



Modeling perspectives on echolocation strategies inspired by bats flying in groups



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HIGHLIGHTS

- We model bats avoiding obstacles by emitting and receiving echolocation pulses.
- We let bats eavesdrop on peers' sensing signals and change pulse emission rate.
- Eavesdropping is beneficial for collision avoidance when measurement noise is low.
- Decreasing emission rate limits sonic interference, but collisions increase.
- Increasing emission rate aids collision avoidance but requires more energy per bat.

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ABSTRACT

Bats navigating with echolocation – which is a type of active sensing achieved by interpreting echoes resulting from self-generated ultrasonic pulses – exhibit unique behaviors during group flight. While bats may benefit from eavesdropping on their peers' echolocation, they also potentially suffer from confusion between their own and peers' pulses, caused by an effect called frequency jamming. This hardship of group flight is supported by experimental observations of bats simplifying their sound-scape by shifting their pulse frequencies or suppressing echolocation altogether. Here, we investigate eavesdropping and varying pulse emission rate from a modeling perspective to understand these behaviors' potential benefits and detriments. We define an agent-based model of echolocating bats avoiding collisions in a three-dimensional tunnel. Through simulation, we show that bats with reasonably accurate eavesdropping can reduce collisions compared to those neglecting information from peers. In large populations, bats minimize frequency jamming by decreasing pulse emission rate, while collision risk increases; conversely, increasing pulse emission rate minimizes collisions by allowing more sensing information generated per bat. These strategies offer benefits for both biological and engineered systems, since frequency jamming is a concern in systems using active sensing.

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1. Introduction

Species of bats in the suborder *Microchiroptera* are unique mammals that primarily navigate in their environment using echolocation (Au and Simmons, 2007). They emit directional ultrasounds in pulses (Surlykke et al., 2009), receive reflected echoes to their auditory system through their deformable pinnae (Gao et al., 2011), and constantly interpret the echoes using a powerful neurological signal processing system (Simmons et al., 1979; Horowitz et al., 2004). By analyzing echo harmonic structures, bats are able to differentiate targets from multiple sound

reflections (Bates et al., 2011). From a behavioral perspective, many species of bats are highly social. They live in colonies that range from tens to millions of individuals (Zahn, 1999; Betke et al., 2008). They may exhibit collective behavior (Couzin, 2007) on fast time scales, such as their motion in group flight in the wild (Betke et al., 2008), and slower time scales, such as their roost selection dynamics (Kashima et al., 2013). Within their colonies, bats are able to fly in high densities (Gillam et al., 2010; Betke et al., 2007) at fast speeds (Theriault et al., 2010), while avoiding collisions with peers and obstacles in the environment.

Bat group flight is a unique phenomenon that involves both complex sensing and behavioral strategies. A major source of the complexity is a bat's use of echolocation as an active sensing mechanism (Kreucher et al., 2005; Musiani et al., 2007) which allows

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interference from peers' sounds. The interference from active sensing can be both constructive and destructive, which is evidenced by bats' so-called eavesdropping and frequency jamming avoidance behaviors, respectively. Eavesdropping behavior is defined as bats listening and reacting to peers' pulses and echoes (Barclay, 1982; Chiu et al., 2008) in situations wherein they do or do not emit pulses. Frequency jamming happens when bats emit pulses of frequencies that overlap the frequency bandwidth of peers' pulses, which may be inevitable for bats flying in large groups in natural settings (Gillam et al., 2010; Betke et al., 2007; Theriault et al., 2010). It has been demonstrated that bats are able to shift the frequencies of their ultrasounds in situations tailored to produce jamming (Gillam et al., 2007; Hiryu et al., 2010; Bates et al., 2008), thus avoiding potentially destructive interference, and recent work has shown incidences of offensive jamming between wild bats during hunting which may necessitate such accommodations (Corcoran and Conner, 2014). Bats are also observed to cease vocalization in the presence of peers in laboratory settings (Chiu et al., 2008; Jarvis et al., 2013), which may allow them to simultaneously eavesdrop on peers' information and avoid jamming. There are currently few studies, however, documenting bats' behavior during flight in the wild and in dense groups.

Mathematically, animal behavior can be modeled as a multi-agent system, where each agent in the group is subject to behavioral rules (Vicsek et al., 1995). Collective behavior at the group level, such as fish schooling (Abaid and Porfiri, 2010; Lopez et al., 2012), bird flocking (Ballerini et al., 2008) and ant lane formation (Couzin and Franks, 2003), may be simulated using these so-called agent-based models when agents are equipped with specific sensing and response schemes (Sumpter, 2006). Rules prescribed to individuals for collective behavior may include repulsion from peers, alignment of velocity directions, and attraction to peers' positions (Aoki, 1982; Couzin et al., 2002). These rules are realized in models by building either discrete decision-making (Vicsek et al., 1995; Aoki, 1982; Couzin et al., 2002) or potential functions (Strefler et al., 2008). Agent-based modeling is also applied to study multi-agent systems in other disciplines, such as population dynamics (Wang et al., 2012; Droz and Pekalski, 2001), predation-prey interactions (Olson et al., 2013; Angelani, 2012; Lin and Abaid, 2013), cell chain migration (Wynn et al., 2012), and disease or parasite transmission (Jiang et al., 2012; Tully et al., 2013).

In this work, we establish an agent-based model to study echolocation strategies which include eavesdropping and changing pulse emission rate inspired by bats emerging from a cave. In the model, bats are designed to fly through a three-dimensional tunnel of rectangular cross-section while avoiding collisions with peers and boundaries, referred to as obstacles. They emit pulses of unique frequencies, and use echoes generated by their own pulses and eavesdropped echoes and pulses from peers to locate obstacles. We note that, although bats echolocate in nature using diverse calls that may be constant frequency or frequency modulated, the acoustic signature of calls are not considered in this model since time is discretized into steps which each can contain a single call. Bats in the model obtain exact obstacle locations with their own pulses, while they estimate obstacle locations using echoes and pulses from their peers perturbed by random noise with a fixed probability distribution; we call this penalty on eavesdropping "measurement noise". In a simulation study, we find that eavesdropping is beneficial in collision avoidance when measurement noise is low. In this case, bat pulse emission rate is balanced between emitting pulses to reliably avoid collisions and varying pulse emission rate to avoid frequency jamming and conserve energy for echolocation, which is quantified using defined cost functions relevant to both biological and engineered systems. This model may help better understand bats' group behavior and inspire control algorithms for robotic teams that use active sensing (Li et al., 2010; Zhuo and Xiao-ning, 2011).

2. Modeling

2.1. Model description

In the following, we describe the model for the acoustic field generation and for bat behavior.

2.1.1. Sensing setup

We consider an agent-based model with the agents, "bats", flying through a three-dimensional tunnel using echolocation and tasked with collision avoidance. The N bats are modeled as self-propelled particles moving with a constant velocity magnitude s in discrete time. The three-dimensional tunnel is a cuboid with side lengths L_x , L_y and L_z , which are the width, length and height of the tunnel, respectively. To model echolocation, we consider that each bat emits a pulse of a unique frequency according to an independent, identically distributed Bernoulli random variable with a constant pulse emission probability p at each time step. The pulse is considered to cover a three-dimensional sensing space, a spherical cone, inspired by a simplified bat sonar beam pattern (Surlykke et al., 2009; Bates et al., 2011; Jakobsen and Surlykke, 2010). The apex of the spherical cone is the bat's position; its side length equals the bat's sensing range r_s ; and its opening angle is the bat's angular range of sensing ϕ . The bat's velocity vector originates at the spherical cone's apex and aligns with its central axis. We define a repulsion zone as a sphere of radius r_r centered at the bat's position. Peers and boundaries with positions in this zone are considered to be obstacles and are perceived by the bat as too close, so the bat performs a collision avoidance maneuver. A schematic of the sensing space and the repulsion zone for bat i , $i = 1, 2, \dots, N$, is shown in Fig. 1.

2.1.2. Echo generation

When a bat emits a pulse at a given time step, echoes are reflected from peers and boundaries that occupy the bat's sensing space simultaneously. These echoes are considered as the bat's "self-echoes" as they result from the bat's pulse. Echoes generated by pulses from peers in the group are called "peers' echoes". Echoes exist for a single time step and they occupy hemispheres of a constant radius r_e , because bats and boundaries are assumed to have surfaces that reflect sound homogeneously. The emitted pulses and reflected echoes are both considered to be incident at the same time step, since we select a discrete time step large enough for sound to propagate through the full echo hemisphere.

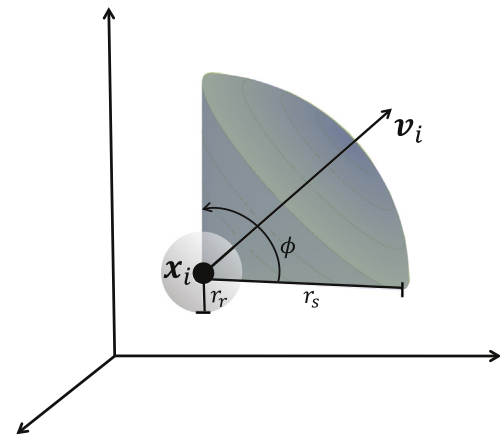


Fig. 1. Schematic of three-dimensional sensing space and repulsion zone for bat i . The bat has position \mathbf{x}_i and velocity \mathbf{v}_i . The spherical cone shows the bat's sensing space with sensing range r_s and angular range of sensing ϕ . The gray sphere shows the bat's repulsion zone with radius r_r .

We define cases for echoes reflected from peers and boundaries separately. In the first case, a bat's sensing space is considered to be occupied by a peer if the distance between the bat and the peer is less than r_s and the angle between the vector from the bat to the peer and the bat's velocity is less than $\phi/2$. In this case, if the bat emits a pulse, a hemispherical echo is simultaneously reflected from the peer with its base centering at the peer's position and its central axis connecting the bat and the peer; the dome of the echo is directed toward the bat emitting the pulse. In the second case, a bat's sensing space is occupied by a boundary, so we can find the cross-section of the sensing cone that passes through the cone's central axis and is orthogonal to the two-dimensional boundary. The intersection of this cross-section with the boundary is a line segment. We consider that a hemispherical echo originates from the point on the line segment which is nearest to the bat's position. The base of the hemispherical echo is on the boundary and the dome is inside the tunnel. If the bat's sensing space is occupied by multiple boundaries, echoes are reflected from each intersecting boundary independently.

2.1.3. Echo interpretation

While a bat's sonar emission is directional according to the geometry of the sensing space described above, its sonar reception is omnidirectional, that is, bats can receive sounds from any angular position. A bat is designed to use all sound information (echoes and pulses) it "hears" to locate obstacles, where hearing is defined in the following. A bat is considered to hear an echo if it occupies the hemispherical echo volume, which means the distance between the echo base center and the bat's position is less than r_e and the angle between the vector from the echo center to the bat and the echo's central axis is less than $\pi/2$ radians. A bat is considered to hear a pulse from a peer if the bat occupies the peer's sensing space. The obstacle locations in the model are taken as the centers of the echo bases when the bat hears echoes or the positions of peers whose sensing space is occupied by the bat when the bat hears peers' pulses.

We enable bats to distinguish between self-information, which are self-echoes, and peers' information, which are peers' echoes and pulses, since bats are considered to emit pulses of unique frequencies. Bats are able to obtain exact obstacle locations by hearing self-echoes reflecting from them, while they obtain perturbed obstacle locations by hearing peers' echoes or pulses. This perturbation is designed as penalty motivated by the fact that bats lack timing information for peers' information in nature. The perturbed location is on the line segment of length r_e that connects the bat and the obstacle's exact location. The distance between the bat and the perturbed location is a random number that has a Gaussian distribution with the exact distance from the bat to the obstacle as the mean and a perturbation parameter η_d as the standard deviation. Since the distance between the bat and the perturbed location is restricted in the interval $[0, r_e]$, we only use realizations of the Gaussian distribution which give random values that belong to the stated interval; otherwise, the random variable value is regenerated.

This model of echo generation and interpretation simplifies the acoustic interactions that occur between bats and their environment. For example, we do not consider echo scattering as a result of an obstacle's surface roughness, which may confound locating the echo source. These simplifications can be eliminated by increasing the detail of the model environment and the resulting acoustic field, which would greatly increase the model's computational complexity. Since we seek to identify macroscopic group behaviors, we neglect these details and instead add a random noise to the bat behavior model as described in the following.

2.2. Position and velocity updates

The update for the position of bat i , \mathbf{x}_i , is defined at time $t + \Delta t$ as

$$\mathbf{x}_i(t + \Delta t) = \mathbf{x}_i(t) + \mathbf{v}_i(t + \Delta t) \Delta t, \quad (1)$$

where $t \in \mathbb{R}^+$, $\Delta t \in \mathbb{R}^+$ is the constant time step, and $\mathbf{x}_i, \mathbf{v}_i \in \mathbb{R}^3$ are the bat's position and velocity vectors, respectively. The velocity in this equation is updated with the goal of the bats avoiding collisions with peers or the domain boundaries.

Specifically, we update bat i 's velocity based on the bat's previous velocity direction, the preferred tunnel direction and a repulsion force from obstacles. The previous velocity direction is the base direction from which the bat turns and ensures the smoothness of the bat's flight trajectory; the preferred tunnel direction describes an external motivation for the bat's flight; and the repulsion force enables the bat to reduce collision risk with peers or boundaries. In particular, the velocity update for bat i at time $t + \Delta t$ is

$$\mathbf{v}_i(t + \Delta t) = s \frac{\mathcal{R}^\eta[\alpha \mathbf{v}_i(t)/s + \beta \mathbf{y} + \gamma \mathbf{r}_i(t)/\|\mathbf{r}_i(t)\|]}{\|\mathcal{R}^\eta[\alpha \mathbf{v}_i(t)/s + \beta \mathbf{y} + \gamma \mathbf{r}_i(t)/\|\mathbf{r}_i(t)\|]\|} \quad (2)$$

where $\mathbf{y} = [0, 1, 0]$ is the constant unit vector representing the preferred tunnel direction, α, β , and γ are weighting coefficients describing the velocity update's dependence on the three summands, and $\mathcal{R}^\eta[\bullet]$ denotes an operator which perturbs a three-dimensional vector in a random direction uniformly distributed in the plane normal to it with a Gaussian-distributed random angle. The Gaussian distribution of this perturbation has mean zero and standard deviation $\eta\pi$ with its value restricted in the interval $[0, \eta\pi]$. Here, η is a parameter that describes how well a bat adheres to the model's desired direction $\alpha \mathbf{v}_i(t)/s + \beta \mathbf{y} + \gamma \mathbf{r}_i(t)/\|\mathbf{r}_i(t)\|$ in the next time step, and can be interpreted as a noise on both the bat's sensing and decision making. The values of η range from 0 to 1, where 0 means that bat i updates velocity in the desired direction and 1 indicates that bat i 's velocity update can be in any direction in the unit sphere.

The repulsion force $\mathbf{r}_i(t)$ is given by

$$\mathbf{r}_i(t) = \mathbf{x}_i(t) - \frac{1}{|\mathcal{N}_i(t)|} \sum_{j=1}^{|\mathcal{N}_i(t)|} \mathbf{y}_j(t) \quad (3)$$

where $\mathcal{N}_i(t)$ is the set of indices of obstacle locations in bat i 's repulsion zone at time step t , denoted as $\mathbf{y}_j(t) \in \mathbb{R}^3$, and $|\bullet|$ is set cardinality. Obstacles locations are accurate if obtained by bat i using self-echoes or perturbed if estimated by bat i using peers' echoes and pulses. Thus, the repulsion force direction is determined by the average relative position of obstacle locations in $\mathcal{N}_i(t)$. Note that a bat may use both exact and perturbed locations of the same obstacle for velocity update, which occurs when the bat obtains both self- and peers' information about an obstacle. When $\mathcal{N}_i(t) = \emptyset$, the term $\mathbf{r}_i(t)/\|\mathbf{r}_i(t)\| = [0, 0, 0]$; this means that the repulsion force is zero when there are no exact or perturbed obstacle locations in bat i 's repulsion zone. A flow chart that illustrates eavesdropping bats' behavior is shown in Fig. 2. We comment that, in order to evaluate the benefit of eavesdropping behavior, we define the case of no eavesdropping when bats do not use peers' echoes or pulses and fly independently. In this case, $\mathcal{N}_i(t)$ is the set of indices of exact obstacle locations obtained by bat i using self-pulses.

Bats' initial positions and velocity directions are generated with uniform probability in the tunnel and in \mathbb{R}^3 , respectively. We consider periodic boundary conditions for the tunnel faces which are orthogonal to the L_y direction. The boundary conditions orthogonal to the L_x and L_z directions are considered as reflective which means, if the position update defines a position outside a face orthogonal to L_x or L_z direction, this position is replaced by another one symmetric about

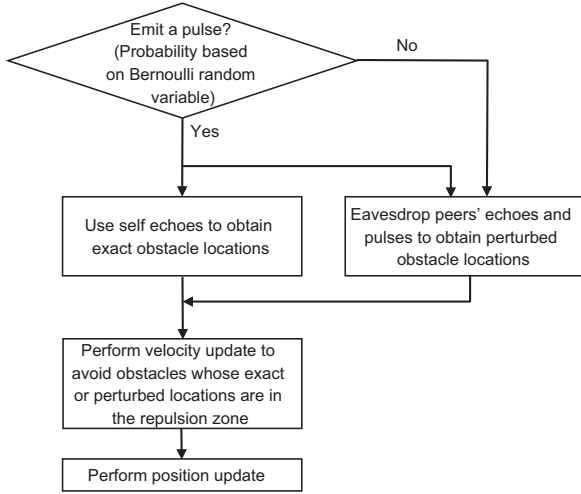


Fig. 2. Flow chart that summarizes the decision making and behavior of a bat at each time step.

the face at the same time step. In this manner, the bats' positions are ensured to be inside the finite domain.

3. Observables

We define three observables to measure the behavior of the bat group: the average collision rate c , the collision/jamming cost s_1 , and the collision/energy cost s_2 . The average collision rate measures the collision avoidance failure of the bat group. The two cost functions are defined to consider natural and engineering settings, respectively. The collision/jamming cost combines average collision rate and potential for frequency jamming, as the frequency band-widths of bats' pulses overlap in natural bat swarm. The collision/energy cost combines average collision rate and energy use per bat, as engineered agents are able to use unique frequencies in their signals but have limited power sources for sensing. Energy is only considered to be used for sensing in this model.

The average collision rate is calculated as the sum of number of bats colliding with peers or boundaries over time divided by the number of bats N and by the total number of time steps T . A bat is defined to collide with a peer if the distance between them is less than the peer collision range r_c and with boundaries when the reflective boundary conditions for the L_x and L_z directions are used. Thus,

$$c = \frac{\sum_{t=1}^T n_c(t)}{NT}, \quad (4)$$

where $n_c(t)$ is the number of bats colliding with peers or boundaries at time t .

The collision/jamming cost s_1 is defined as the weighted sum of the average collision rate c and the average number of pulses over the group Np . The average number of pulses represents the extent of frequency jamming, because a more cluttered acoustic field makes it more difficult for a bat to emit a pulse of a unique frequency in nature. In particular,

$$s_1 = c + \zeta_1 Np, \quad (5)$$

where ζ_1 is the weighting coefficient for frequency jamming.

The collision/energy cost s_2 is computed as the weighted sum of the average collision rate c and the pulse emission rate p , as the pulse emission rate conveys the average energy use per bat. In other words,

$$s_2 = c + \zeta_2 p, \quad (6)$$

where ζ_2 is the weighting coefficient for energy use per bat. Note that small and large values of s_1 or s_2 indicate relatively low and high costs, respectively. We comment that any energy bats use for echolocation may be negligible compared to the high energetic cost of flight (Speakman and Racey, 1991; Salehipour and Willis, 2013). However, the energy used by active sensors in engineered systems is certainly non-trivial, which motivates this observable.

4. Simulation results

We determine the parameter values for the model by taking inspiration from bats emerging from caves in natural settings. We set the nominal width, length, and height of the tunnel to be $L_x = 5$ m, $L_y = 15$ m and $L_z = 5$ m, respectively. We consider the physical parameters of big brown bats, *Eptesicus fuscus*, in the model as they are common in North America and have been widely studied in the biological literature (Agosta, 2002). Big brown bats emit echolocation calls on the order of 10 times per second (Au and Simmons, 2007), which defines the time step $\Delta t = 0.1$ s. In the model, bats are considered to emit pulses and use all received information to perform navigational decisions at one time step. Big brown bats detect small targets that are within 5 m range (Bates et al., 2011; Kick, 1982); thus, we set both the sensing range r_s and echo radius r_e to be 5 m. Bats' angular range of sensing is taken to be $2\pi/3$ radians according to the sonar beam pattern of big brown bats (Surlykke et al., 2009; Bates et al., 2011). Bats' velocity magnitude is set to be 5 m/s, which is considered as the nominal flying speed of big brown bats (Au and Simmons, 2007). The collision range among bats is chosen as the approximate average wingspan of big brown bats, which is $r_c = 0.3$ m (Hamilton and Barclay, 1998). We set the repulsion zone radius to be twice the collision range as $r_r = 2r_c = 0.6$ m, which is considered to be a safe distance for bats to avoid collisions with both peers and boundaries.

The perturbation parameter for bat swarming is defined as $\eta = 0.1$, which adds a small error to a bat's desired swarming direction. The weighting coefficients in the velocity update for previous velocity direction, preferred tunnel direction, and repulsion force direction are taken to be $\alpha = 1$, $\beta = 0.1$, and $\gamma = 1$, respectively, based on inspection of preliminary simulations. The selected dependence of velocity update on the previous velocity direction results in relatively smooth flight trajectories, which matches well with natural bat flight patterns (Tian et al., 2006; Rayner and Aldridge, 1985); the relatively small weighting coefficient for the preferred tunnel direction reduces the straightness of bats' flights in the tunnel direction, while enforcing flight through the tunnel on average; and the selected dependence on the repulsion force direction results in good collision avoidance performance as bats avoid obstacles without blocking peers' flight paths.

In the simulation, bats move subject to the rules defined in the Modeling section with the numbers of bats N taken as 2, 10, 20, 50, and 100; the pulse emission probability p as 0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, and 1; and the perturbation parameter for estimating obstacle locations η_d as 0, 0.1, 1, 2, 10, and $+\infty$. We comment that, when $\eta_d = 0$, bats obtain the exact obstacle locations using peers' information; when $\eta_d = +\infty$, the estimated obstacle locations are uniformly distributed along the line segment of length r_e that connects the bat and the obstacle's exact location. Fig. 3 shows an example frame of 100 bats swarming in the simulation with $p=0.5$ and $\eta_d=0$. In calculating the two flight costs, we set the weighting coefficient for frequency jamming as $\zeta_1 = 8 \times 10^{-4}$ and the weighting coefficient for energy use per bat as $\zeta_2 = 4 \times 10^{-2}$, such that the two summands are approximately equal in magnitude within each cost function. Table 1 gives a summary of all the parameter values used in the simulation study.

For the numerical study, we determine the simulation length for each combination of N , p and η_d values by considering a constant initial transient phase of 999 time steps and 10 simulation

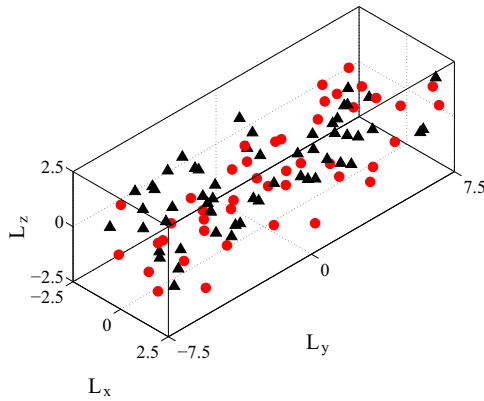


Fig. 3. Example frame of $N=100$ bats flying through the tunnel with $p=0.5$ and $\eta_d=0$. Red circles and black triangles show positions of bats emitting pulses and ceasing emission, respectively. The units for the axes are meters. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

Table 1
Parameter values used in the simulation study.

Parameter	Symbol	Value	Unit
Width of the tunnel	L_x	5	m
Length of the tunnel	L_y	15	m
Height of the tunnel	L_z	5	m
Time step	Δt	0.1	s
Number of bats	N	2–100	–
Bats' velocity magnitude	s	5	m/s
Bats' sensing range	r_s	0.5	m/ Δt
Bats' angular range of sensing	ϕ	$2\pi/3$	rad
Echo radius	r_e	5	m
Perturbation parameter for estimating obstacle locations	η_d	0 to $+\infty$	–
Perturbation parameter for bat swarming	η	0.1	–
Pulse emission probability	p	0–1	–
Weighting coefficient for previous velocity direction	α	1	–
Weighting coefficient for preferred tunnel direction	β	0.1	–
Weighting coefficient for repulsion force direction	γ	1	–
Bats' repulsion zone radius	r_r	0.6	m
Bats' collision range	r_c	0.3	m
Weighting coefficient for frequency jamming	ζ_1	8×10^{-4}	–
Weighting coefficient for energy use per bat	ζ_2	4×10^{-2}	–

replicates whose length is determined by N . The initial transient phase is confirmed to be sufficiently long to exclude the influence of initial conditions by inspecting the time series of the average collision rate for all cases. For each case of N , p and η_d , we compute the average collision rate for each replicate and obtain the mean and standard deviation for the average collision rate over the 10 replicates. We ensure the stationarity of the results by checking that the standard deviation divided by the mean is less than 12%. Table 2 shows the length of one simulation replicate for each N . For larger N , the replicate length reduces because collisions occur with higher probability and the average collision rate approaches steady state faster.

As we vary the three free parameters in the model, we only present a subset of the results that enable understanding the behavior of bats flying in groups. Fig. 4 shows the average collision rate c versus the number of bats N with varying η_d values for a fixed $p=0.5$; simulations with different p values show similar trends and are thus not shown. In Fig. 4, we see that the average collision rate increases as the number of bats increases for all η_d values. For $\eta_d=0$ and $\eta_d=0.1$, the average collision rates are practically equal and both smaller than that for no eavesdropping

Table 2
Simulation replicate length.

N	Replicate length (time steps)
2	2,250,000
5	1,000,000
10	500,000
20	100,000
50	20,000
100	5,000

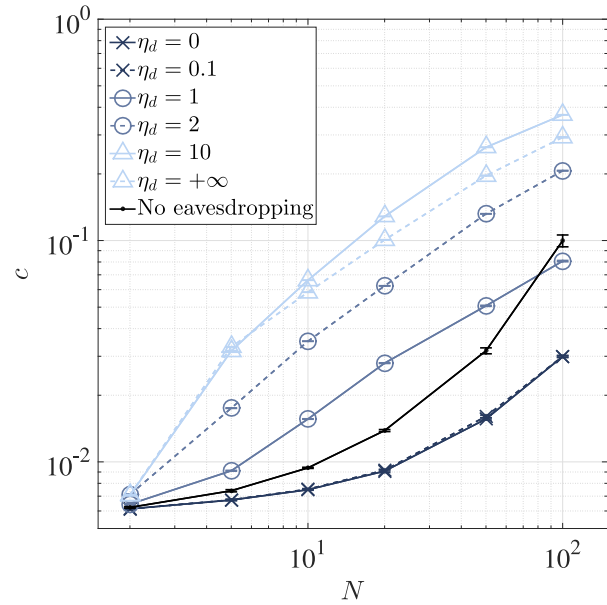


Fig. 4. Average collision rate c versus the number of bats N with varying η_d values for $p=0.5$ and with the case of no eavesdropping. Error bars showing one standard deviation over the 10 replicates are plotted at every point, but are occluded by point markers due to their very small magnitude in almost all cases.

and, for $\eta_d \geq 1$, the average collision rates have larger values than that for no eavesdropping.

We investigate the benefit of eavesdropping through comparison with the situation when bats do not use peers' information and fly independently. We use the case of $\eta_d=0$ to represent the cases with $\eta_d \leq 0.1$, wherein the average collision rates are smaller than that for no eavesdropping as shown in Fig. 4. Fig. 5(a) is a contour plot of the average collision rate for $\eta_d=0$ with varying N and p . From this figure, we see that the average collision rate increases as p decreases and N increases. Fig. 5(b) is a contour plot of the ratio between the average collision rate with $\eta_d=0$ and that for no eavesdropping; it shows that this ratio is smaller for larger bat populations and higher p values.

The collision/jamming and collision/energy costs for $\eta_d=0$ with varying N and p are shown in the contour plots in Fig. 6 (a) and (b), respectively. From Fig. 6(a), for a bat population of fixed size, the collision/jamming cost shows a non-monotonic trend as p decreases. The "optimal" pulse emission rate associated with the minimum cost for each N is connected through a red curve on the contour plot, showing a decreasing trend as N increases in general. We also consider the scenario that bats may seek to keep the same cost as group size increases, so we find p values that correspond to a constant s_1 . For example, such p values for a constant cost of $\log_{10}(s_1) = -2$ are connected through the red dotted curve for smaller N in Fig. 6(a) and show an increasing trend. For larger populations, bats are not able to continue to achieve this constant cost. A similar trend occurs for other different constant s_1 values. From Fig. 6(b), we see that the collision/

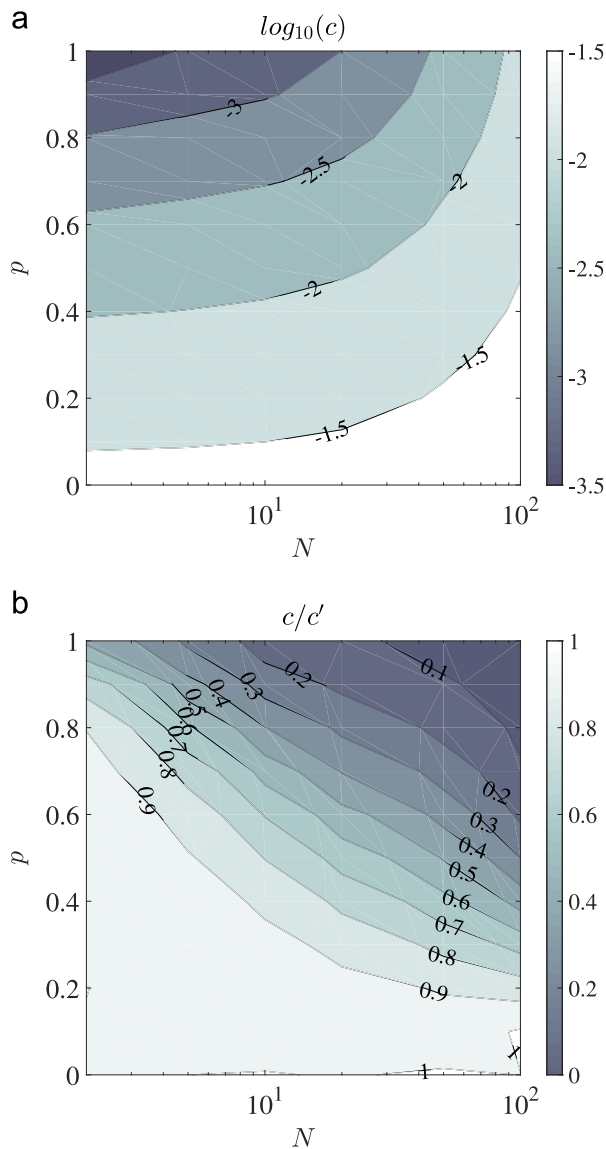


Fig. 5. (a) The average collision rate c with varying N and p for $\eta_d = 0$; (b) the ratio between the average collision rate with $\eta_d = 0$ and the average collision rate with no eavesdropping. Here, c' denotes the average collision rate for simulations with no eavesdropping, which has similar trends as in (a) but with larger values.

energy cost has an analogous nonmonotonic trend for fixed N and varying p . However, the optimal pulse emission rate increases with increasing N , as shown by the blue curve.

5. Discussion

Based on the simulation study, we obtain the following observations regarding bats swarming in groups: (i) if bats are able to estimate obstacle locations using peers' information with low measurement noise, eavesdropping is a better option than flying independently in terms of collision avoidance; (ii) bats are able to suppress pulse emission to accommodate frequency jamming although the collision risk increases; and (iii) bats may increase pulse emission rate to achieve better collision avoidance performance while using more energy individually.

The eavesdropping rule enables bats to use peers' echoes and pulses to obtain information about surrounding obstacles, which is beneficial when the measurement noise is low. In the model, bats

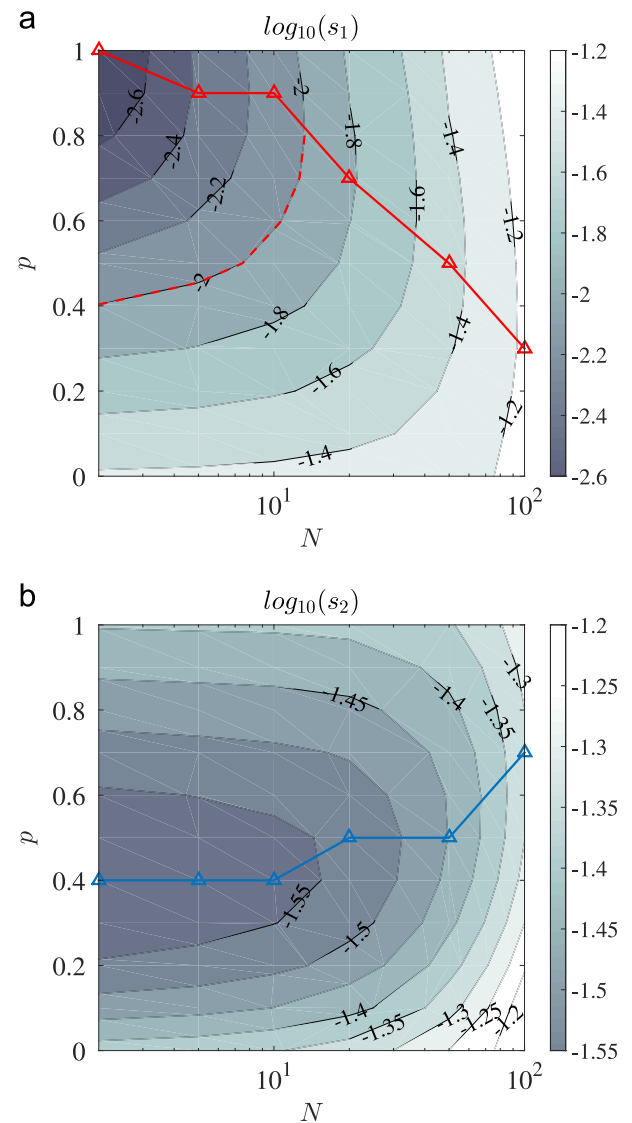


Fig. 6. (a) The collision/jamming cost s_1 and (b) the collision/energy cost s_2 with varying N and p for $\eta_d = 0$. In (a), the red curve denotes the minimum collision/jamming cost for different N ; the red dotted curve shows the pulse emission rates corresponding to a constant collision/jamming cost $\log_{10}(s_1) = -2$. In (b), the blue curve denotes the minimum collision/energy cost for different N . (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

emit directional pulses with which they only sense their environment in the flying direction. With eavesdropping, bats are able to estimate locations of obstacles which are not covered by their sensing space. Moreover, if bats cease pulse emission which may occur when $p < 1$, they receive information about the surrounding environment without generating a signal. Successful collision avoidance may be helped or hindered by this extra information, depending on its accuracy, namely low or high measurement noise. For low noise up to $\eta_d = 0.1$, bats' collision avoidance performance is comparable to $\eta_d = 0$, that is, when bats obtain the exact locations of obstacles from peers. For higher noise with $\eta_d \geq 1$, the estimated obstacle locations are more likely to be perturbed along the limited sound propagation distance that connects the bat and obstacle, which may result in incorrect velocity update decisions that cause more collisions. This is expected to model the biological system since eavesdropping bats garner directional information, but lack time-of-flight, from peers' echoes and pulses. However, the literature is lacking quantitative

studies of this potential effect. We comment that bats are known to exhibit aligned flight formations (Betke et al., 2007) which may enable them to eavesdrop with low measurement noise due to regular patterns of following flight (Chiu et al., 2008). The benefit of eavesdropping is evidenced in Fig. 5(b), where we observe bats having fewer collisions when they eavesdrop with low noise than flying independently. This benefit increases with bat population as bats obtain more information about obstacles from the increasing number of surrounding peers. When the pulse emission rate p reduces, the benefit of eavesdropping vanishes as there are fewer echoes and pulses in the domain. We note that this feature relies on the model's simplification that bats are able to process many signals simultaneously; however, bats perception of numerous signals may be limited in real environments.

Suppressing pulse emission reduces the amount of information in acoustic field, which results in less frequency jamming and lower collision/jamming cost when bats eavesdrop with low measurement noise. With low measurement noise (i.e. situations where eavesdropping is beneficial), the average collision rate increases as p reduces because there is less sound information available for bats to avoid obstacles, see Fig. 5(a). We note that this trend is reversed when bats use peers' information with high measurement noise, due to the destructive influence from high measurement noise causing more collisions for larger p values. Generally speaking, the chance of experiencing frequency jamming in a real system increases for larger N and p values, because the frequency of a bat's emitted pulse is more likely to overlap peers' pulse frequency since there are more pulses overall. The minimum collision/jamming cost occurs at an optimal value of $p < 1$, which captures the benefit of ceasing vocalization for frequency jamming avoidance documented by behavioral studies on big brown and Mexican free-tailed bats (Chiu et al., 2008; Jarvis et al., 2013). This optimal pulse emission rate decreases with N because frequency jamming dominates the collision/jamming cost for larger bat populations. The benefit of ceasing vocalization is also observed in the case of no eavesdropping, where the optimal p is higher due to its larger average collision rate values as compared to the case with eavesdropping. We comment that the bat group uses less energy on average when individuals reduce their pulse emission rate, which may have benefits beyond frequency jamming avoidance. However, we do not include energy consumption per bat in determining bat group behavior in natural settings because it may be a less immediate danger than the risk of collision from frequency jamming; this priority is motivated by engineering applications of this work, since the balance between energy use and collision risk is a dynamic and multifaceted problem for animals and cannot be decisively categorized. We also note that bats may not experience any frequency jamming in very sparse groups in natural settings, which allows for increasing pulse emission rate while keeping a constant safety margin in small populations as shown by the red curve in Fig. 6(a).

The optimal pulse emission rate for minimizing collision/energy cost increases with bat population, as bats obtain greater benefit in collision avoidance by eavesdropping peers' information with low measurement noise, see Fig. 6(b). The very low average collision rate for larger bat groups with high pulse emission rate, shown in Fig. 5(a), results in low collision/energy cost while the energy use per bat given by p increases. In general, the optimal pulse emission rate resulting from increased energy use per bat and decreased collision risk suggests that there is an attainable balance of avoiding collisions and saving energy in engineered systems with analogous acoustic capabilities. In such a system, this tradeoff may be tuned using the weighting coefficient in the collision/energy cost. We comment that, if we consider the total energy use of the bat group given by Np instead of the energy use per bat in calculating the collision/energy cost, we see a decreasing

optimal pulse emission rate, which is the same as the collision/jamming cost.

In conclusion, information sharing among agents in groups and changing pulse emission rate are possible active sensing strategies in nature and in engineering. Using peers' information by eavesdropping may provide substantial benefits for groups in terms of collision avoidance, frequency jamming avoidance and energy saving. Reducing or increasing pulse emission rate, on the other hand, balances collision and jamming avoidance or collision and individual energy use, respectively. We comment that the actual behavior of bats flying in groups in nature may be different from the modeling results. For example, bats may increase pulse emission rate to find unique pulse frequencies as a response to frequency jamming in large groups. In addition, individuals may combine information from peer's pulses and their echoes to lessen timing uncertainty when performing passive sonar. Future work includes obtaining the relationship between the pulse emission rate and the bat population in field studies on wild bat swarms to elucidate behaviors dictating pulse emission strategies, as well as tying these behaviors to the physical acoustic accommodations that bats must make to use variable frequencies for echolocation. We also seek applications of the model in engineered multi-agent systems, such as developing control algorithms for robotic teams that use active sensors for navigation.

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