Swarm Cohesion in Bats Emerges from Stable Temporal Loops

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Abstract. Swarming in echolocating bats presents a compelling example of decentralised coordination driven by acoustic sensing. Unlike visually guided animals, bats navigate and maintain cohesion in dense groups using self-generated sonar signals. I present a biologically grounded simulation framework in which agents operate asynchronously using a closed-loop control policy based on local echo delays. Building on the theory of biosonar responsivity and the deduction of temporal precision in bat echolocation, my model predicts a tight coupling between echo delay, call duration, and call rate, and demonstrates that local, echo-timed interactions suffice to generate stable, self-organised swarm behaviour. To test these predictions, I systematically varied initial velocity and responsivity coefficient (k_r) across a simulation grid and analysed the resulting call dynamics and collision risks. An information propagation model was derived, estimating the effective spatiotemporal speed of behavioural updates across the swarm. I also developed a decay-based model of perturbation attenuation to quantify the spatial limit of influence for local disturbances. Together, these analyses reveal a trade-off between responsiveness and stability: lower k_r yields faster information flow but higher collision risk in denser regions, while higher k_r promotes stability but reduces reactivity. My results align closely with recent empirical findings and provide a generative explanation for swarm cohesion based on the temporal precision of echolocation. These insights offer a promising design framework for decentralised control in bioinspired robotic swarms, where stability, autonomy, and resilience emerge from local sensing and feedback, rather than explicit synchrony or global coordination.

Keywords: Echolocation, Swarm dynamics, Temporal coordination, Responsivity, Collective behaviour, Bats

1 INTRODUCTION

Collective behaviour in aggregations of individuals emerges from local interactions and self-organising dynamics [1], raising fundamental questions in behavioural biology about how individual-level adaptations give rise to stable group cohesion [2, 3]. Large herds of migratory birds and the spectacular emergence of millions of Mexican free-tailed or greater mouse-tailed bats, among other species, present striking examples of these phenomena. In bats, the dynamic processes that maintain coherence during dense flight aggregations are of particular interest, as these animals rely primarily on audition—unlike birds, which depend on vision—to perceive and coordinate with conspecifics.

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A long-standing challenge in understanding swarming bats is the so-called "cocktail party problem"—how each bat can navigate acoustically when surrounded by numerous conspecifics emitting high-intensity calls. Recordings from cave emergence sites reveal dense spectrotemporal overlap, sometimes producing near-continuous acoustic scenes. It has often been presumed that such acoustic scenes reaching an observer's microphone reflect the auditory experience of individual bats [4–6]. However, careful consideration suggests otherwise: the most relevant echoes for any given bat are those returning from the nearest neighbours directly ahead, within the bat's effective sonar range in both distance and beam geometry. Moreover, directional hearing and adaptive modulation of both emission and reception patterns may substantially reduce the impact of distant calls and unrelated clutter. The true extent of interference may therefore be less severe than often presumed.

Summary. The evening emergence of bats from caves-millions streaming into the sky in twisting, coordinated ribbons-has long fascinated observers. Despite the incredible density and speed of these flights, bats rarely collide and maintain fluid, cohesive movement. Unlike birds or fish, bats navigate using sound: they emit high-frequency calls and interpret returning echoes to sense their surroundings. But in a dense swarm filled with thousands of calling individuals, how do they avoid overwhelming acoustic interference?

I present a formal framework and agent-based simulation demonstrating that bats solve the challenge of acoustic interference through a simple yet powerful principle: each bat tracks the echo from its nearest neighbour and times its next call based on this echo delay—a fundamental feature of biosonar behaviour preserved across contexts. This echo-timed coordination forms a closed-loop feedback system, enabling continuous, real-time adjustments without requiring global synchrony or awareness. My simulations show that this local timing mechanism maintains swarm stability even under crowded conditions, with information propagating through the group like a wave—rapid enough to support timely corrections, yet naturally attenuated to prevent overreaction. These findings align closely with a growing body of empirical work and reflect a broader shift in understanding how echolocating animals mitigate acoustic interference in complex social environments.

This model not only explains how bats maintain safe spacing in flight, but also offers insights for designing autonomous robotic swarms that are decentralised, responsive, and robust.

Recent modelling and empirical studies have adopted this view and proposed that a bat's behaviour is primarily guided by echoes from its nearest neighbour [7, 8]. Supporting this, recent empirical work by Goldshtein et al (2025) [9], analysing call parameters during emergence flights, has shown adaptations resembling those observed in cluttered environments, suggesting that bats track their nearest neighbours.

Building on these lines of evidence, I investigate whether local sonar-driven interactions alone can produce stable and cohesive swarm flight. My work is grounded in the responsivity framework [10] and the theory of temporal loop stability [11] developed recently. These models demonstrated that echolocation in bats is governed by a closed-loop control structure, wherein each emitted call initiates a processing cycle triggered by the first relevant echo (FRE). This generates a highly precise call-echo-response loop, with interpulse intervals that show a stable,

hyperbolic relationship to call rate—contradicting any model of random or periodic calling.

I extended the responsivity framework and empirical evidence for temporal precision in echolocation to derive behavioural predictions for swarm flight in dense acoustic environments, such as those observed during emergence from large colonies. According to the velocity–call rate trade-off model [10], a bat's call timing is dynamically modulated by the relative velocity and distance to its target. In the limiting case of near-zero relative velocity—such as when a bat closely trails a conspecific moving at similar speed—the model predicts an infinite pursuit without closure, resulting in a high call rate governed by the relationship $T_b = k_r \cdot T_a$, where T_a is the echo delay and $T_b + T_a$ constitute the interpulse interval. Consequently, under swarm conditions, where many bats maintain similar velocities and distances, one may expect the emergence of high call rates and systematically shortened call durations (cf. call duration model in [10]).

Furthermore, the reaction time constraints derived from the responsivity model impose a fundamental limit: any event unfolding faster than a bat's response latency will not elicit corrective behaviour. In a swarm context, this implies that when time-to-collision (TTC) falls below the bat's effective reaction window (T_b), a collision risk arises. Thus, the theoretical framework predicts that collision risks emerge primarily in scenarios with high relative speeds and insufficient sensorimotor lead time. These predictions form the basis for the simulation experiments presented here, where swarm dynamics and collision events are examined across a systematically varied grid of k_r and v_0 combinations.

Building on this theory, I constructed an asynchronous simulation of swarming *Vespertillio numeralis*, a simulated bat species [10], to test whether fundamental principles of temporal precision in biosonar behaviour can explain swarm dynamics. I modelled each bat as an independent agent following a closed-loop control policy, in which sonar parameters adapt continuously to sensory input from the nearest forward target. The central hypothesis is that this local control suffices to generate coherent, self-organised swarm behaviour without central coordination or explicit spacing rules.

I further analysed local collision risks by applying reaction-time constraints from my previous work [10], quantifying when and where risks are elevated. Importantly, I show that while local perturbations may arise—leading occasionally to close approaches or minor collisions—these do not destabilise the overall swarm structure. Instead, the inherent temporal precision of echolocation enables continuous correction, smoothing out perturbations over time. Further, I derive a model for determining the rate of information transfer across the swarm based on biosonar parameters and inter-individual spacing. This model reveals that the propagation of behavioural changes is governed by the responsivity coefficient k_r and the echo delay geometry, thereby linking swarm-level stability to sensory–motor loop timing. The resulting expression for information velocity provides a mechanistic prediction of how fast a local adjustment can influence distant neighbours, forming a theoretical bridge between micro-level control and macro-level cohesion in bat swarms.

Beyond basic biological insights, I suggest that these principles have promising applications in engineered systems, such as swarms of unmanned aerial vehicles. By incorporating biologically-inspired closed-loop sonar control and reaction-time constraints, it may be possible to develop drone swarms with enhanced stability and resilience to local disturbances. Such interdisciplinary extensions demonstrate the broader relevance of biosonar-inspired technologies, continuing a tradition of biomimetic innovation.

2 METHODS

2.1 Swarm simulation model

I developed a simulation model to test whether purely local, sonar-driven control rules can support stable and cohesive flight in swarming bats. The model builds on the responsivity framework introduced in [10, 11], incorporating the simulated bat species *Vespertillio numeralis*. In this framework, each bat operates an independent, asynchronous control loop in which its sonar inter-pulse interval (IPI) is dynamically adapted to the echo delay from its nearest forward neighbour or environmental obstacle. I extended this closed-loop event-driven principle to simulate group flight, with multiple bats flying simultaneously, each responding only to local sensory input without any central coordination or explicit distance control. The model includes realistic flight dynamics, flexible heading and velocity updates, and explicit detection of potential collision risk. All simulations were implemented in MATLAB (R2024a), and the full history of each bat's dynamics was recorded for quantitative analysis.

2.2 Implementation

The simulation was implemented with a fully asynchronous event-driven architecture in a custom function (`simulateEcholocationSwarm_async()`). Bats were initialised with positions $\mathbf{p}_i(0)$ sampled from a three-dimensional Gaussian distribution with user-defined spatial spread σ_{init} (via `params.initial_sigma`), representing the standard deviation of position along each axis. For instance, with $\sigma_{\text{init}} = 2$, the swarm begins in a loosely clustered configuration in which the average nearest-neighbour distance is approximately 1.6 m for $N = 50$ agents, within a radius of $3\sigma = 6$ m. This value reflects the expected spacing between individuals in a spatially heterogeneous group and provides a plausible baseline for mid-air convergence without inducing artificial clumping. Initial headings were aligned along the $+X$ axis with small angular perturbations, and velocities were sampled from a narrow uniform range ($\pm 10\%$) around the nominal target speed $v_0 = 3\,\text{m/s}$.

Each bat i maintains a heading vector $\mathbf{h}_i(t)$ and velocity $v_i(t)$ which evolve over time. The IPI is updated asynchronously: at each call iteration, only the calling bat updates its IPI, heading, and velocity, while all bats update their positions continuously as a function of time.

The simulation proceeds by selecting the next bat scheduled to call, advancing the global time t_{global} to that bat's scheduled event time. All bats' positions $\mathbf{p}_i(t)$ are forward-integrated from their last update times to t_{global}. The calling bat then performs sonar timing update, heading/velocity update, and reschedules its next call. (Also see the pseudocode of the described algorithm in section 2.9).

2.3 Sonar timing

At each call iteration, bat i selects a target distance $d_i(t)$:

- If a neighbour lies ahead within its frontal field (dot product > 0), $d_i(t)$ is set to the distance to that nearest forward neighbour.
- If no bat is detected ahead, a virtual obstacle at random $d_{\text{obs}} \in [2, 5]$ m is assigned.

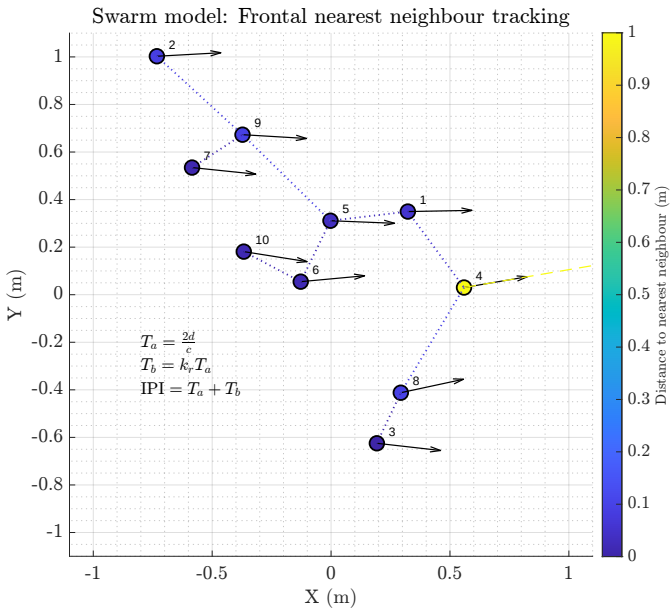

Figure 1: Illustration of the swarm simulation method. Each bat (numbered circles) maintains a heading vector (black arrow) and adapts its sonar inter-pulse interval (IPI) based on the distance to its nearest neighbour within a general frontal region. Lines connect each bat to its selected forward neighbour (dotted) or to a virtual obstacle if no forward target is present (dashed). Colour indicates the distance to the selected target, with short-range tracking (blue) and longer-range tracking (yellow). Equations show the temporal update rules: echo delay T_a, responsivity-scaled reaction interval $T_b = k_r T_a$, and resulting IPI $= T_a + T_b$. This neighbour-following mechanism enables local dynamic adaptation of call timing, which underlies the emergent cohesion of the swarm in the simulation.

The round-trip echo delay is:

$$T_a(t) = \frac{2d_i(t)}{c} \tag{1}$$

where $c = 343\,\mathrm{m/s}$ is the speed of sound. The IPI is computed as:

$$T_b(t) = k_r \cdot T_a(t) \tag{2}$$

$$\mathrm{IPI}_i(t) = T_a(t) + T_b(t) \tag{3}$$

with an enforced maximum call rate (200 Hz).

Call duration is dynamically adapted:

$$T_{\mathrm{call}}(t) = \begin{cases} \frac{T_a(t)}{k_r}, & T_a(t) < k_r \cdot T_{\mathrm{call,init}} \\ T_{\mathrm{call,init}}, & \text{otherwise} \end{cases} \tag{4}$$

with $T_{\mathrm{call,min}} = 0.5\,\mathrm{ms}$.

2.4 Flight dynamics

Each bat's position is updated continuously as:

$$\mathbf{p}_i(t + \Delta t) = \mathbf{p}_i(t) + v_i(t) \cdot \mathbf{h}_i(t) \cdot \Delta t \tag{5}$$

where $\mathbf{p}_i(t)$ is the 3D position of bat i at time t, $v_i(t)$ its current velocity (speed), $\mathbf{h}_i(t)$ its unit heading vector (direction of flight), and Δt is the time elapsed since the last update of that bat's position. In the asynchronous simulation, Δt differs for each bat and corresponds to its

current inter-pulse interval (IPI), thus coupling locomotor updates to sonar control.

Heading and velocity are updated only when each bat emits a sonar call, i.e. at its own echo-processing iteration. At each such iteration, the heading vector $\mathbf{h}_i$ is adjusted by a biologically inspired rule combining several components:

$$\mathbf{h}_i(t+1) = \alpha \mathbf{h}_i(t) + (1-\alpha)\left[\beta\, \bar{\mathbf{h}}_{\text{neigh}} + \gamma\,(\bar{\mathbf{p}} - \mathbf{p}_i(t)) + \delta\, \mathbf{g}\right] \tag{6}$$

where:

- $\alpha = 0.9$ is an inertia term promoting smooth directional changes.
- β, γ, δ are weighting parameters for the three control components:
  - **Neighbour alignment** (β): tendency to align heading with the mean heading of the other bats, $\bar{\mathbf{h}}_{\text{neigh}}$.
  - **Cohesion to swarm centroid** (γ): damping pull toward the average position of the swarm, $\bar{\mathbf{p}}$.
  - **Global drive** (δ): bias toward an overall goal direction $\mathbf{g}$ (set along $+X$).

This update rule belongs to the general class of alignment–cohesion–drive models widely used to describe collective animal behaviour [12, 13]. It was specifically adapted here to reflect the biological constraints of bat flight, which requires maintaining forward progression while preserving local cohesion.

Individual velocities $v_i(t)$ are also allowed to drift gradually between $[0.8, 1.2] \times v_0$, introducing naturalistic variation in speed between individuals. Velocity changes occur stochastically, with small random increments drawn at each bat's call iteration.

Through this scheme, both positional updates and directional dynamics are controlled asynchronously and locally, with each bat responding only to its own sensory input (echoes) and the perceived state of nearby conspecifics.

2.5 Collision risk detection

To evaluate the swarm's ability to maintain safe spacing, I implemented a collision risk detection module based on two criteria.

First, a critical response threshold T_{b^*} was defined, representing the minimum physiological time required for bats to react to a perceived obstacle. Following the responsivity framework of [10], I used $T_{b^*} = 4\,\text{ms}$. If, at any sonar iteration:

$$T_b(t) < T_{b^*} \tag{7}$$

a collision risk is flagged for the emitting bat.

Second, a time-to-collision (TTC) metric was computed at each global iteration for every pair of bats (m, n), based on their current relative position and velocity. For a pair of bats separated by distance d and relative closing velocity v_{closing}:

$$\text{TTC} = \frac{d}{v_{\text{closing}}} \tag{8}$$

if $v_{\text{closing}} > 0$; otherwise, $\text{TTC} = \infty$.

A collision risk was logged if:

$$\mathrm{TTC} < \mathrm{mean}(T_{b,m}, T_{b,n}) \tag{9}$$

where $T_{b,m}$ and $T_{b,n}$ are the current echo-response intervals of the two bats. To avoid redundant reporting, a cooldown interval of 0.1 s was enforced between successive alerts for the same pair.

These criteria allow explicit tracking of instances where bats' current sonar update timing would no longer suffice to avoid imminent collisions, providing a quantitative measure of the swarm's collective safety margin.

2.6 Outputs and analysis

For each bat, I stored full history over time:

- Position $\mathbf{p}_i(t)$
- Heading $\mathbf{h}_i(t)$
- Velocity $v_i(t)$
- Inter-pulse interval $\mathrm{IPI}_i(t)$
- Call duration $T_{\mathrm{call}}(t)$
- Target distance $d_i(t)$
- Nearest neighbour index
- Flight variables: δ_s, δ_t, T_a, T_b, v
- Collision risks (TTC)

This provided full temporal resolution of swarm dynamics, used to produce the plots in Figure 3.

2.7 Parameter grid simulations

To systematically evaluate the effects of sonar responsivity and flight speed on swarm dynamics, I conducted a grid-based parameter sweep using the asynchronous swarm simulation model. For each run, the responsivity coefficient k_r and initial velocity v_0 were varied across a predefined set of values (Table 1 & 2). The simulations were executed with 50 bats over 60 seconds, with full logging of inter-pulse interval (IPI), call duration, call rate, velocity, and inter-individual distances for every bat and time point.

Each parameter combination was simulated independently using a parallelised execution setup (via `parfor` in MATLAB), and outputs were aggregated post hoc to generate summary statistics. For each run, I quantified the number of collision risk events, total update events, and calculated both absolute and normalised collision rates. Additional statistical descriptors (mean, median, standard deviation) were computed for call duration (CD), call rate (CR), flight velocity v, and neighbour distances d.

These data enable a detailed examination of how responsivity and speed jointly affect the spatial organisation and safety margins within the swarm. The results reveal clear trends: higher k_r values lead to increased inter-bat spacing and reduced call rates, consistent with the expected delay scaling from the responsivity rule. Conversely, higher v_0 values increase the likelihood of collision risk events, especially when paired with low responsivity, due to shortened echo delays and reduced reaction time. Together, these findings support the model prediction that precise temporal control at the individual level is sufficient to generate stable swarm dynamics, while also highlighting parameter regimes that elevate collision risk.

2.8 Modelling Information Transfer in Asynchronous Biosonar Swarms

To understand how a local perturbation in the behaviour of one individual bat propagates through the swarm, I developed a theoretical model quantifying the spatiotemporal dynamics of information flow. The model captures both the effective *velocity of information transfer* and the *time taken for a perturbation to influence a distant agent* in an asynchronous swarm of biosonar-guided individuals. These dynamics arise from a chain of sensory–motor reactions, as implemented in my simulation framework.

Propagation Delay and Information Velocity

Let d_i denote the distance between bat i and its nearest frontal neighbour. The corresponding echo delay is $T_{a,i} = 2d_i/c$. Each bat reacts after a latency $T_{b,i} = k_r T_{a,i}$, governed by the responsivity coefficient k_r. As a perturbation propagates across n agents, the total distance covered is $\sum_{i=1}^{n} d_i$, and the cumulative delay is $\sum_{i=1}^{n} T_{b,i}$.

I define the following two quantities:

- **Information latency** $I_t(n)$: the time taken for a perturbation to reach the n-th agent in the chain.
- **Information velocity** I_v: the effective speed at which a perturbation propagates across the swarm.

The information latency is:

$$I_t(n) = \sum_{i=1}^{n} T_{b,i} = \sum_{i=1}^{n} k_r T_{a,i} = k_r \sum_{i=1}^{n} \frac{2d_i}{c} \tag{10}$$

The effective information velocity is then given by:

$$I_v = \frac{\sum_{i=1}^{n} d_i}{I_t(n)} = \frac{\bar{d}}{k_r \cdot \bar{T}_a} = \frac{c}{2k_r} \tag{11}$$

where $\bar{d}$ is the mean inter-bat distance, and $\bar{T}_a = 2\bar{d}/c$ is the average echo delay.

This formulation accounts for spatial heterogeneity and reveals how I_v depends primarily on the biosonar responsivity k_r and the speed of sound c, while $I_t(n)$ depends on both k_r and the summed echo delays across n agents. Denser regions (smaller $\bar{d}$) yield shorter echo delays and smaller $I_t(n)$, facilitating faster local corrections. In contrast, sparser regions increase both delay and spatial reach per step, but the overall information velocity I_v remains invariant for constant

k_r. Thus, k_r regulates the trade-off between speed and stability: lower values enhance corrective responsiveness, while higher values promote robustness by damping rapid fluctuations.

Perturbation Attenuation Model

As a perturbation propagates through the swarm, its influence may diminish due to accumulated noise, variability in heading updates, or stochastic deviations in response. To model this attenuation, I assume that each bat transmits a fraction of the received perturbation to its neighbour, resulting in a multiplicative loss over distance. This leads to an exponential decay of the form:

$$\delta_i = \delta_0 \cdot \exp(-\alpha i) \tag{12}$$

where:

- δ_i is the perturbation magnitude perceived by the ith bat in the interaction chain,
- δ_0 is the initial perturbation magnitude,
- α is the decay coefficient, incorporating the effect of divergence, local noise, and behavioural variability.

To estimate how far a perturbation spreads before becoming negligible, I define a behavioural threshold $\delta_{\min}$ below which the perturbation has no effective influence. The maximum range of influence (in terms of hops) is then:

$$i_{\max} = \frac{1}{\alpha} \cdot \ln\left(\frac{\delta_0}{\delta_{\min}}\right) \tag{13}$$

This defines the *effective communication range* of a perturbation within the swarm. For a given α, smaller initial perturbations or stricter behavioural thresholds reduce the range of effect, while lower α (i.e., more consistent responses) extend the range.

My modelling framework aligns closely with the principles outlined in the general theory of information transfer by Ahlswede et al. [14], particularly in its treatment of information as a spatiotemporal dynamic process shaped by system structure and transmission constraints. In their formalism, information transfer is not merely a passive relay but an active transformation governed by local processing rules and communication delays. Similarly, I define information flow through a biologically grounded mechanism: each agent in the swarm reacts based on temporally precise biosonar feedback, creating a sequential chain of responses. This structure directly mirrors the discrete, causally ordered channels in Ahlswede's theory. Moreover, my explicit formulation of information velocity and perturbation attenuation offers a quantitative instantiation of their abstract transfer functions, adapted for real-time, distributed sensory systems such as bat swarms. In both frameworks, the fidelity and speed of information propagation are critically dependent on the internal system dynamics—in the current case, the responsivity coefficient k_r and the spatial heterogeneity of the swarm.

Interpretation and Application

This model provides a quantitative framework for analysing the swarm's sensitivity to local disturbances. It shows that:

- The reaction time (T_b), governed by k_r, sets the temporal resolution of feedback within the swarm.
- Dense swarms (small d) transmit information faster, but also require more frequent updates to maintain coherence.
- There exists a trade-off: higher responsivity improves reaction speed but reduces tolerance to noise, while lower responsivity improves robustness at the cost of slower adaptation.

In my grid-based simulation, each point in the parameter space defined by (k_r, v_0) corresponds to a different regime of this trade-off. The information velocity model thus allows theoretical prediction of:

1. Whether a perturbation will propagate fast enough to be corrected
2. How far it will spread before becoming negligible
3. The role of k_r in mediating this behaviour across the swarm

This model provides a theoretical lens through which simulation outcomes—such as inter-bat distances, collision rates, and velocity fluctuations—can be interpreted as emergent consequences of biosonar loop dynamics and local sensory delays.

2.9 Pseudocode

Algorithm 1 Asynchronous Bat Swarm Simulation

```
Initialise swarm of N bats with random positions and velocities
Set initial heading near +X direction
Initialise memory structures and parameters
Initialise global time t ← 0
while t < t_max do
    Identify bat i with next event time
    Advance global time to bat i's next event
    for all bats j = 1 to N do
        Update position: p_j ← p_j + v_j Δt
        Record timestamp and position
    end for
    Determine nearest forward neighbour of bat i
    Simulate biosonar loop for bat i
    Update call parameters: T_b, δ_t, T_a, call rate, etc.
    Adjust bat i's heading based on:
        • Neighbour heading average
        • Centre-of-mass attraction
        • Global drive vector
    Update velocity with small random perturbation
    Schedule next event time for bat i
    for all bat pairs (m, n) do
        Compute relative position and velocity
        Estimate time-to-collision (TTC)
        if TTC < mean(T_b^m, T_b^n) then
            Record potential collision
        end if
    end for
end while
Return swarm data and collision log
```

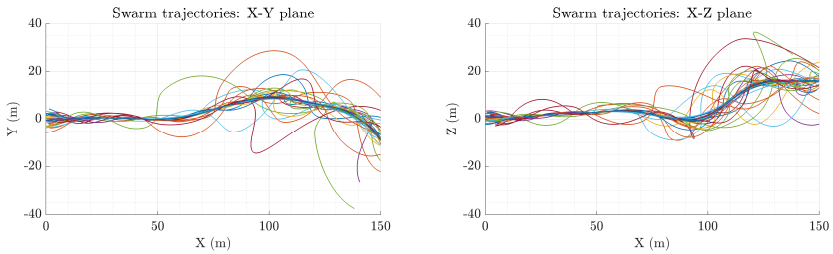

Figure 2: Swarm simulation showing the evolution of bat trajectories in the X–Y plane (left) and X–Z plane (right). Each line traces the path of one individual bat over the course of the simulation. The limited spread along the Z-axis demonstrates vertical cohesion, while horizontal positions (X–Y) exhibit local dispersion within the swarm structure. The forward progression along the X-axis reflects the effect of the global drive **g** applied to all bats. These patterns illustrate the stable, cohesive flow maintained by the simulated swarm under closed-loop sonar guidance.

3 RESULTS

To evaluate whether local echo-driven control alone can sustain swarm cohesion, I implemented a fully asynchronous simulation of echolocating bat aggregations. Each individual, modelled as an autonomous agent, independently emitted sonar calls based on its own sensory feedback loop, governed by the temporal precision theory. Unlike synchronous or discretely-timed models, this asynchronous design captures the natural variability in call emission and echo reception observed in real bats. Each bat adapts its call interval and duration according to its distance to the nearest neighbour ahead, while also updating its heading and speed based on local alignment and centre-of-mass cues. This framework closely mimics the real-world scenario of dense emergence swarms, where thousands of bats operate without central coordination yet maintain fluid, coherent group flight. The model allowed me to probe the emergent dynamics of such decentralised systems under systematically varied responsivity parameters (k_r) and forward drive (v_0), capturing how sonar-based control translates into collective stability, communication load, and collision risk.

I tested the impact of sonar responsivity and initial velocity on swarm dynamics. I conducted a systematic grid-based simulation sweep varying the responsivity coefficient (k_r) and initial velocity (v_0). Each simulation involved 50 bats flying for 60 seconds under closed-loop biosonar control. Output metrics included call rate, call duration, inter-bat distance, velocity, and collision risk events.

Despite the absence of any global coordination rule or prescribed spacing behaviour, all simulations produced globally cohesive swarm formations. As seen in Figure 2, bats maintained forward progression with bounded lateral dispersion and low vertical spread, suggesting that local echo-based timing suffices to preserve group integrity over time.

3.1 Distributional Characteristics

Distributions from a representative run (Figure 3) confirmed key predictions of the model. Call durations were compressed towards the minimum bound (0.5 ms), call rates spanned a wide dynamic range, and velocity distributions centred tightly around v_0. Distance distributions showed long-tailed profiles with a modal spacing near 2–3 m, reinforcing the view of a self-stabilising swarm where each bat dynamically adjusts timing in response to the most salient local cues.

Together, these findings support the central hypothesis: stable swarm dynamics can emerge from asynchronous, locally adapted biosonar timing without the need for central coordination

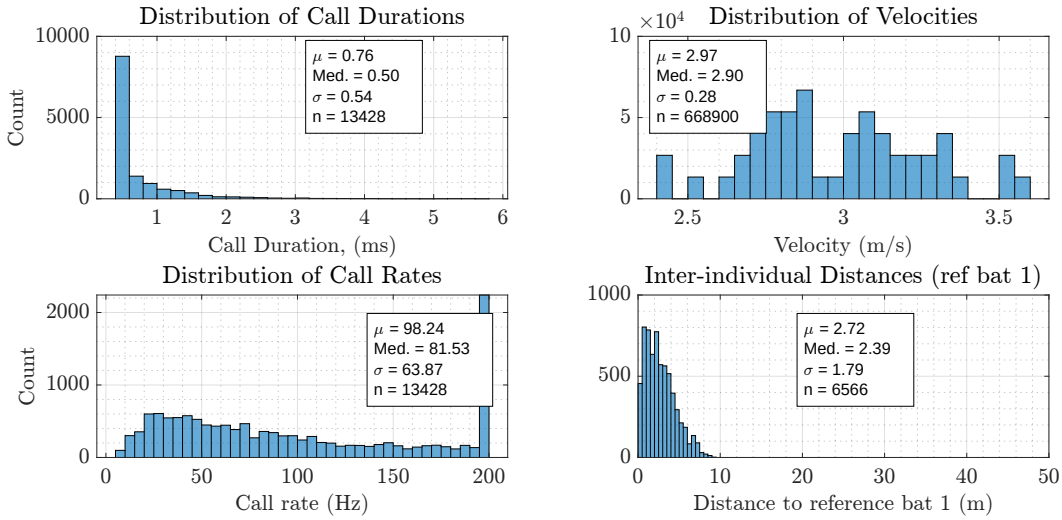

Figure 3: Summary statistics of a swarm simulation under Call-Receive-Process-Call (CRPC) driven closed-loop echolocation behaviour ($N_{bats} = 50$, $T = 5$ s). **Top-left:** Distribution of call durations across all bats and time points. Most calls are dynamically compressed toward the physiological minimum (0.5 ms), reflecting close spacing within the swarm. **Top-right:** Distribution of flight velocities, showing stable speeds tightly centred around the initial target velocity ($\mu = 2.96$ m/s). **Bottom-left:** Distribution of call rates, which adapt over a wide range (peak near 90 Hz) according to local inter-individual spacing. **Bottom-right:** Distribution of distances to a reference bat (bat 1), demonstrating self-organised swarm structure with a median spacing of ∼2.4 m and a long-tailed distribution from occasional forward or backward drift. These results confirm that closed-loop echolocation control can support stable, cohesive swarm flight in the absence of explicit central coordination.

or long-range awareness.

Table 1 presents descriptive statistics for each simulation run. I observed a consistent reduction in call rate and increase in call duration with increasing k_r, while higher v_0 led to wider spacing and modestly elevated velocity variability. The standard deviation in inter-bat distance increased markedly with high v_0, suggesting greater swarm stretching and spatial heterogeneity at faster speeds.

3.2 Swarm-Level Parameter Trends

Figure 4 summarises the effects of k_r and v_0 on mean call rate, call duration, and inter-bat distance. As predicted by the responsivity model, higher k_r increased the inter-pulse interval, leading to reduced call rates and longer call durations. Increased v_0 generally elevated inter-bat spacing, but only when paired with higher k_r, reflecting the interplay between flight speed and echo processing delay.

3.3 Collision Risk Events and Safety Margins

Figure 5 visualises the temporal occurrence and frequency of collision risk events. The top raster shows that collision warnings are sparse but non-zero, concentrated in high-speed, low-responsivity conditions. The heatmap in the lower left quantifies the rate of such events per 100,000 call iterations, revealing a peak at $k_r = 6$ and $v_0 = 6$–7 m/s. These risks remain low overall, with most parameter regimes supporting safe navigation.

The pairwise risk margin plot (lower right) illustrates that for most interactions, the bats' response time (T_b) exceeded the time-to-collision (TTC), ensuring safety. However, a small number of events (highlighted by near-zero or negative margins) occurred when TTC approached or undercut T_b, indicating the boundaries of stability for the control scheme.

k_r	v_0	CD(μ)	CD(med.)	CD(σ)	CR(μ)	CR(med.)	CR(σ)	$v(\mu)$	v(med.)	$v(\sigma)$	$d(\mu)$	d(med.)	$d(\sigma)$
3.0	3.0	0.930	0.500	1.2	151.2	196.5	61.1	3.0	3.0	0.348	6.4	5.7	3.7
3.0	4.0	1.1	0.500	1.5	143.7	179.8	65.2	3.9	3.9	0.427	5.1	4.0	4.7
3.0	5.0	1.7	0.653	2.3	122.2	127.7	71.4	4.9	4.9	0.535	7.3	5.0	9.6
3.0	6.0	1.7	0.676	2.3	120.9	123.3	72.6	5.8	5.8	0.562	9.9	6.6	12.6
3.0	7.0	1.7	0.640	2.3	122.0	130.1	72.4	6.8	6.8	0.648	7.0	4.6	7.2
4.0	3.0	0.811	0.500	0.973	136.7	153.7	64.9	3.0	2.9	0.343	6.3	5.8	3.6
4.0	4.0	1.1	0.500	1.5	116.2	112.9	70.0	3.9	3.8	0.458	11.3	10.1	6.8
4.0	5.0	1.3	0.500	1.7	116.0	117.1	72.8	5.0	5.0	0.526	7.3	4.7	8.0
4.0	6.0	1.3	0.500	1.8	117.8	117.0	72.0	5.9	5.9	0.611	8.7	5.5	10.9
4.0	7.0	1.4	0.539	1.9	106.9	92.8	72.4	6.8	6.8	0.661	8.1	4.7	10.9
5.0	3.0	0.700	0.500	0.809	138.7	163.3	66.4	2.9	2.9	0.332	5.1	4.1	4.5
5.0	4.0	0.878	0.500	1.1	115.5	109.8	70.5	3.9	3.9	0.439	10.2	5.4	10.0
5.0	5.0	1.0	0.500	1.4	111.0	104.6	71.7	4.7	4.6	0.498	14.3	6.9	18.6
5.0	6.0	0.997	0.500	1.5	112.3	104.5	71.4	5.8	5.7	0.533	8.8	5.3	12.0
5.0	7.0	1.2	0.500	1.7	103.4	92.3	71.1	6.8	6.8	0.564	10.6	7.8	12.5
6.0	3.0	0.681	0.500	0.781	126.0	131.2	68.2	3.0	2.9	0.348	6.9	4.3	7.3
6.0	4.0	0.741	0.500	0.942	118.5	116.5	68.8	3.9	3.9	0.422	5.4	3.9	5.2
6.0	5.0	0.927	0.500	1.3	112.2	108.6	73.5	5.0	5.0	0.514	14.3	11.2	11.1
6.0	6.0	0.944	0.500	1.3	92.7	73.1	68.6	5.8	5.8	0.540	12.0	8.2	10.7
6.0	7.0	1.1	0.500	1.5	85.9	64.0	69.0	6.8	6.8	0.550	9.6	5.7	11.2
7.0	3.0	0.656	0.500	0.676	107.7	97.3	68.3	2.9	2.9	0.355	5.5	4.1	5.1
7.0	4.0	0.727	0.500	0.882	111.3	102.9	71.8	3.9	3.9	0.404	7.0	4.6	6.8
7.0	5.0	0.814	0.500	1.1	93.7	74.8	69.6	4.7	4.6	0.487	10.7	6.2	13.4
7.0	6.0	0.838	0.500	1.2	96.2	77.4	70.3	5.8	5.8	0.497	10.7	5.4	13.6
7.0	7.0	0.951	0.500	1.3	81.8	51.5	70.5	6.7	6.6	0.589	17.3	12.6	16.4

Table 1: Summary statistics of swarm simulations across different combinations of initial velocity v_0 and responsivity coefficient k_r. For each simulation, the table reports the mean (μ), median (med.), and standard deviation (σ) of call duration (CD), call rate (CR), velocity (v), and inter-bat distance (d), averaged over all individuals and time points.

k_r	v_0	Collisions	Total Events	Collision Rate (%)	Per 100,000 Events
3	3	0	0	0	—
3	4	0	0	0	—
3	5	2	127143	0.0016	2
3	6	0	0	0	—
3	7	3	96197	0.0031	3
4	3	1	96197	0.0010	1
4	4	0	0	0	—
4	5	0	0	0	—
4	6	6	111233	0.0054	5
4	7	5	96197	0.0052	5
5	3	10	275915	0.0036	4
5	4	6	202653	0.0030	3
5	5	5	104438	0.0048	5
5	6	4	105151	0.0038	4
5	7	10	159796	0.0063	6
6	3	3	224770	0.0013	1
6	4	6	137988	0.0043	4
6	5	4	134747	0.0030	3
6	6	3	86123	0.0035	3
6	7	3	127143	0.0024	2
7	3	6	131425	0.0046	5
7	4	8	219474	0.0036	4
7	5	3	219474	0.0014	1
7	6	6	79718	0.0075	8
7	7	3	83499	0.0036	4

Table 2: Summary of collision events across simulation runs for different combinations of responsivity coefficient k_r and initial velocity v_0. The table reports the absolute number of collisions, total simulated events, collision rate as a percentage, and normalised rate per 100,000 call events. Collision rates remain low overall, but increase slightly with higher k_r and v_0 values, suggesting that slower responsivity (higher k_r) or higher velocities may modestly elevate collision risk within the swarm.

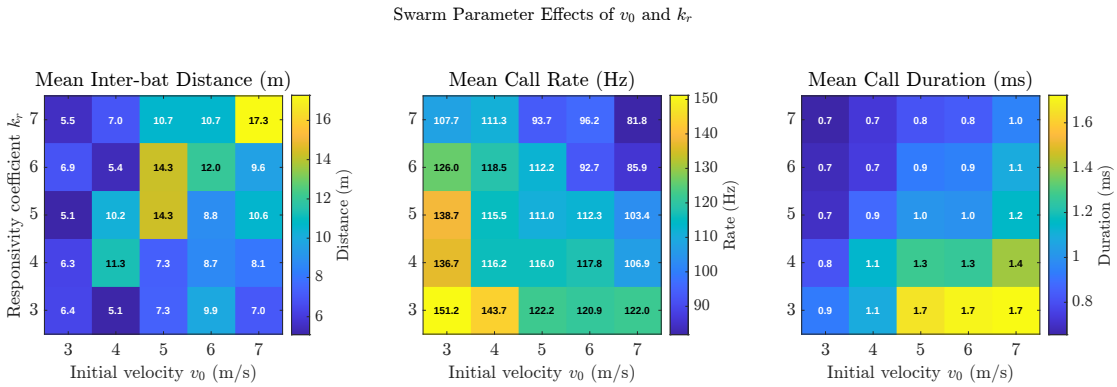

Figure 4: Swarm-level effects of initial velocity v_0 and responsivity coefficient k_r. Left: Mean inter-bat distance increases with higher k_r and peaks at intermediate–high v_0 values, suggesting greater spacing emerges from slower responsiveness. Centre: Mean call rate declines with increasing v_0 and k_r, consistent with longer inter-pulse intervals at high flight speeds and echo delays. Right: Mean call duration shows a reciprocal trend to call rate, decreasing with slower responsiveness and faster speeds. Together, these trends highlight the coupled dynamics of biosonar timing and swarm spatial organisation.

Table 2 summarises the absolute and normalised collision event counts across all simulation conditions. Although higher v_0 increases collision likelihood, particularly at higher k_r, overall rates remain below 0.01%, affirming the robustness of local echo-guided control.

4 DISCUSSION

Understanding the principles that govern stability and coordination in animal swarms requires integrating sensory, motor, and communication constraints into behavioural models. My study bridges this gap by simulating a swarm of echolocating bats where each agent acts autonomously, driven by closed-loop biosonar dynamics. Unlike models that assume externally synchronised control, or reliance of global information, my asynchronous implementation captures the continuous interplay between echo delay, responsivity, and motor response. Through this framework, I provide both a behavioural simulation and a theoretical characterisation of how information flows through the swarm, adapting to spatial structure and echo-timing constraints. The results demonstrate that temporally precise local interactions are sufficient to produce globally coherent swarming behaviour, offering new insight into both biological collectives and potential biomimetic applications.

4.1 Call Characteristics and Adaptations

My simulation framework predicted a coupling between local echo delays and call duration, along with a systematic increase in call rate during close-range interactions. Figures 3 and 4 depict the dynamic modulation of call duration and call rate in response to echo delay and inter-bat spacing. Table 4 shows that shorter echo delays yield shorter call durations, in accordance with the predicted relationship for T_b (also see call duration decrement model in [10]). This coupling is further confirmed in Table 1, where increased call rate corresponds to closer proximity to neighbours, demonstrating the system's sensitivity to local crowding.

Table 1 complements the visualisations by providing a comprehensive statistical overview across simulation conditions. Notably, lower k_r values result in higher mean call rates and shorter call durations, reflecting greater responsivity. The velocity variability also affects these

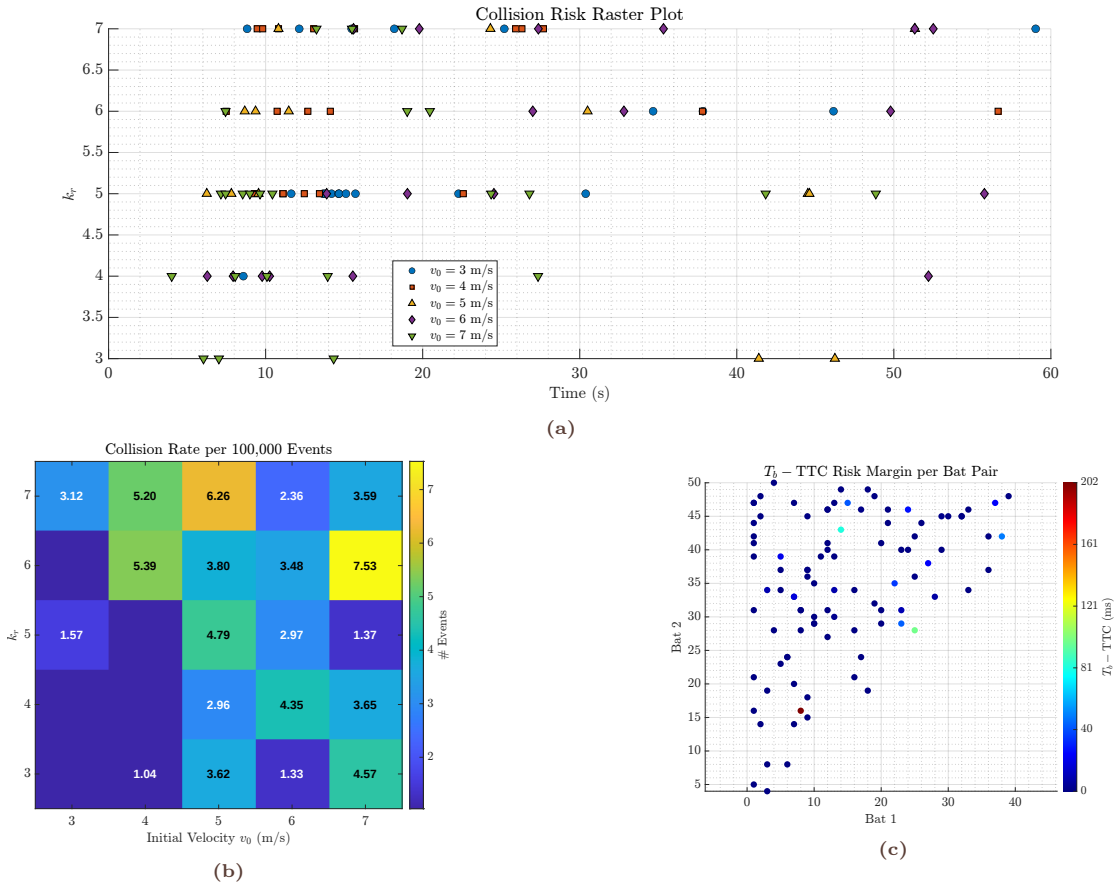

Figure 5: Comprehensive visualisation of collision risk events in the asynchronous swarm simulation with 50 bats and for 60 s. **Top:** Raster plot showing the occurrence of collision risk events over simulation time, stratified by responsivity coefficient (k_r, vertical axis) and colour-coded by initial flight velocity (v_0). Each point represents a collision warning flagged between a unique pair of bats. **Bottom left:** Heatmap showing the mean collision event rate (normalised per 100,000 update events) for each parameter combination of k_r and v_0. Brighter values indicate higher collision frequencies. **Bottom right:** Pairwise risk margin plot across all bat pairs within a selected run, colour-coded by the difference between the response time (T_b) and the time-to-collision (TTC). Positive margins indicate that the bats have sufficient time to respond before collision, while negative or small margins imply elevated risk. These analyses demonstrate that both k_r and v_0 significantly influence collision dynamics, with higher speeds and lower responsivity values associated with increased collision likelihood.

conditions, suggesting a trade-off between responsiveness and kinematic stability.

The model predictions and simulation results align closely with the most recent empirical observations reported by Goldshtein et al. (2025) [9], who analysed onboard acoustic recordings from bats during emergence flights. Their findings reveal that bats increase their call rate and shorten their call duration significantly in response to crowded conditions, paralleling the predicted behaviour of individual agents in my model when the nearest forward target enters the biosonar view. Moreover, the data presented by Goldshtein et al. (2025) support the specific relationship between echo delay and call duration, consistent with the control law (equation 2) tested across my simulation sweeps.

Similar findings have been reported recently in laboratory settings: Wilkinson et al. [15] showed that *Eptesicus fuscus* bats reduced call duration and interval and exhibited enhanced head movements when tracking targets in cluttered environments. These results are consistent with earlier field studies, such as those by Lin et al. (2016) [16], who found that Eastern bent-wing bats (*Miniopterus fuliginosus*) increased their emission rate with swarm size during

natural cave emergence. Likewise, Habersetzer (1981) [17] reported that *Rhinopoma hardwickei* emitted shorter, frequency-modulated calls when flying in groups of 10–70 individuals, indicating an adaptive response to crowding. Furthermore, Chiu et al. (2010) [8] found that big brown bats actively adjusted their sonar beam to monitor conspecifics during flight, suggesting that call timing and beam control are also socially modulated. These findings are further corroborated by field recordings of Brazilian free-tailed bats during dense emergence flights, which show consistent use of short, broadband, high-frequency calls distinct from foraging calls [18].

Taken together, these converging lines of evidence suggest that the acoustic adaptations observed in both natural swarms and controlled experiments—namely, increased call rate, shortened call duration, and directional attention—can emerge from local, echo-timed feedback mechanisms without requiring global awareness or centralised coordination. This supports the hypothesis that temporal precision and closed-loop control at the individual level are sufficient to produce swarm-level acoustic organisation and stability.

4.2 Collision Risks and Management

The asynchronous simulation framework incorporates a biologically inspired collision risk detection mechanism grounded in the principle of sonar loop latency. Each bat emits calls and adjusts its trajectory based on the first relevant echo (FRE), with reaction delays governed by the responsivity control law in equation 2. In the model, a collision is defined likely to occur when the time-to-collision (TTC) between two bats becomes shorter than the average biological reaction time (T_b) of the pair. This condition implies that even if a bat receives an echo, there is insufficient time to react before impact, making the event unavoidable within the bounds of the sensory–motor feedback loop.

My simulations revealed that such collision risks, although rare, do occur under certain conditions, particularly when relative velocities are high or inter-individual spacing is low (Figure 5a). Using a grid sweep over various values of the responsivity constant k_r and initial flight velocities v_0, I observed distinct regimes of swarm stability (Figure 5b). At lower k_r values, the system becomes highly responsive, enabling faster reaction times and improved avoidance, but also introducing instability through overshooting and local oscillations. In contrast, higher k_r values dampen responsiveness, increasing the likelihood of uncorrected perturbations that may lead to close encounters or collisions.

I quantified collision events by logging instances where TTC $< T_b$ and summarised them as raster plots and heatmaps (Figure 5b & 5c). The results show a clear interaction between k_r and v_0: swarms with high velocity and high k_r experienced the most frequent collision risks. Notably, these events were not evenly distributed but tended to cluster during moments of high density and local synchronisation breakdown. Despite these local risks, global swarm cohesion was preserved, and collisions were generally sparse (see Table 2), indicating that local responsivity—even if imperfect—is sufficient to maintain macro-level stability.

The collision model also provides a predictive framework for evaluating the limits of safe interaction timing in swarm systems. By comparing the TTC against the dynamically updated T_b values, I can estimate behavioural margins of safety. Moreover, the model suggests that increasing inter-individual spacing or reducing relative speed can compensate for higher k_r values, offering multiple strategies for risk mitigation. These insights could inform both biological interpretations of swarm dynamics and the design of collision avoidance protocols in engineered

multi-agent systems.

4.3 Group Cohesion and Information Transfer

The mathematical framework developed in this study formalises how information about local perturbations propagates through the swarm. I show that the rate of information transfer—defined as the effective velocity with which changes in state spread across individuals—depends primarily on the responsivity coefficient k_r and the local spatial structure of the swarm. Lower values of k_r allow for faster local adaptation, enabling the swarm to react swiftly to emerging disturbances. Higher values of k_r slow down this process, increasing behavioural latency but also damping sensitivity to small, possibly irrelevant, fluctuations.

Importantly, the model accounts for heterogeneous spacing among individuals, reflecting realistic swarm conditions. In denser regions, the average spacing between bats is smaller, leading to shorter echo delays and hence shorter reaction times. However, since both the spatial and temporal components shrink together, the propagation velocity of information remains relatively stable. Conversely, in more dispersed areas, the longer reaction times are offset by greater spatial reach, again preserving the overall flow of adjustments through the swarm.

I also show that the influence of any perturbation naturally attenuates as it propagates, due to behavioural variability and divergence in headings. This attenuation defines a finite communication radius within which perturbations remain dynamically relevant. Beyond this range, fluctuations are effectively absorbed by the system's internal noise, maintaining swarm-level stability.

Vanderelst and Peremans (2025) [19] proposed that swarming bats could benefit from collective soundscapes, suggesting that local adaptations emerge from global acoustic gradients generated by the group. While their model introduced an elegant mechanism based on spatial filtering and acoustic density, it implicitly assumes that each bat interprets aggregated acoustic information as a coherent signal. By contrast, my model proposes that individual bats operate in a fully local, closed-loop manner—relying not on global gradients but on the direct, temporally structured echo feedback from the nearest neighbour. Rather than processing the collective soundscape, each bat initiates a reaction chain only when the echo delay and target geometry fall within biologically plausible thresholds. This distinction shifts the focus from global signal integration to local precision and offers a mechanistic explanation for decentralised coordination based on biosonar responsivity. The echo-timed loop acts as an intrinsic information gate, avoiding sensory overload while preserving swarm cohesion, even under high-density, asynchronous conditions.

4.4 Robotic Swarm Control

Conventional swarm robotics often draws from global optimisation schemes, as exemplified by the BAT Algorithm (BA) [20], where agent behaviour is steered toward a global fitness maximum using centralised heuristics inspired by echolocation. In contrast, my approach flips this top-down paradigm: I simulate decentralised, biologically grounded control wherein agents respond only to locally available sensory input. Rather than tracing gradients of an objective function, each agent in my model adjusts its trajectory based on echo delay and local sensory–motor latency. This builds a fully distributed control framework that does not require shared state

variables or synchronised timing—resembling natural bat swarms more closely than BA-style abstractions.

A central contribution of this work is the identification of the responsivity coefficient k_r as a regulatory parameter. This single scalar modulates the delay between echo reception and motor output, thereby controlling the responsiveness of the swarm. As demonstrated in my simulations, tuning k_r enables flexible trade-offs between reactivity and cohesion: low k_r values yield faster local adaptation (useful in dynamic environments), while higher k_r values support temporal smoothing and global stability by damping responses to transient fluctuations.

Crucially, this framework supports scalable, fault-tolerant swarm behaviour without the need for explicit communication protocols. The propagation of a local perturbation across the swarm is governed by a mathematically derived information velocity I_v and corresponding delay I_t, which determine how quickly and how far signals spread through the group. These quantities can be tuned via inter-bat distance $\bar{d}$ and k_r, offering system designers predictive control over information dynamics. Moreover, the perturbation attenuation model introduced here allows one to estimate the effective communication radius—beyond which behavioural influence decays exponentially and becomes negligible.

These insights resonate with Müller (2024) [21], who advocates for biologically plausible sensory-based control as a new paradigm for autonomous aerial swarms. Similarly, Diebold et al. (2020) [22] report that bats modulate both echolocation rate and trajectory in response to local spatial context, without requiring centralised coordination. My model mechanistically reproduces this principle, offering a generative framework for implementing such behaviour in robotic platforms.

Taken together, this bioinspired control architecture—grounded in echo-timed closed-loop adaptation—provides a minimal yet powerful design principle for swarm robotics. It sidesteps the overhead of communication, avoids the brittleness of synchronisation, and offers a tunable mechanism for stability–reactivity trade-offs.

5 CONCLUSION

This study demonstrates that stable and collision-averse swarm dynamics in echolocating bats can emerge from decentralised, closed-loop biosonar control governed by temporally precise responsivity rules. By modelling each individual as an autonomous agent adjusting its call timing in response to the first relevant echo, I show that key features of group cohesion, information transfer, and perturbation absorption arise naturally—without any global coordination. The model accurately predicts context-dependent call adaptations observed in empirical studies and highlights how a single parameter, k_r, can flexibly tune the balance between responsiveness and stability. Beyond advancing our understanding of sensory-guided collective behaviour in animals, these findings offer a biologically grounded framework for developing robust, scalable control algorithms in robotic swarms.

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COMPTETING INTERESTS

The author(s) declare no competing interests.

CODE AND DATA AVAILABILITY

The simulation code, experimental data, and analysis scripts are available in a repository archieved at DOI: https://doi.org/10.6084/m9.figshare.29482268.v1
Additionally, a GitHub repository is available with the code at: https://github.com/raviumadi/Swarming_Dynamics

ETHICS STATEMENT

This study did not involve human participants or live animals. All analyses and simulations were conducted computationally, and no ethical approval was required.

AUTHOR CONTRIBUTIONS

Ravi Umadi: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration.

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