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How bats exit a crowded colony when relying on echolocation only - a modeling approach

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eLife Assessment

This potentially **important** model-based study seeks to mimic bat echolocation behavior and flight under high-density conditions. The simulations **convincingly** suggest that the problem of acoustic jamming in these situations may be less severe than previously thought, a finding that would be of broad interest to scientists working in the fields of bat biology and collective behaviour. However, some aspects of the manuscript were found to lack clarity and concerns were raised about some of the assumptions underlying the parameters used for the simulations, which impact both the modeling results and the conclusions that can be made from the data.

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Abstract

Bats face a complex navigation challenge when emerging from densely populated roosts, where vast numbers take off at once in dark, confined spaces. Each bat must avoid collisions with walls and conspecifics while locating the exit, all amidst overlapping acoustic signals. This crowded environment creates the risk of acoustic jamming, in which the calls of neighboring bats interfere with echo detection, potentially obscuring vital information. Despite these challenges, bats navigate these conditions with remarkable success. Although bats have access to multiple sensory cues, here we focused on whether echolocation alone could provide sufficient information for orientation under such high-interference conditions. To explore whether they manage this challenge, we developed a sensorimotor model that mimics the bats' echolocation behavior under high-density conditions. Our findings suggest that the problem of acoustic jamming may be less severe than previously thought. Bats can compensate for potential interference by emitting frequent calls with short inter-pulse intervals (IPI), creating a redundancy in the sensory information that allows them to aggregate echoes over multiple calls. This redundancy, combined with simple pathfinding strategies, such as following walls and avoiding nearby obstacles, enables bats to exit the roost effectively, even when faced with significant sensory interference. Our model indicates that bats' echolocation strategies are robust enough to mitigate the effects of jamming and demonstrates the critical role of signal redundancy in successful navigation. These insights

not only enhance our understanding of bat behavior but also offer implications for swarm robotics and collective movement in complex environments.

Introduction

In many bat species individuals dwell together in caves (or similar roosts), forming large colonies with tens to tens of thousands of individuals[1]. Each evening, at approximately the same time, the bats take off from their roost, navigating through its passages toward the exit. The high density of bats flying simultaneously in great proximity poses many challenges for orientation in such a crowded and noisy environment. Flying while avoiding collisions, often in a pitch-black cave, demands the constant detection and localization of both obstacles and nearby bats[2,3]. Employing echolocation, bats emit strong ultrasonic signals and interpret the reflected echoes to perceive their surroundings[4]. The reception of neighbors' loud calls, which may share similar acoustic features with their own calls, can potentially hinder the bats' ability to detect the faint echoes reflected off the walls and the surrounding bats[4,5]. We examined whether bats could rely solely on echolocation to exit the roost even during such a chaotic 'rush hour'.

The question of how bats cope with acoustic interference has been extensively researched using playback experiments, field observations, on-body tags, and computational simulations[6–15]. However, much of this research has focused on foraging bats in small groups[4,5,8,15–18]. The challenges bats encounter during roost exits (e.g., cave exits), however, differ markedly from those encountered during group foraging. First, during roost exits the bat density is significantly higher, and they need to detect and follow static walls or obstacles, which produce loud echoes, rather than small, sporadic prey items that generate faint echoes[19]. Finally, their flight maneuvers involve flying directionally and avoiding collisions with conspecifics, unlike the hunting maneuvers typically observed while foraging. Echolocation studies during dense collective movement are scarce[3,5,20–23], likely due to the complexities in recording separate echolocation calls and tracking individual flights within the swarm. While collective movement has been extensively studied in various species, including insect swarming, fish schooling, and bird murmuration[24–31], as well as in swarm robotics agents performing tasks such as coordinated navigation and maze-solving[32–34], most studies have focused on movement algorithms while overlooking the sensory challenges involved[35–42].

The present study addresses these gaps by introducing an agent-based sensorimotor model based on the well-documented echolocation capabilities of bats, simulating multiple bats pathfinding their way out of a cave-like structure. We modeled the echolocation behavior of two insectivorous bat species: *Pipistrellus kuhli (*PK*)*, which roosts in abandoned buildings and frequently navigates through conspecific-dense, cluttered corridors and the cave dwelling *Rhinopoma microphyllum* (RM) which emerges from its roosts with thousands of individuals simultaneously. These two species differ in their echolocation signals. In brief, PK echolocation signals are characterized by a wider band width than RM calls. We quantified the performance of an individual bat flying among conspecifics, demonstrating that even a relatively simple sensorimotor algorithm can facilitate successful orientation in such complex environments. The modeling approach enabled us to explore how various biological and ecological factors influence successful navigation under such challenging conditions.

Results

In our 2D simulations[6], each bat emits sound signals and receives the echoes reflected from roost walls and other bats which are often masked by the calls emitted by conspecifics. The bat then estimates the distance and direction of each reflector, adjusts its echolocation accordingly,

and maneuvers in search of an exit while also avoiding collisions. The bats dynamic echolocation responses were modeled following the vast literature (see[6] and Methods). Their reception was modeled using a biologically inspired filter-bank receiver comprising 80 gammatone channels[6,43,44]. Each bat adjusted its flight following a simple pathfinding algorithm based solely on the estimated locations of the detected reflectors (see Methods, **Supplementary Figure 1**, and Supplementary Movie 1 for additional details). The bats had to exit a roost designed as a corridor (14.5 m long x 2.5 m wide), with a right-angle turn located 5.5 m before the exit (**Figure 1A**). Additionally, an obstacle (1.25 m wide) was situated 2.25 m in front of the opening. The simulated bats initiated their flight from the far end of the corridor taking off in the general direction of the exit (±30 degrees), without prior knowledge of the roost's structure. The basic sensory model took all interference signals into account, while assuming that the bat can distinguish between echoes from the walls and echoes from conspecifics. In brief, the bat responded to echoes as follows (see detailed description in the Methods): If a static reflector or a conspecific was detected in front of the bat and was too close (less than 0.4 m), the bat would maneuver to avoid a collision. Otherwise, to find the exit, the bat would follow the direction of the walls by flying toward the farthest static reflector ahead. Finally, if a gap greater than 0.5 m was detected between adjacent reflecting points, the bat directed its flight toward the center of the gap.

The ability of the bats to exit the roost within 15 sec was evaluated for different group sizes, from a single bat and up to 100 individuals. For simplicity, we will refer to the initial density at the cave's far end as the number of bats per $3m^2$ (i.e., for groups of 100 bats, the density is 100 bats/$3m^2$, or 33.3 bats/m^2). The bat densities we tested were chosen to reflect the typical range of bat densities observed in natural caves during emergence events[22,45,46]. Key model parameters, such as the sensory integration window, object target strength, echolocation parameters, and flight velocity (see **Table 1**), were manipulated and their impact on the exit performance was analyzed. To explicitly quantify the effect of sensory masking vs. the effect of collision avoidance only, we turned the acoustic interference on and off to measure its impact.

Bats find their way out of the cave even at high conspecific densities

We first examine how bat density affects bats' ability to exit the cave, alone and in a group. Higher bat densities significantly reduced the probability of exiting the cave in 15 seconds (**Figure 2 A**, see Supplementary Movie 1 for a view of the bats' movement, $p<10^{-10}$, tStat=−23, DF=4077, GLM, see details in **Table 1**). In trials in which a single bat was flying alone, it successfully exited the cave in 100% of the cases. Even without sensory interference, the probability of exiting decreased significantly from 100% to 86%±1.4% and 91%±1.7% at densities of 100 PKs/$3m^2$ and 100 RMs/$3m^2$, respectively (mean ± s.e.). When acoustic interference was added, the exit probability further decreased to 63%±1.4% and 67%±1.4% for 100 PKs and RMs, respectively (see **Figure 2A**).

The difference in exit probability between the two species was not significant (p=0.08, tStat=1.74, DF=4077, GLM as above, **Figure 2A**). Similarly, the difference in echolocation parameters between the two species did not affect the collision rate with the walls (with a maximum of 0.29 and 0.3 collisions per bat per second for PK and RM, respectively, with 100 bats (p=0.63, tStat=−0.48, DF=4077, GLM, **Figure 2C**, see details in **Table 1**). To quantify sensory interference, we defined a jammed echo as an echo entirely missed due to masking. The jamming probability, which was calculated as the number of jammed echoes divided by the total number of reflected echoes, was significantly higher for RM compared to PK with a maximum difference of 14.3% for 10 bats, and 9.8% for 100 bats ($p<10^{-10}$, tStat=6.56, DF=4077, GLM, **Figure 2D**, see details in **Table 1**). Accordingly, PK demonstrated a minor but significant advantage in detecting the cave walls (p=0.024, tStat=−2.25, DF=4077, GLM, **Figure 2E**, see details in **Table 1**). With 100 bats flying together, the probability of detecting a wall echo at a distance of 1 m in a single call was around 50% and 46% for PK and RM, respectively. Despite this minor disadvantage in

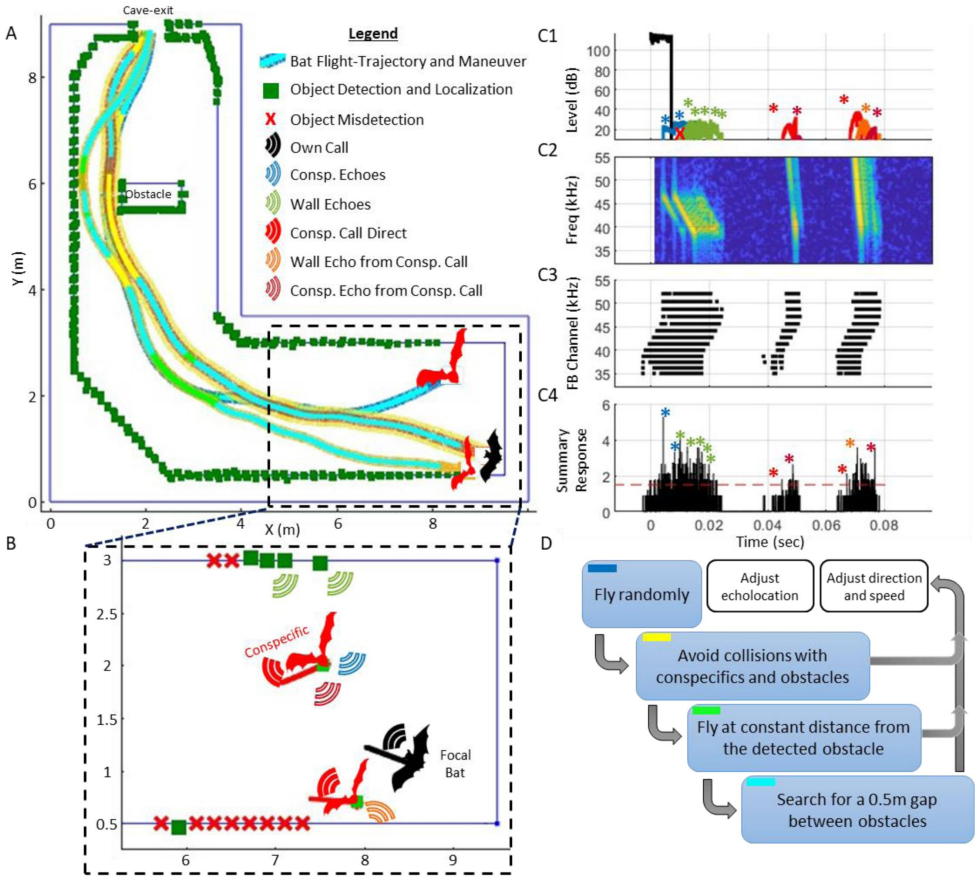


Figure 1.

The sensorimotor model.

(A) Top view of the cave with three bats. Data are presented for the focal bat (black bat, and wide yellow trajectory). The flight trajectories are shown in thick lines, while the bat's moment-to-moment decisions are indicated by the inner colored lines (see panel D). Green squares depict reflectors detected by the focal bat along its route. **(B)** A zoomed-in view of the dashed rectangular area in Panel A, where the focal bat (black) emitted one echolocation call (black filled) and received echoes from the cave walls (green hollow) and from two other bats (blue hollow). It also received conspecifics' calls (red filled) and their reflection from the cave walls (orange hollow), as well as the reflections from other bats (red hollow). Green squares indicate points that were detected by the focal bat from this call and red x's indicate missed points due to acoustic masking. The locations of the detected reflectors (green squares) are marked according to their localization by the bat (with simulated errors). The lines near the bats depict their flight direction. **(C)** The acoustic scene received by the focal bat is as depicted in B, including the emitted call and all received signals (colors as in panel B). **(C1)** The time-domain plot displays the envelope of signals, encompassing the emitted call and the received signals: the desired echoes from the walls and conspecifics; the calls of other bats; the echoes returning from conspecific calls and reflected off the walls and off other bats. Notably, in this example, some of the desired wall-echoes are jammed by the stronger echoes reflected off conspecifics. **(C2)** The spectrogram of all the received signals presented in C1; for clarity, the emitted call is not depicted. **(C3)** The responses of the active channels of the cochlear filter bank after de-chirping. Each channel is represented by its central frequency on the y-axis. Each black dot represents the timing of a reaction that was above the detection threshold in each channel. Note that early reactions in low-frequency channels (marked by yellow arrows) result from the stimulation of those channels caused by the higher frequencies of the downward FM chirp. However, most of these stimulations do not reach the detection threshold and are therefore not detected (see Methods). **(C4)** The detections of each channel are convoluted with a Gaussian kernel, summed, and compared with the detection threshold (dotted red line). The colored asterisks illustrate detections of the received signals (colors of the sources are as defined above). Panel D depicts the navigation algorithm used by the bat. The algorithm involves a correlated-random flight during the search phase (blue), collision avoidance (yellow), flying along the wall at a constant distance (green), and flying toward the center of a gap between obstacles as an indicator of a possible exit (cyan). After each echolocation call, the bat awaits an IPI (Inter Pulse Interval) period before emitting the next call. Based on the received signals, it then modifies its next call design and adjusts its direction and speed accordingly.

Key parameter	Tested range	**Default value**	Effect size			Statistical Test
			Exit-probability (%)	Jamming-probability (%)	Collision rate (sec^{-1})	GLM's explaining factors
Number Of Bats	[1, 2, 5, 10, 20, 40, 100]	**All Values**	-0.37/bat* [63:100]	0.54/bat* [0:54]	0.25/bat* [0.05:0.3]	Number of bats
Bat species	[PK, RM]	**PK**	4.5 [63:67]	9* [54:63]	0.01 [0.29:03].	Number of bats, bat species
Integration Window (#)	[0,1,3,5,10]	**5**	0.41/call* [29:70]	0.01/call [54:55]	0.27/call [0.25:0.53]	Number of bats, integration window size
Nominal flight speed (m/s)	[2,4,6,8,10]	**6**	6/(1m/s), -12/(1m/s)* [15:63]	1.4/(1m/s)* [55:65]	0.18/(1m/s)* [0.07:1.3]	Number of bats, square of number of bats, flight speed
Call level (db-spl)	[100,110,120,130]	**120**	13$^{\Psi}$ [50:63]	0.5/10dB* [53:58]	0.07$^{\Psi}$ [0.29:0.36]	Number of bats, call level
Misidentification	[Yes/No]	**N**	69* [14:83]	1.7* [7.6:9.3]	0.6* [0.2:0.8]	Number of bats, confusion flag
Misidentification and temporal aggregation process	[Yes/No]	**N**	23* [58:83]	1.7* [7.6:9.3]	-0.02* [0.18:0.2]	Number of bats, process flag
Masking	[Yes/No]	**Y**	23* [63:86]	54* [0:54]	0.03 [0.26:0.29]	Number of bats, masking
Wall target strength (db)	[-33, -23, -13, -3]	**-23**	2.13/dB [23:87]	1.16/dB [34:68]	0.01/DB [0.19:0.47]	Number of bats, wall target strength

Table 1.

Key model parameters and their effects on performance metrics.

The table presents the key parameters tested, their ranges, default values, and effect sizes on various performance metrics: exit probability, jamming probability, and collision rate. The parameters comprised the number of bats, bat species (PK-Pipistrellus kuhli, RM –Rhinopoma microphyllum), integration window, nominal flight speed, call level, echo mis-identification with temporal aggregation (yes/no), masking (yes/no), and wall target strength. In each scenario, all parameters except the tested one were set to the default value. The effect sizes for each parameter on exit probability, jamming probability, and collision rate are provided (per bat). Square brackets present the minimum and maximum values of the metric across the tested range. Asterisk (*) indicates a significant impact. Each scenario was tested using Generalized Linear Models (GLMs) with number-of-bats and the tested parameters set as fixed explaining variables. Exit probability and jamming probability were treated as binomially distributed, collision rate was treated as a Poisson distributed, and all other variables were considered normally distributed. Explaining variables were set as fixed factors. The number of repetitions for each scenario was as follows: 1 bat: 240; 2 bats: 120, 5 bats: 48; 10 bats: 24; 20 bats: 12; 40 bats: 12; 100 bats: 6. $^{\Psi}$ A significant difference in call intensity was found only for a bat density of 100 bats/$3m^2$, and between the group with a level of 100dB-SPL and all other groups.

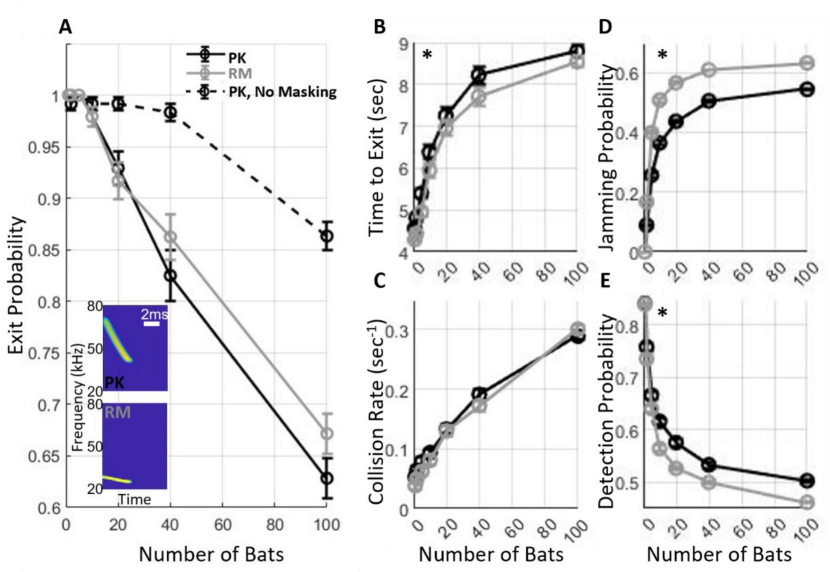


Figure 2.

Exit performance of P. Kuhli (PK) and R. Microphyllus (RM).

(A) Sensory interference significantly impaired the probability of exiting the cave (compare dashed black line with continuous black line). The probability of a successful exit also declined as the number of bats increased, with no significant difference observed between the species when masking interference was applied. The insert shows the spectrograms of the echolocation calls of PK (top) and RM (bottom). **(B)** The time-to-exit, which was calculated for successful trials only, and **(C)** the collision rate with the walls both increased as a function of the number of bats. **(D)** The probability of jamming significantly increased to about 55% and 63% with 100 bats for PK and RM, respectively. **(E)** The detection probability of a wall reflector at one meter or less in front of a bat decreased as a function of the number of bats. In panels (A-E), circles represent means and bars represent standard errors (see details in **Table 1**). Asterisks indicate significant differences between the lines in each panel.

detection, RM bats exhibited a better time-to-exit average than PK bats, being 0.5 seconds faster to exit (p=0.0005, tStat=−4.06, DF=3533, for n=40 bats, **Figure 2B**). It should be noted that the time-to-exit was calculated only for successfully exiting bats. RM bats also suffered from a significantly higher probability of the desired conspecific's echoes being jammed (p=0.00016, tStat=3.8, DF=3593, GLM, see details in **Table 1**).

A longer integration window improves exit performance

We next examined whether bats improve their performance when integrating information from several consecutive calls. The integration window determines the number of previous calls the bat uses at each step to guide its next movement decision (see Methods). The basic model used five calls. The probability of exiting the roost significantly increased when increasing the size of the integration window for all bat densities ($p<10^{-10}$, tStat=28.5, DF=10197, GLM, **Figure 3A**, see details in **Table 1**). For example, at a density of 40 bats/3m^2, the exit probability improved from 20%, to 75%, and to 87% as the window size increased from one, to three, and to 10 previous calls, respectively. In addition, increasing the window size resulted in a significant improvement in the time-to-exit and the avoidance of wall collisions ($p<10^{-10}$, tStat=−12.8, DF=7661; $p<10^{-10}$, tStat=−46.5, DF=10197, respectively, GLM, see details in **Table 1**). With 100 bats, the collision rate decreased by a factor of 2 from 0.53 to 0.25 collisions per second as the window increased from 1 to 10 calls. The size of the integration window had no significant effect on the jamming probability (p=0.37, tStat=0.9, DF=10197, GLM, see details in **Table 1**).

Exit probability was maximal at an intermediate flight-speed

We observed a significant and non-linear effect of the flight speed of the bats on the performance, as shown in **Figure 3B** ($p<10^{-10}$, tStat=−29.9, DF=10196, GLM, see details in **Table 1**). The exit probability increased with flight speed until it reached a maximum at 6-8 m/s and then declined rapidly. This was the case for all bat densities, with the maximal exit probability ranging between 65% to 99%. At the optimal velocity, the time-to-exit was also minimal. However, the collision rate increased monotonically with speed, with a steep incline above the optimal speed.

Call intensity had only a minor effect on exit performance and only at high bat densities

For low bat densities (<40 bats), call intensity did not have a significant impact on either exit probability or collision rate (**Figure 3C**, p=0.89, tStat=0.13, DF=5757; p=82, tStat-0.21, DF=5757, respectively, GLM, see details in **Table 1**). Call intensity affected exit performance only when the intensity dropped to 100 dB-SPL and only at a high bat density of 100 bats/3m^2 (**Figure 3** C). In this scenario, the exit probability declined from approximately 60% to 49.5% (p=0.003, F = 8.45, DF = 2396, One-way ANOVA with 'hsd' post hoc test), and the collision rate increased from 0.3 to 0.35 collisions per second ($p<3{\cdot}10^{-6}$, F = 22.18, DF = 2396). Notably, this low intensity is below the typical search-call intensity of most echolocating bats. At the same bat density (100 bats/3m^2), further increasing the call intensity to above 100dB-SPL had no significant effect on either exit probability (p=0.6) or collision rate (p=0.07). Calling louder also slightly, but significantly, decreased the jamming probability at all bat densities, with a decrease of 3.5%±8% to 5.5%±5% (mean ± s.e.) (p=0.02, tStat=−2.26, DF=8157, GLM, see **Table 1**).

While confusion between the desired echoes and those from conspecific calls may significantly impair exit performance, temporal aggregation helps to mitigate this

We next addressed the challenge of echo classification, assuming that a bat can differentiate an echo resulting from its own calls from echoes resulting from the calls of other bats. To examine this assumption, we tested another model in which bats responded similarly both to wall echoes returning from their own emissions and to those from conspecific emissions, treating all as their

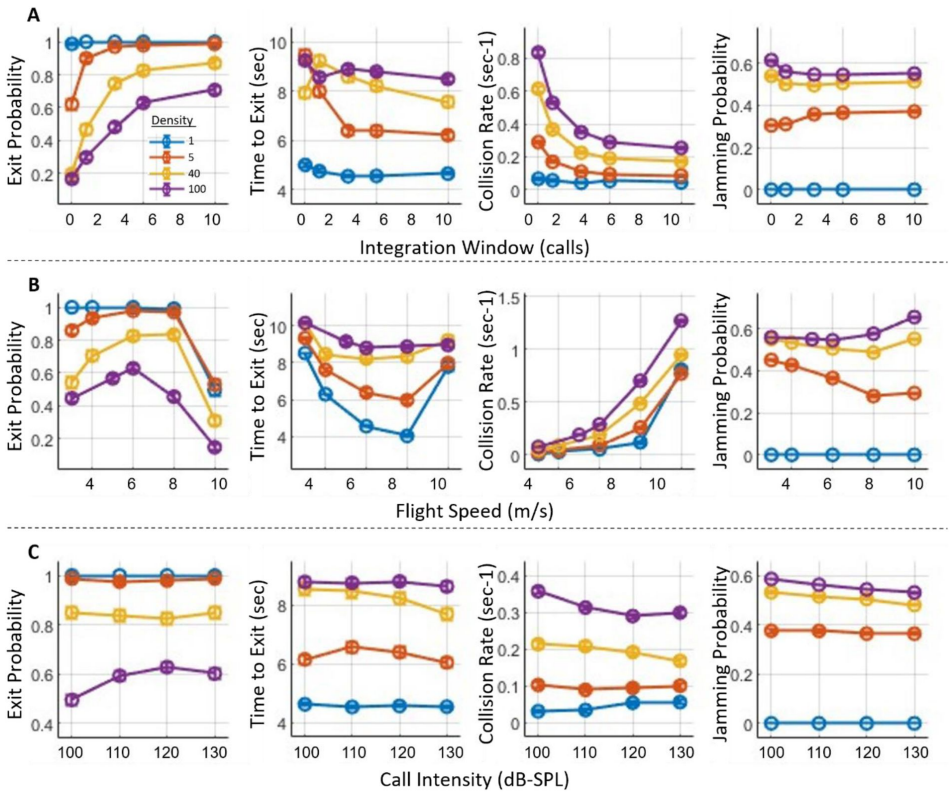


Figure 3.

Exit performance as a function of key sensorimotor parameters.

(A) The effect of the integration window on the probability of exiting the roost, the time-to exit, the rate of collisions with the walls, and the probability of jamming (from left to right, respectively). Each colored line shows the trend as a function of the window-size for different bat densities, with each color representing a specific density. **(B)** The effect of the nominal flight speed of the bats, with panels and line-colors as in panel A. An optimal speed of approximately 6 to 8 m/sec can be observed for all densities above one bat. **(C)** The effect of call intensity on exit performance, panels as in (A). In all panels, circles represent means and bars represent standard errors. See **Table 1** for the number of simulated bats.

own echoes. This confusion significantly decreased exit performance for all bat densities (above one bat). The probability of a successful exit for a density of 40 bats/3m^2 dropped from 83.3±2.4% to 14.6±2.3% ($p<<10^{-10}$, tStat=−20.7, DF=2877, GLM, see details in **Table 1**), the exit time increased from 7.6±0.18 to 9.3±0.2 seconds ($p<<10^{-10}$, tStat=15.5, DF=2157, GLM), and the collision rate increased significantly from 0.2±0.007 to 0.8±0.013 collisions per second ($p<<10^{-10}$, tStat=−30, DF=28777, GLM, see **Figure 4**, red and yellow lines).

To further examine whether this decrease in performance could be mitigated by integrating detections from successive calls, we tested a slightly improved aggregation model that clustered detected reflectors over one second periods (see Methods). This temporal aggregation process significantly improved performance, but exit probability and time-to-exit still remained significantly lower than without echo-confusion: exit probability = 58±3% in comparison to 83.3±2.4% without echo confusion ($p<<10^{-10}$, tStat=18.3, DF=28777, GLM), time-to-exit =9.3±0.2 seconds ($p<<10^{-10}$, tStat=−13.7, DF=1996, GLM), see **Figure 4**, yellow line. The results above are reported for a density of 40 bats/3m^2. Interestingly, the aggregation process restored the collision rate to the levels observed under the “No Confusion” condition (p=0.68, tStat=−0.42, DF= 2877, GLM, see **Figure 4C**, dark-purple and red lines).

Discussion

We present a model-based approach that suggests how echolocating bats might find their way out of a crowded roost while contending with severe sensory interference caused by numerous nearby conspecifics. Our results demonstrate that a single bat, lacking prior knowledge of its location and of the roost’s structure, can reliably find the exit using echolocation alone. As bat density increases, the bats face increased collision risks and more substantial acoustic interference, both of which reduce the probability of efficiently finding the exit. Nevertheless, even at densities of 100 bats/3m^2, most bats (63%) successfully exited the roost within a short timeframe. In brief, we demonstrate how a simple sensorimotor approach can solve this supposedly challenging task. This approach encompasses the following principles: (1) emission of echolocation calls; (2) reception of reflected echoes and interference signals; (3) detection of reflectors (including walls and conspecifics) using a gammatone filter bank biological receiver; (4) localization of the detected objects; (5) employment of short-term integration of acoustic detections; (6) adjustment of flight and echolocation behavior based on the distance and angle to the reflectors; and (7) application of simple pathfinding rules to follow walls and gaps while avoiding collisions. Notably, despite the jamming of a substantial percentage of the echoes (up to approximately 50% of the echoes from a 1 m distance), the bats managed to maneuver correctly even with this simple approach and partial data. Real bats likely use a much more sophisticated approach that also includes memorizing the roost’s structure[47], using landmarks inside the roost[48], reliance on the movement of nearby conspecifics[42,45], and exploitation of other sensory modalities. We thus expect their actual performance to surpass that of our modeled bats.

Our model suggests that acoustic jamming might be less problematic than has been generally assumed[4,10,49] and that movement under severe acoustic masking could be mitigated by increasing the call-rate, creating a redundancy in information across several calls- similar to how real bats react in a complex environment[5], and using simple sensorimotor heuristics. This is consistent with several relatively recent studies that have hinted in this direction[6,22,23].

The bat densities we simulated (ranging from 1 to 100 bats per 3m^2) reflect a wide range of observed bat densities. Although bat colonies can be much larger than 100 bats, the density that we simulated resulted in bats moving very close to each other, with an average distance of 0.27 m to the nearest bat. This density is higher than some of the most-dense reported bat aggregations,

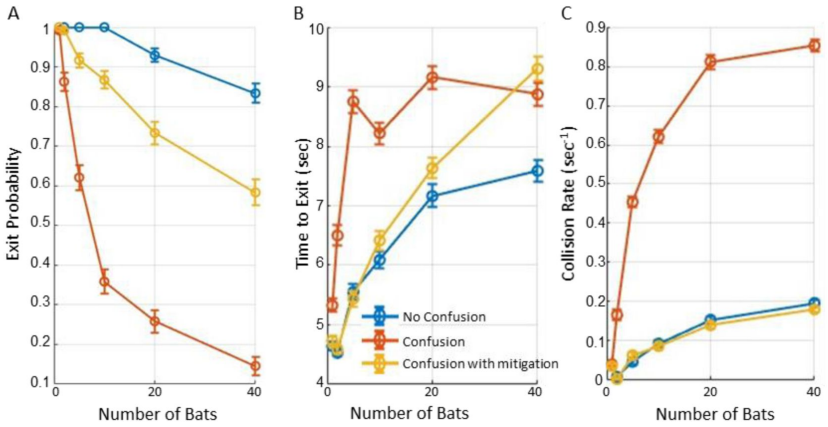


Figure 4.

The impact of confusion on performance.

The figure illustrates the impact of classification confusion on roost-exit performance under various conditions. Blue lines depict trials with masking, while assuming that bats can distinguish between echoes from their own calls and those of conspecifics (referred to as "No Confusion"). Red lines depict performance where confusion between echoes is assumed. Yellow lines depict performance under the confusion condition, with the added capability of temporal aggregation process in a short-term working memory (referred to as "confusion with mitigation", see text for further details). In all panels, circles represent means and bars indicate standard errors. **(A)** The probability of exiting the roost significantly decreased with masking and confusion. In conditions with confusion and no aggregation process, only 15% of bats successfully exited the roost, at a density of 40 bats/3m^2. Temporal aggregation partially mitigated the confusion effect but did not eliminate it. **(B)** Bats with the ability to distinguish between echoes demonstrated significantly shorter exit times than those experiencing confusion. Note that time-to-exit refers only to successful attempts. **(C)** The collision rate with walls was highest for bats experiencing both masking and confusion but decreased significantly when without confusion. Temporal aggregation process restores performance to the "No Confusion" condition, reducing collision rates accordingly, at densities between 1 to 40 bats/3m^2.

including studies on *Miniopterus fuliginosus*[45], *Myotis grisescens*[50], and *Tadarida brasiliensis*[3,46,51], where bats emerge from the roost at rates of 15 to 500 bats per second, but fly with an average distance of 0.5 meters between individual bats.

We compared the performance of two FM echolocating insectivorous bat species: *Pipistrellus kuhli (*PK*)* and *Rhinopoma microphyllum (*RM*)*. PK bats emit wideband echolocation signals that are less prone to jamming than RM bats' narrowband signal[14,52]. Our findings show that PK signals slightly reduce jamming probability (by 9%) and improve wall detection. However, no significant differences in exit probabilities were noted between the two species.

Using a simulation allowed us to separate the effects of sensory and spatial interferences (i.e., avoiding other bats) and revealed new insights into the sensorimotor strategy that is probably applied by real bats. The spatial interference reduced the probability of exiting the roost from 100% to 87%, while the sensory interference further decreased it to 63%. Increasing call intensity had little effect on exit performance, although slightly improving it at high bat densities. When all bats increased their calling intensity, both desired echoes and masking signals intensified equally, resulting in only a marginal effect. There is, thus, no benefit beyond a certain level of calling intensity that is needed to ensure proper obstacle detection (ca. 110dB-SPl, which is in accordance with actual call intensities used by bats). These results align with previous studies that have drawn similar conclusions[6,23].

Bats constantly adjust their flight speed to their surroundings[53–56] and specifically when conspecifics are nearby[57]. Our study suggests that the optimal velocity for flying through a crowded roost ranges from 6 m/sec to 8 m/sec for densities of 2-100 bats/3m^2. Exceeding this velocity-range led to a significant drop in exit probability due to a significant increase in wall collisions. We found that this speed did not depend on bat density in accordance with the observations of Theriault et al.[46]. Notably, the reported velocities of RM when exiting a cave[22] and PK emergence velocity near the cave[58] are close to the speed that appears optimal, based on our simulations.

Our basic model assumed that bats can distinguish between wall echoes and conspecific echoes, as demonstrated in previous studies [59]. We suggest that this is a feasible assumption because echoes from cave walls are longer and exhibit distinct spectro-temporal patterns, whereas echoes from smaller objects, such as conspecifics, are shorter[43,60,61]. However, wall echoes reflected from conspecific calls might resemble those from the bat's own calls in their amplitude and time-frequency characteristics [18,57,62]. This led us to question how the misidentification of such echoes as obstacles might affect navigation. When unable to distinguish between these echoes, the simulated bats responded to all as if they were their own and thus mis-localized conspecific wall echoes. The confusion led to a significant drop in exit performance, in which only 15% of the bats successfully exited (compared to 82% without confusion), and the collision rate rose from 0.2 to 0.85 collisions per second, at a 40 bats/3m^2 density.

Previous studies have demonstrated that bats can aggregate acoustic information received sequentially over several echolocation calls, effectively constructing an auditory scene in complex environments[4,63–66]. Accordingly, we tested how temporal aggregation process, which also included clustering of nearby reflectors and estimating wall orientation based on integration, rather than processing single detections, might assist bats in pathfinding even under the assumption of full confusion. At bat densities of 1 to 40 bats/3m^2, the temporal aggregation process completely restored the collision rate with walls from 0.85 back to 0.2 collisions per second, and significantly improved the exit probability, raising it to 58%, although it did not entirely eliminate the impact of confusion. Our assumption of total confusion between echoes from a bat's own calls and those from conspecifics, as well as our relatively simple integration model, likely underestimates the true capabilities of real bats when flying in complex environments.

Navigation in bats involves processing complex sensory inputs and applying effective decision-making, often requiring an ability to switch strategies[67–73]. Bats possess a highly accurate spatial memory[63,69,73–75], which is essential for tasks like long-distance migration[47], homing[76], and maneuvering in cluttered environments[74]. Additionally, they utilize acoustic landmarks to orient in total darkness[48], occasionally rely on vision[70,71], particularly at the cave edge where light is available, can passively detect echolocating peers, and perhaps eavesdrop on conspecifics' echoes[21]. In this study we focused on whether echolocation alone is sufficient for one of the most difficult orientation tasks that bats perform – exiting a roost at high densities without prior knowledge of the roost's shape, aside from the initial flight direction. Thus, our echolocation-only model, which was based on a five-call integration window during most simulations, probably underestimates real bats' actual performance which also benefits from additional sensory input and can employ addition navigation strategies by sharing information between each other to coordinate and optimize the routes, such as manifested by swarming intelligence[32,77,78].

Our model highlights the importance of considering sensory interference in animal behavior research and illuminates the impressive capabilities of echolocating bats. Additionally, the model showcases the value of simulations and establishes a framework for future studies on collective movement and swarming animals, and on robotics in complex environments.

Methods

The simulated bats rely solely on echolocation to detect and locate obstacles and other bats by analyzing the sound waves they receive. They emit directional echolocation calls and receive the echoes reflected by roost walls and conspecifics, as well as the calls of conspecifics and the echoes returning from their calls. The bats adjust their flight trajectory and echolocation behavior based on the estimated location of the detected objects (range and angle), which deteriorates upon acoustic interference. The detection of the received signals is based on the mammalian gammatone filter bank receiver, under the assumption that bats can differentiate between the desired detected obstacles, conspecifics' echoes, and masking signals. We conducted simulations with varying number of bats (from 1 to 100) to analyze the flight trajectories with and without masking interference by conspecifics. In the trials without masking interference the bats successfully detected walls and conspecifics without any hindrance. For a detailed description of the MATLAB simulation see Mazar & Yovel 2020[6].

All bats in our model start their flight simultaneously within a 0.1 sec window from a random point at the cave's end over a 2 x 1.5 m^2 area, heading in a random direction between −30 and 30 degrees relative to exit direction (see **Figure 1**). They employ a simple navigation algorithm that dynamically adjusts flight direction based on the detected obstacles or conspecifics (**Supplementary Figure 1** and **Figure 1D**). If no obstacles or conspecifics are detected, they continue in a correlated random walk with a maximal turning rate of approximately 30 deg/sec. When obstacles are detected, they are first localized with an error (see below and[6]). Then, if an opening(i.e., a gap of at least 0.5 m between obstacles) is detected, the bats fly through it, if not, they follow the walls while maintaining a 0.8 m distance from them. When approaching a stationary obstacle too closely (<1.5 m and at an angle <60°), they execute an obstacle avoidance maneuver. High proximity to another bat (<0.4 m) triggers an avoidance maneuver away from the nearest conspecific. If the bat collides with a wall, it immediately turns so that its new flight direction is at a 90° angle to the wall. Each decision relies on an integration window that records the estimated locations of detected reflectors from the last five echolocation calls, with the parameter being tested between 1 and 10 calls. This algorithm functions without any prior knowledge of the bats' location or the roost's structure. To assess performance, we measured the

probability of successfully exiting the roost within a 15-second window, chosen because it is approximately twice the average exit time for 40 bats and allows for a second corrective maneuver if needed..

Echolocation behavior and flight speed follow the phases widely reported in insectivorous bats, categorized as “search,” “approach,” and “buzz”[79–82] with specific echolocation parameters for *Pipistrellus khulli* (Kuhl’s pipistrelle)[54] and *Rhinopoma microphyllum* (greater mouse-tailed bat)[22]. The distance to the detected object defines the phase and accordingly determines the following parameters: Inter Pulse Interval (IPI), call duration, and start and stop frequencies. The simulated echolocation call consists of the dominant harmony of the bat’s FM Chirp (1st harmony of the PK and 2nd harmony of the RM). **Table 2** provides the specific echolocation parameters used in the model. During the search phase, the bats fly at a nominal velocity of 6 m/sec, reducing it by half during the approach phase and continuously adjusting their speed according to the relative direction of the target, using a delayed linear adaptive law[6,83,84]. The maneuverability of the bats is constrained to a maximum of 4 m/sec², limiting both angular and linear accelerations.

The sound intensity of the echoes generated by the bat’s own calls and those of its conspecifics are calculated using the sonar equation[6,85] (pp. 196-198), as shown in Equation 1. The received levels of the masking calls are determined by using the Friis transmission equation[86], as shown in Equation 2. Bats are modeled acoustically as spherical reflectors with a uniform target strength of −23dB, reflecting sound isotropically. This acoustic characterization approximates a sphere with a radius of 0.15 m, corresponding to the approximate wingspan of *Rhinopoma microphyllum* (RM) [22,87]. Walls are modeled as composites of individual reflectors placed 20 cm apart; each treated as a sphere with a 20 cm radius and a target strength of −20dB. The directivity of the calls and the received echoes is defined by the piston model[6,82] with radii of 3 mm for the mouth-gap and 7 mm for the ear. Echo delays are calculated as the two-way travel time of the signals from the emitter to the target.

$$\text{Equation 1: } \boldsymbol{P_r = P_t \cdot \frac{G_t(\phi_{target},f)\cdot G_r(\phi_{target},f)\lambda^2}{(4\pi)^3 D^4} \cdot 10^{-2\alpha_{att}(f)/10\cdot(D-0.1)} \cdot \sigma(f)}$$

$$\text{Equation 2: } \boldsymbol{P_{mask} = P_t G_t(\phi_{t_x r_x}) G_r(\phi_{r_x t_x}) \cdot \left(\frac{\lambda}{4\pi D_{txrx}}\right)^2 10^{-\alpha_{att}\cdot(D-0.1)}}$$

$$\text{Equation 3: } \boldsymbol{P_{echoesFromMasking} = P_t \cdot \frac{G_t(\phi_{t_x})\cdot G_r(\phi_{r_x})\lambda^2}{(4\pi)^3 {D_{t_x}}^2 {D_{r_x}}^2} 10^{-\alpha_{att}\cdot(D_{t_x}+D_{r_x}-0.2)} \cdot \sigma(f)}$$

where,

P_r: level of the received signal [SPL]

P_t : level of the transmitted call [SPL]

P_{mask} : level of the masking signal as received by the bat [SPL]

$P_{echoesFromMasking}$: level of the echoes reflected by conspecifics and received by the bat [SPL]

$G_t(\Phi, f)$: gain of the transmitter (mouth of the bat, piston model), as a function of azimuth and frequency (f) [numeric]

$G_r(\Phi, f)$: gain of the receiver (ears of the bat, piston model) [numeric]

Φ_{target} : angle between the bat’s direction and the target [rad]

D: distance between the bat and the target [m]

Table 2.

Echolocation parameters.

The table presents the echolocation parameters of the two bat species we simulated during the specified flight phases (i.e., search, approach, buzz, and final buzz). In each phase, except for the search phase, in which the parameters remain constant, the parameters for each call are determined by the distance to the closest detected object.

***Pipistrellus khulli* (Kuhl's pipistrelle)**						
Flight phase	Search	Approach		Buzz		
Parameter		Start	End	Terminal 1 start	Terminal 1 end	Terminal 2
Inter Pulse Interval [ms]	100	70	35	18	6	5
Call duration [ms]	7	5	2	2	1	0.3
Terminal frequency [kHz]	39	39	39	39	39	39
Chirp bandwidth [kHz]	8	35	30	30	20	20
Call intensity [dB-SPL]	120	120	90	90	80	80
Distance to target [m]	>1.2	1.2	0.4	0.4	0.2	<0.2
***Rhinopoma microphyllum* (greater mouse-tailed bat)**						
Flight phase	Search	Approach		Buzz		

***Pipistrellus khulli* (Kuhl's pipistrelle)**						
Flight phase	Search	Approach		Buzz		
Parameter		Start	End	Terminal 1 start	Terminal 1 end	Terminal 2
Inter Pulse Interval [ms]	100	80	20	18	10	9
Call duration [ms]	12	7	2	2	1.5	0.75
Terminal frequency [kHz]	26	26	26	26	26	23.5
Chirp bandwidth [kHz]	3	4	5	3	3	3
Call intensity [dB-SPL]	120	120	90	90	80	80
Distance to target [m]	>1.2	1.2	0.4	0.4	0.2	<0.2

Φ_{ii}, D_{ii} : angles[rad] and distances[m] between the emitting bat or receiving bat (tx and rx, respectively) and the target

$\alpha_{att}(f)$: atmospheric absorption coefficient for sound [dB/m]

$\sigma(f)$: SONAR cross-section of the target [m^2]

λ: The wavelength of the signal [m]

To model the bat's cochlea, we employed a filter bank receiver[43,88,89] consisting of 80 channels, each with three components: (i) a gammatone filter of order 8, acting as a bandpass filter with center frequencies logarithmically scaled between 10kHz and 80kHz[6]; (ii) a half-wave rectifier; and (iii) a lowpass filter (Butterworth, fc=8kHz, order=6). Object detection and distance estimation are conducted using Saillant's method[6,43,90], based on the sum of detections in the active channels, see **Figure 1C**, D. Initially, a de-chirping process calculates the reference frequency-delay by detecting the peak in the response of each channel to the emitted call in a noise-free environment. Subsequently, the received signal, containing both desired echoes and masking sounds, passes through the filter bank. In each channel, all peaks above a threshold level are detected and time-shifted by the de-chirp reference. Peaks from all channels are aggregated in 5 μs windows and convolved with a Gaussian kernel with σ=5 μs. Output peaks that exceed the threshold level, set at 10% of the number of active channels, and fall within a time window of 100μs around the expected delay, are considered successful detections.

To evaluate the impact of acoustic interference, we conducted the detection procedure twice. The first, termed "interference-free detection", comprised only the desired echoes, with Gaussian noise at a level of 0 dB-SPL and without masking signals. The second, termed "full detection" comprised the desired echoes, Gaussian noise, and the masking signals. Detected echoes in the full detection were defined by the strongest peak within a four-millisecond window (three milliseconds before and one millisecond after, accounting for forward and backward masking) detected within 100μs of the interference-free detections. Jammed echoes were those detected in the interference-free condition and not in the full detection condition. The jamming probability was defined as the ratio of jammed echoes in the full detection condition to the detected echoes in the interference-free condition.

After detection, the bat estimates the range and the Direction of Arrival (DOA) of the reflecting objects. The range is determined by the delay of the detected echo, including any errors derived from the filter-bank process in the "full detection" process (i.e., including all masking signals). The direction is estimated by adding directional errors to the calculated angle between the bat and the target[6]. These errors are normally distributed with a zero mean and a standard deviation that depends on the Signal-to-Noise Ratio (SNR) and the angle. At an angle of 0° and an SNR of 10dB, the standard deviation of the error is 1.5°[91,92].

To evaluate the impact of the assumption that bats can distinguish between echoes caused by their own calls and those caused by other bats (i.e., conspecifics' reflectors), we tested an alternative model in which the simulated bats treat all echoes reflected from walls as if they have originated from their own calls. The distance to the conspecifics' reflectors is estimated based on the time difference between the echo and the bat's last call. The direction of arrival is estimated by the angle between the bat and the physical reflector, with an added random error (the same process used for their own echoes).

In real bats, spatial processing in the brain involves aggregating auditory information over time to construct a coherent map of the environment [4,93]. This neural computation is crucial for navigation and prey detection in complex environments. Therefore, we also examined how the inclusion of temporal aggregation process in the environment perception procedure helps bats

mitigate the confusion problem. The integration comprised the following steps, which were executed within a one-second working memory (or integration window): (i) clustering all detections in memory into groups with a maximum internal distance of 10 cm; (ii) reconstructing the estimated walls positions and directions based on the average of clusters that include at least two detections (and not based on single reflectors); and (iii) looking for openings between wall edges ranging from 0.5 to 2.25 meters in width, see **Supplementary Figure 1**. Note that detections from the last calls, even if not clustered, are still used for obstacle avoidance maneuvers.

Statistical analysis

Statistical analysis and the roost-exit model were conducted using MATLAB© 2023a.

Tests were performed with a significance level of 0.05. For each simulated scenario, we examined the effect of the various parameters on exit probability, time-to-exit, collision rate, and the jamming probability, using Generalized Linear Models (GLMs). The GLM tests were executed with MATLAB built-in function 'fitglm()'. Probability variables (such as exit and jamming probabilities) were treated as binomially distributed; rate variables (such as collision rate) were treated as Poisson distributed, and all other variables were considered normally distributed. Unless otherwise stated, all explaining variables were set as fixed factors. All statistical analyses, including the statistical test and the corresponding sample sizes, are described throughout the text and summarized in **Table 1**.

Data availability

All data and codes generated during this study are included in the manuscript and supporting files. Source code files have been uploaded with a Graphical User Interface and a readme file for explanation. Data are available at: link *https://drive.google.com/drive/folders/1hxnxbd37I2qVOLTWUob7cGhqXaQakEXs*

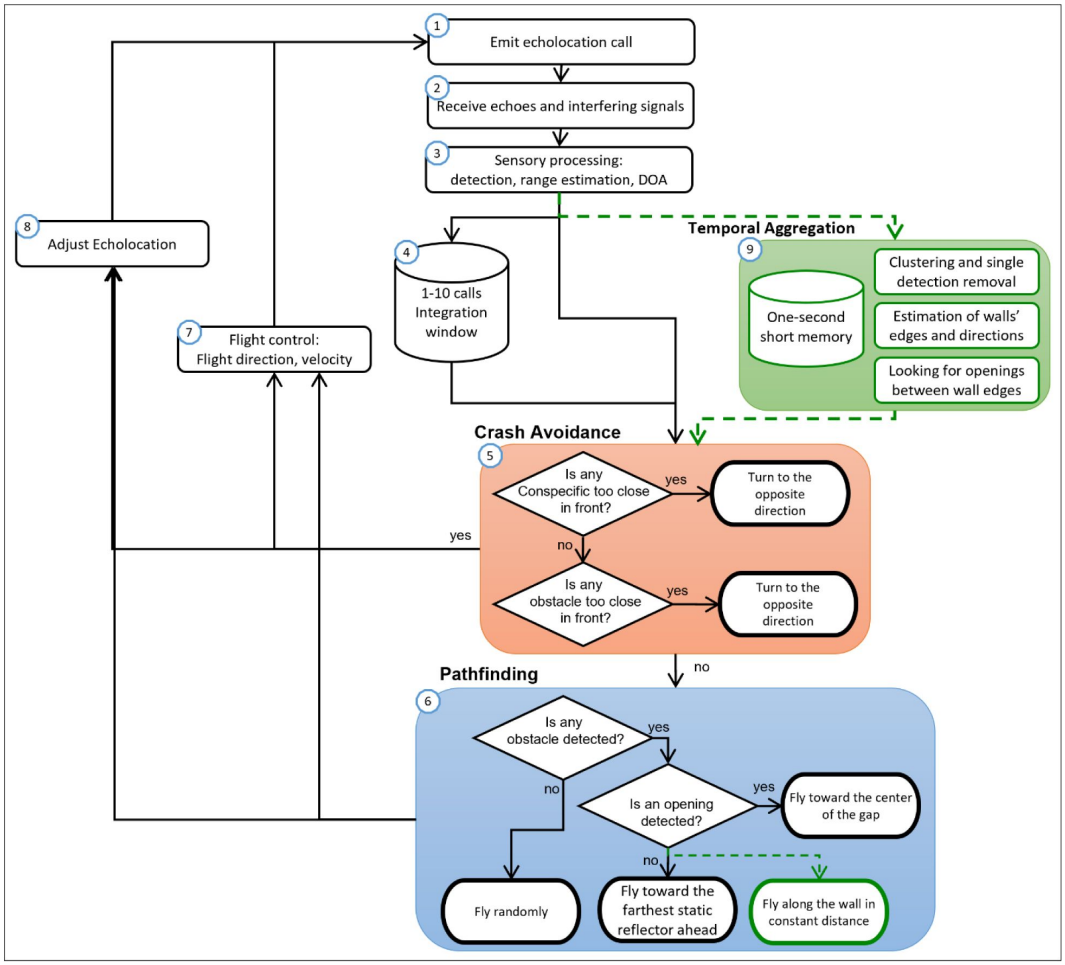
Additional information

Author contributions

O.M - Software, Formal analysis, Data acquisition, Validation, Visualization, Methodology, Writing - original draft, Writing - review and editing. Y.Y - Conceptualization, Resources, Supervision, Funding acquisition, Validation, Investigation, Methodology, Project administration, Writing - review and editing

Additional files

Supplementary Movie 1.



Supplementary Figure 1.

Decision-making in echolocation-based pathfinding

The diagram illustrates the sequential steps in a bat's pathfinding process based on echolocation. This process starts with the emission of an echolocation call (1) and the reception of echoes and interfering signals (2), followed by sensory processing for detection, range estimation, and direction of arrival (DOA) (3). After integrating detections over a 1–10 call window (4), the bat engages in **crash avoidance** (5) by evaluating the proximity of conspecifics and obstacles directly ahead. If either is too close, the bat turns to the opposite direction. If no immediate threat is detected, the bat proceeds to **pathfinding** (6). During pathfinding, it checks for obstacles and, if an opening is detected, flies toward the gap's center. Without the optional **temporal aggregation process** (green), the bat simply integrates detections and flies toward the farthest detected obstacle, interpreting it as a wall edge. If the temporal aggregation is included (9), a one-second short memory aids in clustering detections, estimating wall edges, and identifying openings, while also allowing the bat to follow walls at a constant distance. Throughout, the bat continuously adjusts echolocation parameters (8) and controls flight direction and velocity (7) based on ongoing sensory information and decision-making.

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University of Oxford, Oxford, United Kingdom

Senior Editor
Andrew King
University of Oxford, Oxford, United Kingdom

Reviewer #1 (Public review):

Summary:

Mazer & Yovel 2025 dissect the inverse problem of how echolocators in groups manage to navigate their surroundings despite intense jamming using computational simulations.

The authors show that despite the 'noisy' sensory environments that echolocating groups present, agents can still access some amount of echo-related information and use it to navigate their local environment. It is known that echolocating bats have strong small and large-scale spatial memory that plays an important role for individuals. The results from this paper also point to the potential importance of an even lower-level, short-term role of memory in the form of echo 'integration' across multiple calls, despite the unpredictability of echo detection in groups. The paper generates a useful basis to think about the mechanisms in echolocating groups for experimental investigations too.

Strengths:

(1) The paper builds on biologically well-motivated and parametrised 2D acoustics and sensory simulation setup to investigate the various key parameters of interest

(2) The 'null-model' of echolocators not being able to tell apart objects & conspecifics while echolocating still shows agents successfully emerge from groups - even though the probability of emergence drops severely in comparison to cognitively more 'capable' agents. This is nonetheless an important result showing the direction-of-arrival of a sound itself is the 'minimum' set of ingredients needed for echolocators navigating their environment.

(3) The results generate an important basis in unraveling how agents may navigate in sensorially noisy environments with a lot of irrelevant and very few relevant cues.

(4) The 2D simulation framework is simple and computationally tractable enough to perform multiple runs to investigate many variables - while also remaining true to the aim of the investigation.

Weaknesses:

There are a few places in the paper that can be misunderstood or don't provide complete details. Here is a selection:

(1) Line 61: '... studies have focused on movement algorithms while overlooking the sensory challenges involved' : This statement does not match the recent state of the literature. While the previous models may have had the assumption that all neighbours can be detected, there are models that specifically study the role of limited interaction arising from a potential inability to track all neighbours due to occlusion, and the effect of responding to only one/few neighbours at a time e.g. Bode et al. 2011 R. Soc. Interface, Rosenthal et al. 2015 PNAS, Jhawar et al. 2020 Nature Physics.

(2) The word 'interference' is used loosely places (Line 89: '...took all interference signals...', Line 319: 'spatial interference') - this is confusing as it is not clear whether the authors refer to interference in the physics/acoustics sense, or broadly speaking as a synonym for reflections and/or jamming.

(3) The paper discusses original results without reference to how they were obtained or what was done. The lack of detail here must be considered while interpreting the Discussion e.g.

Line 302 ('our model suggests...increasing the call-rate..' - no clear mention of how/where call-rate was varied) & Line 323 '..no benefit beyond a certain level..' - also no clear mention of how/where call-level was manipulated in the simulations.

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Reviewer #2 (Public review):

This manuscript describes a detailed model of bats flying together through a fixed geometry. The model considers elements that are faithful to both bat biosonar production and reception and the acoustics governing how sound moves in the air and interacts with obstacles. The model also incorporates behavioral patterns observed in bats, like one-dimensional feature following and temporal integration of cognitive maps. From a simulation study of the model and comparison of the results with the literature, the authors gain insight into how often bats may experience destructive interference of their acoustic signals and those of their peers, and how much such interference may actually negatively affect the groups' ability to navigate effectively. The authors use generalized linear models to test the significance of the effects they observe.

In terms of its strengths, the work relies on a thoughtful and detailed model that faithfully incorporates salient features, such as acoustic elements like the filter for a biological receiver and temporal aggregation as a kind of memory in the system. At the same time, the authors' abstract features are complicating without being expected to give additional insights, as can be seen in the choice of a two-dimensional rather than three-dimensional system. I thought that the level of abstraction in the model was perfect, enough to demonstrate their results without needless details. The results are compelling and interesting, and the authors do a great job discussing them in the context of the biological literature.

The most notable weakness I found in this work was that some aspects of the model were not entirely clear to me. For example, the directionality of the bat's sonar call in relation to its velocity. Are these the same? If so, what is the difference between phi_target and phi_tx in the model equations? What is a bat's response to colliding with a conspecific (rather than a wall)? From the statistical side, it was not clear if replicate simulations were performed. If they were, which I believe is the right way due to stochasticity in the model, how many replicates were used, and are the standard errors referred to throughout the paper between individuals in the same simulation or between independent simulations, or both?

Overall, I found these weaknesses to be superficial and easily remedied by the authors. The authors presented well-reasoned arguments that were supported by their results, and which were used to demonstrate how call interference impacts the collective's roost exit as measured by several variables. As the authors highlight, I think this work is valuable to individuals interested in bat biology and behavior, as well as to applications in engineered multi-agent systems like robotic swarms.

https://doi.org/10.7554/eLife.105571.1.sa2

Reviewer #3 (Public review):

Summary:

The authors describe a model to mimic bat echolocation behavior and flight under high-density conditions and conclude that the problem of acoustic jamming is less severe than previously thought, conflating the success of their simulations (as described in the manuscript) with hard evidence for what real bats are actually doing. The authors base their

model on two species of bats that fly at "high densities" (defined by the authors as colony sizes from tens to tens of thousands of individuals and densities of up to 33.3 bats/m2), Pipistrellus kuhli and Rhinopoma microphyllum. This work fits into the broader discussion of bat sensorimotor strategies during collective flight, and simulations are important to try to understand bat behavior, especially given a lack of empirical data. However, I have major concerns about the assumptions of the parameters used for the simulation, which significantly impact both the results of the simulation and the conclusions that can be made from the data. These details are elaborated upon below, along with key recommendations the authors should consider to guide the refinement of the model.

Strengths:

This paper carries out a simulation of bat behavior in dense swarms as a way to explain how jamming does not pose a problem in dense groups. Simulations are important when we lack empirical data. The simulation aims to model two different species with different echolocation signals, which is very important when trying to model echolocation behavior. The analyses are fairly systematic in testing all ranges of parameters used and discussing the differential results.

Weaknesses:

The justification for how the different foraging phase call types were chosen for different object detection distances in the simulation is unclear. Do these distances match those recorded from empirical studies, and if so, are they identical for both species used in the simulation? What reasoning do the authors have for a bat using the same call characteristics to detect a cave wall as they would for detecting a small insect? Additionally, details on the signal creation are also absent, but based on the sample spectrogram in Figure 2A, it appears that the authors used a synthetic linear FM chirp characterized by the call parameters. This simplification of the echolocation signals for these species is not representative of the true emitted signals, which are nonlinear FM for not only the species used within this simulation--PK (Schnitzler et al., 1987; Kalko and Schnitzler 1993 and RM (Schmidt and Joermann 1986)-but also for many other bat species that form large aggregations and undergo dense emergence. Furthermore, echolocation calls of bats emitted during dense emergence flights (see Gillam et al 2010) can be very much different from those emitted during foraging calls, so limiting the simulation to foraging calls may not be valid. Why did the authors not use actual waveforms of calls produced by these species during dense emergence to use biologically relevant signals in their simulation?

The two species modeled have different calls. In particular, the bandwidth varies by a factor of 10, meaning the species' sonars will have different spatial resolutions. Range resolution is about 10x better for PK compared to RM, but the authors appear to use the same thresholds for "correct detection" for both, which doesn't seem appropriate. Also, the authors did not mention incorporating/correcting for/exploiting Doppler, which leads me to assume they did not model it.

The success of the simulation may very well be due to variation in the calls of the bats, which ironically enough demonstrates the importance of a jamming avoidance response in dense flight. This explains why the performance of the simulation falls when bats are not able to distinguish their own echoes from other signals. For example, in Figure C2, there are calls that are labeled as conspecific calls and have markedly shorter durations and wider bandwidths than others. These three phases for call types used by the authors may be responsible for some (or most) of the performance of the model since the correlation between different call types is unlikely to exceed the detection threshold. But it turns out this variation in and of itself is what a jamming avoidance response may consist of. So, in essence, the authors are incorporating a jamming avoidance response into their simulation.

The authors claim that integration over multiple pings (though I was not able to determine the specifics of this integration algorithm) reduces the masking problem. Indeed, it should: if you have two chances at detection, you've effectively increased your SNR by 3dB.

They also claim - although it is almost an afterthought - that integration dramatically reduces the degradation caused by false echoes. This also makes sense: from one ping to the next, the bat's own echo delays will correlate extremely well with the bat's flight path. Echo delays due to conspecifics will jump around kind of randomly. However, the main concern is regarding the time interval and number of pings of the integration, especially in the context of the bat's flight speed. The authors say that a 1s integration interval (5-10 pings) dramatically reduces jamming probability and echo confusion. This number of pings isn't very high, and it occurs over a time interval during which the bat has moved 5-10m. This distance is large compared to the 0.4m distance-to-obstacle that triggers an evasive maneuver from the bat, so integration should produce a latency in navigation that significantly hinders the ability to avoid obstacles. Can the authors provide statistics that describe this latency, and discussion about why it doesn't seem to be a problem?

The authors are using a 2D simulation, but this very much simplifies the challenge of a 3D navigation task, and there is an explanation as to why this is appropriate. Bat densities and bat behavior are discussed per unit area when realistically it should be per unit volume. In fact, the authors reference studies to justify the densities used in the simulation, but these studies were done in a 3D world. If the authors have justification for why it is realistic to model a 3D world in a 2D simulation, I encourage them to provide references justifying this approach.

The focus on "masking" (which appears to be just in-band noise), especially relative to the problem of misassigned echoes, is concerning. If the bat calls are all the same waveform (downsweep linear FM of some duration, I assume - it's not clear from the text), false echoes would be a major problem. Masking, as the authors define it, just reduces SNR. This reduction is something like sqrt(N), where N is the number of conspecifics whose echoes are audible to the bat, so this allows the detection threshold to be set lower, increasing the probability that a bat's echo will exceed a detection threshold. False echoes present a very different problem. They do not reduce SNR per se, but rather they cause spurious threshold excursions (N of them!) that the bat cannot help but interpret as obstacle detection. I would argue that in dense groups the mis-assignment problem is much more important than the SNR problem.

The criteria set for flight behavior (lines 393-406) are not justified with any empirical evidence of the flight behavior of wild bats in collective flight. How did the authors determine the avoidance distances? Also, what is the justification for the time limit of 15 seconds to emerge from the opening? Instead of an exit probability, why not instead use a time criterion, similar to "How long does it take X% of bats to exit?" What is the empirical justification for the 1-10 calls used for integration? The "average exit time for 40 bats" is also confusing and not well explained. Was this determined empirically? From the simulation? If the latter, what are the conditions? Does it include masking, no masking, or which species?

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Author response:

> ***Public Reviews:***
>
> ***Reviewer #1 (Public review):***

We thank the reviewer for his valuable input and careful assessment, which have significantly improved the clarity and rigor of our manuscript.

> *Summary:*
>
> *Mazer & Yovel 2025 dissect the inverse problem of how echolocators in groups manage to navigate their surroundings despite intense jamming using computational simulations.*
>
> *The authors show that despite the 'noisy' sensory environments that echolocating groups present, agents can still access some amount of echo-related information and use it to navigate their local environment. It is known that echolocating bats have strong small and large-scale spatial memory that plays an important role for individuals. The results from this paper also point to the potential importance of an even lower-level, short-term role of memory in the form of echo 'integration' across multiple calls, despite the unpredictability of echo detection in groups. The paper generates a useful basis to think about the mechanisms in echolocating groups for experimental investigations too.*
>
> *Strengths:*
>
> *(1) The paper builds on biologically well-motivated and parametrised 2D acoustics and sensory simulation setup to investigate the various key parameters of interest*
>
> *(2) The 'null-model' of echolocators not being able to tell apart objects & conspecifics while echolocating still shows agents successfully emerge from groups - even though the probability of emergence drops severely in comparison to cognitively more 'capable' agents. This is nonetheless an important result showing the direction-of-arrival of a sound itself is the 'minimum' set of ingredients needed for echolocators navigating their environment.*
>
> *(3) The results generate an important basis in unraveling how agents may navigate in sensorially noisy environments with a lot of irrelevant and very few relevant cues.*
>
> *(4) The 2D simulation framework is simple and computationally tractable enough to perform multiple runs to investigate many variables - while also remaining true to the aim of the investigation.*
>
> *Weaknesses:*
>
> *There are a few places in the paper that can be misunderstood or don't provide complete details. Here is a selection:*
>
> *(1) Line 61: '... studies have focused on movement algorithms while overlooking the sensory challenges involved' : This statement does not match the recent state of the literature. While the previous models may have had the assumption that all neighbours can be detected, there are models that specifically study the role of limited interaction arising from a potential inability to track all neighbours due to occlusion, and the effect of responding to only one/few neighbours at a time e.g. Bode et al. 2011 R. Soc. Interface, Rosenthal et al. 2015 PNAS, Jhawar et al. 2020 Nature Physics.*

We appreciate the reviewer's comment and the relevant references. We have revised the manuscript accordingly to clarify the distinction between studies that incorporate limited

interactions and those that explicitly analyze sensory constraints and interference. We have refined our statement to acknowledge these contributions while maintaining our focus on sensory challenges beyond limited neighbor detection, such as signal degradation, occlusion effects, and multimodal sensory integration (see lines 61-64):

While collective movement has been extensively studied in various species, including insect swarming, fish schooling, and bird murmuration (Pitcher, Partridge and Wardle, 1976; Partridge, 1982; Strandburg-Peshkin et al., 2013; Pearce et al., 2014; Rosenthal, Twomey, Hartnett, Wu, Couzin, et al., 2015; Bastien and Romanczuk, 2020; Davidson et al., 2021; Aidan, Bleichman and Ayali, 2024), as well as in swarm robotics agents performing tasks such as coordinated navigation and maze-solving (Faria Dias *et al.*, 2021; Youssefi and Rouhani, 2021; Cheraghi, Shahzad and Graffi, 2022), most studies have focused on movement algorithms , often assuming full detection of neighbors (Parrish and Edelstein-Keshet, 1999; Couzin *et al.*, 2002, 2005; Sumpter *et al.*, 2008; Nagy *et al.*, 2010; Bialek *et al.*, 2012; Gautrais *et al.*, 2012; Attanasi *et al.*, 2014). Some models have incorporated limited interaction rules where individuals respond to one or a few neighbors due to sensory constraints (Bode, Franks and Wood, 2011; Jhawar *et al.*, 2020). However, fewer studies explicitly examine how sensory interference, occlusion, and noise shape decision-making in collective systems (Rosenthal *et al.*, 2015).

> *(2) The word 'interference' is used loosely places (Line 89: '...took all interference signals...', Line 319: 'spatial interference') - this is confusing as it is not clear whether the authors refer to interference in the physics/acoustics sense, or broadly speaking as a synonym for reflections and/or jamming.*

To improve clarity, we have revised the manuscript to distinguish between different types of interference:

· Acoustic interference (jamming): Overlapping calls that completely obscure echo detection, preventing bats from perceiving necessary environmental cues.

· Acoustic interference (masking): Partial reduction in signal clarity due to competing calls.

· Spatial interference: Physical obstruction by conspecifics affecting movement and navigation.

We have updated the manuscript to use these terms consistently and explicitly define them in relevant sections (see lines 87-94 and 329-330). This distinction ensures that the reader can differentiate between interference as an acoustic phenomenon and its broader implications in navigation.

> *(3) The paper discusses original results without reference to how they were obtained or what was done. The lack of detail here must be considered while interpreting the Discussion e.g. Line 302 ('our model suggests...increasing the call-rate..' - no clear mention of how/where call-rate was varied) & Line 323 '..no benefit beyond a certain level..' - also no clear mention of how/where call-level was manipulated in the simulations.*

All tested parameters, including call rate dynamics and call intensity variations, are detailed in the Methods section and Tables 1 and 2. Specifically:

· Call Rate Variation: The Inter-Pulse Interval (IPI) was modeled based on documented echolocation behavior, decreasing from 100 msec during the search phase to 35 msec (~28 calls per second) at the end of the approach phase, and to 5 msec (200 calls per second) during the final buzz (see Table 2). This natural variation in call rate was not manually manipulated in the model but emerged from the simulated bat behavior.

· Call Intensity Variation: The tested call intensity levels (100, 110, 120, 130 dB SPL) are presented in Table 1 under the “Call Level” parameter. The effect of increasing call intensity was analyzed in relation to exit probability, jamming probability, and collision rate. This is now explicitly referenced in the Discussion.

We have revised the manuscript to explicitly reference these aspects in the Results and Discussion sections.

> ***Reviewer #2 (Public review):***

We are grateful for the reviewer’s insightful feedback, which has helped us clarify key aspects of our research and strengthen our conclusions.

> *This manuscript describes a detailed model of bats flying together through a fixed geometry. The model considers elements that are faithful to both bat biosonar production and reception and the acoustics governing how sound moves in the air and interacts with obstacles. The model also incorporates behavioral patterns observed in bats, like one-dimensional feature following and temporal integration of cognitive maps. From a simulation study of the model and comparison of the results with the literature, the authors gain insight into how often bats may experience destructive interference of their acoustic signals and those of their peers, and how much such interference may actually negatively affect the groups' ability to navigate effectively. The authors use generalized linear models to test the significance of the effects they observe.*
>
> *In terms of its strengths, the work relies on a thoughtful and detailed model that faithfully incorporates salient features, such as acoustic elements like the filter for a biological receiver and temporal aggregation as a kind of memory in the system. At the same time, the authors' abstract features are complicating without being expected to give additional insights, as can be seen in the choice of a two-dimensional rather than three-dimensional system. I thought that the level of abstraction in the model was perfect, enough to demonstrate their results without needless details. The results are compelling and interesting, and the authors do a great job discussing them in the context of the biological literature.*
>
> *The most notable weakness I found in this work was that some aspects of the model were not entirely clear to me.*
>
> *For example, the directionality of the bat's sonar call in relation to its velocity. Are these the same?*

For simplicity, in our model, the head is aligned with the body, therefore the direction of the echolocation beam is the same as the direction of the flight.

Moreover, call directionality (directivity) is not directly influenced by velocity. Instead, directionality is estimated using the piston model, as described in the Methods section. The directionality is based on the emission frequency and is thus primarily linked to the behavioral phases of the bat, with frequency shifts occurring as the bat transitions from search to approach to buzz phases. During the approach phase, the bat emits calls with higher frequencies, resulting in increased directionality. This is supported by the literature (Jakobsen and Surlykke, 2010; Jakobsen, Brinkløv and Surlykke, 2013). This phase is also associated with a natural reduction in flight speed, which is a well-documented behavioral adaptation in echolocating bats (Jakobsen et al., 2024).

To clarify this in the manuscript, we have updated the text to explicitly state that directionality follows phase-dependent frequency changes rather than being a direct function

of velocity, see lines 460-465.

> *If so, what is the difference between phi_target and phi_tx in the model equations?*

ϕ_{target} represents the angle between the bat and the reflected object (target).

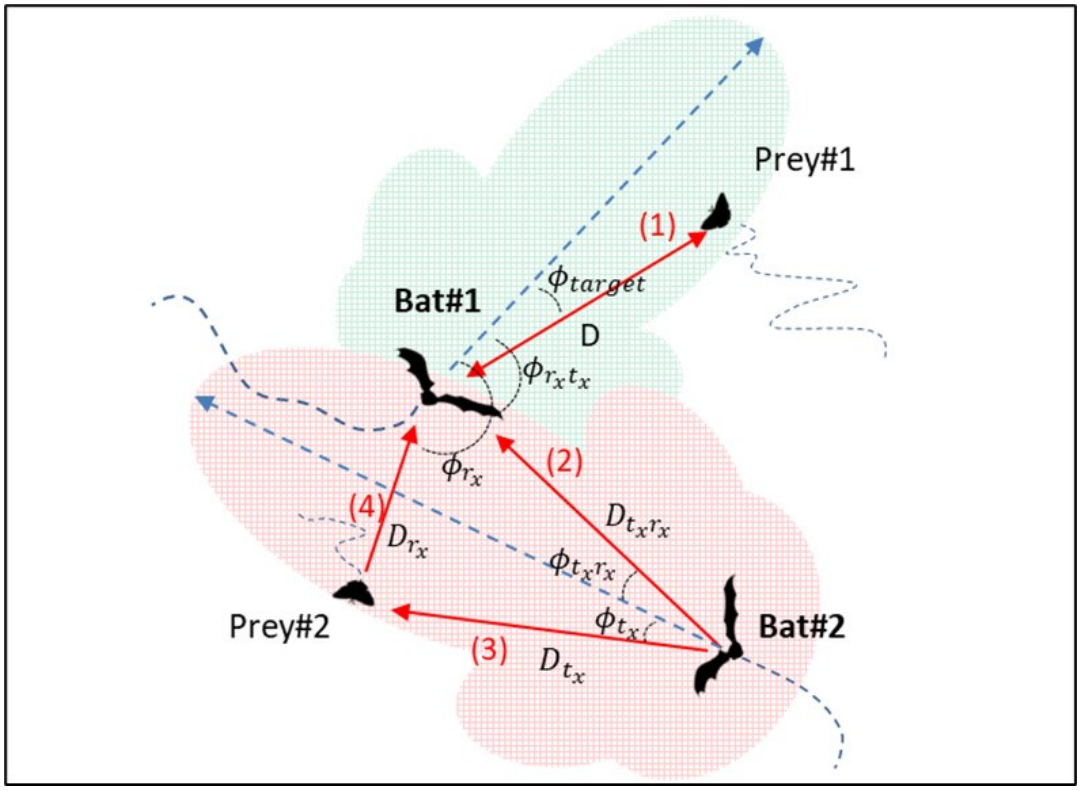
ϕ_{Tx} the angle [rad], between the masking bat and target (from the transmitter's perspective)

ϕ_{TxRx} refers to the angle between the transmitting conspecific and the receiving focal bat, from the transmitter's point of view.

ϕ_{RxTx} represents the angle between the receiving bat and the transmitting bat, from the receiver's point of view.

These definitions have been explicitly stated in the revised manuscript to prevent any ambiguity (lines 467-468). Additionally, a Supplementary figure demonstrating the geometrical relations has been added to the manuscript.

Author response image 1.



> *What is a bat's response to colliding with a conspecific (rather than a wall)?*

In nature, minor collisions between bats are common and typically do not result in significant disruptions to flight (Boerma *et al.*, 2019; Roy *et al.*, 2019; Goldstein *et al.*,

2024).Given this, our model does not explicitly simulate the physical impact of a collision event. Instead, during the collision event the bat keeps decreasing its velocity and changing its flight direction until the distance between bats is above the threshold (0.4 m). We assume that the primary cost of such interactions arises from the effort required to avoid collisions, rather than from the collision itself. This assumption aligns with observations of bat behavior in dense flight environments, where individuals prioritize collision avoidance rather than modeling post-collision dynamics.

> *From the statistical side, it was not clear if replicate simulations were performed. If they were, which I believe is the right way due to stochasticity in the model, how many replicates were used, and are the standard errors referred to throughout the paper between individuals in the same simulation or between independent simulations, or both?*

The number of repetitions for each scenario is detailed in Table 1, but we included it in a more prominent location in the text for clarity. Specifically, we now state (Lines 274-275):

"The number of repetitions for each scenario was as follows: 1 bat: 240; 2 bats: 120; 5 bats: 48; 10 bats: 24; 20 bats: 12; 40 bats: 12; 100 bats: 6."

Regarding the reported standard errors, they are calculated across all individuals within each scenario, without distinguishing between different simulation trials.

We clarified in the revised text (Lines 534-535 in Statistical Analysis)

> *Overall, I found these weaknesses to be superficial and easily remedied by the authors. The authors presented well-reasoned arguments that were supported by their results, and which were used to demonstrate how call interference impacts the collective's roost exit as measured by several variables. As the authors highlight, I think this work is valuable to individuals interested in bat biology and behavior, as well as to applications in engineered multi-agent systems like robotic swarms.*
>
> ***Reviewer #3 (Public review):***

We sincerely appreciate the reviewer's thoughtful comments and the time invested in evaluating our work, which have greatly contributed to refining our study.

We would like to note that in general, our model often simplifies some of the bats' abilities, under the assumption that if the simulated bats manage to perform this difficult task with simpler mechanisms, real better adapted bats will probably perform even better. This thought strategy will be repeated in several of the answers below.

> *Summary:*
>
> *The authors describe a model to mimic bat echolocation behavior and flight under high-density conditions and conclude that the problem of acoustic jamming is less severe than previously thought, conflating the success of their simulations (as described in the manuscript) with hard evidence for what real bats are actually doing. The authors base their model on two species of bats that fly at "high densities" (defined by the authors as colony sizes from tens to tens of thousands of individuals and densities of up to 33.3 bats/m2), Pipistrellus kuhli and Rhinopoma microphyllum. This work fits into the broader discussion of bat sensorimotor strategies during collective flight, and simulations are important to try to understand bat behavior, especially given a lack of empirical data. However, I have major concerns about the assumptions of the parameters used for the simulation, which significantly impact both the results of the simulation and the conclusions that can be made from the data. These details are elaborated upon below,*

> *along with key recommendations the authors should consider to guide the refinement of the model.*
>
> *Strengths:*
>
> *This paper carries out a simulation of bat behavior in dense swarms as a way to explain how jamming does not pose a problem in dense groups. Simulations are important when we lack empirical data. The simulation aims to model two different species with different echolocation signals, which is very important when trying to model echolocation behavior. The analyses are fairly systematic in testing all ranges of parameters used and discussing the differential results.*
>
> *Weaknesses:*
>
> *The justification for how the different foraging phase call types were chosen for different object detection distances in the simulation is unclear. Do these distances match those recorded from empirical studies, and if so, are they identical for both species used in the simulation?*

The distances at which bats transition between echolocation phases are identical for both species in our model (see Table 2). These distances are based on well-documented empirical studies of bat hunting and obstacle avoidance behavior (Griffin, Webster and Michael, 1958; Simmons and Kick, 1983; Schnitzler *et al.*, 1987; Kalko, 1995; Hiryu *et al.*, 2008; Vanderelst and Peremans, 2018). These references provide extensive evidence that insectivorous bats systematically adjust their echolocation calls in response to object proximity, following the characteristic phases of search, approach, and buzz.

To improve clarity, we have updated the text to explicitly state that the phase transition distances are empirically grounded and apply equally to both modeled species (lines 430-447).

> *What reasoning do the authors have for a bat using the same call characteristics to detect a cave wall as they would for detecting a small insect?*

In echolocating bats, call parameters are primarily shaped by the target distance and echo strength. Accordingly, there is little difference in call structure between prey capture and obstacles-related maneuvers, aside from intensity adjustments based on target strength (Hagino *et al.*, 2007; Hiryu *et al.*, 2008; Surlykke, Ghose and Moss, 2009; Kothari *et al.*, 2014). In our study, due to the dense cave environment, the bats are found to operate in the approach phase nearly all the time, which is consistent with natural cave emergence, where they are navigating through a cluttered environment rather than engaging in open-space search. For one of the species (*Rhinopoma M.*), we also have empirical recordings of individuals flying under similar conditions (Goldstein *et al.*, 2024). Our model was designed to remain as simple as possible while relying on conservative assumptions that may underestimate bat performance. If, in reality, bats fine-tune their echolocation calls even earlier or more precisely during navigation than assumed, our model would still conservatively reflect their actual capabilities.

We actually used logarithmically frequency modulated (FM) chirps, generated using the MATLAB built-in function chirp(t, f0, t1, f1, 'logarithmic'). This method aligns with the nonlinear FM characteristics of *Pipistrellus kuhlii* (PK) and *Rhinopoma microphyllum* (RM) and provides a realistic approximation of their echolocation signals. We acknowledge that this was not sufficiently emphasized in the original text, and we have now explicitly highlighted this in the revised version to ensure clarity (sell Lines 447-449 in Methods).

> *The two species modeled have different calls. In particular, the bandwidth varies by a factor of 10, meaning the species' sonars will have different spatial resolutions. Range resolution is about 10x better for PK compared to RM, but the authors appear to use the same thresholds for "correct detection" for both, which doesn't seem appropriate.*

The detection process in our model is based on Saillant's method using a filter bank, as detailed in the paper (Saillant *et al.*, 1993; Neretti *et al.*, 2003; Sanderson *et al.*, 2003). This approach inherently incorporates the advantages of a wider bandwidth, meaning that the differences in range resolution between the species are already accounted for within the signal-processing framework. Thus, there is no need to explicitly adjust the model parameters for bandwidth variations, as these effects emerge from the applied method.

> *Also, the authors did not mention incorporating/correcting for/exploiting Doppler, which leads me to assume they did not model it.*

The reviewer is correct. To maintain model simplicity, we did not incorporate the Doppler effect or its impact on echolocation. The exclusion of Doppler effects was based on the assumption that while Doppler shifts can influence frequency perception, their impact on jamming and overall navigation performance is minor within the modelled context.

The maximal Doppler shifts expected for the bats in this scenario are of ~ 1kHz. These shifts would be applied variably across signals due to the semi-random relative velocities between bats, leading to a mixed effect on frequency changes. This variability would likely result in an overall reduction in jamming rather than exacerbating it, aligning with our previous statement that our model may overestimate the severity of acoustic interference. Such Doppler shifts would result in errors of 2-4 cm in localization (i.e., 200-400 micro-seconds) (Boonman, Parsons and Jones, 2003).

We have now explicitly highlighted this in the revised version (see Lines 468-470).

> *The success of the simulation may very well be due to variation in the calls of the bats, which ironically enough demonstrates the importance of a jamming avoidance response in dense flight. This explains why the performance of the simulation falls when bats are not able to distinguish their own echoes from other signals. For example, in Figure C2, there are calls that are labeled as conspecific calls and have markedly shorter durations and wider bandwidths than others. These three phases for call types used by the authors may be responsible for some (or most) of the performance of the model since the correlation between different call types is unlikely to exceed the detection threshold. But it turns out this variation in and of itself is what a jamming avoidance response may consist of. So, in essence, the authors are incorporating a jamming avoidance response into their simulation.*

We fully agree that the natural variations in call design between the phases contribute significantly to interference reduction (see our discussion in a previous paper in Mazar & Yovel, 2020). However, we emphasize that this cannot be classified as a Jamming Avoidance Response (JAR). In our model, bats respond only to the physical presence of objects and not to the acoustic environment or interference itself. There is no active or adaptive adjustment of call design to minimize jamming beyond the natural phase-dependent variations in call structure. Therefore, while variation in call types does inherently reduce interference, this effect emerges passively from the modeled behavior rather than as an intentional strategy to avoid jamming.

> *The authors claim that integration over multiple pings (though I was not able to determine the specifics of this integration algorithm) reduces the masking problem.*

> *Indeed, it should: if you have two chances at detection, you've effectively increased your SNR by 3dB.*

The reviewer is correct. Indeed, integration over multiple calls improves signal-to-noise ratio (SNR), effectively increasing it by approximately 3 dB per doubling of observations. The specifics of the integration algorithm are detailed in the Methods section, where we describe how sensory information is aggregated across multiple time steps to enhance detection reliability.

> *They also claim - although it is almost an afterthought - that integration dramatically reduces the degradation caused by false echoes. This also makes sense: from one ping to the next, the bat's own echo delays will correlate extremely well with the bat's flight path. Echo delays due to conspecifics will jump around kind of randomly. However, the main concern is regarding the time interval and number of pings of the integration, especially in the context of the bat's flight speed. The authors say that a 1s integration interval (5-10 pings) dramatically reduces jamming probability and echo confusion. This number of pings isn't very high, and it occurs over a time interval during which the bat has moved 5-10m. This distance is large compared to the 0.4m distance-to-obstacle that triggers an evasive maneuver from the bat, so integration should produce a latency in navigation that significantly hinders the ability to avoid obstacles. Can the authors provide statistics that describe this latency, and discussion about why it doesn't seem to be a problem?*

As described in the Methods section, the bat's collision avoidance response does not solely rely on the integration process. Instead, the model incorporates real-time echoes from the last calls, which are used independently of the integration process for immediate obstacle avoidance maneuvers. This ensures that bats can react to nearby obstacles without being hindered by the integration latency. The slower integration on the other hand is used for clustering, outlier removal and estimation wall directions to support the pathfinding process, as illustrated in Supplementary Figure 1.

Additionally, our model assumes that bats store the physical positions of echoes in an allocentric coordinate system (x-y). The integration occurs after transforming these detections from a local relative reference frame to a global spatial representation. This allows for stable environmental mapping while maintaining responsiveness to immediate changes in the bat's surroundings.

See lines 518-523 in the revied version.

> *The authors are using a 2D simulation, but this very much simplifies the challenge of a 3D navigation task, and there is an explanation as to why this is appropriate. Bat densities and bat behavior are discussed per unit area when realistically it should be per unit volume. In fact, the authors reference studies to justify the densities used in the simulation, but these studies were done in a 3D world. If the authors have justification for why it is realistic to model a 3D world in a 2D simulation, I encourage them to provide references justifying this approach.*

We acknowledge that this is a simplification; however, from an echolocation perspective, a 2D framework represents a worst-case scenario in terms of bat densities and maneuverability:

· Higher Effective Density: A 2D model forces all bats into a single plane rather than distributing them through a 3D volume, increasing the likelihood of overlap in calls and echoes and making jamming more severe. As described in the text: the average distance to the nearest bat in our simulation is 0.27m (with 100 bats), whereas reported distances in very

dense colonies are 0.5m, as observed *in Myotis grisescens* and *Tadarida brasiliensis* (Fujioka et al., 2021; Sabol and Hudson, 1995; Betke et al., 2008; Gillam et al, 2010)

· Reduced Maneuverability: In 3D space, bats can use vertical movement to avoid obstacles and conspecifics. A 2D constraint eliminates this degree of freedom, increasing collision risk and limiting escape options.

Thus, our 2D model provides a conservative difficult test case, ensuring that our findings are valid under conditions where jamming and collision risks are maximized. Additionally, the 2D framework is computationally efficient, allowing us to perform multiple simulation runs to explore a broad parameter space and systematically test the impact of different variables.

To address the reviewer's concern, we have clarified this justification in the revised text and will provide supporting references where applicable: (see Methods lines 407-412)

> *The focus on "masking" (which appears to be just in-band noise), especially relative to the problem of misassigned echoes, is concerning. If the bat calls are all the same waveform (downsweep linear FM of some duration, I assume - it's not clear from the text), false echoes would be a major problem. Masking, as the authors define it, just reduces SNR. This reduction is something like sqrt(N), where N is the number of conspecifics whose echoes are audible to the bat, so this allows the detection threshold to be set lower, increasing the probability that a bat's echo will exceed a detection threshold. False echoes present a very different problem. They do not reduce SNR per se, but rather they cause spurious threshold excursions (N of them!) that the bat cannot help but interpret as obstacle detection. I would argue that in dense groups the mis-assignment problem is much more important than the SNR problem.*

There is substantial literature supporting the assumption that bats can recognize their own echoes and distinguish them from conspecific signals (Schnitzler and Bioscience, 2001; Kazial, Burnett and Masters, 2001; Burnett and Masters, 2002; Kazial, Kenny and Burnett, 2008; Chili, Xian and Moss, 2009; Yovel et al., 2009; Beetz and Hechavarría, 2022). However, we acknowledge that false echoes may present a major challenge in dense groups. To address this, we explicitly tested the impact of the self-echo identification assumption in our study see Results Figure 4: The impact of confusion on performance, and lines 345-355 in the Discussion.

Furthermore, we examined a full confusion scenario, where all reflected echoes from conspecifics were misinterpreted as obstacle reflections (i.e., 100% confusion). Our results show that this significantly degrades navigation performance, supporting the argument that echo misassignment is a critical issue. However, we also explored a simple mitigation strategy based on temporal integration with outlier rejection, which provided some improvement in performance. This suggests that real bats may possess additional mechanisms to enhance self-echo identification and reduce false detections. See lines XX in the manuscript for further discussion.

> *The criteria set for flight behavior (lines 393-406) are not justified with any empirical evidence of the flight behavior of wild bats in collective flight. How did the authors determine the avoidance distances? Also, what is the justification for the time limit of 15 seconds to emerge from the opening? Instead of an exit probability, why not instead use a time criterion, similar to "How long does it take X% of bats to exit?"*

While we acknowledge that wild bats may employ more complex behaviors for collision avoidance, we chose to implement a simplified decision-making rule in our model to maintain computational tractability.

The avoidance distances (1.5 m from walls and 0.4 m from other bats) were selected as internal parameters to ensure coherent flight trajectories while maintaining a reasonable collision rate. These distances provide a balance between maneuverability and stability, preventing erratic flight patterns while still enabling effective obstacle avoidance. In the revised paper, we have added supplementary figures illustrating the effect of model parameters on performance, specifically focusing on the avoidance distance.

The 15-second exit limit was determined as described in the text (Lines 403-404): “A 15-second window was chosen because it is approximately twice the average exit time for 40 bats and allows for a second corrective maneuver if needed.” In other words, it allowed each bat to circle the ‘cave’ twice to exit even in the most crowded environment. This threshold was set to keep simulation time reasonable while allowing sufficient time for most bats to exit successfully.

We acknowledge that the alternative approach suggested by the reviewer—measuring the time taken for a certain percentage of bats to exit—is also valid. However, in our model, some outlier bats fail to exit and continue flying for many minutes, Such simulations would lead to excessive simulation times making it difficult to generate repetitions and not teaching us much – they usually resulted from the bat slightly missing the opening (see video S1. Our chosen approach ensures practical runtime constraints while still capturing relevant performance metrics.

> *What is the empirical justification for the 1-10 calls used for integration?*
>
> *The "average exit time for 40 bats" is also confusing and not well explained. Was this determined empirically? From the simulation? If the latter, what are the conditions? Does it include masking, no masking, or which species?*

Previous studies have demonstrated that bats integrate acoustic information received sequentially over several echolocation calls (2-15), effectively constructing an auditory scene in complex environments (Ulanovsky and Moss, 2008; Chili, Xian and Moss, 2009; Moss and Surlykke, 2010; Yovel and Ulanovsky, 2017; Salles, Diebold and Moss, 2020). Additionally, bats are known to produce echolocation sound groups when spatiotemporal localization demands are high (Kothari et al., 2014). Studies have documented call sequences ranging from 2 to 15 grouped calls (Moss et al., 2010), and it has been hypothesized that grouping facilitates echo segregation.

We did not use a single integration window - we tested integration sizes between 1 and 10 calls and presented the results in Figure 3A. This range was chosen based on prior empirical findings and to explore how different levels of temporal aggregation impact navigation performance. Indeed, the results showed that the performance levels between 5-10 calls integration window (Figure 3A)

Regarding the average exit time for 40 bats, this value was determined from our simulations, where it represents the mean time for successful exits under standard conditions with masking.

We have revised the text to clarify these details see, lines 466.

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