions using the technique of nearest neighbours [23]. This method requires defining a fixed number of nearest neighbours for building the distribution, which we take to be $k=6$ after considering values $k = 4, \ldots, 10$ in line with the literature [22]. When using this method to calculate TE, JIDT may produce a small negative non-zero value which we regard as zero in line with the literature [23]. Additionally, Kraskov et al. recommends adding a small amount of noise to the data so that large data sets with potentially non-unique samples do not neglect data points. This causes small differences in the TE each time the PDF is calculated (i.e., the coefficient of variation is usually 2%, but may be up to 15% for conditions with small values of TE).

In order to test whether the transfer entropy found using the given source and destination time series were significant, we partitioned the data in the source time series into one-second intervals and randomly permuted them to get a dummy source. This permuted source, which creates a statistical control condition, retains some relevant temporal structure but which destroys the dynamic relationship between the true source and destination. TE was then calculated with the permuted source and the destination time series, which we expect to give very low values by construction. This process was repeated for one hundred realizations of permuted sources and we calculated the z score of each data point in comparison to the permuted TE distribution. The transfer entropy for a specific case is considered significant if the z score corresponds to a 95% confidence interval. To find an appropriate time step, we compared the transfer entropy and the corresponding significance for time steps between 1/60 seconds and 6/60 seconds. Almost all experimental conditions (discussed in Results section) showed significant TE for all choices of time steps; we selected 1/30 seconds for the following analysis.

Sparse identification of non-linear dynamics

Sparse identification of non-linear dynamics (SINDy) was developed by Brunton, Proctor, and Kutz in 2016 to identify dynamical systems from data in an optimal way [17]. SINDy aims to solve $\dot{\mathbf{X}} = f(\mathbf{X}) = \Theta(\mathbf{X})\Xi$ for the matrix $\Xi \in \mathbb{R}^{f\times m}$, given the input data $\mathbf{X} \in \mathbb{R}^{n\times m}$ and a library of basis functions $\Theta(\mathbf{X}) \in \mathbb{R}^{n\times f}$ such as polynomials and trigonometric functions of $\mathbf{X}$. The columns of Ξ represent the sparse coefficients that solve the row equation $\dot{\mathbf{x}}_k = \Theta(\mathbf{x}^T)\xi_k$ where ξ_k is a column vector of Ξ [17]. To solve these systems with a sparse regression, Brunton et al. use a sequence of least squares approximations. An initial least squares approximation is used to estimate the system, then coefficient values less than a set threshold, $\lambda > 0$, are set to zero. This process of implementing least squares and sparsifying the system is iterated until all non-zero elements of Ξ have absolute values greater than λ. Depending on the desired sparsity of the problem, λ can be tuned to effect the sparsity constraint of the problem.

We used SINDy to develop a model that represents the change in call properties with respect to the number of bats. For our data, we define $\mathbf{X} = \begin{bmatrix} \hat{N} & \hat{C} & \hat{P} \end{bmatrix}$ where $\hat{N} \in \mathbb{R}^{T\times 1}$ is the number of bats, $\hat{C} \in \mathbb{R}^{T\times 1}$ is the total number of calls, and $\hat{P} \in \mathbb{R}^{T\times 1}$ is the total acoustic power for $T = 7200$ time steps (computed from 60 seconds sampled at 1/60 seconds). We used this time step for SINDy as it presented the best goodness of fit. We choose not to normalize the number of calls and acoustic power in this case so that the identified models capture data analogous to what can be captured with a microphone. We set the library of basis functions, Θ, up to order two polynomials of $\mathbf{X}$. Our vector $\dot{\mathbf{X}}$ was calculated by taking the differences between adjacent elements of $\mathbf{X}$. Due to the large differences in value sizes between the number of calls made per bat and the total power, we normalized the columns of Θ and $\dot{\mathbf{X}}$ by subtracting the mean from each value and dividing by the standard deviation.

The normalized data was split into data for testing, training, and validation of SINDy. To choose a suitable λ, we first used the testing data (12.5% of total) to iteratively calculate a Ξ matrix for a set of λ values from zero to one (one being the highest value in Ξ when $\lambda = 0$). We then found which λ minimized the mean Euclidean distance between the known testing data $\dot{\mathbf{X}}$ and the calculated $\Theta(\mathbf{X})\Xi$ for the columns containing the number of calls and the acoustic power (75% of total). If the value found for λ was small, the final Ξ matrix was not sparse, and therefore not preferred for the analysis going forward. To combat the lack of sparsity, we used the largest λ that still maintained an error of within 0.003 of the minimum value. This helped the system keep a low error while still making our Ξ matrix sparse. The training data is then used to calculate Ξ with the appropriate λ value. The goodness of fit for the system is then verified by calculating the R^2 value between the validation data of $\dot{\mathbf{X}}$ and the corresponding $\Theta(\mathbf{X})\Xi$ (12.5% of total).

Results

We seek to understand the effect of physical geometry and local group density on the bats' calling behaviour, which motivates the definition of our experimental conditions. Specifically, the data is sampled in four conditions pertaining to a combination of both the presence of obstacles and the average number of bats in the video data. Examples of the bat flight trajectories in relation to the cameras and obstacles can be seen in Aung's paper [24]. The conditions are as follows, with the mean and standard deviation (SD) of the number of bats in parentheses: no obstacles with few bats (NF) (0.68 ± 0.85), obstacles with few bats (OF) (0.96 ± 0.95), no obstacles with many bats (NM) (3.30 ± 1.75), and obstacles with many bats (OM) (5.03 ± 2.46). Notably, conditions with few bats have a large proportion of time steps with no bats visible by definition (51% of total time steps for NF and 38% for OF), while many-bat conditions NM and OM have fewer than 5% of time steps with no visible bats. While both conditions only include a relatively small number of individuals in the recorded control volume, we know that other social animals that fly in groups interact primarily with a small set of nearest neighbours [25], which suggests that the results of our analysis may be relevant to the behaviour of nominally larger groups.

For each condition, we computed the transfer entropy with the number of bats as the source time series and the number of calls and acoustic power per bat as the destination time series. Fig 3 shows the results. The transfer entropy was considered significant for each of the four conditions for the number of calls made per bat and acoustic power per bat. For verification, the transfer entropy was calculated for the other direction, where the source time series were the properties of the calls while the destination time series was be the number of bats. This calculation gave us $T_{Y\rightarrow X} = 0$, or insignificant values, which we would expect since it indicates that the properties of calls at time t do not help predict the number of bats present at the next time step.

Calls per bat

Considering the number of calls being made per bat, when we examine the conditions with no obstacles, we see an decrease in TE between the condition with few bats (NF) and the condition with many bats (NM). However, with obstacles,

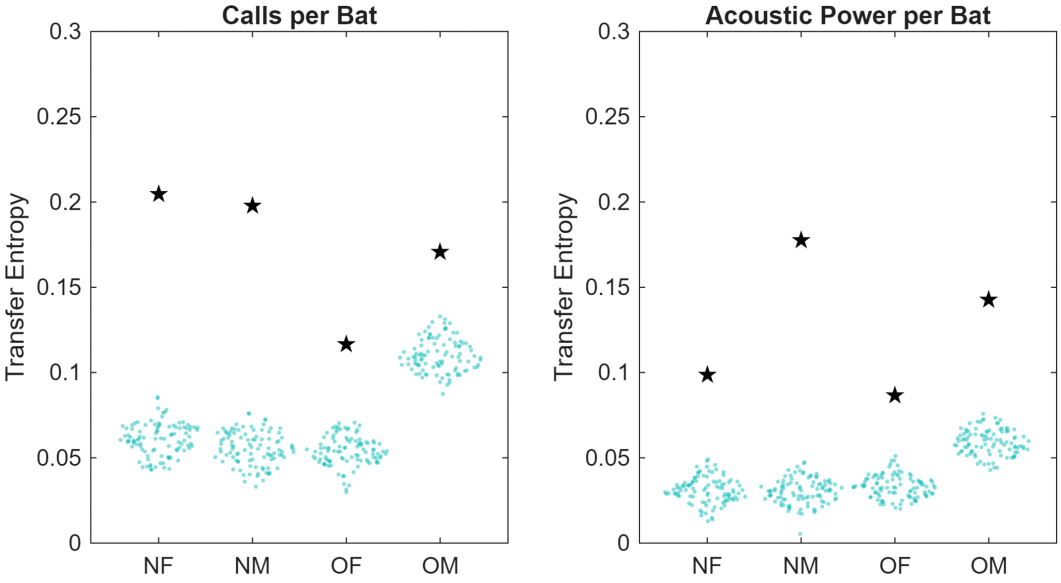

Fig 3. Transfer entropy from the number of bats to the number of calls per bat (left) and the acoustic power per bat (right). Values from experimental data are shown as the black star for each condition (no obstacles, few bats (NF); no obstacles, many bats (NM); obstacles, few bats (OF); and obstacles, many bats (OM)). The violin of teal points show the distribution of the transfer entropy values obtained from the one hundred permutations of the source time series.

https://doi.org/10.1371/journal.pcsy.0000100.g003

we see an increase in TE. The calculated TE for few bats with obstacles (OF) is lower than all the other conditions, which tells us that little information is transferred when there are few bats and obstacles, meaning smaller groups facing obstacles do not carry as much information about their number of calls as the other conditions. The condition for few bats without obstacles (NF) has the highest TE for this property which tells us that when small groups fly without obstacles, it is more likely that we can predict their number of calls at the next time step.

Acoustic power per bat

Considering the acoustic power per bat, for the condition with obstacles, we see a similar pattern to that of the number of calls made. There is a higher amount of information flow for the condition where there are more bats (OM) than condition with few bats (OF). This suggests that an increase in the number of bats influences how much sound is produced when there are obstacles present. This may indicate an increase or decrease in usage of the specific frequency bands, which has been documented in the literature [4]. When obstacles are not present, we also see an increase in the amount of information transfer between the conditions of few and many bats. Similar to the property of the number of calls made, we see that case of few bats with obstacles (OF) has the lowest TE, while the highest TE is now seen when there are no obstacles with many bats (NM). This tells us there is an increase in the information transferred in cases of many bats without obstacles, meaning the larger the group, the more their numerosity predicts the acoustic power they use at the next time step.

Interpretation

The biological interpretation of TE is subtle for this data due to our choice of the time series. Unlike previous studies on biological collective behaviour, which look at the TE between individuals (see for example in [20]), we consider the TE between properties of the same group. Rather than saying individual A drives the behaviour of individual B, we test whether a group's size drives its members' calling behaviour. TE does not, however, tell us how the property changes. An increase in TE tells us there is more information flowing from the property of group size to the call property. In other words, a higher TE helps us better predict the call property of the group given what we know about the size of the group, which motivates the following analysis.

Sparse identification of non-linear dynamics

Since the TE analysis supports that the number of bats and presence of obstacles drives both acoustic variables, we use SINDy to identify a model for their dynamics. When performing SINDy with linear and quadratic polynomials, we consider models of the form

$$\dot{C} = \alpha_1 + \alpha_2 N + \alpha_3 C + \alpha_4 P + \alpha_5 N^2 + \alpha_6 NC + \alpha_7 NP + \alpha_8 C^2 + \alpha_9 CP + \alpha_{10} P^2$$
$$\dot{P} = \beta_1 + \beta_2 N + \beta_3 C + \beta_4 P + \beta_5 N^2 + \beta_6 NC + \beta_7 NP + \beta_8 C^2 + \beta_9 CP + \beta_{10} P^2$$

where N, C, P are scalar variables for the number of bats, the number of calls, and the acoustic power. Here, α_i and β_i, for $i = 1, \ldots, 10$, are the coefficients that show the weight of each of the variables in the identified model. The equations given by SINDy, and their goodness of fit for the data, are summarized by the Table 1. A colour map depicting the values for these coefficients for both $\dot{C}$ and $\dot{P}$ is given in Fig 4.

SINDy uncovers the nature of the dynamic relationship between the number of bats at a given time and properties of their calls. The testing/training/validation process was performed independently for each condition (NF, NM, OF, and OM), resulting in unique λ values, reported with the identified models in Table 1. The models are generally capable of fitting well to the data, as demonstrated by the R^2 values above 0.3 in all of the conditions, see Table 1.

For most of the identified models, linear terms tend to contribute more to the models, as can be seen from the many zero entries in the arrays shown in Fig 4. Notably, for both models, we see strong negative coefficients on linear terms of the state being considered. That is, for $\dot{C}$ and $\dot{P}$, we see negative values multiplying C and P in all conditions, respectively. These negative coefficients indicate a decay in the change of the number of calls when more calls are made, and similarly for power. Considering the number of calls, the strength of this decay term increases when the number of bats increases (-0.55 in NF compared to -0.71 in NM) and when obstacles are introduced (-0.55 in NF compared to -0.74 in OF, -0.71 in NM compared to -0.74 in OM). Considering the power, this pattern is more nuanced. In conditions with more bats, the strength of decay decreases with more bats and no obstacles (-0.86 in NF compared to -0.72 in NM), but increases with

Table 1. SINDy-identified models for the number of calls ($\dot{C}$) and acoustic power ($\dot{P}$) in each experimental condition using the respective λ values. Each equation has a corresponding R^2 value to measure goodness of fit.

Condition	λ	Equation	R^2
NF	0.129	$\dot{C} = -0.55C$	0.4559
		$\dot{P} = 0.35N - 0.86P + 0.24N^2 - 0.32NP + 0.16P^2$	0.5490
NM	0.121	$\dot{C} = .12N - 0.71C$	0.4726
		$\dot{P} = 0.29N - 0.72P$	0.4710
OF	0.139	$\dot{C} = -0.74C + 0.25N^2$	0.4798
		$\dot{P} = 0.25N + 0.26C - 0.71P + 0.18N^2 - 0.14NP - 0.21CP$	0.4312
OM	0.149	$\dot{C} = 0.31N - 0.74C$	0.3942
		$\dot{P} = 0.50N - 0.80P$	0.3732

https://doi.org/10.1371/journal.pcsy.0000100.t001

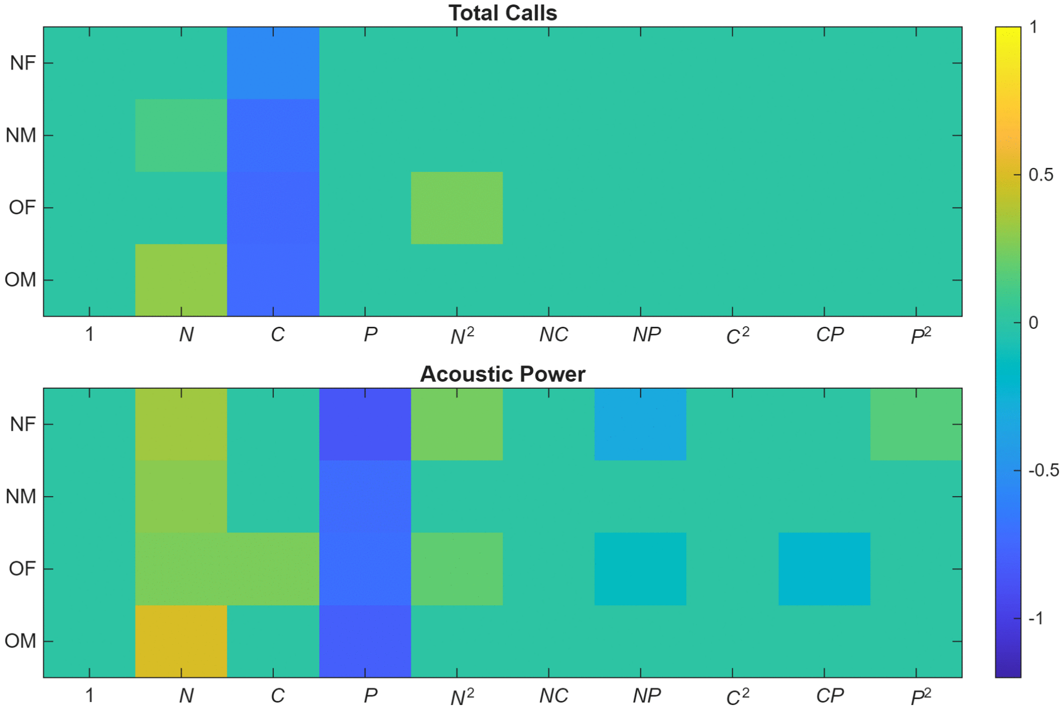

Fig 4. Output of SINDy analysis. Values of coefficients (α_i and β_i for $i = 1, \ldots, 10$) in the SINDy-identified models for number of calls $\dot{C}$ (top) and acoustic power $\dot{P}$ (bottom). For each value, the column corresponds to the basis function it multiplies in the model and the row corresponds to the experimental condition to which it refers (no obstacles, few bats (NF); no obstacles, many bats (NM); obstacles, few bats (OF); and obstacles, many bats (OM)).

https://doi.org/10.1371/journal.pcsy.0000100.g004

more bats when obstacles are present (-0.71 in OF compared to -0.80 in OM). Introducing obstacles at fixed group sizes results in a similar pattern (-0.86 in NF compared to -0.71 in OF, -0.72 in NM compared to -0.80 in OM).

For the number of calls made, SINDy-identified models are primarily linear and only comprise terms of *N* and *C*. For models with a non-trivial *N* term, its coefficient is positive, indicating that changes in the number of calls depends positively on the number of bats, and of smaller magnitude than the coefficients of *C*. For the acoustic power, all models contain terms of *N* and *P*. Each model includes a positive *N* term indicating that the change in acoustic power depends positively on the number of bats. We also note that the magnitude of the terms of *N* follow the same pattern as the terms of *P* as described above, and that they always smaller in magnitude than *P* terms. The presence of both positive and negative linear terms respecting this pattern suggests there is a balance between the number of bats and their acoustic properties that drive the dynamics. As a note, there are two conditions (NF and OF) in which there are non-linear terms that are considered significant for the model. Notably their coefficients are smaller in magnitude than the linear terms in each case.

Discussion

Our analysis demonstrates that the presence of conspecifics and obstacles in the environment of flying bats drive their calling behaviour. The transfer entropy analysis shows that both group size and presence of obstacles help to predict acoustic call properties normalized per bat in all experimental conditions. While transfer entropy is a powerful tool for measuring the flow of information between time series, it does not tell us what the underlying dynamics of the system are. Towards this end, models identified by SINDy for the two acoustic properties suggest that the change in the number of calls is generally described with a linear model, while the change in acoustic power may require a non-linear model with both linear and quadratic terms.

The models capture a complex relationship between the dynamics of the number of bats and the acoustic properties of their calls. Increasing group size has a positive influence on the change of both the number of calls and their power, evidenced by the positive coefficients on linear *N* terms in the SINDy-identified models where they appear. On the other hand, each acoustic property's rate has a negative dependence on its value, so that the change in the number of calls is smaller when a larger number of calls is observed and the change in the acoustic power is smaller when larger power is observed. Interestingly, we see that, as the number of bats increases between the conditions with few and many bats, individuals in larger groups restrict their number of calls more compared to individuals in smaller groups. This pattern of restriction is echoed in the acoustic power when obstacles are present, but reversed in the absence of obstacles.

Nevertheless, the overall rate of change in the call properties is the result of combining these effects. In Fig 5, we plot the resultant functions for the number of calls and their power, combining time instances with the same number of bats. Consistently with the results in [8] (where Mexican free-tailed bats are studied while not flying), we see that the call rate per bat and their acoustic power both decrease as group size increases, suggesting that the animals may employ call restriction or attenuation as a jamming avoidance response.

The identified models also evidence the influence of environmental obstacles on the acoustic properties of bats' calls. Specifically, both groups of few bats and many bats suppress their number of calls more when flying with obstacles compared to without, seen in the increase in magnitude of the coefficient of the decay term when obstacles are introduced. This pattern is consistent with acoustic power for groups of many bats, but is reversed for groups of few bats. In other words, we note that in the presence of obstacles, bats in larger groups adjust their acoustic power more compared to bats in smaller groups. We note that in Jones and Moss's paper, the number of calls made by an individual bat increases as the bat gets closer to a common landing area, but in the presence of visual obstacles, bats will suppress their number of calls more compared to when there are no obstacles present [9]. However, literature does not give us the relationship of number of calls made per bat when there are multiple bats flying together. In addition to these already complex relationships, some models show additional non-linear dependencies for the rate of change in acoustic power. While this is likely to be an interesting area of future work, our current models for these cases, described by Table 1 and Fig 5, show a general decrease in acoustic power per bat similar to the cases with only linear terms.

In conclusion, we have shown that bats modulate their acoustic calling behaviour in response to the number of conspecifics they fly with and the clutter in their environment, as evidenced by data-driven methods. Specifically, we see that the number of calls and acoustic power are often driven by a positive term of the number of bats as well as a decay term of the given state. Other terms, such as the second order polynomials seen in the equations for acoustic power, give the models additional complexities that can be further analysed using the current ground work of the present study. Both acoustic properties follow similar rules in relation to the number of observed bats and the value of the corresponding property. Though these results may seem self-evident, we underscore that our inputs were only time series, meaning that SINDy was able to predict the governing rules of our system mathematically without assuming the form these rules would take. The use of TE allowed us to identify which time series were appropriate model variables, given that one variable causes another to change. Without undercutting the biological significance of our results, we emphasize that the method we have used may extend to many research questions about biological systems where the presence and form of interactions between salient variables is not known.

Acknowledgments

We would like to thank Dr. W. Mark Ford for help identifying a field site and obtaining permits and Amanda Hashimoto for help with data collection.

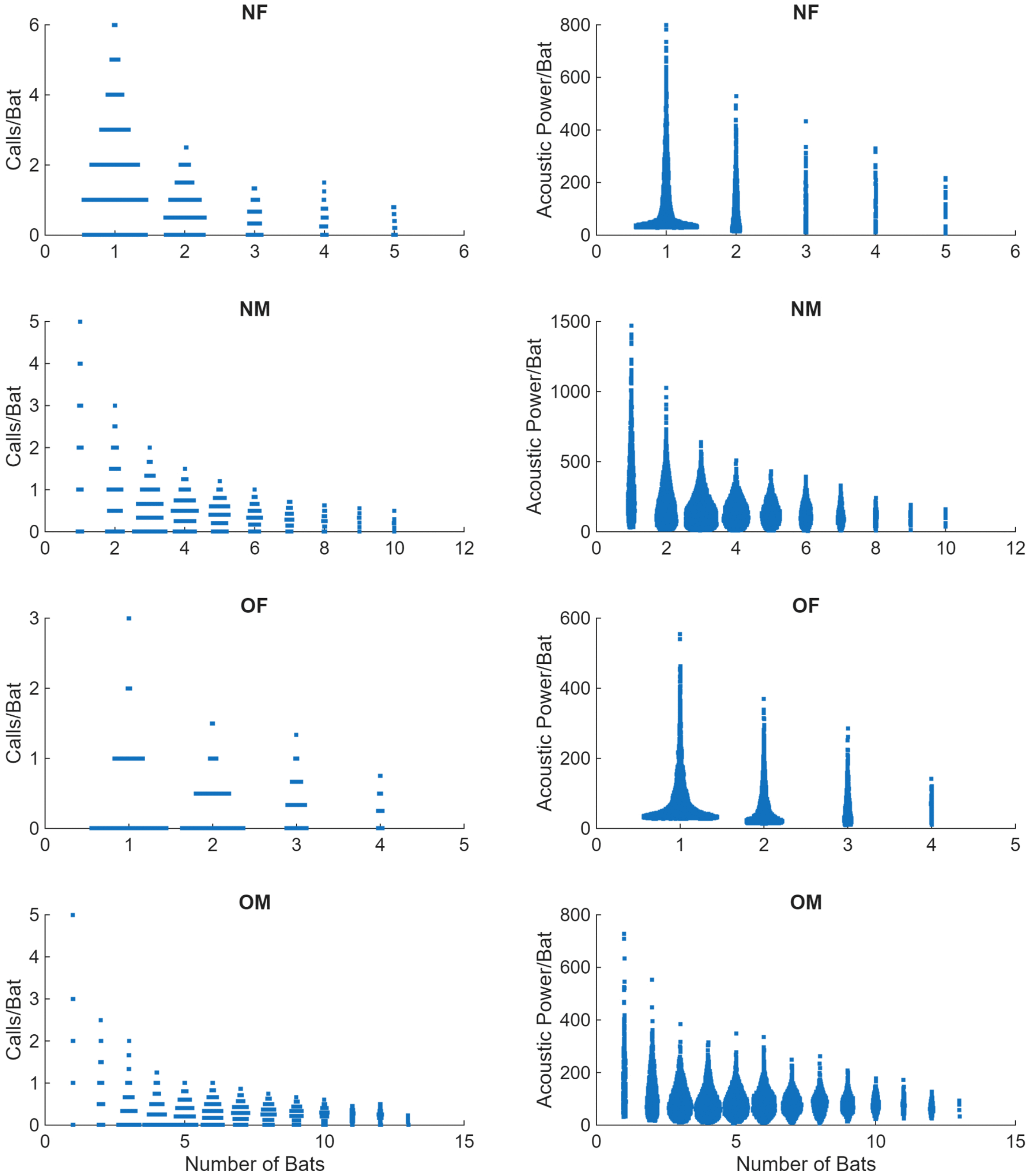

Fig 5. Experimental data of call properties changing with number of bats, with data jittered to show density. Violin plots of the number of calls per bat (left) and acoustic power per bat (right) versus the total number of bats present for each observed condition. The equations used are based on the models found using SINDy, summarized in Table 1.

https://doi.org/10.1371/journal.pcsy.0000100.g005

Author contributions

Conceptualization: Megan Grey, Nicole Abaid.

Data curation: Megan Grey, Eighdi Aung.

Formal analysis: Megan Grey, Nicole Abaid.

Funding acquisition: Nicole Abaid.

Project administration: Nicole Abaid.

Software: Megan Grey, Eighdi Aung.

Supervision: Nicole Abaid.

Visualization: Megan Grey.

Writing – original draft: Megan Grey.

Writing – review & editing: Megan Grey, Eighdi Aung, Nicole Abaid.

References

1. Harvey MJ, Altenbach JS, Best TL. Bats of the United States and Canada. JHU Press. 2011.
2. Jones G. Echolocation. Current Biology. 2005;15(13):R484-8.
3. Corcoran AJ. Automated acoustic identification of nine bat species of the astern United States. Humboldt State University. 2007.
4. Ulanovsky N, Fenton MB, Tsoar A, Korine C. Dynamics of jamming avoidance in echolocating bats. Proc Biol Sci. 2004;271(1547):1467–75. https://doi.org/10.1098/rspb.2004.2750 PMID: 15306318
5. Adams AM, Patricio A, Manohar R, Smotherman M. Influence of signal direction on sonar interference. Animal Behaviour. 2019;155:249–56. https://doi.org/10.1016/j.anbehav.2019.05.024
6. Corcoran AJ, Conner WE. Bats jamming bats: food competition through sonar interference. Science. 2014;346(6210):745–7.
7. Chiu C, Xian W, Moss CF. Flying in silence: Echolocating bats cease vocalizing to avoid sonar jamming. Proc Natl Acad Sci U S A. 2008;105(35):13116–21. https://doi.org/10.1073/pnas.0804408105 PMID: 18725624
8. Jarvis J, Jackson W, Smotherman M. Groups of bats improve sonar efficiency through mutual suppression of pulse emissions. Frontiers in Physiology. 2013;4:140.
9. Jones TK, Moss CF. Visual cues enhance obstacle avoidance in echolocating bats. J Exp Biol. 2021;224(9):jeb241968. https://doi.org/10.1242/jeb.241968 PMID: 33942102
10. Brigham RM, Grindal SD, Firman MC, Morissette JL. The influence of structural clutter on activity patterns of insectivorous bats. Can J Zool. 1997;75(1):131–6. https://doi.org/10.1139/z97-017
11. Orbach DN, Fenton B. Vision impairs the abilities of bats to avoid colliding with stationary obstacles. PLoS One. 2010;5(11):e13912. https://doi.org/10.1371/journal.pone.0013912 PMID: 21085481
12. Hansen MJ, Burns AL, Monk CT, Schutz C, Lizier JT, Ramnarine I, et al. The effect of predation risk on group behaviour and information flow during repeated collective decisions. Animal Behaviour. 2021;173:215–39. https://doi.org/10.1016/j.anbehav.2021.01.005
13. Porfiri M. Inferring causal relationships in zebrafish-robot interactions through transfer entropy: a small lure to catch a big fish. AB&C. 2018;5(4). https://doi.org/10.26451/abc.05.04.03.2018
14. Bossomaier T, Barnett L, Harré M, Lizier JT. An introduction to transfer entropy information flow in complex systems. Springer. 2016.
15. Shaffer I, Abaid N. Transfer Entropy Analysis of Interactions between Bats Using Position and Echolocation Data. Entropy. 2020;22(10):1176. https://doi.org/10.3390/e22101176
16. Bolker BM. Linear and generalized linear mixed models. Ecological Statistics. Oxford University PressOxford. 2015. p. 309–33. https://doi.org/10.1093/acprof:oso/9780199672547.003.0014
17. Brunton SL, Proctor JL, Kutz JN. Discovering governing equations from data by sparse identification of nonlinear dynamical systems. Proc Natl Acad Sci U S A. 2016;113(15):3932–7. https://doi.org/10.1073/pnas.1517384113 PMID: 27035946
18. Khaldi B, Keyvan EE, Şahin M, Turgut AE, Şahin E. Towards data-driven discovery of governing swarm robots flocking rules. In 2023 European Conference on Mobile Robots (ECMR) 2023 Sep 4 (pp. 1-6). IEEE.
19. Feller KD, Lagerholm S, Clubwala R, Silver MT, Haughey D, Ryan JM, et al. Characterization of photoreceptor cell types in the little brown bat Myotis lucifugus (Vespertilionidae). Comp Biochem Physiol B Biochem Mol Biol. 2009;154(4):412–8. https://doi.org/10.1016/j.cbpb.2009.08.006 PMID: 19720154
20. Orange N, Abaid N. A transfer entropy analysis of leader-follower interactions in flying bats. Eur Phys J Spec Top. 2015;224(17–18):3279–93. https://doi.org/10.1140/epjst/e2015-50235-9
21. Stilz W-P, Schnitzler H-U. Estimation of the acoustic range of bat echolocation for extended targets. J Acoust Soc Am. 2012;132(3):1765–75. https://doi.org/10.1121/1.4733537 PMID: 22978903

22. Lizier JT. JIDT: An Information-Theoretic Toolkit for Studying the Dynamics of Complex Systems. Front Robot AI. 2014;1. https://doi.org/10.3389/frobt.2014.00011

23. Kraskov A, Stögbauer H, Grassberger P. Estimating mutual information. Phys Rev E Stat Nonlin Soft Matter Phys. 2004;69(6 Pt 2):066138. https://doi.org/10.1103/PhysRevE.69.066138 PMID: 15244698

24. Aung E, Abaid N. Gray bats spatially segregate when navigating flight with conspecifics in complex environments. bioRxiv. 2025. https://doi.org/10.64898/2025.12.26.696615

25. Ballerini M, Cabibbo N, Candelier R, Cavagna A, Cisbani E, Giardina I, et al. Interaction ruling animal collective behavior depends on topological rather than metric distance: evidence from a field study. Proc Natl Acad Sci U S A. 2008;105(4):1232–7. https://doi.org/10.1073/pnas.0711437105 PMID: 18227508